Age determination of the blue wildebeest *Connochaetes taurinus* in Zululand

C.A.M. Attwell
Department of Zoology, University of Natal, Pietermaritzburg

Age determination methods for the blue wildebeest employed the use of tooth eruption sequence, cementum layers from macroscopic tooth sections, eye lens mass, and tooth attrition. Eleven eruption classes were arrived at, providing a reliable method of age determination up to 3,5 years. The times of eruption of specific teeth were compared with data from East Africa. The restricted birth interval of wildebeest enabled some sub-adult animals to be regarded as 'known-age' which were used to arrive at a value for the number of cementum layers laid down per annum, and to provide a 'correction factor' for the period before eruption and cemental deposition. The nature of tooth cementum lines in wildebeest is discussed, and changes in infundibular patterns were related to cementum or eruption age, providing an age-wear chart with 14 adult classes, adequate for life-table data. Incisiform wear in wildebeest appears to follow a curvilinear relationship. When eye lens mass was plotted against cementum or eruption age, the resultant curve served only to distinguish between animals below one year old and the older age classes. Anomalies in dentition are discussed. Some criteria for age determination in the field are presented.
S. Afr. J. Zool. 1980, 15: 121–130

Ouderdomsbepalingsmetodes vir die blouwildebees het die gebruik van tandsnypatrone, tandsementumlae in makroskopiese deursnitte, ooglensmassa en tandslytasie ingesluit. Elf tandsnyklasse, as 'n betroubare metode vir ouderdomsbepaling tot 3,5 jaar is geïdentifiseer. Die sny van spesifieke tande is met gegewens uit Oos-Afrika vergelyk. Die beperkte kalfseisoen van wildebeeste het daartoe gelei dat die ouderdom van sommige onvolwasse diere as bekend beskou kan word, en is gebruik om te bepaal hoeveel sementumlae jaarliks neergelê word en om 'n korreksiefaktor vir die periode voor die sny en sementumring neerlegging te verskaf. Die aard van tandsementumlyne in wildebeeste word bespreek. Die veranderinge in infundibulêre patrone is met sementum- of tandsnyouderdom vergelyk, en 'n ouderdomslytasiekaart met 14 klasse vir volwasse diere vir lewenstabelgegewens kon opgestel word. Snytandslytasie in wildebeeste volg blykbaar 'n kromlynige verwantskap. Die verwantskap tussen ooglensmasse en sementum- of tandsnyouderdom kan slegs diere jonger as een jaar van diere in ander ouderdomsgroepe onderskei. Afwyking in tandekry word bespreek. Etlike maatstawwe vir ouderdomsbepaling in die veld word aangebied.
S.-Afr. Tydskr. Dierk. 1980, 15: 121–130

C.A.M. Attwell
Department of Zoology, University of Natal,
P.O. Box 375, Pietermaritzburg 3200, South Africa.
Present address: Department of Biology, University College of Swaziland,
Private Bag, Kwaluseni, Swaziland.
Received 23 June 1979; accepted 26 February 1980

Age determination in bovids originally centred on tooth eruption in animals with immature dentition, and on tooth attrition in adults. The sequence of eruption appears to be constant within a species, but eruption times may be altered by genetic or environmental factors. In adult animals, the shapes of the infundibula on molariform teeth change with wear: patterns so formed may be used as indices of wear. More recent approaches have involved the use of incremental growth rings in dental histology. This approach is of note because it facilitates the assignment of absolute ages, provided that it can be established that a specific number of annuli is laid down within a set period.

Cementum is laid down on the roots of all teeth in an uneven layer, favouring the root apices. As layers are laid down throughout life, the process may serve to continue eruption and consequently compensate for loss of crown height resulting from tooth wear. The alternating broad, translucent layers and the narrower dark layers are caused by differences in the rate and nature of calcification. The cementum layer technique in age determination was initially developed by Laws (1952) on marine mammals; its subsequent application to African mammals has been reviewed by Spinage (1973, 1976).

An age determination technique unrelated to dentition is the use of eye lens mass, reviewed by Friend (1968) and Morris (1972). The eye lens is an ectodermal structure, and consequently displays apparent deposition throughout life.

Age determination of wildebeest has received previous attention (Talbot & Talbot 1963; Watson 1969; Schaller 1972; Braack 1973). The last author found that the method of Talbot and Talbot (1963) drawn up for *C.t.hecki* in East Africa overestimated ages of Kruger Park wildebeest, particularly in the four-year-old age class, where the error was as great as 2,5 years. This is ample justification for the need to establish separate criteria for age determination in separate areas, particularly where differences in nutrition and soil types are marked. Further, the above workers did not attribute absolute age intervals for adult classes.

Materials and Methods

Data were derived largely from culling operations in Umfolozi Game Reserve, and from skulls found in the field. These data were supplemented by additional information from Mkuzi Game Reserve.

Tooth eruption

In species having an annual period of parturition which is short and distinct, it is relatively simple to assign immature dentition to specific age classes, because the young born in any one year constitute a uniform and easily recognizable group within the population. Eighty-two skulls of immature dentition were available for the determination of the eruption sequence.

For each skull, the eruption phase for each tooth was recorded against one of five possible categories on a specially-designed eruption/wear sheet (Attwell 1977). Horn growth usually indicated whether the wildebeest had died in the first, second or third year of life. If any doubt was apparent, reference was made to Talbot and Talbot's (1963) calendars. An age was then ascribed to a specific skull by estimating the interval from the date of death back to the assumed birth period. This period was defined as six weeks, from mid-November until the end of December, and was based on observation and extrapolation of foetal weights. For convenience, the central point of this period, i.e. the end of the first week in December, was taken as an arbitrary birth date. Results were expressed with reference to this central point, but with the understanding that the error would be of the order of one month. To arrive at the eruption calendar, those sheets with the same or closely similar ages were grouped. The predominant eruption pattern from each group was then taken as being characteristic of that group or age class. Sheets within a group which showed marked deviations from the relatively consistent eruption phase of that group were discarded on the grounds that these related to out-of-season births (Attwell & Hanks in press). The rarity of discarded sheets lent support to the supposition that they did indeed relate to aseasonal parturition.

Adult dentition

For examination of cementum annuli, the first molar (M1) and third molar (M3) were extracted from either the mandible or the maxilla. Teeth were sectioned dorsoventrally along the long axis, using a lapidary saw with a 0,5 mm diamond blade. As there was no method whereby the blade could be made to pass unfailingly through that section of the tooth displaying the broadest 'pad' of cementum, no attempt was made to relate the thickness of the pad to age. Some cementum layers were clearly visible after this initial sectioning, but the majority required further processing by polishing on a geological Cut Rock Lapping Machine.

Various authors have reported on the necessity of preparing stained, decalcified sections (Low & Cowan 1963; Spinage 1967; Simpson & Elder 1969; Hall-Martin 1976). Cementum layers in wildebeest teeth were considered sufficiently clear not to warrant decalcification and staining. Instead, the method of Mitchell (1967) was adopted, whereby facial sections were viewed by reflected light under a low-power binocular dissecting microscope. Sections were examined under a power of 25X, but sometimes 12X power was used in order to see if the continuity of a particular band persisted along the entire depositional layer. Both light and dark bands were counted, but those lines lying on or close to the dentino-cement border were discounted, as they were considered to correspond to 'eruption lines' (Spinage 1967).

In the absence of known-age adult material, sub-adult wildebeest (for which eruption age could be fairly accurately determined) were regarded as 'known-age', and provided a sample of first and third molars. As the approximate age at eruption of a particular tooth was known, the number of annuli on eruption allowed the determination of an adjustment factor to compensate for those annuli laid down prior to eruption.

The approach to infundibular patterns was as follows: the pattern for each molariform tooth from 175 adult skulls was drawn in outline on the tooth sheet. The right tooth row was chosen in the maxilla, and the left in the mandible. This was considered to be a more efficient alternative to 'averaging' infundibular patterns between, for example, the two maxillary rows. Individuals containing the same or closely similar cementum ages were then grouped, and an attempt was made to assign a characteristic infundibular pattern for each tooth to a specific cementum age. Infundibular patterns were drawn on the chart in such a way that maxillary and mandibular toothrows could be examined side by side, by viewing the maxilla from a ventral aspect, and the mandible dorsally. Because the right tooth row was considered in the maxilla, and the left in the mandible, the drawings for both maxillary and mandibular teeth showed lingual aspects on the left, and buccal on the right. Teeth were drawn with the anterior aspects towards the bottom of the chart.

It was considered that relating cementum age to wear would only be of value if the rate of wear was shown to be reasonably uniform with age. Thus, to give a measure of the reliability of the age-wear chart produced, the percentage dissimilar infundibular patterns which were 'excluded' from the final characteristic patterns, was assigned for each tooth.

In order to relate incisor heights and widths to wear and age, the height of the first left incisor was measured from the tip of the tooth to the gum line. Measurements were taken as soon after death as possible to obviate errors resulting from gum shrinkage. The greatest width of the same tooth was measured across the occlusal surface with a Vernier caliper to 10^{-2}mm for subsequent relation to cementum or eruption age.

Eye lens mass

The left eyeball was excised as soon after death as possible, and was injected with 10% formalin into the vitreous humor. The organ was left to fix in formalin for at least two weeks. A superficial circular incision was then made through the cornea, and the lens carefully expelled into 10% formalin until such time as it could be dried. Before drying, the lenses were washed in methanol and freed of any remaining attached ciliary muscle. One hundred and thirty-eight lenses from animals of all ages were used; this figure excluded those which appeared damaged or had obvious cataracts. Drying took place in an oven at 98°C. Lenses were weighed to 10^{-3}g, and lens mass was then plotted against eruption or cementum age.

Results and Discussion

Tooth eruption

The complete original dentition of placental mammals is believed to have consisted of three incisors, one canine, four premolars, and three molars in each jaw half (Hyman 1942). The first premolar (P1) has been lost in Artiodactyl evolution (but retained in Suidae); for this reason the most anterior premolar is termed P2. This tooth is found in both upper and lower jaws of most ungulates, except in the case of wildebeest, where P_2 is lost in adults, leaving only two premolars (P_3 and P_4) in the lower jaw. One may tentatively conclude from this that the wildebeest shows the most advanced stage in the evolution of ungulate dentition, if one accepts that progressive premolar loss is an evolutionary trend.

The formula for wildebeest deciduous teeth is:

$$2\left(i\frac{\cdots}{123},\ c\frac{\cdot}{1},\ p\frac{.234}{.234}\right) = 20;$$

and for adult dentition:

$$2\left(I\frac{\cdots}{123},\ C\frac{\cdot}{1},\ P\frac{.234}{..34},\ M\frac{123}{123}\right) = 30$$

Table 1 contains 11 eruption classes arrived at for *C.t.taurinus* in this study. Adult dentition can be taken as complete at about 38 months, but the great variability in canine eruption may prolong the attainment of adult dentition, if the criterion for the latter status is taken as uniformity in the level of the incisiform teeth. Spinage (1973) also noted this variation in canine eruption. The variation may be related to the decreased importance the canine shows in function.

Some departure from the calendar occurs, which is related to individual variation, and not to aseasonal births. The more consistent deviations noted were:

- The second and fourth maxillary milk premolars may persist into the 28–32 month age class. Of the 11 specimens in this age class, three (27,3%) showed this variation.
- The second mandibular milk premolar may persist beyond the 25–28 month age class. It was recorded twice (18,2%) in the 28–32 month age class, and once in the 38–46 month age class (9%). It is also maintained in some adult animals: of 178 adult mandibles examined, 6 (3,4%) showed the persistence of this tooth. The maximum age of a wildebeest with this deviation was 13 years.
- The adult maxillary premolars may not be fully erupted in the 38–46 month age class. This occurred in two out of 11 specimens (18,2%).

Both Caughley (1965) and Steenkamp (1969) found that the age at which a tooth erupted was dependent upon the age at eruption of the preceding one, and variability in eruption increased the later the tooth appeared. Consequently the probability of placing an individual in the wrong class increases with the age of the animal.

Table 1 Eruption calendar for *C.t. taurinus* based on specimens from Zululand

Age	MAXILLA						MANDIBLE										
Class	Premolars			Molars			Incisors			CA	Premolars			Molars			Sample size used
Months	2	3	4	1	2	3	1	2	3	1	2	3	4	1	2	3	
Birth	M■^{1}						M■^{1}				M■^{1}						0
0,5–0,75	M	M△^{2}	M□^{2}				M	M▲	M▲	M▲	M	M^{1}	M△^{3}				2
5–<6	$\bar{M}$	M	M	A△^{2}			M	M	M	M	M	M	M	A△^{2}			5
6–8	$\bar{M}$	M	M	A△			M	M	M	M	M	M	M	A▲	A■^{2}		6
12–<16	$\bar{M}$	M	M	A	A△^{2}		A□	M	M	M	M	M	M	A	A△		5
16–<18	$\bar{M}$	M	M	A	A△		A△	M	M	M	M	M	M	A	A▲	A■^{3}	6
18–20	$\bar{M}$	$\bar{M}$	M	A	A▲	A□^{2}	A	M	M	M	M	$\bar{M}$	$\bar{M}$	A	A	A△	9
21–24	$\bar{M}$	A□^{1}	$\bar{M}$	A	A	A△	A	A■	$\bar{M}$	$\bar{M}$	$\bar{M}$	A□^{1}	A□^{1}	A	A	A△	7
25–<28	A■^{1}	A■	A□^{1}	A	A	A△	A	A	$\bar{M}$	$\bar{M}$	$\bar{M}$	A■	A■	A	A	A△	10
28–32	A△	A△	A△	A	A	A△	A	A	A■	$\bar{M}$		A△	A△	A	A	A▲	11
33–<38	A▲	A▲	A▲	A	A	A	A	A	A▲	A△		A▲	A▲	A	A	A	10
38–46	A	A	A	A	A	A	A	A	A	A▲		A	A	A	A	A	11

Explanation of symbols:

Superscripts show number of cusps present

M = milk tooth

A = adult tooth

CA = canine

(a) □ tip of erupting tooth just visible, level with or below the bone line. If the erupting tooth is preceded by a deciduous tooth, then this stage may sometimes only be discernible on removal of the deciduous tooth.

(b) ■ tip of tooth now projecting above bone line. In adult premolar or adult incisiform eruption, the overlying deciduous tooth is often still *in situ*.

(c) △ intermediate between (c) and (d)

(d) ▲ eruption nearly complete; tooth is almost level with other fully-erupted teeth in the tooth row.

$\bar{M}$ indicates heavy wear on a milk tooth, with smooth surfaces and no dentine/enamel ridges.

(Eruption stage at birth based on Talbot and Talbot, 1963).

Comparison of the blue wildebeest eruption calendar from Zululand with Talbot and Talbot's (1963) calendar for East Africa shows that, in general, the Zululand subspecies has earlier eruption times, with eruption proceeding over a longer period. The major differences are summarized in Table 2. A similar deviation in eruption between two populations of the same species has been noted for impala *Aepyceros melampus*. Roettcher and Hoffman (1970) found much later eruption of the first molar in Kenyan impala, when compared to the Rhodesian chronology of eruption given by Child (1964). Variation in eruption and replacement times between geographically separate populations occurs as a result of different nutritional planes. Steenkamp (1970) has shown that the age at which eruption occurs in cattle is accelerated by a high plane of nutrition.

Differences in eruption times may have functional or adaptational significance. Steenkamp (1969) maintained that the early loss of deciduous teeth might influence the pattern of wear of the permanent teeth, resulting in reduced food intake and delayed growth in later life. It can however be assumed with some confidence that replacement within the same population will be consistent, for Hemming (1969) has shown consistency over 16 years in a study on dall sheep, *Ovis dalli*.

Table 2 Comparison of eruption pattern between *C.t. taurinus* and *C.t. hecki*

Deciduous dentition		Minimum age at which milk tooth is lost (months)		Difference
		C.t.taurinus	*C.t.hecki*	
MANDIBLE	i_1	8	20	12
	i_2	20	26	6
	i_3	28	33	5
	c	32	37	5
	p_2	28	33	5
	p_3	20	33	13
	p_4	20	28	8
MAXILLA	p^2	24	33	9
	p^3	24	*	*
	p^4	28	28	0

Permanent dentition		Minimum age at eruption of permanent tooth (months)		Difference
		C.t.taurinus	*C.t.hecki*	
MANDIBLE	I_1	12	20	8
	I_2	21	26	5
	I_3	28	33	5
	C	33	37	4
	M_1	5	6	1
	M_2	6	15	9
	M_3	16	26	10
MAXILLA	M^1	5	6	1
	M^2	12	15	3
	M^3	18	30	12

*denotes insufficient data

Cementum annuli

The first molar was found to be consistently preferable in distinguishing cementum annuli owing to the degree of development of the cementum pad between the roots. In contrast, the mandibular third molar almost invariably showed a relatively thin accretion with annuli ill-defined. In cases where the accretion was uniformly distributed around the roots and in the zone of root bifurcation, the annuli were better defined within the latter region. In some teeth there was a distinct break between annuli in the pad and those displayed on the inner lateral aspects of the roots. Although counts from the two regions may be the same, the annuli are in these cases not confluent from one region to the other. This suggests that accretion of cementum occurs simultaneously in different zones, but that there is a possible physiological mechanism preventing continuity between the zones.

Usually the first layer laid down tends to be thicker than subsequent layers, in some cases up to five times thicker. This is suggestive of a functional feature in anchoring a newly-erupted tooth. The rates of accretion were found to vary between teeth of the same animal, and within the same tooth. In general, the annuli appeared to be compressed with increasing age, apparently because growth of the cementum slows and more annuli must be accommodated within a narrower layer. In cases of exceptional wear in a molar tooth, attrition of the dentine may result in exposure of the cementum pad at the tooth cusp, thus extending the useful life of the tooth by providing a grinding surface after the dentine has been worn away.

Longitudinal tooth sections confirmed that the exposed cementum was confluent with root cementum, thus distinguishing it from secondary dentine, which may be formed as a result of severe wear (Starkey 1971). Cemental exposure of this nature does not detract from the possibility of counting annuli, as teeth of this age have pronounced accretion at the roots which can be used instead.

Klevezal and Kleinenberg (1967) postulated that the thin dark lines corresponded to periods of arrested growth and the broader light bands to periods of optimal nutrition. Although this supposes that growth is only related to food and not to some endogenous factor, most workers have assumed that a biannual season would result in a dark and a light annulus for each year. To validate this, the 30 molars and permanent premolars from sub-adult 'known-age' individuals were tabulated in terms of increasing age (derived from the eruption calendar), with the numbers of light and dark annuli recorded opposite each tooth. In the summary of results below, 'band' represents one light annulus and one dark annulus combined.

For M_1:

15 months ($\simeq$ 1 year) had $\frac{1}{2}$ band.

30 months ($\simeq$ $2\frac{1}{2}$ years) had $1\frac{1}{2}$ bands.

40 months ($\simeq$ $3\frac{1}{2}$ years) had $2\frac{1}{2}$ bands.

46 months ($\simeq$ 4 years) had 3 bands.

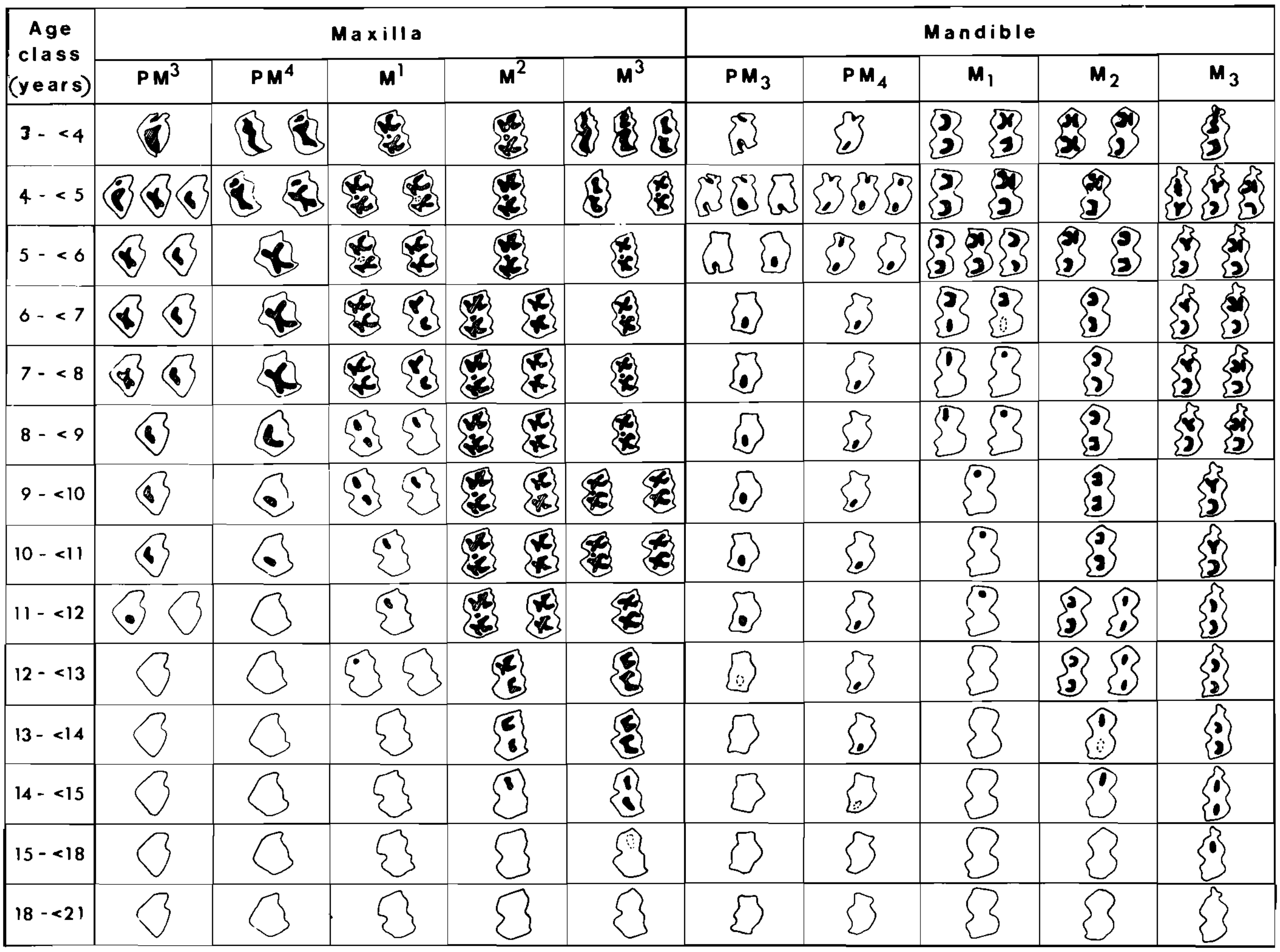

Fig. 1 Tooth wear chart for adult wildebeest. Where more than one pattern occurs for a specific tooth in any age class, these patterns are alternatives for that class.

This clear pattern did not hold for all teeth; variation from the pattern in a minority of first molars was discounted in arriving at the above sequence. Those teeth not conforming to the pattern were assumed either to represent deviation from the eruption calendar, or to exhibit anomalous accretion. This latter phenomenon is discussed below.

The results show a sequence from which it can be concluded that one band is in fact laid down per year. For M_1, one year must be added to the number of bands to arrive at the true age. This formula must also apply to M^1, as this tooth shows the same age at eruption. The $\frac{1}{2}$ band shown by M1 from 15-month old animals consisted of a single broad light annulus, and thus the light annulus must be laid down first. In a similar way, correction factors for third molars were determined. It was found that an addition of 2,5 years was required to compensate for the later eruption of these teeth.

If the deposition of cementum around a tooth exhibits layering, and if the layers are laid down in all teeth at the same time of the year, there should be a consistent difference in the number of these annuli in teeth that erupt at different ages. When the number of annuli on M1 were compared with the number on M3 from the same animal, the mean difference was 1,86 (S.D. = 1,17). With an interval of about 13 months between the eruption times of M1 and M3, one would expect (if two annuli are laid down per annum) the difference to approximate two annuli. The departure from expectation may be explained in part by individual variation in eruption times, or possibly by misinterpretation of annuli. Closer agreement with the expected value would probably have resulted had stained, decalcified sections been used instead of the macroscopic preparations.

Tooth attrition

Figure 1 shows the changes in infundibular patterns in each molariform tooth with age. Fourteen adult age classes are distinguished. The more conventional approach of drawing the entire tooth row has been dispensed with by considering each tooth separately. The chart may be used for rapid age estimation of skulls found in the field; a characteristic feature of such skulls in Zululand is that the full toothrow is rarely present, particularly in young animals. Anterior portions of both mandible and maxilla are often consumed by hyaenas *Crocuta crocuta,* leaving only the more posterior molariform teeth.

The reliability of tooth wear charts is open to question. First, it is naive to assume that the same degree of wear represents the same age (Ransom 1966; Spinage 1967; Roettcher & Hoffman 1970). A measure of the chart's reliability is given by Table 3. The results indiciate that M^3 and M^2 are the most 'reliable' teeth; they show least variation in wear patterns at the same age. When all teeth are considered together, only 68,2% will show the same wear pattern at the same age.

A more detailed interpretation of the reliability of the

Table 3 Comparison of numbers of tooth wear categories used in the compilation of age-wear chart, with numbers of categories discarded

	Tooth	Number of wear categories conforming to chart	Number of wear categories falling in 'adjacent' wear classes	Total	% conforming to chart
MAXILLA	P^2	No infundibular change: pattern consistent			100
	P^3	91	26	117	77
	P^4	80	46	126	63,5
	M^1	84	46	130	64,6
	M^2	106	31	137	77,4
	M^3	86	47	133	64,7
MANDIBLE	P_3	65	43	108	60,2
	P_4	74	46	120	61,7
	M_1	86	30	116	74,1
	M_2	74	42	116	63,8
	M_3	86	31	117	73,5
	Total	832	388	1 220	68,2

Table 4 Estimates of reliability of wear chart, considering each age class

Cementum age class (years)	Number of specimens used (both sexes)	Total number of teeth for which infundibular patterns were recorded[2]	Maximum number of infundibular patterns the same[1]	% of total number of patterns: 'variability' or 'reliability'
3-< 4	9[3]	78	47	60,3
4-< 5	37	340	243	71,5
5-< 6	25	235	143	60,8
6-< 7	11	105	72	68,6
7-< 8	9	87	60	70,0
8-< 9	7	58	42	72,4
9-<10	6	40	26	65,0
10-<11	6	47	34	72,3
11-<12	7	63	53	84,0
12-<13	5	51	30	58,8
13-<14	6	54	25	46,3
14-<15	8	61	23	37,7
15-<18	2	41	9	22
18-<21	2			

[1] The maximum numbers of conforming patterns were used as the final definitive pattern for that age class.

[2] 10 patterns are possible for each skull (Total number of adult teeth is 11, but P^2 was not used as no infundibular pattern was apparent). The third column is not, however, merely 10 × the second column, because teeth, mandibles or even maxillae were sometimes missing.

[3] The sample size in the 3-< 4 year age class is small because the majority of these skulls had their ages determined by eruption.

chart may be achieved by referring to Table 4, where each age class is considered separately. The conclusion is that the chart is consistently 'reliable' (over 60% reliability) up to 12 years. Thereafter the reliability drops rapidly to 37,7% in the 14−<15 years age class. Both the 15−<18 and 18−<21 years age classes must be regarded as extremely unreliable, as these classes were based on minimal numbers of specimens, and because wear patterns are by now very diverse for the same cementum age.

Despite these limitations, it is considered that the chart provides a rapid field age determination technique, without resorting to the laborious preparation of sections. Any particular specimen will allow an estimate of age, with the range in which that estimate will lie. The range will vary with the age of the individual, and with the number of teeth that can be examined.

The results of incisor height and width measurements are presented graphically in Figs. 2 and 3. The height rela-

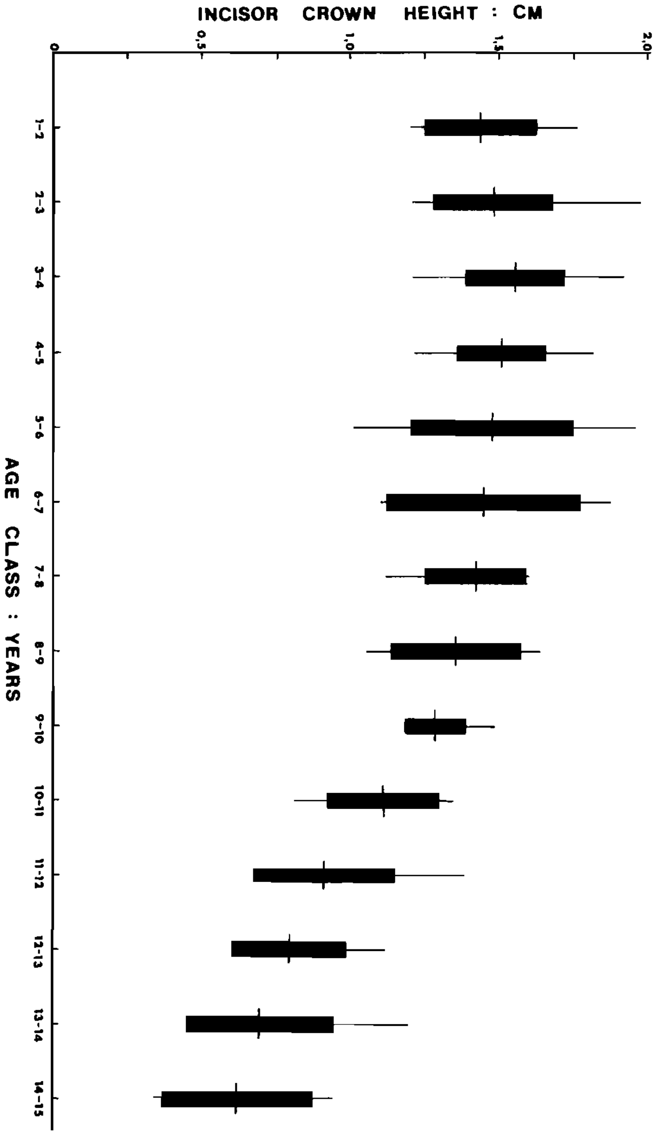

Fig. 2 Mean values (horizontal lines) of incisor crown height against age. (Bars represent one S.D.; vertical lines, ranges).

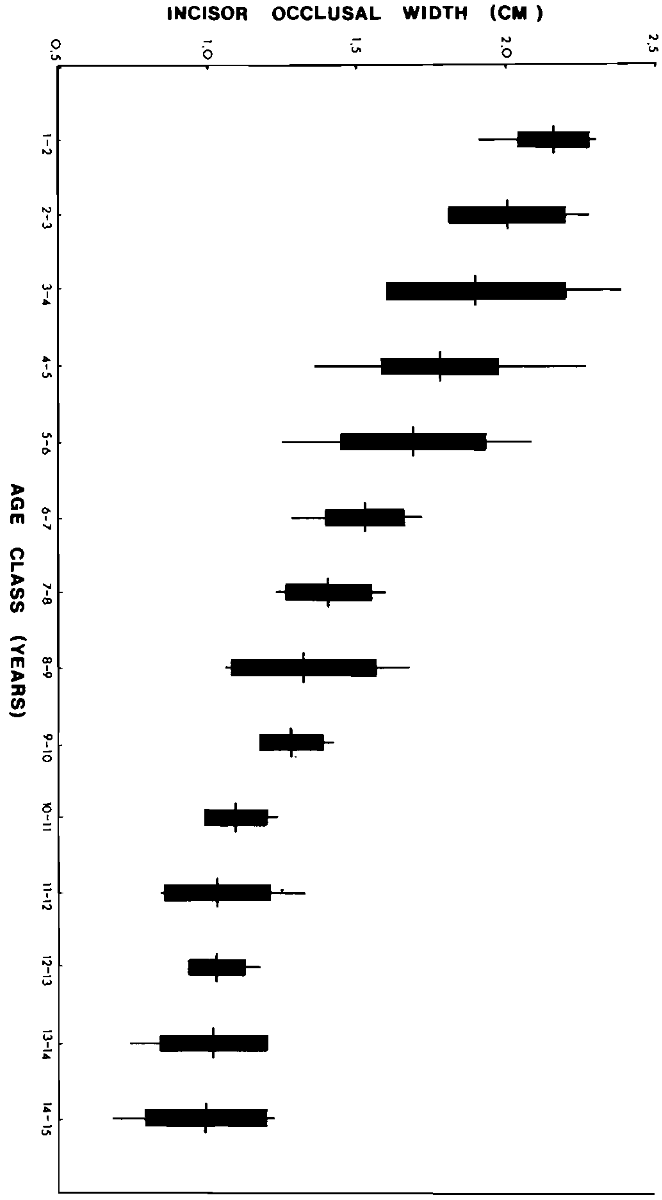

Fig. 3 Mean values of incisor width plotted against age. Notation as for Fig. 2.

tionship (Fig. 2) during the first three years of life is not a true reflection of wear. Although wear is taking place during this period (confirmed by Fig. 3), the rate of eruption of the tooth exceeds the downward wear. The incisor is a wedgeshaped tooth, the broad dorsal edge tapering ventrally towards the roots. Consequently, as an animal ages, the occlusal width will become narrower and downward wear (decrease in incisor height) will become more rapid. This is clearly apparent from Fig. 2 after about nine years. Conversely, with occlusal width (Fig. 3), the rate of change is initially rapid, and then slows down at about the same age. Towards the tooth roots the angle of the 'wedge' is less marked and the sides of the tooth tend towards the parallel. At this point little change in occlusal width will occur with wear. Both graphs illustrate that incisiform wear is not linear. This confirms the findings of Spinage (1967) and Simpson and Elder (1969). A curvilinear relationship is apparent. Similar relationships for molariform teeth have been described by Watson (1967), Grimsdell (1973) and Hall-Martin (1976).

Spinage (1973) considers that incisiform teeth show greater variability in wear than molariform teeth, and this may account for the overlap between age classes in my results. The overlap is pronounced in older age classes of the occlusal width graph, and in younger age classes of the incisor crown height.

Anomalies in dentition and wear

Dental anomalies may be expected in most families of mammals (Colyer 1936). The presence of supernumary maxillary canines was noted in a single calf skull, of about 2—3 weeks old, but of undetermined sex. The canines were situated at the posterior end of the premaxilla, at the suture between maxilla and premaxilla. An adult female (6—7 years) showed remnants of maxillary canines. Mitchell (1965) recorded maxillary canines in a 10-month-old wildebeest (*C.t. taurinus*) from Barotseland. The incidence of maxillary canines has also been recorded in Cervids (Chaplin & Atkinson 1968; Chapman & Chapman 1973).

In adults, two cases were noted where P^2 did not erupt at all. One occurred on the left side (5-year-old male), and the other on the right (4,5-year-old male). Failure of P^3 to erupt was recorded in a single 5-year-old male, from the right tooth row.

Occasional pronounced discrepancy in wear between incisiform and molariform teeth occurs. In these cases, wear on the incisiforms is far heavier. Differences in wear also take place between upper and lower jaws. One 14-year-old male had maxillary premolars and first molar worn completley flat, whilst the corresponding mandibular surfaces had experienced relatively little wear. With heavy wear (in animals older than 13 years), M_1 may split between the buccal and lingual aspects. This is often caused by differential wear: adjacent sides of P^4 and M^1 together form the apex of a wedge which extends beyond the level of other teeth in the tooth row. The 'wedge' impinges on M_1, resulting in highly differential wear of that tooth, particularly on the anterior cusp. This phenomenon may be related to the staggered eruption sequence of apposing teeth. A more frequent phenomenon in adult dentition is seen in the anomalous juxtaposition of the anterior cusp of M1 with the posterior cusp of P4, in both mandible and maxilla. A 'shearing' effect results, with enamel worn off at the points of contact, so that the infundibula of the two teeth become confluent.

Eye lens mass

In Fig. 4, two straight line regressions of lens mass against age have been plotted. For animals less than one year old the equation is y = − 0,048 + 1,106 x; (r = 0,76; p<0,001). For animals between one and four years old, the regression equation is y = 0,5496 + 0,085 x; (r = 0,89; p<0,01). The pattern of lens growth is fairly rapid up to about four years, followed by a rectilinear relationship between mass and age. This biphasic growth pattern agrees with results in other African mammals (Laws 1967; Fairall 1969; Rautenbach 1971; Smuts 1974; Hall-Martin 1976).

To illustrate the reliability with which age classes could be separated from lens mass data, a further computer-based curve was plotted (Fig. 5). This curve was based on the von Bertalanffy growth equation, using a program identical to that employed by Hanks (1972), who provides a lucid account of the uses and concepts of the equation. The equation for the curve is $m_t = 1{,}019\ (1 - e^{-0{,}378(t+3{,}394)})^3$ where m_t is mass at age t.

Clear differentiation occurs only between animals below one year old and the older age classes. The general conclusion is that the technique is of little value for age deter-

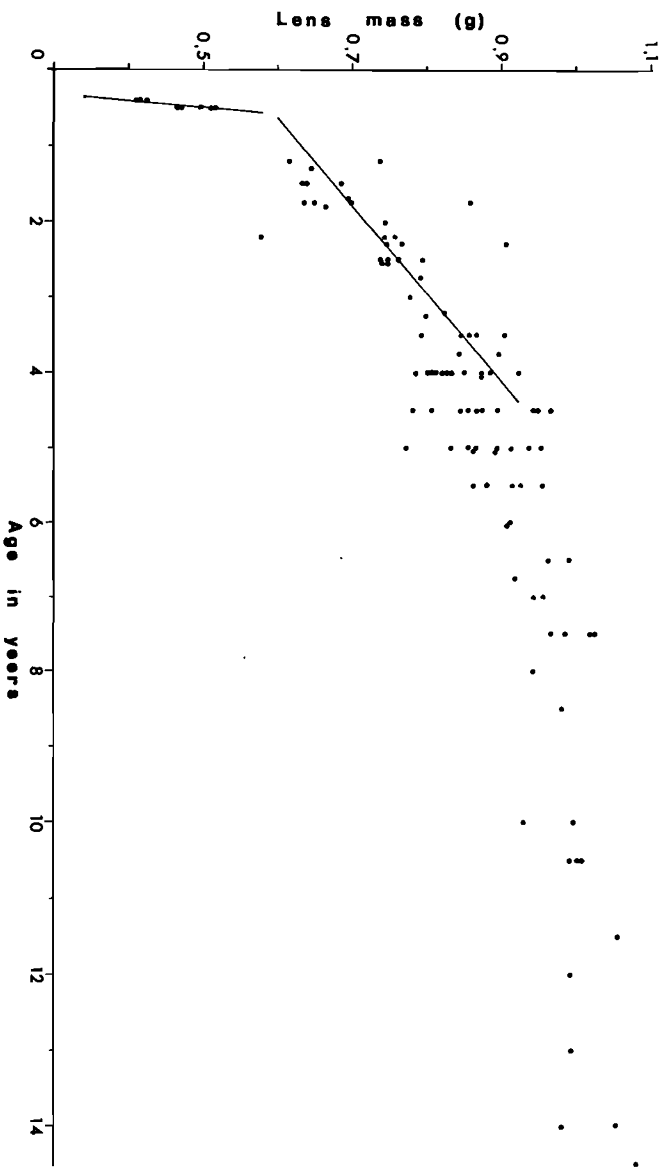

Fig. 4 Straight-line regressions of lens mass against age for animals under four years of age.

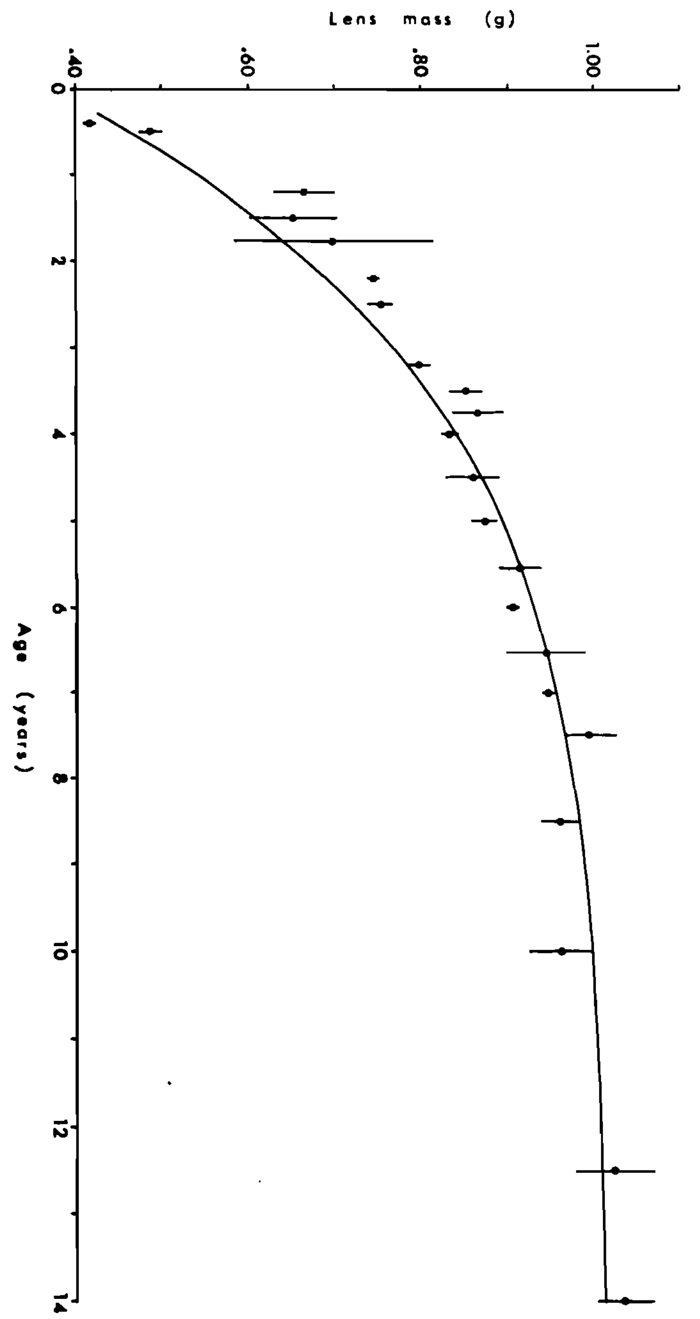

Fig. 5 Von Bertalanffy growth curve for eye lens mass. Circles indicate mean values; vertical lines extend for one standard error either side of the mean.

mination of wildebeest. Because the rate of growth of the lens is not constant, only the very young age classes are distinguishable with any confidence. Ages of these classes are more easily and more accurately determined from the tooth eruption calendar.

Errors in determining lens mass have been summarized by Attwell (1977), but these inherent or experimental errors cannot wholly account for the overlap between age classes. It is suggested that if workers wish to persevere with the use of eye lenses in age determination of larger mammals, then attention should be diverted to biochemical methods rather than lens mass. Only increased accuracy would minimize the overlap in older age classes. Otero and Dapson (1972) consider the biochemical assay of eye lens proteins to be 'the most accurate method known to date for estimating age of wild vertebrates'.

Field age and sex determination

Determination of age in the field requires considerable experience. Talbot and Talbot (1963) differentiated six age classes for females based on horn configuration, and seven for males. Their adult classes were of little use in the field, and the severe wear shown by their oldest male class was never observed in Zululand. The following notes may be of use in distinguishing between age classes and sexes:

Calves

Readily distinguishable on size, colour and horn development. The fawn colour contrasts strongly with that of other age classes, but is usually lost by about May (5–6 months old), and sometimes as early as the end of February. Fawn colouration is maintained on the face into the yearling class. (A single calf specimen was observed with a wholly black face.) By the end of July, most Zululand calves display full development of brindle stripes on the neck, with faint brindles on the thorax.

The horns first appear at about three months, initially growing straight out but begin to curve outwards and then inwards at about 7,5 months. No field sex differentiation is possible.

Yearlings

The yearling is distinguished by the fawn colouring on the front of the face, between the eyes. Size may be useful early in the year, but becomes less reliable later. The fawn colouration is not always reliable (it may be lost, or may even be found in adults). A more reliable characteristic is the degree of exposure of the base of the horns: in yearlings the boss is not visible, and has the appearance of being covered by a tuft of hair. Sexual differentiation is difficult but possible, particularly towards the end of the year when male horn development is more marked. The belly shape (see adults, below) may also be used.

2-3 Year olds

Reliable recognition of this class can only take place in about the first six months of the year. Criteria for sex are as for adults.

Adults

The male is the more easily distinguished. The spread of the horns extends beyond the ears when the latter are extended horizontally. The boss of the horns is well developed, much larger than in females. The scrotum is seldom observed in the field, but the penis shaft extends anteriorly in a downward straight line to the centre of the belly, so that an angular appearance is presented from the flank. In contrast the belly of the female is more uniformly rounded, lacking the 'angle' of the adult male.

In general, the laterally extended ears of the female project beyond the spread of the horns. No single criterion should however be used, as the above are largely generalizations. The ear/horn-spread feature is fallible, for example, and the angular male belly is lost in animals in very poor condition.

Acknowledgements

This study was supported by C.S.I.R. funding, and supplemented by a grant from the Natal Parks Board. The advice and assistance of Professor J. Hanks are gratefully acknowledged. The manuscript was typed by Mrs I. Martyn of the University of Natal, Durban.

References

ATTWELL, C.A.M. 1977. Reproduction and Population Ecology of the blue wildebeest *Connochaetes t.taurinus* in Zululand. Ph.D. thesis, University of Natal.

ATTWELL, C.A.M. & HANKS, J. (in press). Reproduction of the blue wildebeest *Connochaetes taurinus taurinus* in Zululand, South Africa. *Saug. Mitt.*

BRAACK, H. 1973. Population dynamics of the blue wildebeest, *Connochaetes taurinus taurinus* (Burchell 1823), in the Central District of the Kruger National Park. Project report submitted to the University of Rhodesia. 85 pp.

CAUGHLEY, G. 1965. Horn rings and tooth eruption as criteria of age in the Himalayan thar, *Hemitragus jemlahicus*. *N.Z.J. Sci.* 8: 333–351.

CHAPLIN, R.E. & ATKINSON, J. 1968. The occurrence of upper canine teeth in Roe deer (*Capreolus capreolus*) from England and Scotland. *J. Zool. Lond.* 155: 141–144.

CHAPMAN, D.I. & CHAPMAN, N.G. 1973. Maxillary canine teeth in Fallow deer, *Dama dama*. *J. Zool. Lond.* 170: 143–162.

CHILD, G.F.T. 1964. Growth and ageing criteria of impala *Aepyceros melampus*. *Occ.Pap.natn.Mus.Sth.Rhod.* 4(27B): 128–135.

COLYER, F. 1936. Variations and diseases of the teeth of animals. John Bale, Sons and Davidsson Ltd., London.

FAIRALL, N. 1969. The use of the eye lens technique in deriving the age structure and life table of an impala population. *Koedoe* 12: 90–96.

FRIEND, M. 1968. The lens technique. *Trans.N.Am.Wildl.Conf.* 33: 279–298.

GRIMSDELL, J.J.R. 1973. Age determination of the African buffalo, *Syncerus caffer* Sparrman. *E.Afr.Wildl.J.* 11: 31–53.

HALL-MARTIN, A.J. 1976. Dentition and age determination of the giraffe, *Giraffa camelopardalis*. *J.Zool. Lond.* 180: 263–289.

HANKS, J. 1972. Growth of the African Elephant (*Loxodonta africana*). *E.Afr. Wildl. J.* 10: 251–272.

HEMMING, J.E. 1969. Cemental deposition, tooth succession, and horn development as criteria of age in dall sheep. *J. Wildl. Mgmt.* 33: 552–558.

HYMAN, L.H. 1942. Comparative vertebrate anatomy. University Chicago Press, Chicago. 544 pp.

KLEVEZAL, G.A. & KLEINENBERG, S.E. 1967. Age determination of mammals from annual layers in teeth and bones. Nauka Publishing House, Moscow (and Israel Program for Scientific Translations, P.O.B. 7147, Jerusalem, Israel).

LAWS, R.M. 1952. A new method of age determination for mammals. *Nature Lond.* 169: 972–973.

LAWS, R.M. 1967. Eye lens weight and age in African elephants. *E. Afr. Wildl. J.* 5: 46–52.

LOW. W.A. & COWAN, I. McT. 1963. Age determination of deer by annular structure of dental cementum. *J. Wildl. Mgmt.* 27: 466–471.

MITCHELL, B.L. 1965. The presence of canine teeth in the upper jaw of wildebeest and oribi. *Puku* 3: 178–179.

MITCHELL, B.L. 1967. Growth layers in dental cement for determining the age of red deer (*Cervus elaphus*). *J.Anim. Ecol.* 36: 279–293.

MORRIS, P. 1972. A review of mammalian age determination methods. *Mammal Rev.* 2: 69–104.

OTERO, J.G. & DAPSON, R.W. 1972. Procedures in the biochemical estimation of age of vertebrates. *Res. Popul.Ecol.* 13: 152–160.

RANSOM, A.B. 1966. Determining the age of white-tailed deer from layers in cementum of molars. *J.Wildl.Mgmt.* 30: 197–199.

RAUTENBACH, I.L. 1971. Ageing criteria in the springbok, *Antidorcas marsupialis* (Zimmermann 1780) (*Artiodactyla: Bovidae*). *Ann. Tvl. Mus.* 27: 83-133.

ROETTCHER, D. & HOFFMAN, R.R. 1970. The ageing of impala from a population in the Kenya Rift Valley. *E. Afr. Wildl. J.* 8:37-42.

SCHALLER, G.B. 1972. The Serengeti Lion. University of Chicago Press, Chicago and London. 480 pp.

SIMPSON, C.D. & ELDER, W.H. 1969. Tooth cementum as an index of age in greater kudu. *Arnoldia Rhod.* 4(20): 1-10.

SMUTS, G.L. 1974. Growth, reproduction and population characteristics of Burchell's zebra (*Equus burchelli antiquorum*, H. Smith, 1841) in the Kruger National Park. D.Sc. thesis University of Pretoria.

SPINAGE, C.A. 1967. Ageing the Uganda defassa waterbuck *Kobus defassa ugandae* Neumann. *E.Afr.Wildl. J.* 5: 1–17.

SPINAGE, C.A. 1973. A review of the age determination of mammals by means of teeth with especial reference to Africa. *E. Afr. Wildl. J.* 11: 165–187.

SPINAGE, C.A. 1976. Incremental cementum lines in the teeth of tropical African mammals. *J. Zool. Lond.* 178: 117–131.

STARKEY, W.E. 1971. Dimensional changes associated with enamel maturation in rabbits. *Arch. Oral Biol.* 16: 479–493.

STEENKAMP, J.D.G. 1969. Wear in bovine teeth. *Proc. Symp. Anim. Prod.* 2: 11–23.

STEENKAMP, J.D.G. 1970. The effect of breed and nutritional plane on the chronology of teeth eruption in cattle. *Rhod.J.agric.Res.* 8: 3–13.

TALBOT, L.M. & TALBOT, M.H. 1963. The wildebeest in Western Masailand, East Africa. *Wildl. Monogr.* 12: 1–88.

WATSON, R.M. 1967. The population ecology of the wildebeest (*Connochaetes taurinus albojubatus* Thomas) in the Serengeti. Ph.D. thesis University of Cambridge.

WATSON, R.M. 1969. Reproduction of wildebeest *Connochaetes taurinus albojubatus* Thomas, in the Serengeti region, and its significance to conservation. *J. Reprod. Fert.*, Suppl. 6: 287–310.