Age determination of eland *Taurotragus oryx* (Pallas, 1766) in the Natal Highveld

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Techniques for the age determination of highveld eland in Natal were investigated. Tooth eruption and replacement sequence, and growth in horn length, were suitable criteria for the age determination of young eland with deciduous dentition. The most accurate technique for the age determination of *post mortem* adult eland was based on counts of cementum annuli from molar teeth. Animals without distinctive cementum annuli may be assigned ages from measurements of M_3 crown height. The ages of live restrained eland could be derived from measurements of I_1 occlusal width or I_1 crown height. Horn morphology was adequate for age and sex classification of free-ranging eland up to adult status.

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Tegnieke vir die ouderdombepaling van elande van die Natalse hoëveld is ondersoek. Die deurbraak en volgorde van tandvervanging en toename in horinglengte was geskikte maatstawwe vir ouderdombepaling van jong elande met tydelike gebit. Die akkuraatste tegniek vir nadoodse ouderdombepaling in volwasse elande was gebaseer op tellings van sementbande van molaartande. Die ouderdomme van diere sonder herkenbare sementbande kon bepaal word op grond van afmetings van M_3 kroonhoogte. Die ouderdomme van lewendige elande onder bedwang kon afgelei word van afmetings van die bytwydte of kroonhoogte van I_1. Horingmorfologie was voldoende vir ouderdom- en geslagbepaling van vry elande tot op die volwasse stadium.

S.-Afr. Tydskr. Dierk. 1981, 16: 113 – 122

In order to satisfy the most demanding requirements of management and research, it is necessary to establish techniques for age determination which are both rapid to use and reliable. Numerous techniques are available and the majority are reviewed by Morris (1972). The purpose of the present study is to provide a choice of techniques for the age determination of the common eland (*Taurotragus oryx oryx*) in the Natal Highveld. For the practical use of fieldworkers, techniques based on destructive sampling are distinguished from those which can be used for live sampling. The study examines age determination from tooth eruption and replacement sequence, incremental lines of tooth cementum, tooth wear, and horn growth and morphology.

Methods

The principal site for data collection was Coleford Nature Reserve in the foothills of the Natal Drakensberg Mountains (29°27′E; 29°58′S). The majority of mandibles and all skulls were found and collected in the Drakensberg reserves of Natal including Giant's Castle Game Reserve and Loteni Nature Reserve. All these areas constitute the Natal Highveld.

Three sources of material were available for this study.

(i) Live known-age eland. The incisiform teeth of 21 female eland at Coleford Nature Reserve were examined. Horn measurements and photographs were collected from 40 female eland and 12 male eland at Coleford. Measurements were taken from the captive eland by driving the herd into a crush and physically restraining individual animals in a weighbridge (Jeffery 1978).

(ii) *Post mortem* known-age eland. The mandibles of 15 known-age eland (10 females : 5 males) which had died in captivity at Coleford were collected for dental examinations.

(iii) *Post mortem* unknown-age eland. A collection of 42 found mandibles (17 females : 13 males : 22 of unknown sex) was available for dental studies. The skulls of 13 adult males were used to supplement the study of horn growth and morphology. Only four of these skulls had mandibles attached allowing examination of the maxillary teeth only in the remaining nine skulls.

Tooth eruption and replacement sequence

The dentition of eland was examined from the *post mortem* samples and the eruption and replacement se-

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quence classified by age. Twenty mandibles with incomplete adult dentition were available, of which seven were of known ages. Six mandibles of unknown ages had known dates of death enabling approximate ages to be assigned to them assuming that they were born during the September calving peak of wild eland in Natal (Stainthorpe 1972).

Cementum annuli

Varying rates of accretion and calcification of cementoid tissue around the roots of ungulate teeth are responsible for the alternating dark and light lines known as cementum annuli which may be seen in sections cut through the tooth cementum (Morris *ibid.*). These correspond to the translucent and opaque layers described by Douglas (1969).

Except when teeth were missing or worn out, all fully erupted first, second and third permanent mandibular molars were extracted from *post mortem* samples and examined. These included teeth from eight known-age mandibles and 29 mandibles of unknown ages. The permanent first molars from the maxillae of nine skulls of unknown ages were also examined. The sexes were not differentiated for cementum annuli counts. Teeth were sectioned dorso-ventrally along either their longitudinal or transverse axes using a 0,5-mm diamond blade lapidary saw. The facial sections chosen for counting were smoothed with progressively finer-grained Corumdum powder as described by Attwell (1977). The cementum lines were counted through a binocular microscope with reflected light (Mitchell 1967), never using more than 25x magnification. The total number of dark and light annuli which could be distinguished as separate lines were counted in the cementum pad arch. Indistinct or branched lines not conforming to the overall pattern of annulations were considered to be the 'supplementary streaks' described by Klevezal & Kleinenberg (1967) and were not counted. The correlations between age and the numbers of annuli counted in the permanent first, second and third molars were calculated for the known-age teeth sections.

Using the larger sample size of results from the unknown-age teeth, the mean difference between numbers of annuli counted in the first and second molars and the mean difference between numbers in the first and third molars were calculated. Having initially derived an estimate of the number of annuli layed down per year, the mean numbers of annuli deposited between eruptions of the first and second molars and between eruptions of the first and third molars could be converted to intervals in years. Mean eruption intervals were finally used as correction factors to compute cementum ages from the number of annuli counted in the second and third molars from each jaw. No correction factor was required for computing cementum ages from the number of annuli in the first molars since these teeth begin to erupt at birth (Figure 1). A similar method was used by Simpson & Elder (1969) for the age determination of greater kudu (*Tragelaphus strepsiceros*) except that cementum annuli were counted from C_1, PM_4 and M_1.

Tooth attrition

I_1 crown height from the anterior enamel-dentine interface to the crown of the tooth and I_1 occlusal width (Figure 2) were measured from 21 live known-age females at Coleford. The teeth were measured to the nearest 0,1 mm with vernier calipers. Both first incisors from each eland were measured and the mean values used to compute their correlations with absolute age. Measurement of I_1 crown height from young live eland was prone to error in locating the enamel-dentine border. This was because the gum-line in such eland had not receded enough to expose the interface. In young eland therefore, it was assumed that the gum-line approximated the posi-

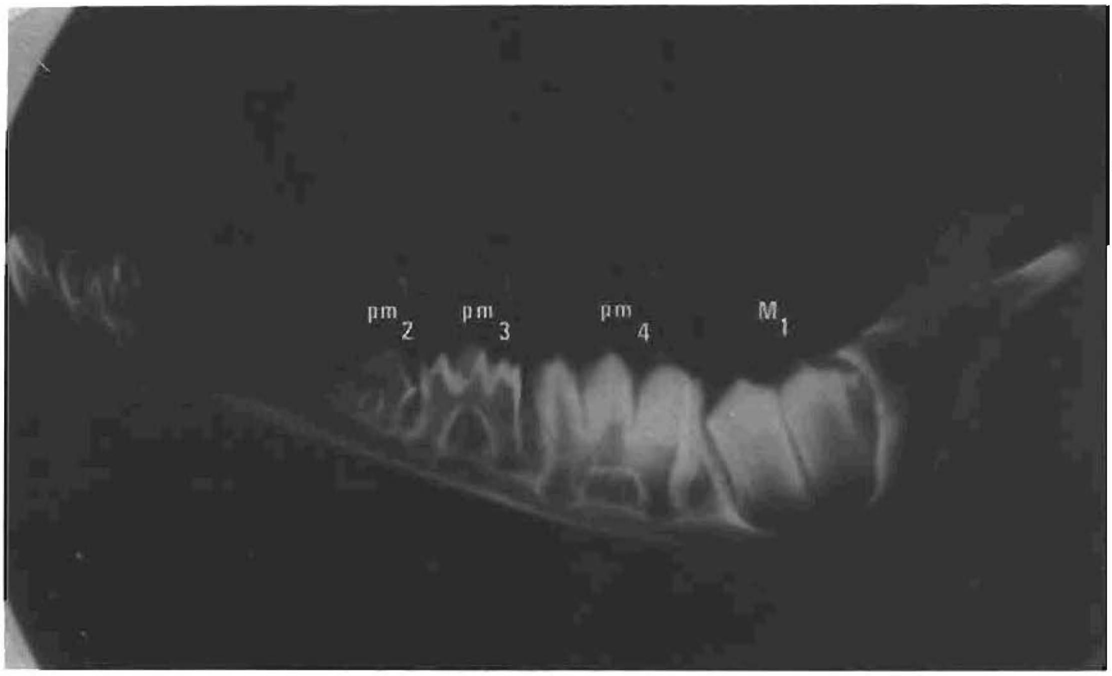

Fig. 1 Radiograph of the mandible of a four day old male eland showing that M_1 begins erupting at birth.

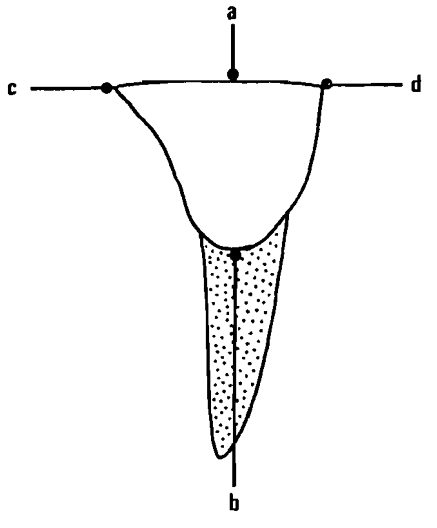

Fig. 2 Anterior of I_1, showing the measurement of crown height (a—• •—b) and occlusal width (c—• •—d).

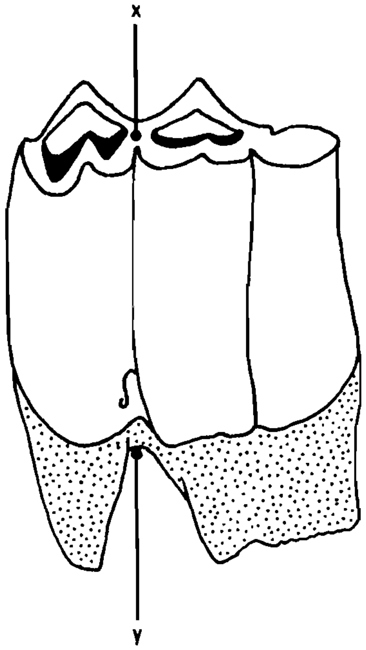

Fig. 3 M_3 of eland from buccal aspect, showing measurement of M_3 crown height (x—• •—y).

tion of the enamel-dentine interface. The alternative, a consistent measurement between gum-line and I_1 crown was rejected because recession of the gums was often considerable (as much as 5 mm in older eland). Measurement of I_1 occlusal width was not prone to such problems of definition.

The same measurements were collected *post mortem* from one male known-age jaw and seven jaws of unknown ages. In *post mortem* samples there was no difficulty in locating the enamel-dentine interface for I_1 crown height measurement. In order to increase the sample size, the results from the *post mortem* known-age and unknown-age jaws were combined. To be consistent, the mean cementum ages were used for all the male jaws when calculating the correlations of I_1 height and width with age.

Measurements of the molar teeth were recorded from the *post mortem* jaw collection. Sexes were treated separately (10 male jaws and 13 female jaws were available) and measurements were related to mean cementum age as described for the I_1 wear analysis of males. The large number of potential measurements defining molar wear was finally reduced to mass of M_3 and height from cementum pad arch to crown between the anterior and median cusps of M_3 ('crown height' — see Figure 3). The measurement of crown height was used by Spinage (1971) for the age determination of impala (*Aepyceros melampus*). Mass was measured to the nearest 0,01 g and crown height was measured with vernier calipers to the nearest 0,1 mm.

Horn growth and morphology

The horns of 40 female and 12 male known-age eland from Coleford and 13 adult male found skulls were measured. Horn length was the distance in a straight line between the lower, foremost point of cornified horn tissue and the horn tip, measured to the nearest 0,5 cm. This is not the same method as that described by Rowland Ward (Best 1962) where the distance between the two points follows the axis of the horn rather than along a straight line. Circumference at the base of the horn was the basal circumference at the most proximal plane which was at right angles to the long axis of the horn, measured to the nearest 1,0 mm. The same method is described by Rowland Ward (Best *ibid.*). Both horns were measured on each individual and the mean values recorded.

Due to the paucity of horn measurements from live adult males, those from the 13 adult male found skulls were used with their assigned cementum ages. To create meaningful sample sizes for the adult males, we combined the data from five males between five and seven years of age, three between eight and ten years of age and five of 10+ years of age, assigning each group a group mean cementum age. Growth curves of horn length and basal circumference of males and females were derived from theoretical von Bertalanffy equations (von Bertalanffy 1938; Beverton & Holt 1957) using a computer program as described by Hanks (1972).

Black and white photographs were taken of the horns of calves, yearlings, subadults and adults. The photographs were used to describe the changing morphology of male and female horns with age.

Results and Discussion

Tooth eruption and replacement sequence

The small sample size available for this study limited the reliability of observations of tooth eruption and replacement. The situation was further aggravated by the uneven distribution of the age classes. Only one mandible had fully erupted permanent first incisors and none of the known-age jaws was older than 11 months at death. However, since the eruption and replacement stages of all known-age mandibles correspond to the eruption and replacement calendar for *Taurotragus oryx livingstonei* in Zimbabwe (Kerr & Roth 1970), we have used their classification for the tooth eruption and replacement sequence of eland between 28 and 40 months of age.

The complete tooth eruption and replacement sequence in the lower jaw of eland is shown in Table 1. Eland dentition is diphyodont and similar to that of most bovids. The dental formula for the deciduous teeth of eland is:

$$2(\mathrm{i}\,\frac{\bullet\ \bullet\ \bullet}{1\ 2\ 3},\ \mathrm{c}\,\frac{\bullet}{1},\ \mathrm{pm}\,\frac{\bullet\ 2\ 3\ 4}{\bullet\ 2\ 3\ 4}) = 20$$

The dental formula for the permanent teeth of eland is:

$$2(\mathrm{I}\,\frac{\bullet\ \bullet\ \bullet}{1\ 2\ 3},\ \mathrm{C}\,\frac{\bullet}{1},\ \mathrm{PM}\,\frac{\bullet\ 2\ 3\ 4}{\bullet\ 2\ 3\ 4},\ \mathrm{M}\,\frac{1\ 2\ 3}{1\ 2\ 3}) = 32$$

Table 1 may be used to determine the ages of eland which have not obtained their adult dentition, but fieldworkers should be aware that although the eruption sequence remains constant within a species, eruption times may be altered by genetical or environmental factors (Attwell 1977). Sowls & Phelps (1968) found that ages at eruption of specific teeth of the African bushpig (*Potamochoerus porcus*) varied considerably. Due to the small sample size, the sensitivity of this method of age determination for eland could not be established.

The technique finds its greatest application in *post mortem* sampling but it should be possible to examine the teeth from the jaws of live suitably restrained animals either directly or by taking tooth impressions (Barnes & Longhurst 1960).

Tooth cementum annuli

The same degree of clarity of annuli in the first molar examined in a series from a single jaw persisted in the second and third molars (Figure 4). It was impossible to count any annuli in the teeth from three (9%) jaws of unknown sex and age. The maximum number of cementum annuli were found to lie above the apex of the cementum pad arch. Although in clear sections these lines were continuous and unbranched, they faded progressively and sometimes disappeared as the cementum layers became thinner down the sides of the roots in longitudinal sections and up the sides of the teeth in transverse sections (Figure 4). Lines usually reappeared around the lower half of the roots but they were more indistinct than the cementum pad annuli and were sometimes apparently branched. For this reason, annuli should only be counted from the roots when a cementum pad count is impossible. A further advantage of counting annuli in the cementum pad is that resorption of cementum may occur first at the root apices in old animals (Spinage 1973). However, this phenomenon may depend on the physiological condition of the individual since evidence of this feature was found in only one jaw, that of a 13 year old female in poor condition at death. Apart from this case, it was found that cementum was actively being deposited in discrete nodules below the roots of the oldest animals. In one case, a cementum nodule the size of a tooth was found in the lower jaw just posterior to and below the roots of M_3 (Figure 5).

The different zones on a tooth where cementum accretion occurs simultaneously (Attwell 1977) appear to be the cementum pad and root apices. Accretion of cementum about these two zones emanates further around the

Table 1 Tooth eruption and replacement in the lower jaw of eland combining data from Natal with those of Kerr & Roth (1970)

Age	Incisors			Canine	Premolars			Molars			Known-age samples	Sample
(months)	1	2	3	1	2	3	4	1	2	3	(months)	size
Birth	e	e	e	e	e	e	e	Ⓔ			(1) 0 (2) 0,2	2
1 – 5	M	M	M	M	M	M	M	E̮				2
6 – 8	M	M	M	M	M	M	M	E			(1) 6,2 (2) 6,46	7
9 – 13	M	M	M	M	M	M	M	P	Ⓔ		(1) 9,6 (3) 10,9 (2) 10,8	3
14 – 20	M	M	M	M	M	M	M	P	E		(1) 14* (3) 20* (2) 20*	3
21 – 23	Ⓔ	M	M	M	M	M	M	P	E	Ⓔ	(1) 21* (2) 22*	2
24 – 27	P	Ⓔ	M	M	M	M	M	P	P	E	(1) 26*	1
28 – 29	P	P	M	M	M	M	M	P	P	P	Kerr & Roth (1970)	
30 – 31	P	P	P	E	M	M	M	P	P	P		
32 – 35	P	P	P	P	M	M	M	P	P	P		
36 – 37	P	P	P	P	P	P	E	P	P	P		
38 – 40	P	P	P	P	P	P	P	P	P	P		

Explanation of symbols:

e = erupting milk tooth

M = fully erupted milk tooth in full wear

Ⓔ = erupting permanent tooth-cusps level with or below bone line

E̮ = erupting permanent tooth-cusps level with or just visible above bone line

E = erupting permanent tooth not in full wear

P = fully erupted permanent tooth in full wear

* = Estimated ages derived from known dates of death and assuming births were during September (Stainthorpe 1972).

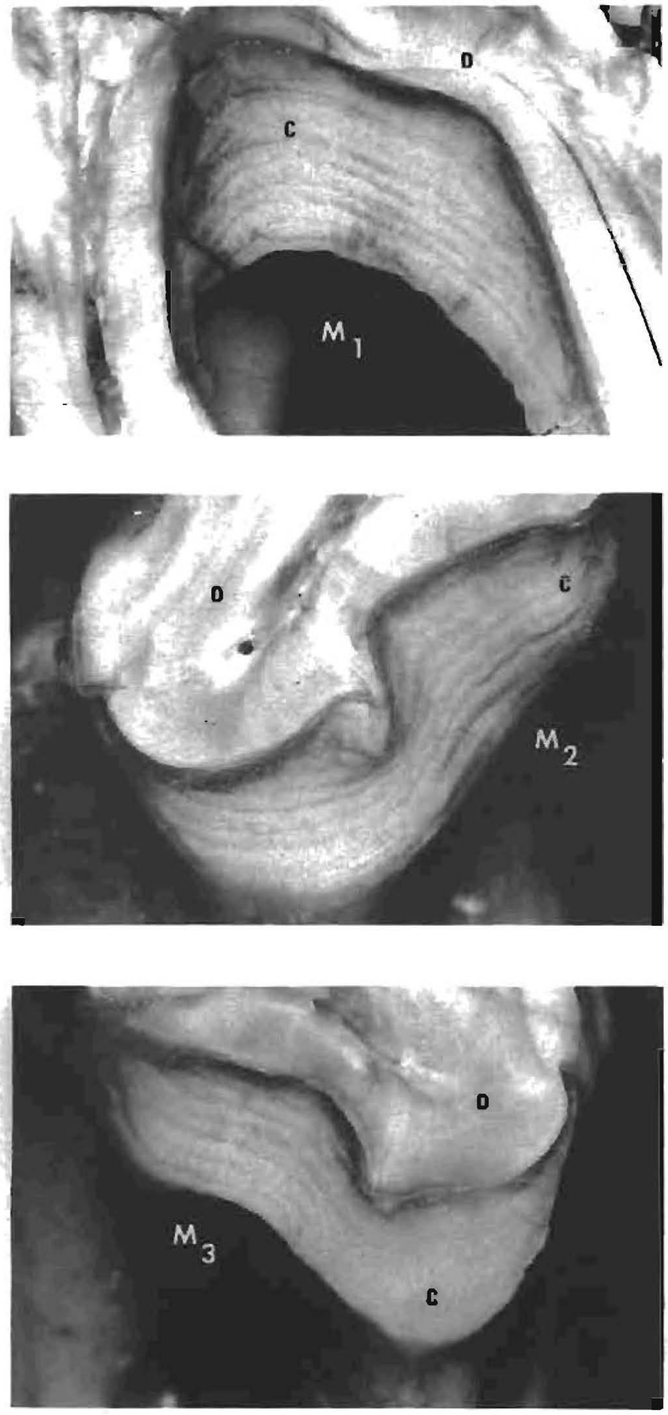

Fig. 4 Dorso-ventral sections of M_1 (longitudinal), M_2 (transverse) and M_3 (transverse) of adult male eland showing well-defined cementum annuli. Note the constriction of the cementum layer and disappearance of annuli in the upper part of the roots of the longitudinal section and a similar feature up the sides of the teeth in the transverse sections. C = cementum pad; D = dentine.

tooth with each successive layer. This hypothesis is supported by the observation that the enamel-dentine border clearly demarcating root from crown in teeth of young eland is usually hidden by sheets of cementum in the teeth of old animals (Figure 6). Furthermore, the first layers of secondary cementum around the root apex are nearly always the thickest suggesting a functional significance in anchoring a newly erupted tooth. The thick cementum pad in older animals may extend the useful life of the tooth by providing a grinding surface after the dentine has been worn away (Attwell *ibid.*).

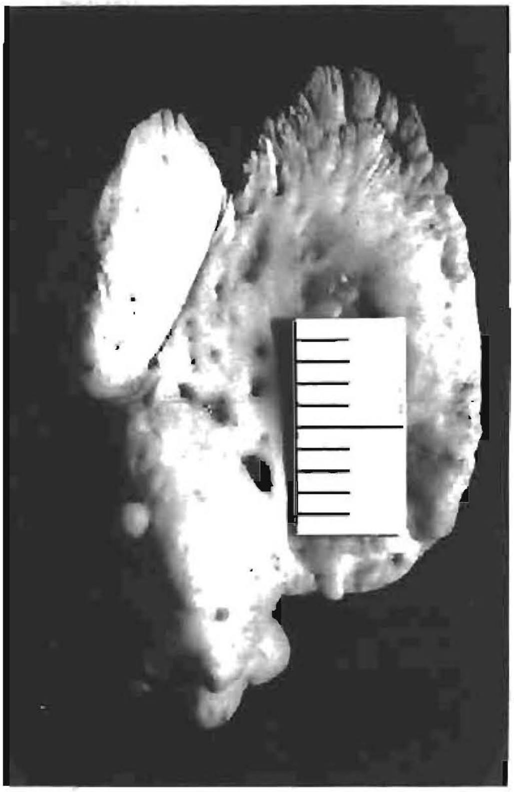

Fig. 5 Cementum nodule found just posterior to and below M_3 of a female eland estimated to be 15,5 years old. Scale is 10 mm.

Fig. 6 Transverse facial section of eland molar showing the enamel-dentine border covered by a thick layer of cementum. No cementum annuli can be seen in this sample. C = cementum pad; D = dentine; E = enamel.

The mean numbers of cementum annuli counted in the permanent molars of known-age eland are shown in Table 2. The relationships between absolute age and the numbers of cementum annuli are given by the following equations where x is age in years and y the number of annuli.

For M_1:

$$y = 1{,}72x + 1{,}66\ (n = 5;\ r = 0{,}986;\ p < 0{,}001)$$

For M_2:

$$y = 1{,}86x - 1{,}63\ (n = 8;\ r = 0{,}988;\ p < 0{,}001)$$

For M_3:

$$y = 2{,}01x - 5{,}19\ (n = 8;\ r = 0{,}996;\ p < 0{,}001)$$

The above equations show that to the nearest whole number, two annuli were deposited per year. This value fell well within the 95% confidence limits of the coefficients of x in all three equations. We therefore propose that two annuli (one dark and one light) were normally laid down per year in the cementum pad of the Highveld eland.

Table 2 Mean numbers of cementum annuli counted in M_1, M_2 and M_3 of known-age eland (with adult dentition) from Coleford Nature Reserve. The equations for the calculation of mean cementum ages from cementum annuli counts are given in the text

Absolute age (years)	M_1	M_2	M_3	Mean cementum age (years)
3,67	7,4	4,6	2	3,51
3,83	9	6	2	4,00
8,92	–	15	13,5	8,88
9,25	16	14	14	8,50
9,5	19	18	14,6	9,77
11,67	22	20	18	11,17
12,5	–	20,8	19	11,7
13,0	–	23	21	12,75

The mean numbers of cementum annuli counted in the permanent molars from unknown-age jaws are shown in Table 3. There were high positive correlations between the numbers of annuli counted in M_1 and M_2 and between those in M_1 and M_3. This phenomenon was described by Attwell (*ibid.*) and Anderson (1978). The equations are $y = 1{,}00x - 2{,}46$ ($n = 21$; $r = 0{,}99$; $p < 0{,}001$) for the M_1/M_2 combination and $y = 0{,}95x - 3{,}78$ ($n = 22$; $r = 0{,}96$; $p < 0{,}001$) for the M_1/M_3 combination. The mean difference between the numbers of annuli in M_1 and M_2 was 2,43 annuli and the mean difference between the numbers of annuli in M_1 and M_3 was 4,6 annuli. Assuming that two annuli were deposited per year, these values correspond to an M_1-M_2 eruption interval of 1,2 years and an M_1-M_3 eruption interval of 2,3 years. These are similar but slightly higher than those values which could be deduced from the eruption calendar (approximately 1,1 and 2,0 years). It is assumed that the former values are more accurate since they were derived from larger sample sizes.

Table 3 Mean numbers of cementum annuli counted in M_1, M_2 and M_3 from eland of unknown ages with adult dentition. The equations for the calculation of mean cementum ages from cementum annuli counts are given in the text

Specimen No.	M_1	M_2	M_3	Mean cementum age (years)
1	–	7	5,5	4,88
2	11,25	7,6	6	5,31
3	10,5	9	6	5,42
4	10,5	8,5	8	5,67
5	–	9	–	5,7
6	12,5	9	6,4	5,82
7*	12	–	–	6,0
8	14	11	8	6,67
9	13	11	9	6,67
10	13,2	11,4	8,6	6,7
11*	13,5	–	–	6,75
12	13	11	11	7,0
13	14	12	10	7,17
14	16,3	13,4	11	7,95
15*	16	–	–	8,0
16*	16	–	–	8,0
17	18	14,5	12	8,58
18	17	15	14	8,83
19	18,3	16	12,5	8,97
20	18	16	14	9,17
21	19	–	–	9,5
22	20	17	15	9,83
23*	19,5	–	–	9,75
24	–	17	–	9,8
25	19	17	17	10,0
26	22	18,7	15	10,44
27*	21	–	–	10,5
28*	21	–	–	10,5
29	22	20	17	11,0
30*	22	–	–	11,0
31	25	22	19	12,17
32	24,5	23	19	12,25
33	–	22,5	20	12,38
34	–	23	20	12,5
35*	25	–	–	12,5
36	27	25	23	13,46
37	29	–	25,3	14,73
38	31	–	–	15,5

*Maxillary teeth used because mandibles not available.

Knowing the number of cementum lines deposited annually and the M_1-M_2 and M_1-M_3 eruption intervals, it was possible to use the cementum counts of all three molars from each jaw to derive cementum ages as follows:

Since M_1 erupts at birth,

$$M_1 \text{ cementum age} = \frac{\text{number of annuli in } M_1}{2} \text{ years}$$

Since M_2 erupts 1,2 years after M_1,

$$M_2 \text{ cementum age} = \frac{\text{number of annuli in } M_2}{2} + 1{,}2 \text{ years}$$

Since M_3 erupts 2,3 years after M_1,

$$M_3 \text{ cementum age} = \frac{\text{number of annuli in } M_3}{2} + 2{,}3 \text{ years}$$

A mean cementum age derived from all three mandibular molars (or those available) could minimize counting errors from individual teeth. Mean cementum ages were thus computed for the known-age and unknown-age jaws (Tables 2 and 3). Cementum ages of the nine skulls were calculated from M^1 alone. Although the eruptions of mandibular molariform teeth slightly precede those of corresponding maxillary teeth (Kerr & Roth, *ibid.*), the eruptions of both M_1 and M^1 are considered to occur at birth.

There was a high positive correlation between absolute ages of the known-age jaws and their mean cementum ages. The regression equation is $y = 0{,}94x + 0{,}25$ years ($n = 8$; $r = 0{,}995$; $p < 0{,}001$) where x is absolute age and y is mean cementum age.

The use of cementum annuli counts for the age determination of eland can give highly accurate results although anomalies may occur as a result of the difficulty of distinguishing annuli in some tooth sections and perhaps as a result of inconsistencies in annual patterns of growth and condition.

It should be noted that the total number of cementum annuli in the cementum pad were counted excluding 'supplementary streaks'. This presumably includes the primary cementum (eruption line) deposited during eruption (Spinage 1973). Since M_1 is fully erupted by nine months, cementum deposited between nine and twelve months may produce a second annulus. This would be consistent with the findings presented above and may also apply during the year following the eruptions of M_2 and M_3. However, the cementum counts of eland with deciduous dentition appear to be inconsistent in their relationships with age (Table 4). Douglas (1969) found that half the yearlings in his study group of red deer (*Cervus elaphus*) failed to produce a summer opaque layer as recorded in adults. Thus it is inadvisable to use cementum counts for age determination of eland of less than 40 months of age. Apart from the uncertainty concerning cementum deposition in newly erupted teeth, a counting error of one cementum line will be more misleading in a young animal than an old animal.

Finally, because it is impractical to extract molar teeth from live animals without impairing their feeding efficiency, age determination of eland from counts of molar cementum annuli is only suitable as a *post mortem* technique.

Table 4 Mean number of cementum annuli counted in M_1 and M_2 from eland with deciduous dentition. The equations for the calculation of mean cementum ages from cementum annuli counts are given in the text

Absolute age (years)	M_1	M_2	Mean cementum age (years)
0,8	1	–	0,5
0,9	1	–	0,5
0,9	2	–	1,0
1,8*	1,5	1	1,2
1,8*	4	2	2,1
2,2*	5	3	2,6

*Estimated ages derived from known dates of death and assuming births were during September (Stainthorpe 1972).

Tooth attrition

(i) *Quantification of* I_1 *wear.* It has been found that I_1 wear has a sigmoidal relationship with age (Spinage 1967, Simpson & Elder 1969, Attwell 1977). In this study there was no evidence that the relationships of I_1 crown height and occlusal width with age were anything but linear between the range of ages examined. It is possible that the sigmoid portions of the present data were excluded by an inadequate range of ages.

The relationships of I_1 crown height and occlusal width with absolute age of live female eland at Coleford are given by the following equations where x is the I_1 wear measurement, and y is age in years.

I_1 crown height: $y = -0{,}64x + 17{,}47$ years
($n = 21$; $r = -0{,}855$; $p < 0{,}001$)

I_1 occlusal width: $y = 1{,}16x + 30{,}18$ years
($n = 21$; $r = -0{,}933$; $p < 0{,}001$).

The high correlation reported earlier between absolute age and mean cementum age justifies the use of cementum ages in all the remaining analyses of tooth wear.

The relationships of I_1 crown height and occlusal width with mean cementum age of the male *post mortem* samples are as follows.

I_1 crown height: $y = -0{,}56x + 18{,}41$ years
($n = 8$; $r = -0{,}883$; $p < 0{,}001$)

I_1 occlusal width: $y = -0{,}89x + 26{,}63$ years
($n = 8$; $r = -0{,}812$; $p < 0{,}01$).

Spinage (1973) considered that tooth wear measurements such as crown height and occlusal width are only pseudo-objective in that they may remove observer bias but cannot correct for varying rates of wear. Variations in measurement must also be expected as a result of differences in absolute sizes of individuals of the same age in a population. Such variations may be reduced by calculating a ratio of the chosen wear parameter to an associated parameter which remains constant throughout the animal's life. Thus, a ratio such as I_1 occlusal width : I_1 transverse diameter at a point immediately above the enamel-dentine interface could be investigated.

Incisiform teeth may be measured on live restrained animals or *post mortem* samples.

(ii) *Quantification of* M_3 *wear.* The equations describing the relationships of mass and crown height of M_3 with mean cementum age are given below where x is the measurement of M_3 wear and y is age in years.

M_3 mass (females): $y = -0{,}30x + 18{,}06$ years
($n = 13$; $r = -0{,}830$; $p < 0{,}001$)

M_3 crown height (females): $y = -0{,}27x + 15{,}33$ years
($n = 13$; $r = -0{,}919$; $p < 0{,}001$)

M_3 mass (males): $y = -0{,}31x + 18{,}66$ years
($n = 10$; $r = -0{,}895$; $p < 0{,}001$)

M_3 crown height (males): $y = -0{,}29x + 16{,}03$ years
($n = 10$; $r = -0{,}977$; $p < 0{,}001$)

M_3 crown height gave the best correlations with age.

Because it is necessary to extract M_3 for measurement, this method is only suitable for *post mortem* sampling.

Horn growth

The growth curves and equations describing growth in horn length and basal circumference with age are shown in Figures 7 – 9.

Female and male growth in horn length with age was similar. Female asymptotic horn length was 2,5% less than that of males, but this difference would be indistinguishable in the field. In contrast, male and female growth in horn basal circumference with age differed considerably. Asymptotic horn basal circumference of females was 29% less than that of males. The data demonstrate that horn growth is of no value for age determination after about 40 months of age. Horn basal circumference values illustrate the marked sexual dimorphism in horn growth. Taking the standard errors of means into consideration, one can use the measurement of horn basal circumference to distinguish between sexes by at least three months of age and possibly sooner. Using the table of tooth eruption and replacement to determine the ages of non-adult found skulls, it should be possible to derive their sexes from Figure 9. Since non-adult growth in horn length was so similar in males and females, a more rapid field-method for sex determination is to determine the age of the found skull from horn length and classify the sex of the sample according to horn basal circumference at the assigned age. The sexes of adult skulls can more readily be distinguished at a glance by their size and morphology.

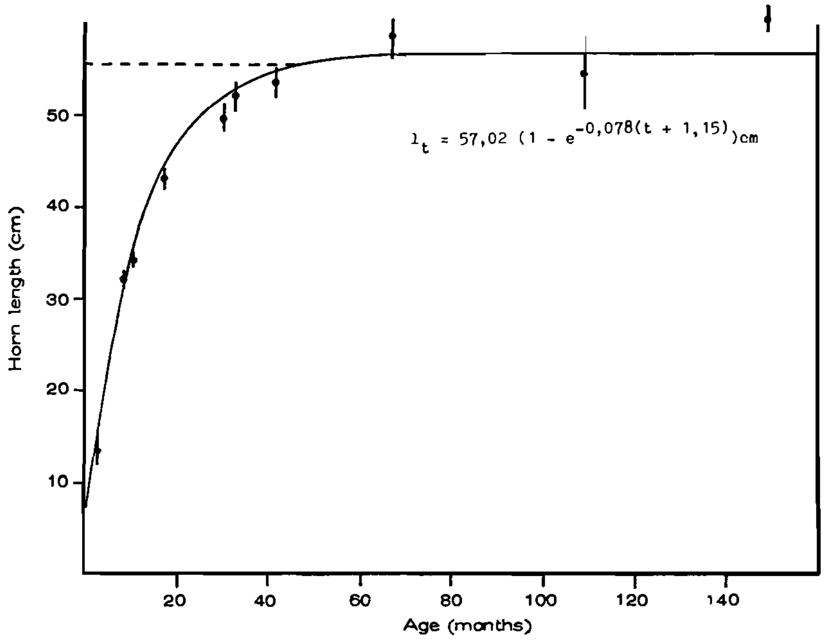

Fig. 7 Theoretical von Bertalanffy growth curve of horn length for female eland from Coleford. Circles denote mean horn length at age. Vertical lines denote one standard error either side of the mean. Asymptotic horn length (dashed line) was 57,02 cm and age at 2,5% less than this value (the corrected asymptote — Attwell 1977, Jeffery 1978) was 46,1 months.

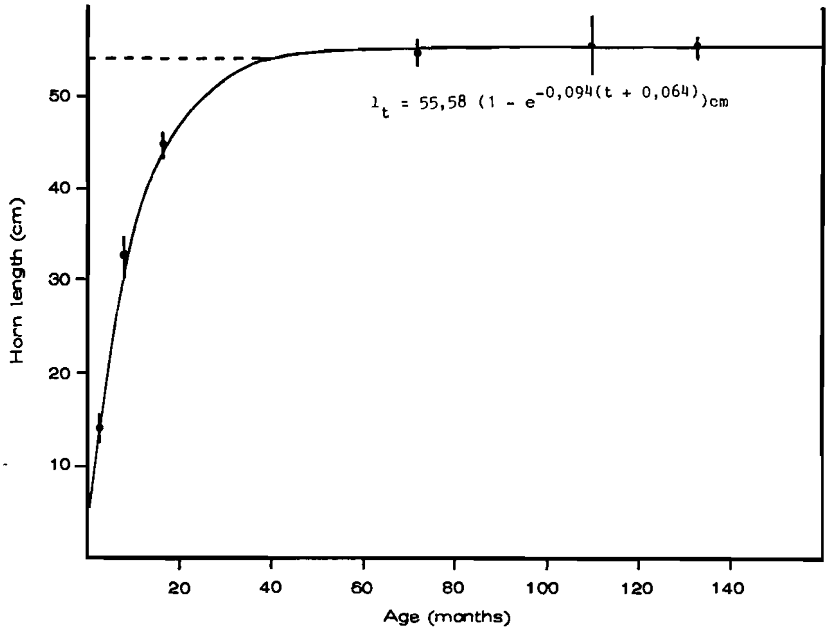

Fig. 8 Theoretical von Bertalanffy growth curve of horn length for male eland from Coleford and the Natal Highveld. Circles denote mean horn length at age. Vertical lines denote one standard error either side of the mean. Asymptotic horn length (dashed line) was 55,58 cm and age at the corrected asymptote was 39,2 months.

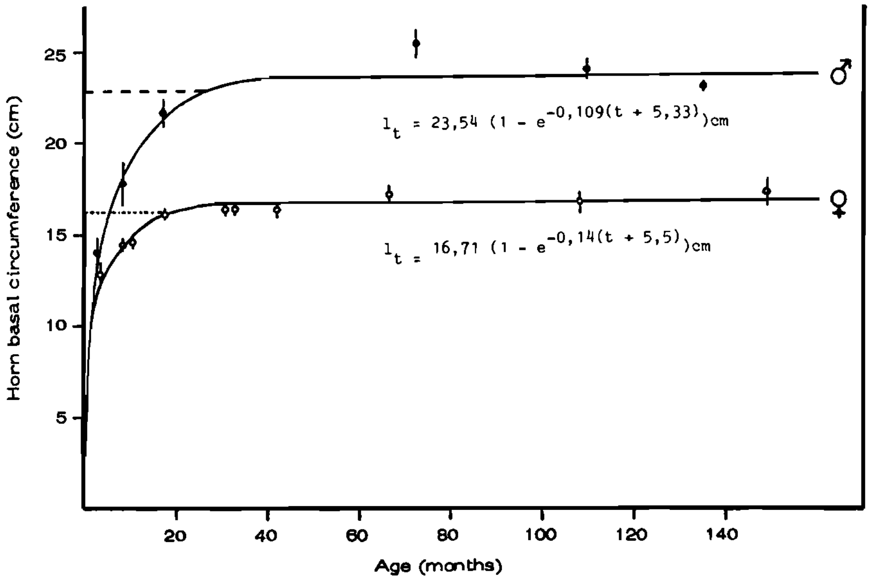

Fig. 9 Theoretical von Bertalanffy growth curves of horn basal circumference for female and male eland from Coleford and the Natal Highveld. Circles denote mean basal circumference at age. Vertical lines denote one standard error either side of the mean. Asymptotic basal circumference for females (dotted line) was 16,71 cm and age at the corrected asymptote was 20,8 months. Asymptotic basal circumference for males (dashed line) was 23,54 cm and age at the corrected asymptote was 28,5 months.

Horn morphology

Horn development and morphology of *T.o.livingstonei* have been described by Kerr & Roth (1970) and closely resemble the observations of *T.o.oryx* in Natal (Figure 10). Both sexes bear horns which are distinctly sexually dimorphic. The more massive development of male horns is a true secondary sexual character (Kerr & Roth *ibid.*) and may be used for the differentiation of the sexes. It is the development of a close spiral in the basal half of the horn which can be related to age (Kerr & Roth *ibid.*).

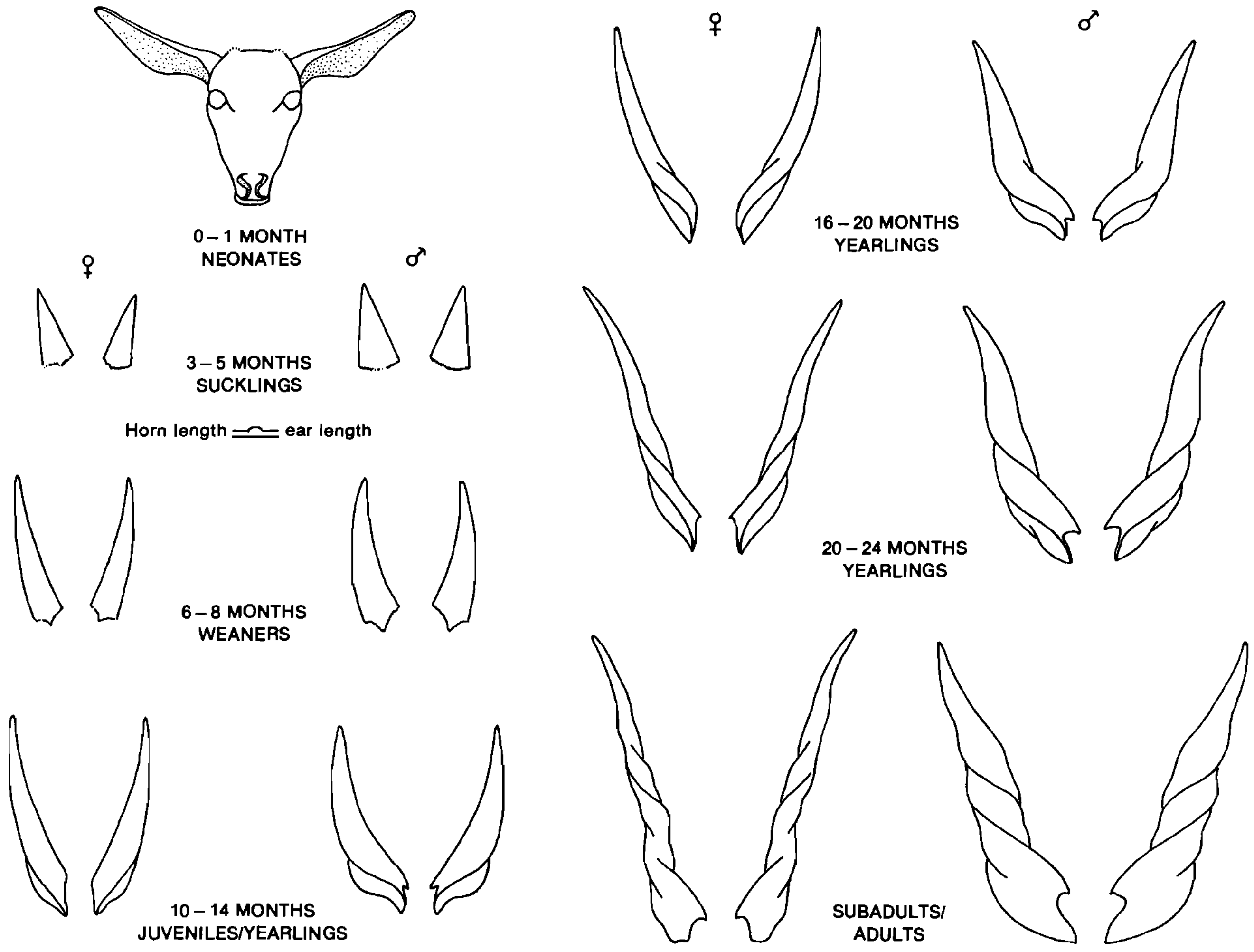

Fig. 10 The changing morphology of eland horns with age in Natal. Class I: Neonates (birth to one month); Class II: Sucklings (up to five months); Class III: Weaners (six to eight months) (Classes I – III — calves); Class IV: Juveniles/yearlings (10 to 14 months); Class V: Yearlings (16 to 20 months); Class VI: Yearlings (20 to 24 months); Class VII: Subadults and adults (from 26 months).

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