

A review of the age determination of mammals by means of teeth, with especial reference to Africa

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Summary

A growing requirement exists to determine the ages of the larger African mammals, concomitant with increasing management. Teeth offer the most practicable means of age determination, but no wholly reliable method, based on teeth, has been demonstrated. Tooth structure, growth and function, are considered, and related to methods of age determination. Methods are divided into those separating groups, and those for determining the chronological ages of groups. The various methods used in these two procedures are evaluated. It is pointed out that studies on the most promising method, cementum line counts, have been neglected in Africa, while methods of determining the ages of large carnivores are virtually uninvestigated, and there is a lack of basic studies describing tooth growth and changes for most large African mammals.

Introduction

With increasing sophistication of African wildlife management, it has become necessary in many fields of application to determine the ages of species. Age determination by means of teeth, not 'ageing' which means to make old, is a practice of some antiquity among animal husbandmen; but its use for African mammals is recent.

In the past it was considered that crude groupings of ages sufficed, as, once mature size was attained, each animal would contribute much the same to the population. With increasing refinement of age determination methods, more precise attempts at age determination have followed. Knowledge of the ages of individuals is essential to understanding the rates of growth, onset of sexual maturity, fertility peak, senescent decline and life span, as well as social behaviours. However, extreme precision in age determination is often more of academic than of practical interest. Thus relatively crude methods, empirically speaking, are often sufficient.

Despite increasing interest in this aspect of wildlife biology, no wholly reliable method for African mammals has yet been demonstrated. This communication aims to review some of the methods of age determination by teeth used to date, and to comment on their further development.

Before considering methods of age determination by means of tooth changes, it is necessary to consider tooth growth, structure and function, and to understand the use of these characteristics in age determination.

Tooth structure

The permanent tooth comprises three hard substances, enamel, dentine and cementum, all of which show certain lines in section.

Enamel is the hard, outer coating of the crown, laid down before eruption. After eruption begins there is no further addition, so that any incremental structures relate to the pre-eruption period. Ground longitudinal sections may reveal two types of lines or bands. Firstly, there is a series of alternating light and dark bands running more or less longitudinally. These are the Hunter-Schreger lines and are the result of an optical phenomenon due to the prism arrangement of the enamel. Secondly, there are the Brown Striae of Retzius, which are true incremental lines. Schour & Hoffman (1939) found that calcification of both enamel and dentine, in all species, took place in a basic incremental rhythm recurring at intervals of 16 μm . The Striae of Retzius tended to recur at intervals which were multiples of 16 μm , and they considered this to be physiologic or pathologic accentuations of the normal rhythm.

Dentine comprises the major tooth substance, and is present as both primary and secondary dentine. As with enamel, the formation of primary dentine is rhythmic, resulting in incremental lines visible in ground sections. At eruption, little more than the coronal portion is formed, complete root formation occurring later. Before eruption a second process of dentine formation is initiated, which will gradually fill the pulp cavity. This dentine is physiological secondary dentine, and its formation continues until the pulp cavity is occluded, or nearly so. It also shows rhythmic deposition portrayed by alternate light and dark bands in ground section, known as the Contour Lines of Owen. These run at an oblique angle to the tooth surface. Schour & Hoffman (1939) found that they possessed the same rhythmic characteristics as the Striae of Retzius in the enamel, and deduced the same cause for their formation. A finer pattern of parallel lines may occasionally be seen, which are also incremental and are known as the Lines of Von Ebner. Sometimes a third type is present, running in the same direction as the Contour Lines of Owen, which result from variations in calcification and are not true incremental lines.

If excessive abrasion of the tooth crown takes place, such that the surface is worn to the forming secondary dentine, 'irregular secondary dentine' is formed. This can be distinguished microscopically by its fewer, less regularly arranged, dentinal tubules; or their complete absence. Its formation is an emergency reaction to caries or excessive wear. If the latter was suspected in an animal, it should be possible to confirm it by the presence of this type of dentine.

In old age, starting at the root apex and spreading upwards, the dentine becomes translucent, due to occlusion of the dentinal tubules by calcific deposits. The extent of this translucency in section can be used in age determination.

Cementum normally covers the root of the tooth, but in some species extends over the crown as well. The thickness covering the root varies among species; it is thick in ungulates, and thin in primates, rodents and carnivores. Two types can be identified, the first-formed acellular cementum adjacent to the dentine, and the cellular secondary cementum which starts to be laid down when the tooth commences eruption. Both types show incremental layering starting after eruption, and continuing throughout life, which is very distinctive in some species, visible often in ground sections and staining well in decalcified sections. Schour & Hoffman (1939) did not extend their studies of calcification rhythm to cementum, but accretion is probably continuous with

disturbances, such as cold winters or dry seasons, causing interruption of the process. The marked lines which result have been described as 'fibre-free amorphous substance' representing successive intervals between cementum deposition (Scott & Symons, 1971); but the concept that the life span of cementum is restricted, forming a series of dead bands (Sicher, 1962), is now considered to be unlikely. In Spinage (1967) it was postulated that seasonal lack of phosphate might result in a line of hypocalcification, as the calcium-phosphate balance is critical in mammals (French, 1957; White, 1959). Current thought, however, considers calcium and phosphate levels are usually sufficient for mineralization processes, and that it is the growth of the ostein matrix which is checked. Mineralization continues at uniform rate, thus forming a line of greater density when growth of the matrix slows up. Thus the broad, translucent bands seem to be regions of active growth, and the narrow, dark lines, regions of reduced growth. In tropical herbivores these could be formed after the onset of the rains, when the animals are most affected by vegetation changes (Payne, 1964). Their occurrence in carnivores, however, could not be explained on this basis.

Despite the fact that oestrogens play a role in calcium-phosphate retention, there is little evidence as yet of cementum lines being related to parturition, lactation or sexual activity, an exception being the red deer *Cervus elaphus* L. stag in Scotland, a 'rutting line' apparently forming (Mitchell, 1967). This could be due to nutritional features rather than sexual.

Cementum accretion continues through most of life, most conspicuously in bovids on the posterior of the incisor root apices, and in a pad under the crown of the molars. In senescence, resorption takes place, commencing at the root apex, and in very old animals may extend to the lower part of the dentine as well (Spinage, 1967). Once initiated this process proceeds very rapidly, apparently resulting from an imbalance of calcium ions between the blood and the calcified tissues. In cattle the excretion of unabsorbed calcium in the blood increases three-fold in old age (Hansard, Comar & Davis, 1954). The tooth roots seem to be the first tissues drawn upon to correct this imbalance. The importance of this does not seem fully appreciated in age determination studies, for it means that cementum line counts can only give the minimum age an old animal has reached, as an unknown number of lines are likely to have been resorbed.

Tooth morphology

If descriptive studies of dentition are to become more precise, it is necessary to use terms which are already established and understood. Correct nomenclature for individual teeth is that given by Flower & Lydekker (1891). The incisors, maximum number three on either side, are those teeth originating in the premaxilla and their dentary counterparts. The canine, maximum number one on either side, originates in the maxilla. It is followed by the premolars, maximum number four on either side, and the molars, maximum number three on either side. All these have their dentary counterparts, so that the complete permanent dentition has the formula:

$$I \frac{3}{3} \quad C \frac{1}{1} \quad Pm \frac{4}{4} \quad M \frac{3}{3}.$$

Recognized descriptive terms covering the structure of each tooth have been in use by palaeontologists for 90 years, but biologists have been slow to adopt them. These are the terms applied to the tritubercular theory of Cope, modified by Osborn (Gregory, 1934). Although the tritubercular theory of the origin of the mammalian molar is not today accepted in all of its original tenets, its descriptive names of parts of the tooth crown have been retained without implying acceptance of the theory.

In descriptive morphology there are four sides to a tooth: anterior, posterior, buccal (cheek) and lingual (tongue). The tooth can be divided into three major parts: the crown, neck and root. The root varies from a single one in most incisors and canines, to two in the lower premolars and molars, and three in their upper counterparts. The root is characterized by an absence of covering enamel, and is that part of the tooth embedded, initially, in the jaw bone. The neck marks the division between the root and the crown, the latter being the exposed portion which is covered with enamel. In the Carnivora the neck broadens into a ridge, the cingulum, which protects the gingiva. The crown frequently attains considerable complexity of structure, as in the sexi-tubercular tooth of the bovid.

In maxillary teeth the cusps of the crown are suffixed by the designation cone, with secondary cusps termed conules. In the mandible they are conid and conulid respectively. A bovid maxillary molar is considered to consist of four cusps, from anterior to posterior: two buccal cusps the paracone and metacone; and lingual cusps, the protocone and hypocone. In addition there are two secondary cusps derived from elevations of the crown, termed the paraconule and metaconule. Around the cusps are additional pillars termed styles. Buccally there are the parastyle, mesostyle, and metastyle; and lingually the protostyle, entostyle and hypostyle. In the mandible these cusps become buccally the paraconid, metaconid and entoconid; and lingually the protoconid, and hypoconid. Of the secondary cusps there exists only the hypoconulid. The buccal stylids are the parastylid, metastylid and entostylid; and the lingual are the protostylid, ectostylid and hypostylid (Fig. 1).

In the premolars these cusps are considerably reduced in structure and number, while the incisors and canines are simply paracones or paraconids.

The ridges joining the cusps are termed lophs, ectolophs lying buccally and endolophs lingually. These are formed by the fusion of styles and stylids which may lose their identity. Between the cusps may be a pocket termed the infundibulum.

In the zebra molar the same origins can be traced, but the teeth of Carnivora are much simpler. The most specialized carnivore teeth, the carnassials, possess only protocone, paracone and metacone in the maxilla (Pm 4); and paraconid and protoconid in the mandible (M 1).

Tooth tribology

Every & Kühne (1971) suggest that tooth attrition results from two processes: abrasion, and thegosis, or sharpening. Abrasion begins as soon as the tooth cuts the gum, from the contact of tooth with food. The food forms a loose, abrasive medium, acting on the tooth non-directionally as a consequence of mastication. In herbivores the abrasive factors are mainly plant phytoliths and accidentally ingested gritty bodies. Cutress & Healy (1966) considered that the enzymes and acids released during mastication had an insignificant effect upon the erosion of sheeps' teeth, mechanical wear being the most important factor.

To maintain the cutting edges of the cusps, which would otherwise be blunted by

Tooth physiology

Two related processes of movement continue throughout life. One is that of continuous eruption into the mouth cavity, so that the opposing crowns will always remain in contact with one another. Thus, as the teeth erupt, the roots become exposed at the gingiva, a process known as periodontosis. A second process is that of mesial drift, the continuous movement of the teeth towards the mid-line which serves to maintain contact between the crowns antero-posteriorly. This results in shortening of the tooth row through life, due to the wear on the antero-posterior surfaces (Table 1). These features are not seen in Carnivora, except for some periodontosis in very old animals, as they do not experience the same rate of wear and do not have to maintain a united grinding surface.

Table 1. Change in length with age (to nearest mm) of the tooth row in the Defassa waterbuck

Age (years)	Sample size	Length of maxillary tooth row	Sample size	Length of mandibular tooth row
3	1	100	1	103
4	8	101	7	103
5	29	104	24	106
6	23	102	22	104
7	32	101	29	103
8	10	102	10	104
9	26	101	25	103
10	31	98	28	102
11	8	101	11	102
12	11	92	9	99
13	2	96	3	97
14	8	98	8	103

Methods of age determination

Methods of age determination can be divided into two categories: methods separating age groupings, and methods of determining chronological age of the groups. Methods of separating age groupings will be dealt with under four headings: eruption and replacement of teeth, attrition of the permanent teeth, cementum line counts, and 'other methods'.

Eruption and replacement

This method, applicable with one exception only to young animals, has been used for age determination of domestic stock for well over a century, dating from Girard (1824). Rörig published data on eruption times for red deer, fallow deer *Dama dama* L., and roe deer *Capreolus capreolus* L., in Europe in 1905 (Rörig, 1905). American workers have used the method for deer age determination since the early 1930's (Cahalone, 1932; McLean, 1936).

Variation in time of eruption and replacement may occur from place to place, and as a result of different nutritional levels, which may have some importance in precise studies of growth and productivity, but generally speaking are unlikely to be significant. Brown (1902) observed eruption times in stock for 52 years, and could find no marked change in timing with improvement in breed. But several authors have shown the exact time of sheep incisor eruption to vary considerably with genetic and environmental factors (Kammlade, 1947; Franklin, 1950; Weiner & Purser, 1957;

Duckworth *et al.*, 1962; Geist, 1971). Within a population, however, there is probably some constancy; Hemming (1969) considered replacement timing to be consistent over a 16-year study of the Dall sheep *Ovis dalli*. In a recent study of barren ground caribou *Rangifer tarandus greenlandicus* in northwest Canada, Miller (1972) found that eruption times agreed relatively closely with those for caribou in Lapland, Russia, Alaska and Newfoundland. Kellog (1956) recorded that when extreme winter malnutrition caused retardation of tooth replacement in white-tailed deer *Odocoileus hemionus*, this was made up for later in the season when diet improved. Severinghaus (1949) found very little variation in eruption timing between dam fed and bottle fed white tailed deer fawns.

In populations with restricted breeding a useful approach is: (a) to assess the percentage number of calves born within a certain period; and (b) by capture of samples from the same calving season at set intervals, to assess the percentage which have attained permanent first incisors, second incisors, etc. Caughley (1965) has described such an approach for the Himalayan thar *Hemitragus jemlahicus* in New Zealand. If the time of replacement of any one tooth is normally distributed, which is expected for biological characters (Laws, 1968), the cumulative percentages should cluster around a straight line when plotted on a normal probability scale against age. From the distribution, the mean age of time of replacement can be read off, which is 50% probability, and the standard deviation can be calculated. In the thar, Caughley (1965) found considerable variability in replacement times when analysed in this manner, variability increasing the later the tooth appeared. From this he deduced that the age at which a tooth erupted was dependent upon the preceding one; thus the probability of placing an animal in the wrong age class increased with age of the animal. This is also shown for sheep by Boyd *et al.* (1964). Caughley thought other workers may have underestimated variability as objective analyses were lacking, but the thar is an introduced animal into New Zealand, which has undergone rapid population expansion. This may have led to greater genetic variability than might be met with in more conservative populations.

Unfortunately there is no comparable study for African mammals to that of Miller (1972) on the caribou, in which eruption times are compared from different areas. But for general population studies, age determination to the nearest year is often sufficient. If mean age at puberty is required, or specific weight for age determinations, then a more precise determination of age is necessary, involving not only knowledge of variability in time of replacement, but also rates of attrition of the deciduous teeth. Plowright (1965), and Plowright, Parker & Pierce (1969) in a study of the course of the viral disease malignant catarrh in free-living wildebeest *Connochaetes taurinus taurinus* Burchell, and of African swine fever in free-living warthogs *Phacochoerus aethiopicus* Pallas, required to know the ages of these animals to the nearest month and 3 months respectively (Fig. 2). Such refinement may become of increasing necessity in disease studies.

Age determination from incisor replacement is an attractive method as it can be readily applied to live animals with a minimum of handling. Its disadvantage in bovids is that the incisiform canine shows the greatest variability in time of replacement, although the incisors and canines are usually the last teeth to show full replacement, so that age determination can be taken further with these teeth than with the cheek teeth. It is wise, however, to correlate incisor replacement with premolar and molar replacement. In the buffalo *Syncerus caffer caffer* Sparrman it allows age determination

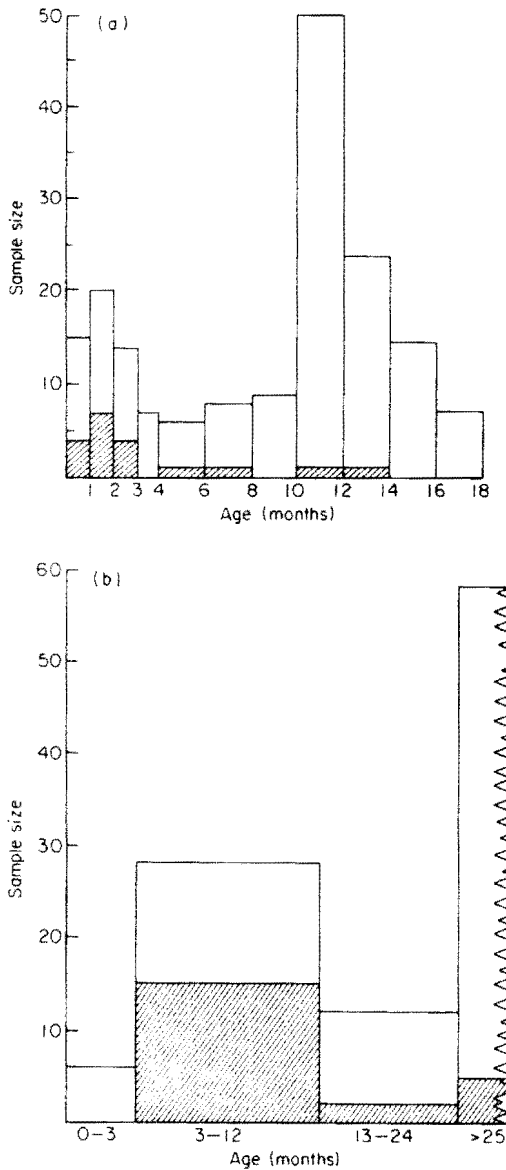


Fig. 2. (a) Presence of malignant catarrhal fever virus in wildebeest calves from Ngorongoro Crater, Tanzania. Shaded, present; unshaded, absent. Redrawn from Plowright (1965). (b) Presence of African swine fever virus in warthog piglets from Ruwenzori National Park, Uganda. Shaded, present; unshaded, absent. Redrawn from Plowright *et al.* (1969).

up to 5-6 years (Grimsdell, 1969), and in zebra *Equus quagga boehmi* Matschie up to 4 years (Klingel & Klingel, 1966).

The exception to only young animals being age determined by tooth replacement is the elephant. What takes many mammals the first quarter of their life span to complete, takes the elephant two-thirds; with each molar erupting in sequence over a period of 30-40 years. The ages of replacement for the Indian elephant *Elephas maximus* L. have been known for some time (Widdowson, 1946), and Laws (1966)

has worked out a detailed age determination method for the African elephant *Loxodonta africana africana* Blumenbach.

Attrition of the permanent teeth

Attrition of the permanent teeth provides the most ready means of estimating ages of adult animals, and has thus been used in Europe and America for many years. A collection of known-age white tailed deer jaws for comparative purposes was started in New York State in 1940, and 127 had been collected by 1946 (Severinghaus, 1949). The method has been introduced relatively recently into African wild life studies.

In age estimation by attrition, wear is compared against a set of typical specimens for age, or, if age is not known, a series of easily separable specimens; separation being dependent upon the degree of wear of the crowns. The use of measurements is only pseudo-objective, it may remove observer bias, but it can not correct for varying rates of wear. If wear is accentuated for age, then measurements will give the same false impression as visual appraisal.

A number of American workers has checked the validity of visual age estimation from wear, against cementum line counts, the latter giving reasonably positive ages for temperate zone animals. Gilbert & Stolt (1970) found in white tailed deer that there was a tendency to overestimate the age of younger classes, and underestimate the old. Kerwin & Mitchell (1971) achieved the opposite result with pronghorn antelope *Antilocapra americana*. The former error is likely to be more prevalent as the overall pattern of attrition should tend to follow a negative exponential rate of decay. Thus, rapid rate of wear in the young age classes makes them look older, whilst flattening of the curve in the older classes makes them difficult to separate from younger ones (Fig. 3).

In their analysis, Gilbert & Stolt (1970) found that 'wear age' matched with cementum line age, gave only 58.4% agreement. Kerwin & Mitchell (1971) obtained 60.9%; Erickson *et al.* (1970) obtained 63% with mule deer *Odocoileus hemionus*; and Keiss (1969) obtained 50% with elk *Cervus canadensis*, using the same matching technique.



Fig. 3. The negative exponential curve of wear. The shaded portion indicates the range over which animals are likely to be over estimated in age due to the rapid attrition; the unshaded portion indicates the range over which they may be underestimated in age due to the slow attrition.

Lockard (1972) obtained agreements of 74% and 83% with two different populations, but pointed out that the errors were not compensating. These authors all concluded that visual assessment was not a reliable method. In the Uganda waterbuck *Kobus defassa ugandae* Neumann, Spinage (1967) obtained only 38% agreement, possibly due to a much smaller sample size. But when extended to ± 1 year, the agreement was increased to 76%.

Lowe (1967) studying red deer in Scotland, claimed 88% agreement when jaws of unknown age were tested against known-age specimens, and concluded that the method of visual assessment 'as used traditionally on the continent of Europe' was the best. But his argument for this, as Douglas (1970) has pointed out, seems circuitous. The problem is not in matching degrees of wear, but whether the same degrees of wear represent the same ages. Nevertheless, several authors are of the same opinion, that visual estimation is a good method. Quimby & Gaab (1957) listed five 'key features' for elk teeth, whose presence or absence in young animals with permanent dentition could be related to age; but they regarded the visual method as better.

Robinette *et al.* (1957) proposed a 'molar tooth ratio' for determining the ages of mule deer, which Robinette & Archer (1971) subsequently used on Thomson's gazelle *Gazella thomsoni* Günther. The 'molar tooth ratio' was defined as the sum of the occlusal widths of the seven buccal crowns, divided by the sum of the corresponding lingual crown heights, measured to the nearest 0.1 mm. Erickson *et al.* (1970) tested this against cementum line counts in mule deer and obtained 62% agreement, compared with 63% for visual estimation.

When known-age jaws from other regions of America were compared with the New York State collection (Severinghaus, 1949), they were found to agree in age categories with two exceptions. These exceptions were jaws from a sand-blown coastal area, and from a dry, dusty area. The molars of these jaws showed greater wear for age; but the comparisons were made only on young animals (Kellog, 1956). Often quoted against the reliability of wear-age techniques is the work of Healy & Ludwig (1965a, b); Ludwig, Healy & Cutress (1966); Cutress & Healy (1966), and Arnold, McManus & Bush (1966), concerning the wear of sheep incisor teeth in New Zealand and Australia. These workers demonstrated that excessive wear was correlated with high ingestion of soil, but it should be stressed that the conditions causing excessive wear were related to stocking rate, and the observations only concerned incisor teeth. It is unrealistic to make comparisons of this nature between wild and domestic stock, for the latter are not selected for the hardness of their teeth, and may be exposed to environments which do not suit them. In this I disagree with Chaplin (1971), who considers that rates of tooth wear should be more uniform in domestic stock than in wild animals, as the latter inhabit a more diverse environment.

In my experience incisor teeth show more variable rates of wear for age than do molariform teeth; variability being greater in browsers or semi-browsers. To test this hypothesis, height of the crown of the first incisor was plotted against height of the crown of the first mandibular molar, in a heterogeneous sample of buffalo. This gave a correlation coefficient (r) of 0.838, or approximately 84% agreement. A homogeneous population from another area was tested in the same way, and r was equal to 0.899, or 90% agreement. When the correlation was tested for a sample of Grant's gazelle *Gazella granti granti* Brooke, r was equal to 0.591, or 60% (Table 2, Fig. 4). In the waterbuck *Kobus defassa ugandae* Neumann incisor crown height showed considerable overlap for age (Fig. 5), although the mean weight of the incisors remained an

approximately constant percentage of the mean weight of the maxillary plus mandibular molariform teeth (Table 3). Unfortunately M 1 crown heights were not recorded for this species. These analyses suggest that incisor wear is not a reliable guide to age in the pecora, for an uneven rate of wear is to be expected when a hard substance, the tooth, is apposed to a soft substance, the dental pad.

Table 2. The relationship between height of the crown of the first incisor and the first maxillary molar, in buffalo and Grant's gazelle

Sample	Sample size	Regression*	S_{yx} †	(r)‡	P §
Buffalo, heterogeneous	43	$y=1.042x-2.999$	3.9	0.838	$\ll 0.001$
Buffalo, homogeneous	22	$y=0.824x+0.8$	1.7	0.899	$\ll 0.001$
Grant's gazelle ♀	44	$y=0.329x+8.65$	1.3	0.591	< 0.001

* Regression of height of first incisor enamel (y) on height of buccal cusp enamel of M 1 (x).

† S_{yx} means that a mean value of incisor height has this standard deviation.

‡ The coefficient of correlation.

§ The probability at the 95% level that the measurements are not correlated.

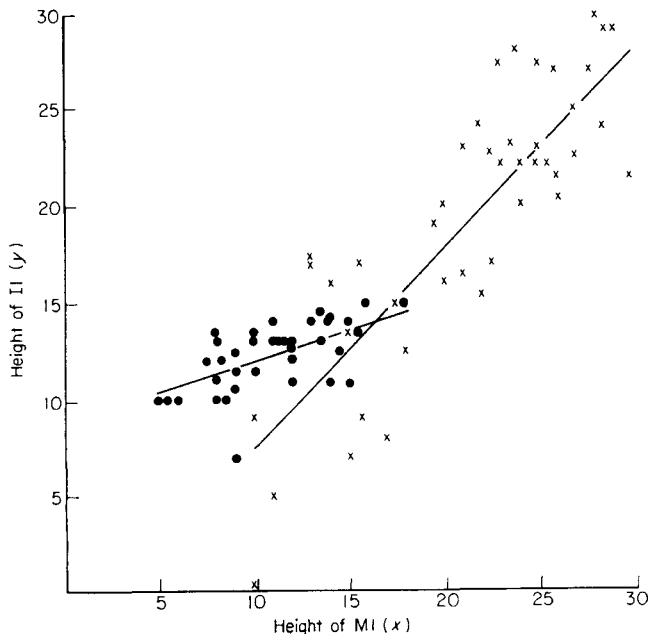


Fig. 4. The relationship between the wear of incisor teeth and molar teeth in buffalo, a grazer (X—X): and Grant's gazelle, a semi-browser (●—●).

In the *Equidae* the upper and lower incisors are apposed, and a more uniform rate of wear is probably achieved. Due to the distinctive change in shape of the incisors along their length, and both the presence of, and change in shape of, an infundibulum, equid incisor teeth have long been found to be a useful guide to age estimation. Girard (1824) age-determined horses up to 20 years from the changes in shape of the

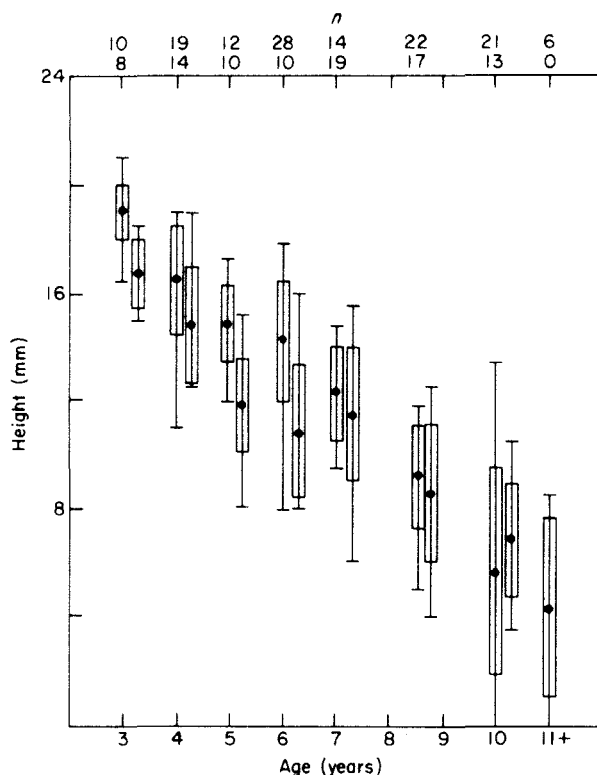


Fig. 5. Wear of the first incisor teeth in relation to age in the defassa waterbuck; mean value, one standard deviation and range. Each pair of measurements shows left, dead animals; right, live animals.

Table 3. The relationship between weight of incisor teeth and molar teeth with age, in defassa waterbuck

Age (years)	Sample size	Mean wt of maxillary + mandibular teeth (g)	Mean wt of incisor teeth (g)	Incisors as %
5	7	125	6	4.8
6	7	123.5	6	4.9
7	13	108.5	5.3	4.9
8	6	122.3	5.7	4.7
9	3	112.3	4.9	4.4
10	8	81.3	4.2	5.2
11	6	105.9	4.6	4.4
12+	13	62.2	3.2	5.1

incisors; while Galvayne (1905), using a lateral groove in the third incisor, estimated ages up to 30 years. This groove, now known as Galvayne's groove, appears at 10 years in the horse, has grown halfway down the tooth at 15–16 years, reached the edge of the crown at 21 years, and by 25 has started to disappear, being completely absent by the age of 30. Although a good method of age determination for old animals, it is frequently absent altogether, and I have yet to find a distinctive groove in zebra; but it may exist in some races. Age estimation of zebra by reference to incisor changes was first used by Klingel & Klingel (1965), but the range these authors give for wear

classes is much wider than most authors give for wear estimates of the molariform teeth of artiodactyla. Owing to the crown pattern of equid molariform teeth showing little variation until old age, visual assessment is difficult to apply. Spinage (1973) has shown, however, that height of M 1 is a useful estimator when incisor teeth are absent.

To summarize, visual estimation from jaws is often the only means available for age determination. In answer to criticisms levelled against the method, we must again remember that the biological character being assessed, wear on teeth, is likely to follow a normal curve of distribution in relation to specific age, and it is unrealistic to expect precise agreement. Rather, one should take the mean age of samples, when, unless there is observer bias, a confident result should be obtained. Caughley's (1965) statement that the assumption of compensatory errors is 'both theoretically and demonstrably false' is essentially true, as Lockard (1972) has recently shown. Nevertheless, in my opinion, Lockard's figures show a satisfactory result, and certainly justify the use of the technique in the absence of more refined methods.

Eberhardt (1960) argued that if age data are grouped to avoid errors, information about survival and mortality is lost. Again, this depends upon the degree of precision required, and I would consider that in most studies, errors would have to be very great indeed for information to be lost in this way; especially when one considers that a single age-specific life table has yet to be constructed for a large mammal other than man.

Cementum line counts

Rhythmical calcification in dental tissues has been known since 1932, when Eidmann (1932) first proposed that red deer could be age determined from rings, in the secondary dentine of their incisors, which he believed to be annual. It was not until the early 1950's that the value of cementum lines for age determination was realized with respect to marine mammals (Laws, 1952), and in 1959 Sergeant & Pimlott extended the use to moose *Alces alces*, using incisor teeth. This was followed in 1963 by Low and Cowan's work on mule deer, when standard decalcification and staining procedures were applied with success. The method has since become well established in North America, including the use of the cementum pad underlying the crown of the first molar (Ransom, 1966; Wolfe, 1969). In temperate climates, where species are subjected to harsh winters, such lines apparently provide a definitive method of age determination, with one light and one dark annulus representing a year's growth. The phenomenon has been the subject of reviews by Laws (1962), Sergeant (1967) and Klevezal' & Kleinenberg (1967).

Klevezal' & Kleinenberg (1967) list the following families in which cementum layering has been found in the teeth, but not necessarily correlated with annual rhythms: Soricidae, Vespertilionidae, Castoridae, Sciuridae, Muridae, Physteridae, Delphinidae, Ursidae, Canidae, Mustelidae, Odocoileidae, Otariidae, Phocidae, Equidae, Cervidae and Bovidae. To which can be added Felidae, Hyaenidae (Spinage, 1967), and Hominidae (Gustafson, 1950). The occurrence of cementum layering thus seems to be almost universal among the Mammalia.

There has not always been agreement on its annual incidence. Mitchell (1963, 1967) found annual layers in the cementum pad of M 1 of red deer in Scotland, but Lowe (1967) was unable to establish a satisfactory correlation for specimens from Rhum, an island west of Scotland. Douglas (1970) found layering in a variety of introduced deer in New Zealand, which he tentatively concluded might be annual.

Layering was found in the first incisor cementum of waterbuck living on the equator in Uganda (Spinage, 1967). At this latitude cementum accretion appeared to follow an inherent rhythmical pattern of growth, but some lines stood out above others. Two such 'bold lines' appeared to be formed each year, which would correlate with the two wet and two dry seasons experienced at this latitude. Independently, Klevezal & Kleinenberg (1967) found 'supplementary streaks' in some species, and considered that these should be ignored when counting 'annual' layers. A similar relationship to that found in the waterbuck, was found in buffalo from the same area by Grimsdell (1969), who used the M 1 cementum pad. Robinette & Archer (1971) found layering in the M 1 pad of Thomson's gazelle from an equatorial latitude in Tanzania, which also suggested that two distinct lines were formed each year. These authors were able to relate an exceptionally distinct line in an old animal to a bad drought year which was followed by floods. However, Simpson & Elder (1969) found, on average, two clear lines per year in greater kudu *Tragelaphus strepsiceros* Pallas in southwest Rhodesia, where there is only one dry season each year. These authors concluded that the layering must be due to 'hormonal balance on the one hand and nutritional stress on the other'. By comparing the layering in teeth of different eruption times, the canine, Pm 4 and M 1, they found that there was not total agreement, one jaw showing teeth up to 1 year out. Thus, they concluded that counting of cementum layers was not a definitive technique. It should be pointed out that the sample size was small (ten animals), and that technique may account for discrepancies. Cementum may sometimes be detached with the jawbone, resorption may occur even in young animals if remodelling due to stresses is taking place, some lines may fail to stain adequately, and sometimes the section may not pass through the region of maximum discernible number.

In a study of the impala *Aepyceros melampus* Lichtenstein Spinage (1971) was unable to find regular cementum lines in the incisor teeth, which confirmed the finding of Grafton (1965). But it is possible that in some cases an acid decalcifying solution interferes with the staining properties of the tissue (Drury & Wallington, 1967). More work is needed on this species.

Clearly, insufficient is known about cementum layering in tropical mammals. Work is currently in process on a collection of buffalo teeth from an area of southern Tanzania, with only one wet and one dry season per year. If the pattern of two bold lines per year holds good for this area, this would suggest that the dominant physiological rhythm is one of two main lines of reduced growth per year, and that this persists in equatorial species. The annual correlation may be spurious, and the pattern represent nothing more than an expression of the 16 μ m calcification rhythm of Schour & Hoffman (1939).

Other methods

Methods applicable to many herbivorous ungulates with their complex tooth rows, are not generally so for carnivores with their relatively simple teeth. Many marine carnivores show annual cementum ridges on the outside of their canine roots (Laws, 1952). This has also been found to be evident in Alaskan black bears *Ursus americanus* up to 6 years old, after which the annuli are not discernible (Rausch, 1961). No external annulations could be detected on the roots of lion *Leo leo* L. canines which I examined (Fig. 6), neither on those of leopard *Leo pardus* L. This method would seem to have limited or no applicability to African Carnivora.

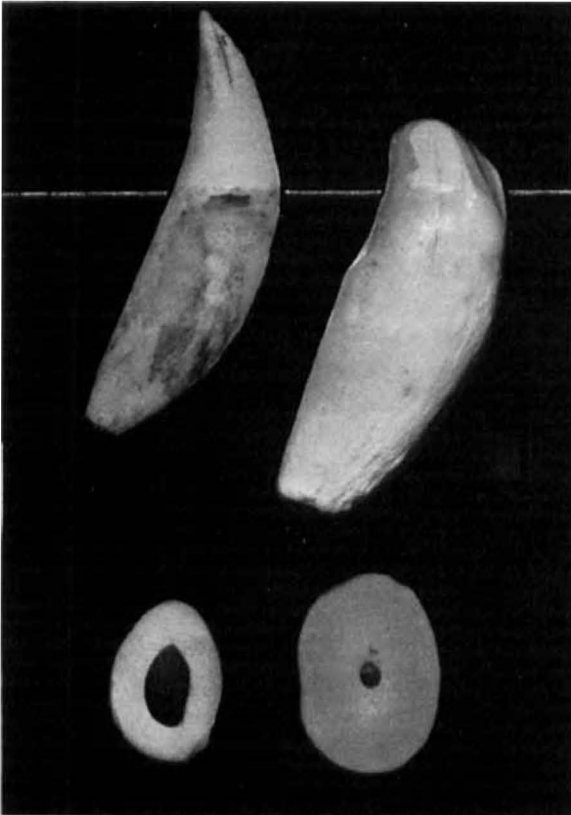


Fig. 6. Mandibular canines of the lion. Left, about 3 years of age; right, about 10 years of age. Note absence of annulations on the roots, and change in size of pulp cavity with age.

A promising alternative is to measure the decreasing diameter of the pulp cavity in transverse section, at the line of the neck of the canine, as first proposed by Smirnov (1960). The internal apposition of secondary dentine to the walls of the pulp cavity is a physiological process, and its increase in thickness should be closely correlated with age. If a standard curve could be fitted to a series of measurements, then further teeth could simply be X-rayed to avoid destruction. The degree of closure of the pulp cavity orifice is probably also directly related to age, as in man (Gustafson, 1950), but may complete its closure relatively early in life.

A successful method of age determination of human teeth has been devised by Gustafson (1950). Points, of value 0–3, are awarded to the state of six characters as seen in longitudinal ground section, to give a maximum of 18 points for the oldest. The characters are as follows (Fig. 7):

(i) Attrition. The degree of wear on the crown is divided into zero wear, attrition of the enamel, exposure of the dentine, and exposure of the secondary dentine.

(ii) Periodontosis. Recession of the gingiva from the neck of the tooth is classified as zero, some recession, one-third of the root exposed, and two-thirds of the root exposed, at which stage cementum is usually showing.

(iii) Amount of secondary dentine. Again the classification commences with zero, dentine beginning to form in the upper part of the pulp cavity, cavity half-filled, and cavity nearly or completely filled.

(iv) Amount of cementum. Lines were not counted, cementum was rated as 'normal amount', a little greater than 'normal', a thick layer, and a very thick layer.

(v) Root resorption. Classified as no resorption, isolated spots of cementum resorbed, resorption beginning at root tip, and finally much resorption.

(vi) Degree of root translucency. This commences at the root apex and ranges from zero, to translucency just visible, visible over the apical third of the root, and visible over two-thirds of the root.

Plotting the points awarded against a known-age sample, a linear regression was calculated with an estimated mean error of ± 3.6 years, over the range from 11 to 69 years. This represents a high correlation for such a long time span, and for teeth which are subject to such varied conditions of care and diet. The reason for the good correlation is that, apart from the first character, the characters are all physiological aspects of ageing. As the method needs to be calculated from a set of known-age teeth, it has not yet found practical application in wildlife studies, but it holds great promise where cementum line counts are impractical, or for use in combination on teeth of older animals in which lines may have become resorbed. It is not suggested that the method will be found suitable without modification; a preliminary examination of buffalo first incisors shows that their mode of growth and change differs somewhat to that of human teeth (Fig. 8).

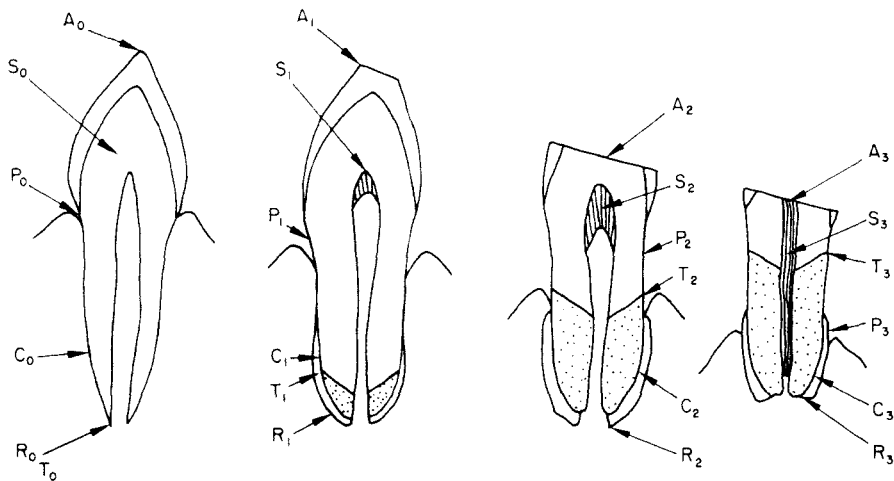


Fig. 7. Gustafson's points system for the determination of age from teeth. A, wear of crown; S, formation of secondary dentine; P, periodontosis; C, formation of cementum; R, resorption; T, translucency of dentine.

Determination of chronological age

Separating degrees of wear, counting cementum lines, measuring secondary dentine deposition, and other methods, are, in themselves, not difficult. The problem arises in assigning specific ages to categories when the birth date of an animal is not known. In finding the relationship for a species as many complementary methods as possible should be used. Laws (1966, 1968) has shown how several methods were used to assign ages to the wear classes of elephant and hippopotamus *Hippopotamus amphibius* L. In this review, although fully appreciating the value of other criteria, discussion is restricted to the part which teeth may play.

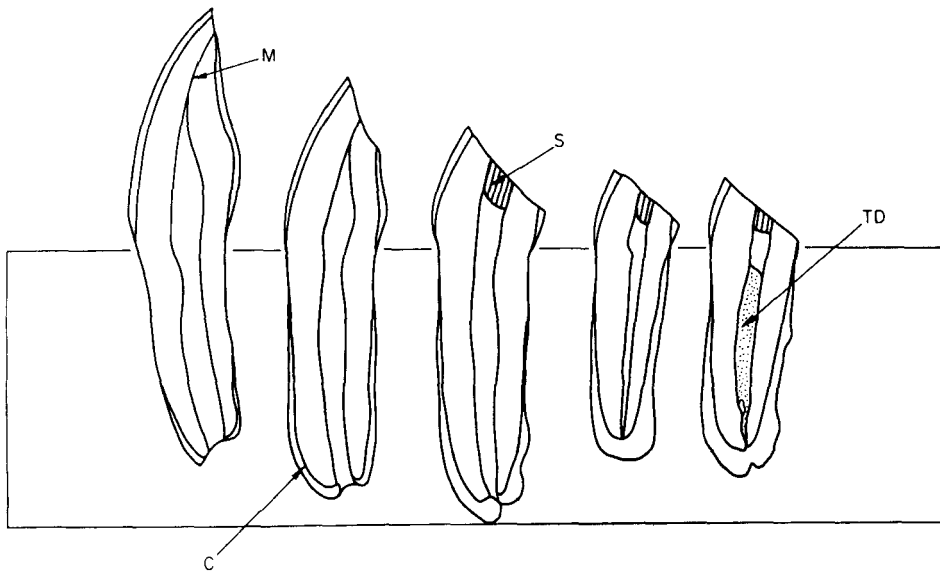


Fig. 8. Change with age in the first incisor of the buffalo. M, 'mark'; C, cementum; S, secondary dentine; TD, translucent dentine. Drawn from photographs.

Several methods making use of teeth can be suggested:

(1) Known-age specimens. Although obviously the best reference, serious attempts to compile collections of known-age material in Africa appear to be wanting. As many calves as possible should be marked; or better still animals known to be 1 year of age, which will be less likely to suffer heavy mortality. Marking is best done in hunting areas, so that when a marked animal is shot the hunter can bring in the jaw. Animals marked in protected areas are likely to die without their remains being recovered.

(2) Tooth impressions. This method, modified after Barnes & Longhurst (1960), has been described in Spinage (1967). By capturing marked animals at annual intervals, and taking an impression of the tooth row, the annual rate of wear can be assessed, and hence the period elapsing between age groupings.

(3) Vital staining. This can be used to determine the amount of secondary dentine deposited per unit of time, or the number of cementum lines produced. Its history goes back to 1771, when Hunter studied the development of pig teeth, by feeding the animals madder *Rubia tinctorum* (Hunter, 1771). Alizarine Red, the extract of madder, has since been used by Schour & Hoffman (1938), and more recently by Lowe (1971), to study tooth calcification processes. Alizarine Red is apparently non-toxic, but some workers, studying marine mammals, have used toxic lead salts, killing the animals (Yagi, Nishiwaki & Nakajima, 1963). The advent of the tetracyclines (McCormick *et al.*, 1957), antibiotics which chelate with calcium ions to form a golden-yellow fluorescence under ultra-violet light, has provided a remarkable new method for studying calcification. Tetracyclines chelate the calcium ions wherever active calcification is taking place, but are non-toxic in small amounts, and are now widely used in therapeutic doses.

Spinage (1967) demonstrated that 2.5 g of demethylchlortetracycline in 60 cc of sterile water, when injected intraperitoneally into waterbuck weighing 182–228 kg liveweight, produced clearly fluorescing lines in both cementum and dentine of the

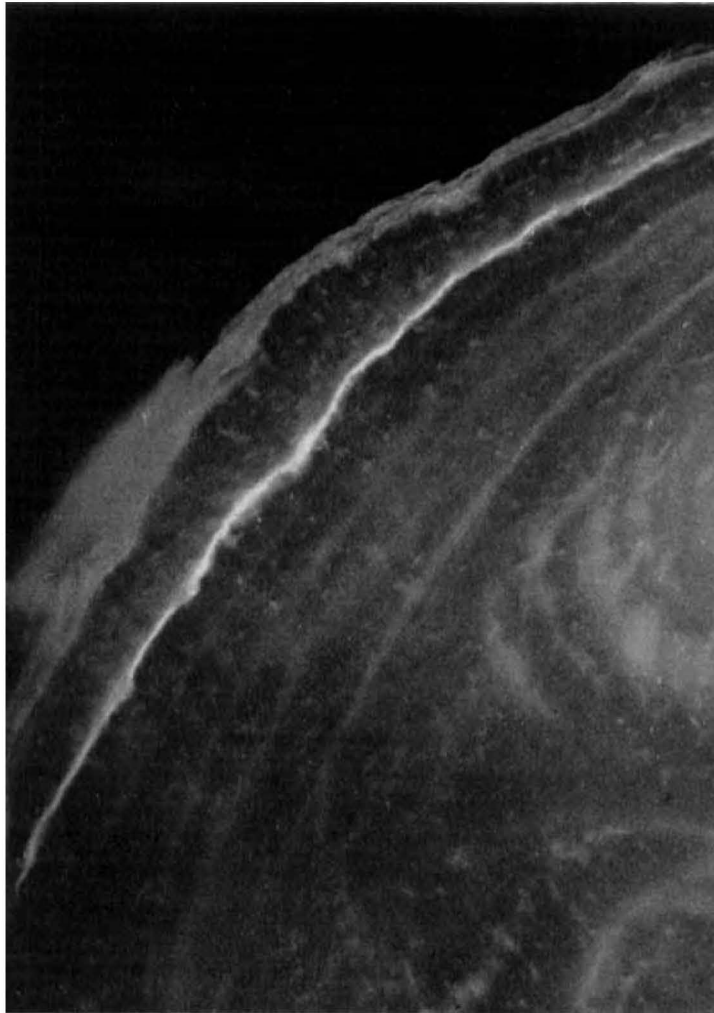


Fig. 9. Photomicrograph of the cementum of a defassa waterbuck first incisor, labelled with demethyl chlortetracycline. Ultraviolet light.

incisors, visible when the animals were sacrificed 1 year later (Fig. 9). Circumstances have precluded further investigation, but the actual labelling is a simple operation which can easily be performed on captured animals. Linhart & Kenelly (1967) showed that coyotes *Canis latrans* could be labelled by placing tetracycline in baits; Crier (1970) demonstrated this with laboratory rodents. But using baits the amount ingested can not be controlled: overdosage can interfere with calcification processes, whereas underdosage makes the operation futile.

(4) Wear models. Spinage (1971, 1972), Spinage & Jolly (1973), have suggested that in the absence of known-age specimens, age may be determined by the use of models which approximate to the rates of growth or wear of the teeth. Attrition of M 1 in the impala appeared to follow a negative exponential curve (Spinage, 1971), such that if the beginning and end points were known, ages of intermediate stages could be derived from the curve from a knowledge of crown height. Such a model depends

upon variations being random, and cannot be more accurate than visual assessment of wear, as it itself is an expression of wear. But criticisms of the method based on variability of the data, are equally criticisms of the method of visual estimation. From visual estimates we can separate stages, but we can not determine ages for these categories without prior knowledge. The conceptual wear model is an attempt to overcome this. Using decreasing height of M 1 in the zebra, it was found that age, calculated from a 'wear curve', gave good agreement with that estimated from incisor wear, when the mean age of samples was compared (Spinage, 1972).

The warthog presents special problems of age determination, due to its unique dentition. The premolars and first two molars are low-crowned teeth which are worn out, and may be shed, early in life. The warthog then depends upon an enlarged third molar, which grows and is worn down continuously until old age. When the antecedent teeth have been worn down, or shed, age can only be determined from the combination of growth and wear of M 3; with the possible alternative of secondary dentine layering in the continuously-growing canines. Spinage & Jolly (1973) found that the relationship between growth and attrition of M 3 appeared to be linearly related with time over part of its range. A prediction formula was thus calculated, from the linear regression of growth in length of the crown divided by decreasing height at the anterior, with which ages up to 10 years could be predicted. The validity of the approach is open to confirmation, as no old known-age warthog were available to check the prediction formula; but studies are being pursued with regard to the layering of secondary dentine in the canines.

In conclusion, wear models may offer a means of determining specific age in the absence of known-age data, but should only be used for predicting the mean age of samples, and not the age of individuals.

Use of captive animals for age comparisons

Due to the paucity of known-age material workers must usually refer to animals reared or maintained in captivity, when age comparisons are sought. This has invited the criticism that such animals are unlikely to show the same rates of tooth wear as those in the wild, because, it seems, they are likely to be fed softer foods, so that the teeth should show less wear for age (Laws, 1968; Goddard, 1970). Although this may be true to some extent, the physiology of tooth growth does not support this view entirely. The process of eruption is continuous throughout life, so that if teeth are not worn down at a rate dictated by their ontogenetic development, we may suppose that either eruption slows down, or the jaws will tend to be pushed apart if eruption continues. Either alternative would lead to reactions inducing thegosis, so that the crowns would be kept ground down. This might explain tooth grinding in some captive and domestic animals. If an animal was subjected to an excessively abrasive diet, the converse would hold. If the rate of wear was faster than the secondary dentine could be deposited internally, sensitivity, and ultimately caries, would result; making the animal reluctant to masticate. As a consequence of these two processes it may be inferred that tooth wear is unlikely to depart widely from a mean value which will be found in the wild. A tooth is a complex organ, which develops its perfectly occluding crown surface before it comes into contact with its opposite number (Glasstone, 1938), the occlusion not being produced by abrasion. For an organ which has made its appearance so early in mammalian evolution it would be surprising to find very variable rates of wear among any one species.

Knowledge of the maximum age to which an animal may live comes entirely from captive specimens, and the criticism is often levelled that such records have no relevance to wild animals. This overlooks the fact that captivity can not prolong life beyond its physiological maximum, which is the same whether the animal is captive or wild. Herbivores are likely to reach this maximum in the wild, under favourable circumstances, but the same is not true of carnivores, which are unable to capture prey once senescent decline sets in.

Conclusion

The use of refined age determination techniques is an important tool in the initial stages of wildlife investigations, although a high degree of precision would seem to be more of academic than of practical value. There are exceptions, such as the detailed tracing of the course of diseases. We do, however, want to know how fast our animals grow, how soon and for how long they will reproduce, and for how long they may be expected to live. A knowledge of age is also illuminating in understanding social organization and behaviour (e.g. Spinage, 1969).

The most promising method of age determination, cementum line counts, does not seem to have received the attention it merits in African studies, and the relationship of the lines to age is not yet clearly defined. Even the elementary preliminary of gathering known-age series is lacking, and age estimation of carnivores is almost an untouched field. It is to be hoped that in the future more attention will be paid to basic age determination methods, so that we will have the knowledge upon which to base sound management and sound conclusions.

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