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Dentition and age estimation of Elephants in the Etosha National Park, Namibia

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ABSTRACT

Variation in the number of laminae per molar, and in the number and position of foramina mentale in mandibles from elephants in the Etosha National Park rules out the use of referenced laminary counts for age estimation purposes. Premature loss of anterior molar fragments occurred in 18% of mandibles, as an additional source of confusion and subjectivity in the identification of age classes. Classification of mandibles according to the degree of eruption and attrition of anterior and posterior molars independently, result in different age distributions, and indicates that the loss of molar fragments is more irregular than the eruption sequence of molars. Anomalous peaks in the age distribution corresponding to the loss of molars were less distinctive in the samples from the Etosha National Park, than in all other populations studied. The age estimation method of Laws (1966, 1967) could not be shown to be inaccurate and age distributions based on the original schedule and recent revisions were not significantly different.

INTRODUCTION

Aspects of the dentition of elephants from several populations have been described in attempts to facilitate the estimation of age of individuals, determination of the sex and describing interpopulation differences in demographic parameters. Both recent methods of estimating ages of elephants rely on the forward progression of the six molars in each half of the upper or lower jaw. Laws (1966) and Sikes (1966, 1968) provide detailed descriptions of the dentition of elephants in East Africa and both propose methods of age estimation based on the earlier work of Morrison-Scott (1947), Perry (1954), Bourlière & Verschuren (1960 in Laws 1966) and Johnson & Buss (1965). This entails the classification of the relative position, development and attrition of the molar series into discrete categories related to chronological age. A scarcity of known-age individuals, however, left many assumptions and approximations made by Laws (1966) and Sikes (1968) unconfirmed. Subsequent use of their methods on other populations showed several inconsistencies and both methods are currently regarded as suspect (Croze, Hillman & Lang 1981; Eltringham 1982; Jachmann 1985, 1988).

At least three major processes combine to produce the appearance of the molar complement in a given mandible. Forward movement, resorption of roots of functional molars and eruption of a newly consolidated molar should be coordinated to some degree for the jaw to function properly. Minor variation in the rate of appearance and disappearance of a molar should, however, not adversely affect mastication. Small variations in either eruption, forward movement or attrition could nevertheless result in misclassification of a mandible in both the methods of Laws (1966) and of Sikes (1968).

Laws (1966), Sikes (1968) and Hanks (1972a, b) show that several methodological errors may influence age estimation, notably in the correct identification of molars and laminae which are crucial to either age estimation method. Hanks (1972a) suggested that cycles of recruitment in populations, as indicated by age distributions, were artifacts of the age estimation method of Laws (1966), and he was supported, if indirectly, by Sherry (1975), Smuts (1975), Williamson (1976) and Kerr (1978). "Cycles of recruitment" or peaks in the age distributions occurred at more or less the same ages in the populations they studied and the five studied by Laws (1969a) and Laws & Parker (1968), although this was obviously not correlated to rainfall prior to conception or birth.

Jachmann (1985) has suggested that the method of Laws (1966) overestimates the age of individual elephants over the range 10-30 years of age, based on photographs of the mandibles of three known-age elephants in Lang (1980) and one in Laws et al. (1975). Jachmann (1988) therefore proposed a tentative revision of the age estimation method of Laws (1966) over the range 10-30 years of age, based on molar replacement and growth in shoulder height of six captive elephants (Lang 1980), and photographs of the mandibles of the four known-age elephants mentioned. All studies of the demography of African elephants, including Jachmann's own study in Malawi (Jachmann 1980, 1988), have nevertheless relied on the age estimation method of Laws (1966). The original method of Laws (1966) was used in this study in favour of the tentative revisions by Jachmann (1988), to facilitate comparison with previous studies, and also because the revision is not final (Jachmann 1988).

The aim of this paper is to describe the utility of, and problems encountered with accepted age classification methods in a sample of mandibles from the Etosha National Park (Etosha).

METHODS

The mandibles of 525 elephants were collected during culling operations in the western part of Etosha in 1983 (219) and 1985 (306). Each mandible was marked with a numbered metal tag and painted with polyester resin after the soft tissue had been removed by scavengers. Standard body measurements following Laws (1966) were recorded for all culled individuals, but only used as a direct indication of age in 44 juveniles captured live during the 1985 cull.

Mandibular molars were identified by their relative sizes (Laws 1966, Hanks 1972b). Maximum widths and lengths of intact and incomplete molars were measured as in Laws (1966). The full laminary complement was recorded in intact molars, as well as the number of laminae posterior to a vertical line through the foramen mentale, i.e. the laminary index of Sikes (1968). The incidence of incompletely developed first and last laminae was recorded, as well as the number of functional laminae in each molar. Alveolar sockets were classed as open (molar lost recently), semi-filled, closed but visible with some small cavities, and closed entirely, grading into matrix (longest interval since molar was lost). The number and relative position of the foramina mentale were recorded for both sides of each mandible.

All mandibles were allocated to the 30 age classes of Laws

(1966), as based on the characteristic stage of molar progression, as well as the revised age schedule of Jachmann (1988). Only right halves were used as is conventional. As a test for personal subjectivity, all mandibles were furthermore reclassified twice, based on the appearance of the anterior and posterior molars independently. Chronological age limits were assigned to age classes by Laws (1966) later refined by Laws (1967) and modified by Jachmann (1988). The frequency of individuals in year groups were calculated using equal representation of the number of individuals in each age class over the number of years represented by each age class, or by using three-year running averages.

After identification of molars situated above the foramen mentale, the laminary index, or "FM formula" of Sikes (1968), was identified by counting the number of laminae posterior to the imaginary vertical line passing through the foramen mentale, of the molar above the foramen. Chronological ages were assigned to six of the 57 possible molar age groups of Sikes (1968). The standard notation for elephant molars is followed, where M1 refers to mandibular molar 1.

Age structures were compared using a contingency analysis as recommended by Caughley (1966).

RESULTS

Identification of molars

Figure 1 illustrates the sizes of molars of males (A) and females (B) from Etosha. M1, M2 and M3 showed no overlap in size, while M6 could be identified by the absence of an alveolus posterior to it. M4 and M5 were distinguished by their relative sizes and the presence or absence of a preceding M3. Molars of males were generally more massive than those in females, but sizes overlapped as is shown in Hanks (1972b). This overlap was only in part due to the inclusion of partially worn or incompletely developed teeth in the series (Figure 1 A-'A', B-'B'). One supernumerary molar (M7) was found, giving an incidence of 0.2% in the total sample. One mandible in the 1985 sample was abscessed and had a fractured M4, possibly as the result of a gunshot wound, while one mandible in the 1983 sample showed the loss of an entire M5 soon after complete eruption with no further development of M6. The other half was normal.

Number of laminae

Frequency distributions of the number of laminae in each molar are shown in Figure 2. Variation in the number of laminae per molar occurred in all molars, with overlapping numbers from M3 to M6. Apart from the number of rudimental laminae described by Sikes (1968), which may or may not be counted, the visible number of laminae is further reduced by another process. The first, or anterior, lamina of all molars is usually smaller than the rest, and probably does not last as long. The first laminae of M4-6 are in addition sometimes absent or incompletely developed where the developing buttress remains confined below the last lamina of the preceding molar. Not all molars show this reduction to the same degree and the incidence of incomplete first laminae as the only remaining evidence, is shown in Table 1. The last functional laminae in M1-5 might similarly be suppressed due to the development of the succeeding first lamina of the next molar. More last laminae are in fact incomplete or absent than first laminae (Table 1).

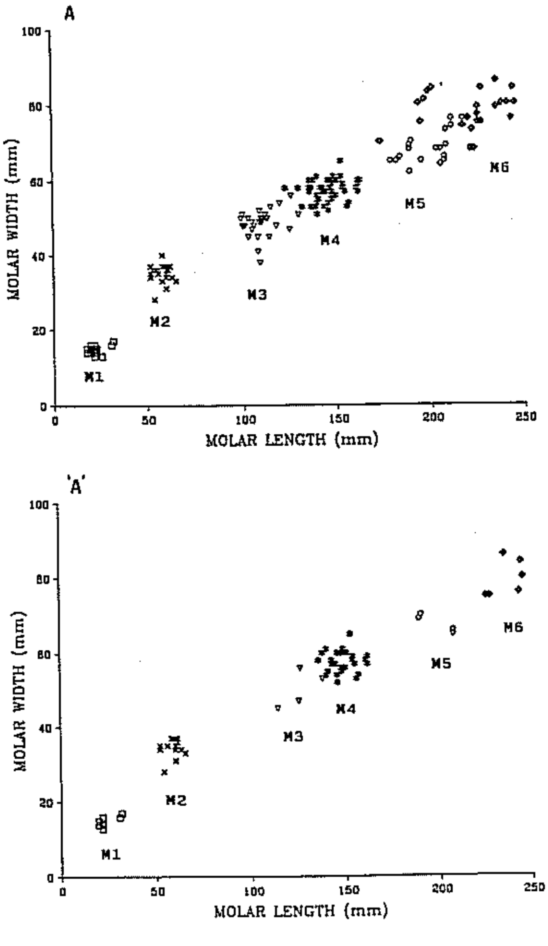

FIGURE 1A: Widths and lengths of M1-M6 in the total sample of males (A) and of intact molars only ('A') of elephants culled in Etosha National Park.

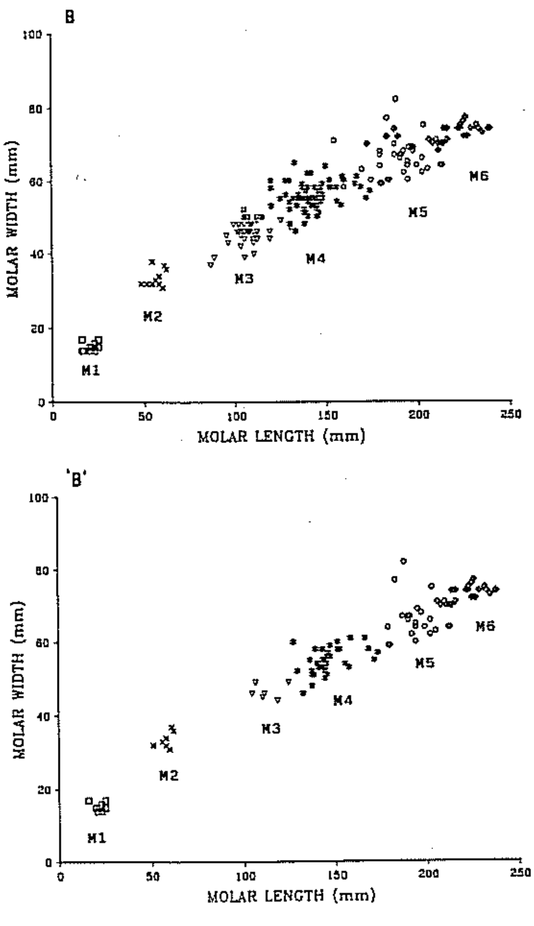

FIGURE 1B: Widths and lengths of M1-M6 in the total sample of females (B) and of intact molars only ('B') of elephants culled in Etosha National Park.

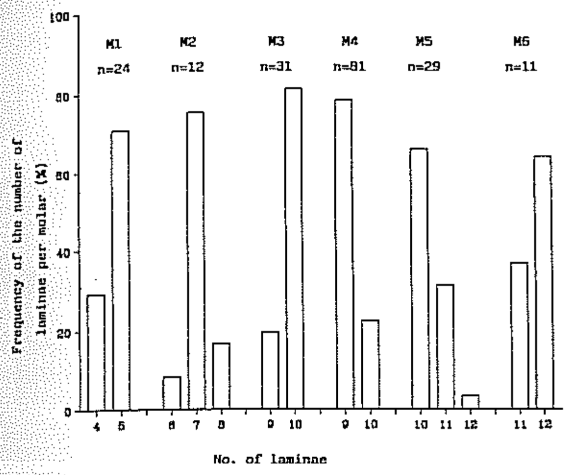

FIGURE 2: Frequency distribution of the number of laminae in intact elephant M1-6 in Etosha National Park (n denotes sample size).

Variation occurred in the position and number of foramina mentale (Table 2), and the position of foramina on left and right mandibles differed in 7.3% of the total sample. Counts of laminae differed in up to three laminae in M1-M3 and up to two laminae in M4-6 when counted from the posterior and anterior foramina mentale.

TABLE 1: Number of incomplete first and last laminae in fully erupted molars of elephants culled in 1983 and 1985 in Etosha National park. Percentage incidence given in parenthesis.

Molar	Total no. of elephants examined	No. with incomplete first laminae	No. with incomplete last laminae
M1	29	0	2 (6.9)
M2	53	0	28 (52.8)
M3	181	0	76 (42.0)
M4	154	16 (10.4)	52 (33.8)
M5	50	2 (4.0)	23 (46.0)
M6	34	3 (8.8)	0
	501	21 (4.2)	181 (36.1)

TABLE 2: Variation in the number and position of the foramina mentale in mandibles of elephants culled in Etosha National Park. Percentage incidence given in parenthesis.

Anterior molar present in mandible	No. of mandibles	No. of foramina mentale expected	No. of foramina mentale present	No. of mandibles with >2 foramina mentale	No. of displaced foramina mentale in L & R mandibles
M1	32	64	82	12 (37.5)	0 (-)
M2	42	84	110	20 (23.8)	4 (9.5)
M3	69	138	181	32 (46.4)	8 (11.6)
M4	63	126	155	22 (34.9)	4 (6.3)
M5	44	88	106	16 (36.4)	1 (2.3)
M6	32	64	90	16 (50.0)	0 (-)

Seventeen percent of mandibles had no molar situated directly above the foramen mentale reference point, thus occupying intermediate positions relative to Sikes' age groups. The variable degree of filling of the alveolus above the foramen, and variable degree of abrasion of the anterior edge of the next molar, indicate that some molars are lost at irregular intervals. Although not mentioned as such by Sikes (1966, 1968), the absence of a molar lamina above the foramen is not totally abnormal, as the last few laminae of a particular molar are usually lost in unison. Complete resorption of molar roots occur above the foramen and the part of a molar anterior to the foramen projects as an unrooted shelf. The entire molar progressively loses its roots *en passage* over the foramen, and the occlusal surface is therefore lost bit by bit. The anterior part of the alveolus itself retrogresses as soon as one or more roots are resorbed, and the alveolus is therefore only visible in the molar row when the last section of the anterior molar of the two or three present is lost. Two different molars are present in a mandible, except in age class III where three molars (M1-3) are present, and age classes XXIII-XXX where only one molar (M6) is present. In the normal sequence of events all mandibles will on occasion have recently evacuated alveoli over the foramen, while partially or completely filled alveoli above and posterior to the foramen indicate the premature loss of a molar. It is not possible to judge from the size of the alveolus which lamina would have been situated above the foramen, thus further limiting the use of Sikes' method based on counting laminae. The incidence of lost molars and therefore alveoli situated above the foramen mentale is presented in Table 3, as well as the degree of filling of the alveolar socket (Table 4). It is not known how rapidly the entire cavity is filled by secondary bone growth, but at least the closed-absent class represents premature losses of M1-4.

TABLE 3: Number of mandibles with no molar over the foramen mentale in elephants culled in 1983 and 1985 in Etosha National Park. Percentage incidence given in parenthesis.

Anterior molar present	Total no. of mandibles examined in 1983	No. of mandibles with no molar over foramina mentale
M1	46	16 (34.8)
M2	76	38 (50.8)
M3	170	27 (15.9)
M4	128	5 (3.9)
M5	44	1 (2.3)
M6	32	- -
	496	87 (17.5)

TABLE 4: Condition of the alveolus of lost molars in mandibles with no molar over the foramen mentale, from elephants culled in Etosha National Park.

Alveolus of	No. of alveoli examined	Fresh fully open (%)	1/2 filled (%)	3/4 filled (%)	Closed - absent (%)
M1	16	8 (50.0)	1 (6.3)	1 (6.3)	6 (37.5)
M2	38	3 (7.9)	2 (5.3)	10 (26.3)	23 (60.5)
M3	27	4 (14.8)	4 (14.8)	4 (14.8)	14 (51.9)
M4	5	1 (20.0)	2 (40.0)	1 (20.0)	1 (20.0)
M5	1	1 (100.0)	-	-	-

Comparisons between ages assigned following Sikes (1968) and Laws (1966)

Figure 3 illustrates the correlation between ages of the elephants from Etosha as derived from the methods of Laws (1966) and Sikes (1968), with ages derived from Laws in general greater than those according to Sikes. Table 5 presents the range of laminary indices (Sikes 1968) allocated to mandibles in each of Laws' age classes, in the samples from Etosha, as well as similar ranges described by Sikes (1968). The wide range of FM indices in each of the Lawsian age classes in the samples from Etosha indicates that the two methods correspond less well than they should, as both describe the same process of anterior progression of molars. Ages derived from one method are therefore not directly convertible to the other system.

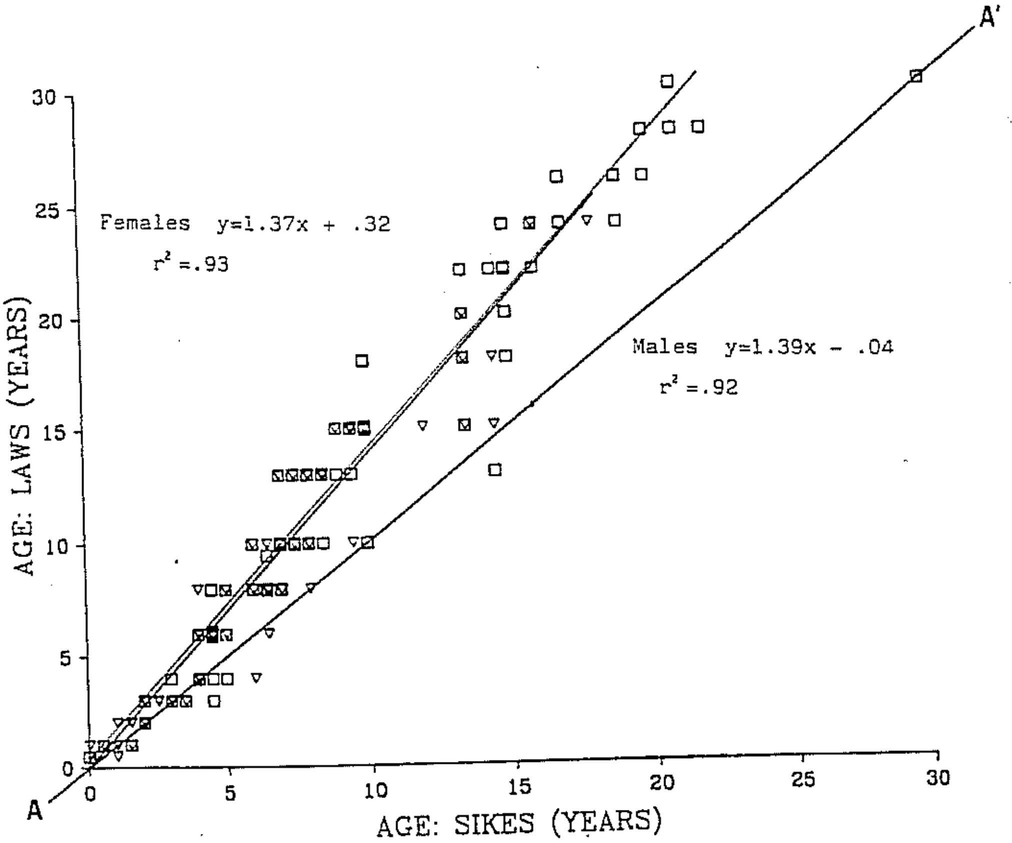

FIGURE 3: Comparison between the ages allocated to female (▼) and male (■) elephants in Etosha National Park according to the methods of Laws (1966) and Sikes (1968) (the diagonal line A-'A' represents exact correspondence between the two methods).

TABLE 5: Range of laminary indices per Lawsian age class in elephants in Etosha National Park.

Age class (Laws 1966)	Corresponding laminary index in Sikes (1968)	Range of laminary indices in Etosha elephants	Modal laminary index in Etosha elephants
I		I/0*	I/0
II	I/1-3	I/0	I/0
III		I/0 - II/0	I/1
IV	I/4-5	I/3 - II/2	II/0
V	II/1-7	II/0 - II/7	II/1
VI	III/1-2	II/0 - III/3	III/0
VII	III/3	III/0-4	III/0
VIII	III/4	III/0-7	III/3
IX	III/5-6	III/1 - IV/1	III/7
X	III/7 - IV/1	III/5 - IV/4	III/8
XI	IV/2	III/9 - IV/4	IV/0
XII	IV/3	IV/0-5	IV/0
XIII	IV/4	IV/3-5	IV/4
XIV	IV/5	IV/3-6	IV/5
XV	IV/6-9	IV/5-9	IV/6
XVI	IV/10 - V/1	IV/7 - V/4	IV/9
XVII	V/2	V/0 - V/5	V/0
XVIII	V/3	V/0 - V/6	V/5
XIX	V/4	V/5 - V/7	-
XX	V/5	V/5 - V/8	-
XXI	V/6-9	V/6-9	V/8
XXII	V/10-12	V/8-10	V/9
XXIII	VI/1-2	V/11 - VI/4	-
XXIV	VI/3	V/9 - VI/4	-
XXV	VI/4-8	V/12 - VI/5	-
XXVI		VI/4-VI5	VI/4
XXVII		VI/4 - VI/6	VI/8
XXVIII	VI/9-10	-	-
XXIX		-	-
XXX	VI/11	VI/8-9	-

*entire molar situated posterior to a vertical line through the foramen mentale.

Age distribution

As a fair degree of subjectivity is involved when allocating mandibles to one of Laws' (1966) age classes, it was suspected that a biased use of the method could be responsible for the inaccurate assignment of individual mandibles to a particular age group. As a test, all mandibles were re-allocated to age classes using the appearance of the anterior and posterior molars independently. Entirely different numerical distributions are produced in this way (Figures 4 & 5). Smoothing by using the estimated age ranges in Laws (1966) and (1967) increased the similarity between anterior-molar biased and posterior-molar biased distributions (Figures 4 B & D, 5 B & D). Anterior-molar bias results in slightly more uneven distributions than posterior-molar bias, the more so in the distributions that emerge using age ranges in Laws (1966) rather than the age ranges in Laws (1967). This may indicate that eruption of molars is more regular than the eventual loss of their fragments.

Age distributions of the elephant from Etosha samples, as derived from the method of Sikes (1968) are illustrated in Figure 6. Peaks do not generally correspond with the loss of molars M2-4, and these distributions are potentially useful. Variations in the number of laminae per molar or the position of the mental foramen are not taken into account in Sikes' method. The only modification that could be made to her method was the allocation of prematurely lost molars to the last laminary age group (Figure 6 A,C) or the last two laminary stages of the missing molar (Figure 6 B,D). Age groups 20-30, following Sikes (1968) are underrepresented in both the 1983 and 1985 samples, as compared to the Lawsian age distributions (Figures 7 & 8).

Figure 9 A-J illustrates female age structures derived from culled samples of elephants from Etosha and seven other populations (data from graphs in Laws 1969b, Hanks 1972a, Sherry

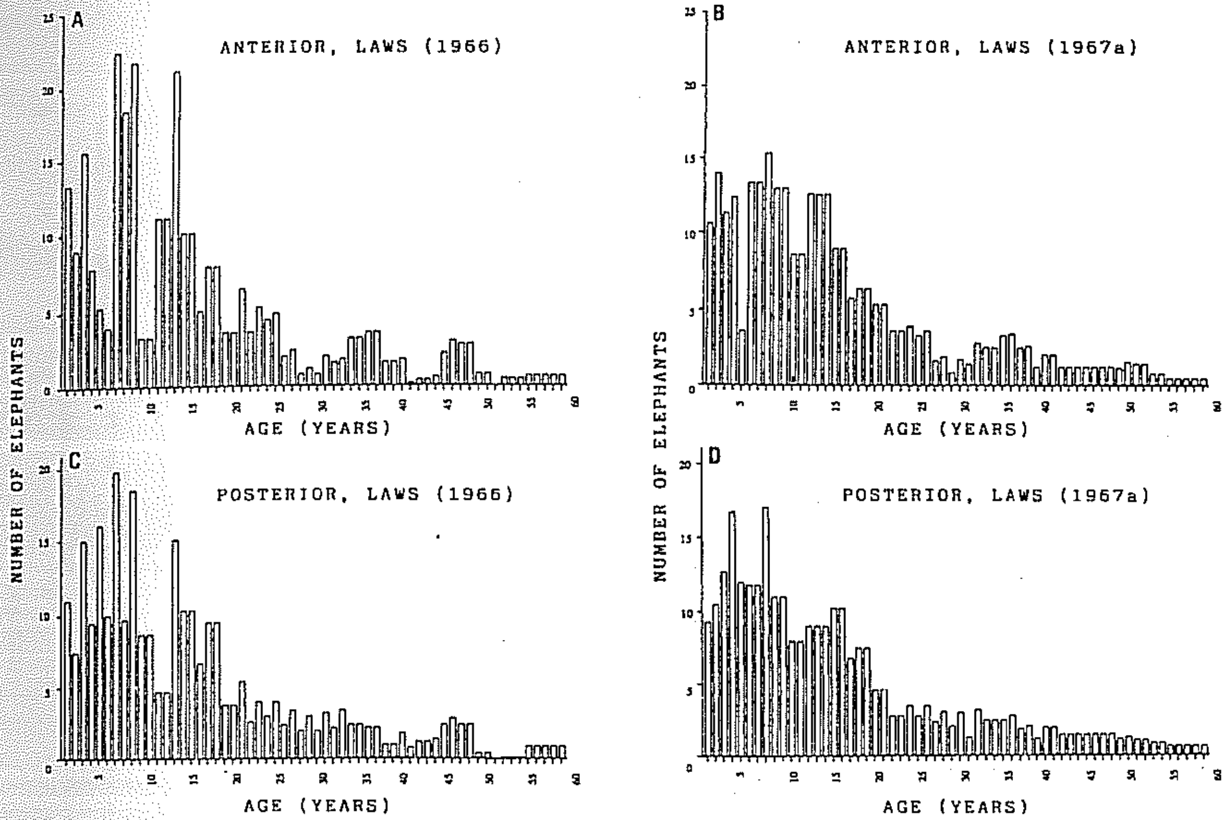

FIGURE 4: Age distributions of female elephants in the 1985 sample from Etosha National Park based on the appearance of the anterior (A & B) and posterior (C & D) molars independently, and smoothed using the age ranges of Laws (1966) and Laws (1967a).

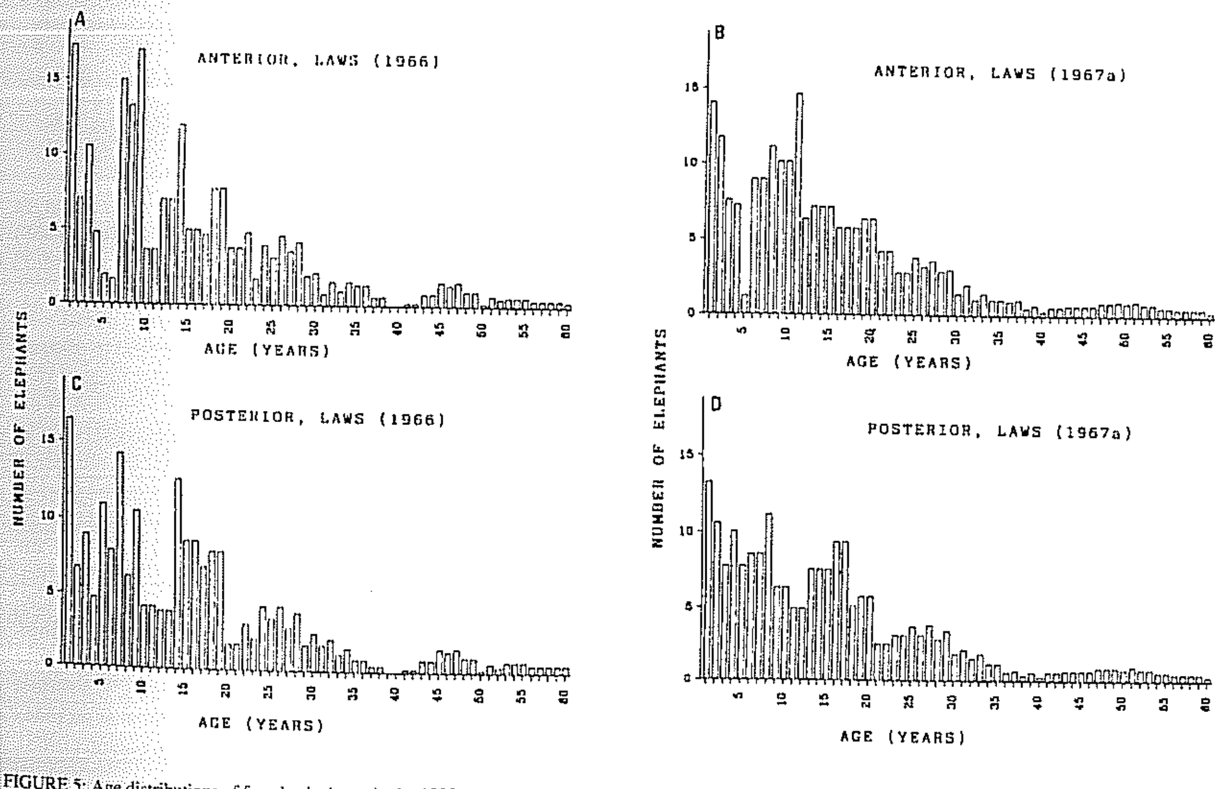

FIGURE 5: Age distributions of female elephants in the 1983 sample from Etosha National Park based on the appearance of the anterior (A & B) and posterior (C & D) molars independently, and smoothed using the age ranges of Laws (1966) and Laws (1967a).

1975, Williamson 1976, Kerr 1978 and Fatti *et al.* 1980). All age structures in Figure 9 are three-year running averages based on age estimations following Laws (1966) except those in Fig. 9 A & C which were based on the revised method of Jachmann (1988). The age structures derived from the original and revised methods of Laws of female elephants in Etosha are not significantly different in both the 1983 and 1985 samples ($_{1983}\chi^2_{59}$= 13.435; NS and $_{1985}\chi^2_{59}$= 12.839; NS).

DISCUSSION

Molar width and length are generally sufficient to identify a particular molar. When a molar is partially eroded, fragmented or not fully erupted and therefore not identifiable by measuring its width and length as in Figure 1, the relative sizes of other molars present in the mandible reveal its identity. Confusion between M4, M5 and M6 is resolved in this way, and there was

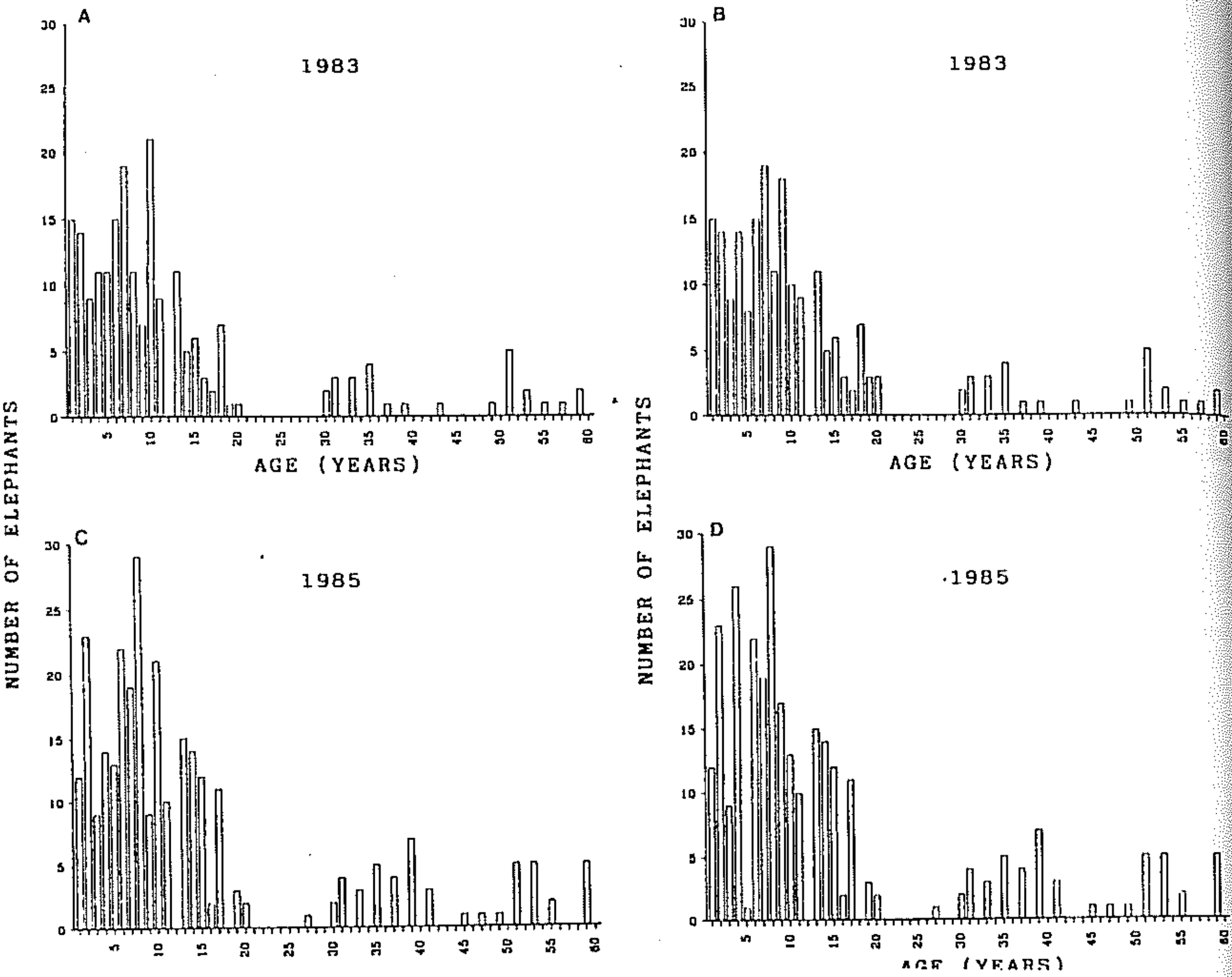

FIGURE 6: Age distributions of female elephants in the 1983 (A & B) and 1985 (C & D) samples from Etosha National Park using the method of Sikes (1968).

no need to resort to laminae counts or exposing roots for identification, as was found by Laws (1966), Hanks (1972b) and Jachmann (1988). Laws (1966) ascribes the overlap in size between molars as possibly due to the inclusion of both sexes in his sample, but Hanks (1972b) and the present study show that even by separating the sexes, the overlap remains, albeit reduced. The respective widths and lengths of molars from the sample from Etosha are similar to those from Zambia (Hanks 1972b) and smaller samples from Uganda (Laws 1966) and Kenya (Sikes 1968). Molars 3-6 from elephants in Malawi are considerably smaller than M3-6 from Etosha, Uganda and Kenya (Jachmann 1985). Few abnormalities occurred in molars in the Etosha samples, similar to the sample of Hanks (1972b). Molar abscesses are regarded as indicative of loss in condition and population stress (Laws & Parker 1968), with a high incidence in Uganda (approximately 10%) but were rare in Etosha (0.4% of all jaws) and absent in Zambia (Hanks 1972b). Supernumerary molars in Etosha (0.2%) and Zambia (0.1%) were likewise less abundant than in Uganda (1.0%).

As both the methods of Sikes and Laws are based on the forward progress of the molar series in the jaw, the degree of correlation between age distributions derived from both methods is to be expected. This was also found by Malpas (1978, in Eltringham 1982) and Lark (1984). Individual ages assigned using the two methods may, however, differ greatly. The use of both methods require a degree of subjectivity, and no two workers will assign all mandibles to the same categories using either method. Ages derived by the method of Laws (1966) cannot be converted directly into Sikesian ages, as shown by the range of laminary indices occurring in each age class of Laws (1966). Such ranges were greater in Etosha elephants than suggested by Sikes (1968) and may reflect interpopulation differences.

Apart from Hanks (1972b) and Jachmann (1985, 1988) who counted laminae but used the Laws (1966) method to allocate ages, only Corfield (1973), Malpas (1978) and Lark (1984) seem to have used Sikes' method. Variation occurred in the number of laminae in the intact and fully developed M1-6 in all populations studied. There appears to be no standard number of laminae for each molar and variable numbers are more common than suggested by Sikes (1968). The same degree of variation was found in Etosha as by Laws (1966), Hanks (1972b) and Jachmann (1988), in Uganda, Zambia and Malawi. Identification of molars can therefore not rely on lamina counts only. Variation in the degree of reduction of the rudimental laminae, and complete development of first and last functional laminae due to the state of development of adjacent molars, is a further drawback in the use of referenced laminary counts as an index of age, as also found by Corfield (1973) and Jachmann (1988). Additional uncertainty is caused by the variation in the number and position of the foramina mentale which are supposed to be a fixed reference point for counting laminae. Variation in the number of laminae, reduction of rudimental laminae, and the position of the foramen mentale disqualify Sikes' method, and have consequently restricted its use.

Sikes (1968) furthermore provides only six ages for her 57 classes, but maintains that intermediary ages can be read off her age reference chart. This is problematical, as there is no

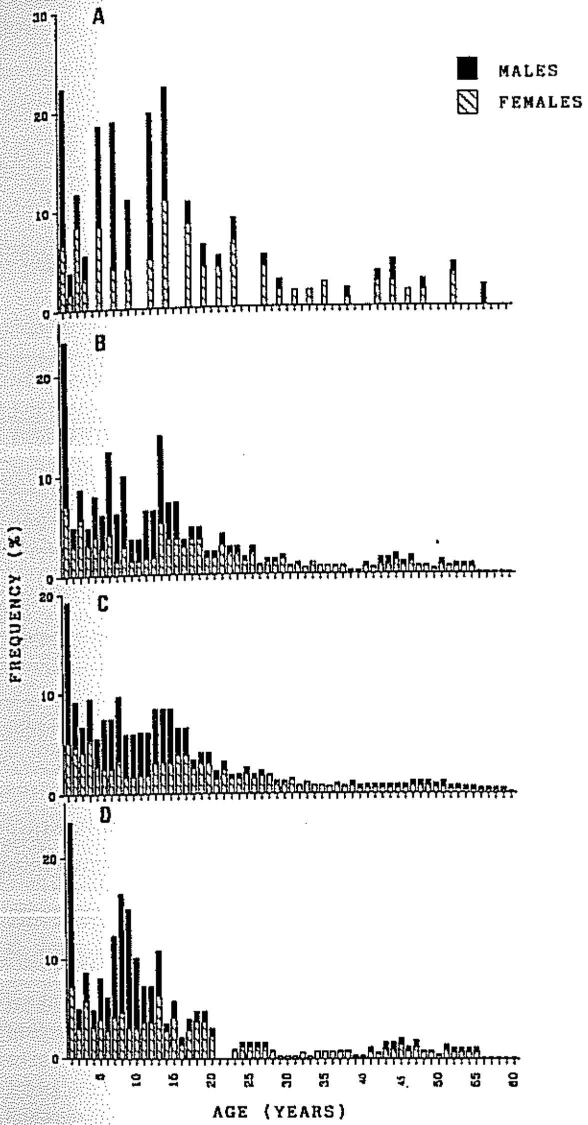

FIGURE 7: Frequency distribution of elephants in each Lawsian age class (A) and in year groups adjusted according to the ranges given in Laws (1966) (B), Laws (1967a) (C) and the age schedule of Jachmann (1988) (D) in the 1983 sample from Etosha National Park.

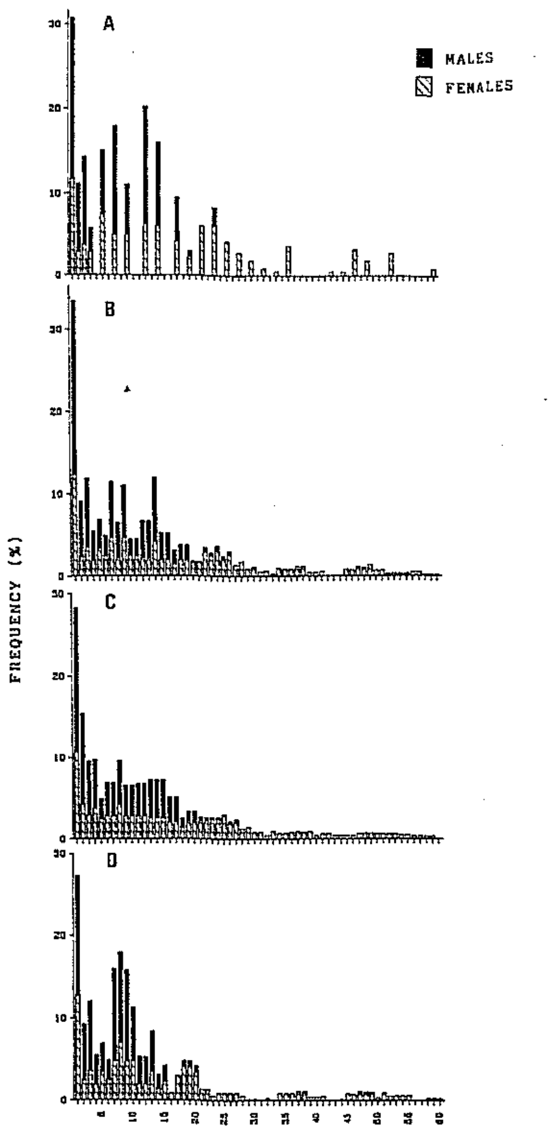

FIGURE 8: Frequency distribution of elephants in each Lawsian age class (A) and in year groups adjusted according to the ranges given in Laws (1966) (B), Laws (1967a) (C) and the age schedule of Jachmann (1988) (D) in the 1985 sample from Etosha National Park.

evidence that intermediate groups follow in regular increments when in fact the six known ages do not. In Etosha at least, it seems wrong to regard the presence of the last lamina of M6 as placing an elephant in the terminal age group. This lamina is only a small portion of the normal occlusal surface of M6 in adult elephants, and death through starvation will ensue long before only the last lamina remains.

The most severe shortcoming of the use of Sikes' method for determining the age of the mandibles of elephants from Etosha, is that up to 18% of mandibles have no molar situated over the mental foramen, due to the premature loss of the last portion of the anterior molar present. It would not be correct to regard alveoli above the foramen mentale as equivalent to the last laminary group of the now lost molar, as a variable degree of erosion of the next molar and variation in the appearance of the empty socket from fresh to undetectable indicate that the preceeding molar is lost at different stages in molar progression in different elephants.

Premature loss of molars is regarded as premature only in terms of the age estimation methods, as no detrimental effects should necessarily be experienced by the individual elephant. Not only may individual elephants have different rates of molar progression, but other factors may also contribute to premature or delayed loss of some molars. At least two molars are lost coincidentally with major life history events, both of which may occur at variable ages, namely weaning and first lactation in females (Laws 1966, Laws 1969a). Calves are weaned at age 2-4 years, which coincides with the loss of M2. Increased demands on the occlusal surface during and after weaning may well unseat the partially resorbed roots of M2 earlier than otherwise. Cows may start lactating from 10-18 years, and greater nutritional demands during this phase may similarly affect the time of loss of M3. This of course would only affect females, and any such effect would have been easy to describe, were it not that males from about 10-20 years old are underrepresented in breeding herds and by consequence also in typical culled samples.

Fatti *et al.* (1980) suggest that misclassification accounts for the ubiquitous peak in 2-4 year-olds in elephant age distributions, while misclassification of completely different age groups accounts for two peaks, at 12-16 years and 20-28 years respectively. All three peaks coincide with the actual loss of a molar, M2, M3 and M4 respectively. The identification of M4 and M5 are not foolproof, the more so in the absence of an intact preceeding tooth such as in age classes XI and XVI (Laws 1966), and may result in the allocation of jaws of completely different ages to these classes. The other alternative cause of

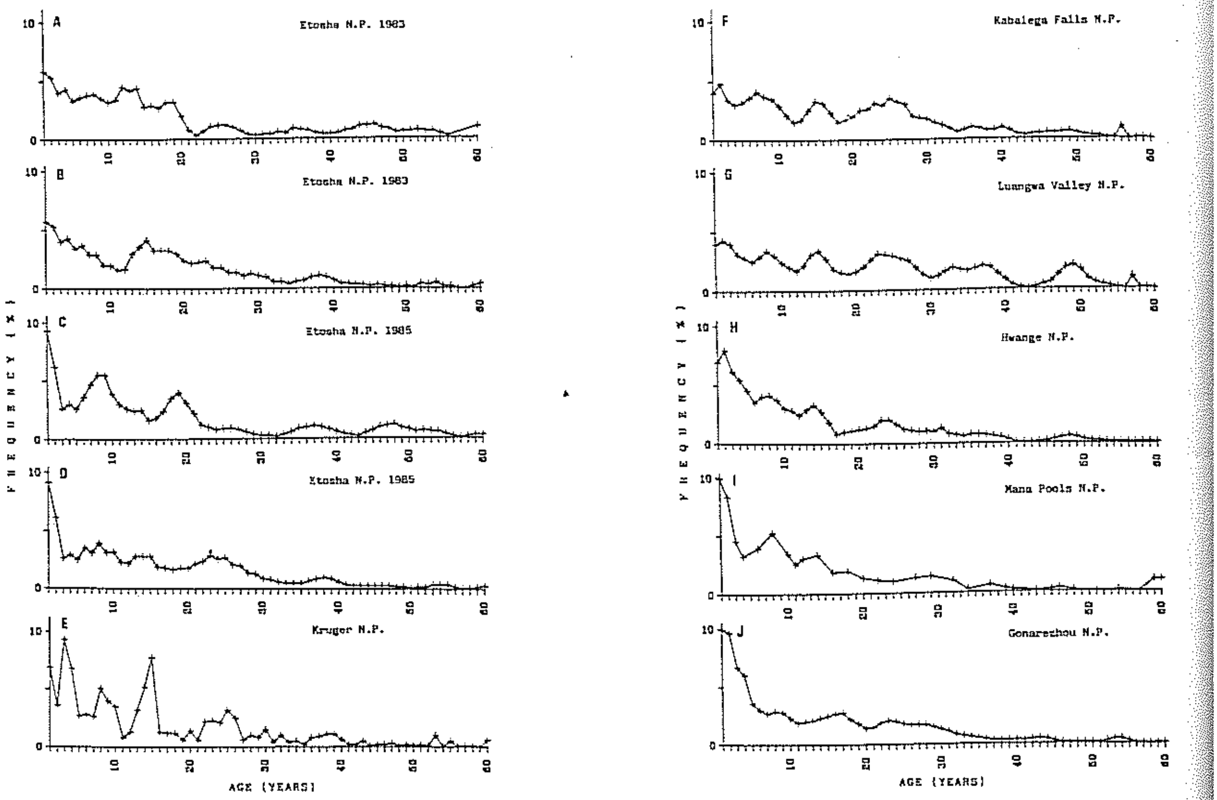

FIGURE 9: Age structures of female elephants derived from the revised age estimation method (Jachmann 1988): A & C, and the method of Laws 1966 (B, D-J), for culled samples from Etosha National Park (A-D), Kruger N.P. (E), Kabalega Falls N.P. (F), Luangwa Valley N.P. (G), Hwange (H), Mana Pools N.P. (I) and Gonarezhou N.P. (J). Data are three-year running averages from references in text.

misclassification of 12-16 and 20-28 year-olds could be that incorrect intervals are allocated to the various stages of loss of M3 and M4.

For unknown reasons, the refined age ranges in Laws (1967) were ignored by Hanks (1972a), Sherry (1975), Smuts (1975), Williamson (1976) and Fatti *et al.* (1980). Age ranges in Laws (1966) are arbitrary, while those in Laws (1967) were based on variation in the only independent criterion of age used in elephants other than molar progression, namely growth of the eye lens. Age distributions constructed from age class frequencies with the age ranges of Laws (1967) are far more even than those using ranges in Laws (1966). It would be informative to have a sample from one of the populations with markedly uneven age distributions reassessed by more than one person, with regard to emphasis on eruption or loss of molars, and the ignored age ranges in Laws (1967).

The validity of using a single series of captive elephants in Basel Zoo (Lang 1965, 1980) to discredit Laws' (1966, 1967) method is questionable. Artificial diets and individual variation in the loss of molars as found in this study complicate this issue. Observations that individual growth rates are faster than previously believed and individual ages are overestimated by Laws' method will have to be substantiated in Africa. The revision of Laws' (1966) method proposed by Jachmann (1988) could be a step in the right direction, but caution has to be exercised in the use of this revision. The fact that elephants in Malawi, on which the revision was based in part, are apparently smaller than savanna elephants (*Loxodonta africana africana*) elsewhere, and show some differences in their molars (Jachmann 1985, 1988) might not support the use of the revised method in other populations. The use of the molar progression method of age estimation by Laws (1966, 1967) has proved to be the most useful in this study. Chronological limits assigned to age classes should ideally be verified by known-age individuals, but this is unlikely to be achieved.

The most vexing issue regarding the elephants in the Etosha samples is the evenness of their Lawsian age distributions. Is this a mere chance effect of individual variation in molar progression combining with local environmental effects on occlusion and possibly interpopulation differences in the rate of molar progression, to make an age estimation method said to be biased in other situations, appear adequate? In this study, greater caution was applied in the identification of molars and allocation of mandibles to age classes in view of the findings of Fatti *et al.* (1980). Less emphasis was possibly placed on the status of a single feature in the mandible in favour of the overall appearance. The absence of peaks in the age distribution could well be of biological significance and suggests the operation of another mechanism on molar progression or population age structure, such as the premature loss of molars, synchronized breeding or even periodic changes in the mortality rate.

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REFERENCES

BOURLIÈRE, F. & VERSCHUREN, J. 1960. Introduction à l'écologie des ongulés du Parc National Albert. *Explor. Parc natn. Albert Miss. F. Boulière, J. Verschuren.* 1: 1-158.

CAUGHLEY, G. 1966. Mortality patterns in mammals. *Ecology* 47: 906-918.

CORFIELD, T.F. 1973. Elephant mortality in Tsavo National Park, Kenya. *E. Afr. Wildl. J.* 11: 339-368.

CROZE, H., HILLMAN, A.K.K. & LANG, E.M. 1981. Elephants and their habitats: How do they tolerate each other. In: FOWLER, C.W. & SMITH, T.D. (eds.). New York: Wiley & Sons.

ELTRINGHAM, S.K. 1982. Elephants. Poole: Blandford Press.

FATTI, L.P., SMUTS, G.L., STARFIELD, A.M. & SPURDLE, A.A. 1980. Age determination in African elephants. *J. Mammal.* 61: 547-551.

HANKS, J. 1972a. Reproduction of elephant (*Loxodonta africana*) in the Luangwa Valley, Zambia. *J. Reprod. Fert.* 30: 13-26.

HANKS, J. 1972b. Aspects of dentition of the African elephant, *Loxodonta africana*. *Arnoldia* 5(36): 1-8.

JACHMANN, H. 1980. Population dynamics of the elephants in the Kasungu National Park, Malawi. *Neth. J. Zool.* 30: 622-634.

JACHMANN, H. 1985. Estimating age in African elephants. *Afr. J. Ecol.* 23: 199-202.

JACHMANN, H. 1988. Estimating age in African elephants: a revision of Laws' molar evaluationtechnique. *Afr. J. Ecol.* 26: 51-56.

JOHNSON, O.W. & BUSS, I.O. 1965. Molariform teeth of male African elephants in relation to age, body dimensions and growth. *J. Mammal.* 46: 373-384.

KERR, M.A. 1978. Reproduction of elephant in the Mana Pools National Park, Rhodesia. *Arnoldia* 8(29): 1-11.

LANG, E.M. 1965. Zahnbeobachtungen bei Elefanten. *Z. Saugetierk.* 30: 287-297.

LANG, E.M. 1980. Observations on growth and molar change in the African elephant. *Afr. J. Ecol.* 18: 217-234.

LARK, R.M. 1984. A comparison between techniques for estimating the ages of African elephants (*Loxodonta africana*). *Afr. J. Ecol.* 22: 69-71.

LAWS, R.M. 1966. Age criteria for the African elephant, *Loxodonta africana*. *E. Afr. Wildl. J.* 4: 1-37.

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

LAWS, R.M. 1969a. Aspects of reproduction in the African elephant, *Loxodonta africana*. *J. Reprod. Fert. Suppl.* 6: 193-217.

LAWS, R.M. 1969b. The Tsavo Research Project. *J. Reprod. Fert. Suppl.* 6: 495-531.

LAWS, R.M. & PARKER, I.S.C. 1968. Recent studies on elephant populations in East Africa. *Symp. zool. Soc. Lond.* 21: 319-359.

LAWS, R.M., PARKER, I.S.C. & JOHNSTONE, R.C.B. 1975. Elephants and their habitats. Oxford: Clarendon Press.

MALPAS, R.C. 1978. The ecology of the African elephant in Rwenzori and Kabalega Falls National Parks. Unpubl. Ph.D. thesis, Univ. of Cambridge.

MORRISON-SCOTT, T.C.S. 1947. A revision of our knowledge of African elephants' teeth with notes on forest and "pygmy" elephants. *Proc. zool. Soc. Lond.* 117: 505-527.

PERRY, J.S. 1954. Some observations on growth and tusk weight in male and female African elephants. *Proc. zool. Soc. Lond.* 124: 97-104.

SHERRY, B.Y. 1975. Reproduction of elephant in Gonarezhou, southeastern Rhodesia. *Arnoldia* 7(29): 1-13.

SIKES, S.K. 1966. The African elephant, *Loxodonta africana*: a field method for the estimation of age. *J. Zool.* (Lond.) 150: 279-295.

SIKES, S.K. 1968. The African elephant, *Loxodonta africana*: a field method for the estimation of age. *J. Zool.* (Lond.) 154: 235-248.

SMUTS, G.L. 1975. Reproduction and population characteristics of elephants in the Kruger National Park. *J. sth. Afr. Wildl. Mgmt. Ass.* 5: 1-10.

WILLIAMSON, B.R. 1976. Reproduction in female African elephant in Wankie National Park, Rhodesia. *S. Afr. J. Wildl. Res.* 6: 89-93.