Assessment of African elephant (*Loxodonta africana*) molars and mandibles and their association with estimated age and sex

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Abstract

Introduction: Estimates of an elephant's age are made by observing the movement of their molars through the mandible. Established ageing techniques have produced varying results and problems have been exacerbated by the difficulty of molar identification. Molar identification is made easier when the sex of the individual is known, as male teeth tend to be larger than female teeth. Elephant mandibles (n = 323) and molars of Zimbabwean origin where gender was known were studied in an attempt to identify relationships between molar/mandible size and sex. Measurements of molars and mandibles were recorded.

Results: From the molar measurements made, the crown-base length of complete molars proved to be useful in determining molar type and may be suggestive of sex in some molar types. On each mandible body, a novel marker, the age reference point, was determined and a measurement based on this point was found to be significantly associated with sex ($p \leq 0.05$) at given ages. Furthermore, inter-rami width was found to be associated with sex between 0–5 y and highly significantly so after 12 y of age. This study also addressed the question of the impact of the number of lamellae present in a given molar type on molar occlusal life; the results suggest that the variable number of lamellae counted in this Zimbabwean population did not affect occlusal life and therefore should not influence ageing techniques.

Conclusion: This is the first detailed study in published literature of both male and female complete elephant molars of the left and right mandible from within the same populations. The results of molar size described here, together with mandible width, should aid in molar identification and sexing of found mandibles, and should therefore improve the estimation of elephant age using existing ageing techniques.

Résumé

Introduction: Les estimations de l'âge d'un éléphant sont faites en observant le mouvement de leurs molaires par la mandibule. Les techniques de vieillissement établies ont produit des résultats variables et les problèmes ont été aggravés par la difficulté d'identification des molaires. L'identification des molaires est facilitée lorsqu'on connait le sexe de l'individu, car les dents des mâles ont tendance à être plus grandes que les dents des femelles. On a étudié les mandibules et les molaires des éléphants (n = 323) d'origine zimbabwéenne où l'on connaissait le sexe dans le but d'identifier les relations entre la taille des molaires/mandibules et le sexe. On a enregistré les mesures des molaires et des mandibules.

Résultats: A partir des mesures des molaires faites, la longueur de leur base couronnée complète s'est avérée utile pour déterminer leur type et peut suggérer le sexe dans certains types de molaire. Sur chaque corps de mandibule, on a déterminé un nouveau marqueur, le point de référence de l'âge, et on a trouvé qu'une mesure basée sur ce point était associée de manière significative avec le sexe ($p \leq 0.05$) à des âges donnés. En outre, on a trouvé que la largeur inter-rami était associée au sexe entre 0-5 ans et très considérablement après l'âge de 12 ans. Cette étude a également abordé la question de longue date de l'impact du nombre de lamelles présentes dans un type de molaires donné sur leur vie occlusale; les résultats suggèrent que le nombre variable de lamelles comptées dans cette population zimbabwéenne n'a pas d'incidence sur la vie occlusale et ne devrait donc pas influencer les techniques de vieillissement.

Conclusion: C'est la première étude détaillée dans la littérature publiée sur des molaires complètes des éléphants mâles et aussi femelles de la mandibule gauche et droite au sein des mêmes populations. Les résultats de la taille des molaires décrits ici, ainsi que la largeur de la mandibule, devraient faciliter l'identification et la détermination du sexe des mandibules trouvées, et devraient donc améliorer l'estimation de l'âge des éléphants en utilisant des techniques de vieillissement existantes.

Introduction

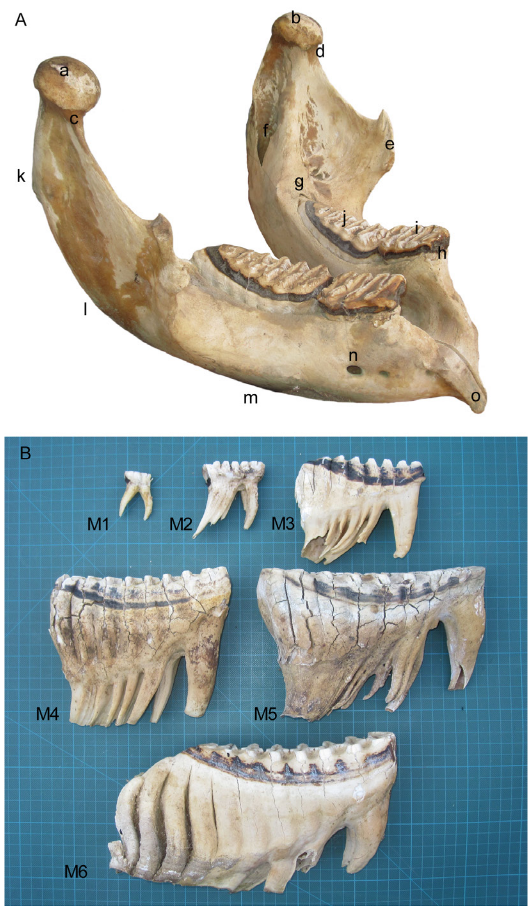
The ability to assign a good estimate of age and sex to African elephant carcasses found in the wild is important in order to study the demographics of a population and thereby allow appropriate long-term management of remaining elephant populations.

The most commonly used method to obtain the above information is to observe the mandible (Figure 1A) and molars (Figure 1B). Six progressively larger cheek teeth or molars (M) move horizontally and progressively upward through each quadrant of the elephant jaw during life and this progression can be related to an animal's age (Laws 1966; Lee et al. 2012). Ageing first requires accurate identification of the molar in wear in the mandible, this being simplified if the sex of the animal is known.

Methods of aging African elephants from their mandibles have been used since the 1960s (Laws 1966; Sikes 1966). There have, however, been difficulties in applying these techniques, particularly with regard to the molars in wear (Hanks 1972; Fatti et al. 1980; Lark 1984; Jachmann 1985; Haynes 1993; Rasmussen et al. 2005; Shrader et al. 2006; Craig and Peake 2011). Furthermore, there has been long-standing interest in the impact of the number of lamellae in each molar type and its effect on ageing methods (Morrison-Scott 1947; Laws 1966; Sikes 1966; Hanks 1972; Craig and Peake 2011; Lee et al. 2012).

This study therefore set out to describe molar and mandible measurements of a collection of specimens from Zimbabwean elephants of known sex, with the aim of providing new information that would aid in molar identification and ageing and also in allocating gender to mandibles of unknown sex. The results from this study have been collated and formed the basis of a new objective method of ageing elephant mandibles (Stansfield 2015).

Figure 1. Anatomical points of the African elephant mandible
1A a) Right mandibular condyle, b) left mandibular condyle c) base of right mandibular condyle, d) base of left mandibular condyle, e) left coronoid process, f) left mandibular foramen, g) distal end of dental alveolus, h) mesial end of dental alveolus, i) mesial molar, j) distal molar, k) right mandibular ramus, l) right mandibular angle, m) right mandibular body, n) right posterior foramen mentale, o) mandibular symphysis. **1B** Molar teeth of African elephants. Examples of molars M1 to M6 from female mandibles. Grid = 1 cm^2.



Material and methods

Elephant mandibles (n = 323) of unknown age were obtained as described previously (Stansfield 2015). To allow statistical analyses, it was necessary to place the mandibles into age groups. This was performed objectively by determining the type of the most mesial molar (Table 1). Description of tooth orientation uses the standard dental terms of mesial (toward the mandibular symphysis) and distal (away from the mandibular symphysis).

The first 7 measurements (as shown in Figure 2A, B and C) were made on 323 mandibles; i) the height at two sites (Figure 2C) from the surface on which the mandible sat to the top of the mandibular condyle, and to the base of the mandibular condyle, this allowed for measurements to be taken on jaws where the softer bone of the condyle had been removed by scavengers; ii) two measurements of length (Figure 2A) taken between a flat board (or wall), directly behind the mandibular rami distally, and the curve of the mandibular symphysis, and also on to the outer tip of the symphysis, two measurements were made to attempt to capture any gender difference there may be

Table 1. Age groups into which African elephants were divided for statistical analysis based on the identification of the mesial molar

Group	Sex F/M	Description	Age (y)[1]	n[3]	Group age mean (y)	sd	p[4]
1	F	M1 present	0 to 1.4	7	1.0	0.4	
1	M			10	1.1	0.28	0.36
2	F	M1 lost	1.5 to 4.9	11	3.3	0.93	
2	M			13	3.9	0.58	0.07
3	F	M2 lost	5.0 to 11.9	27	8.7	2.24	
3	M			18	6.8	1.49	<0.01
4	F	M3 lost	12.0 to 25.9	61	20.1	4.47	
4	M			11	21.9	2.88	0.21
5	F	M4 lost	26.0 to 42.9	56	33.8	4.51	
5	M			73	34.4	4.25	0.46
6	F	M6 only	43.0 to >70[2]	14	57.7	9.01	
6	M			9	51.9	7.06	0.11

[1] Aged according to Laws (1966) and Lee et al. (2012)
[2] >70 reflects ages over 70 years but with a maximum of 75 years
[3] The number of elephants in each group varied due to the nature of specimen collection from either family group culls or professional hunts. The younger animals in Groups 1 and 2 were from culled family groups and were therefore approximately equal in number. In Group 3, the number of females was much higher than the number of males as at the top of this age group (age 10–12) males had a looser association with the family group and therefore may have escaped a family group cull. In Group 4 there were many more females than males as these females could have been shot both in family culls or as tuskless female hunts. The fewer males that were shot in Group 4 were present as young trophy bulls or individuals involved in problem animal control; all were over the age of 18. The majority of trophy bulls shot belonged to Group 5.
[4] p values reflect the difference between the mean ages of males and females in the same age group.

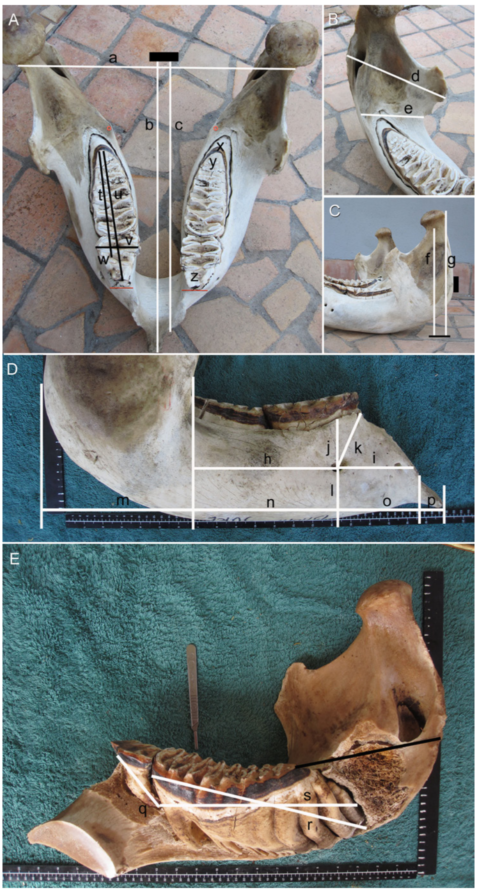


Figure 2. A range of measurements made on 323 intact mandibles of African elephants
A; two mandibular length measurements (b and c) and mandibular ramus width (a). Molar measurements include (t) grinding length on the right mandible to the foramen mentale (FM), (u) full grinding length, (v) maximum grinding width; and points, (w) marking the right mandible FM point according to Sikes 1967, (x) the rearmost erupted lamella, (y) the rearmost worn lamella, and (z) the foremost worn lamella. The red circles indicate the right and left age reference points (ARP) and the red line indicates the mesial end of the dental alveolus (or the crest) **B;** measurements of the flare of the mandibular ramus (d) and the thickness of the mandibular body (e). **C;** the two height measurements excluding (f) and including (g) the mandibular condyle. The black rectangles in A and C mark the point between the mandibular rami from where the length measurements are made.
D; The lateral surface of a bisected mandible showing attempts to describe the position of the foramen mentale (h, i, j, k, l) and measurements of the length of the jaw (m, n, o, p). **E;** the medial surface of a mandible showing the opened dental alveolus; (q) the crown-base length of the mesial molar (if it were to be measured on this mostly eroded molar), (r) the crown-base length of the distal molar, (s) the length of the distal molar. The black line indicates a step in the description of the ARP, the line extends from the tip of the distal occlusal surface to the base of the mandibular foramen on to the back of the ramus. The scalpel handle indicates the position of the foramen mentale on the lateral surface of the jaw.

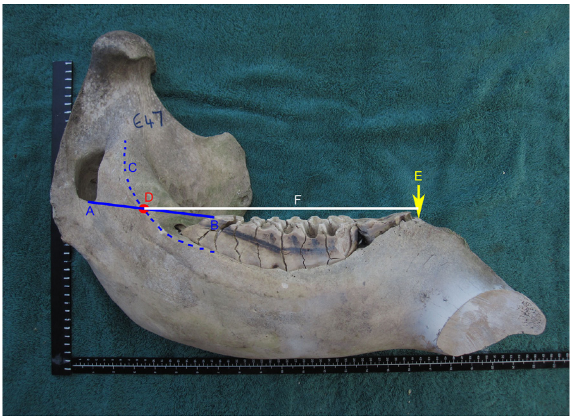


Figure 3. Determination of the age reference point on a left mandibular body
A straight line (blue) is drawn from point A at the base of the mandibular foramen to the distal end of the occlusal surface at point B. A second curved line is visualised or drawn along the apex of the mandibular ridge (blue dotted line). The lines intersect at the age reference point (ARP; red dot at Point D). The length of the line drawn from Point D to the mesial end of the dental alveolus, Point E (marked by the yellow arrow) was significantly associated with the sex of mandibles within the same age group, i.e. males had significantly longer mandibular bodies than females; p ≤0.05).

in the shape of the symphysis; iii) the inter-ramus width (Figure 2A) between the outer surface of the left and right mandibular rami directly below the mandibular condyles; iv) the width of the mandibular ramus bone (Figure 2B) as described by Lee et al. (2012) along with v) the flare from the caudal aspect of the ramus to the rostral edge of the coronoid process (Figure 2B), as also described by Lee et al.

A further important reference point marking the apex of the dental alveolus was determined [this is discussed in greater detail in an accompanying paper (Stansfield 2015); but briefly, the 'age reference point' (ARP) falls at the intersection of a line drawn from the base of the mandibular foramen to the most distal grinding surface of the distal molar, and a line which tracks the apex of the ridge on the medial (inner) surface of the mandibular ramus; see Figure 3]. This point was found to vary little throughout life.

Measurements on each molar and on the occlusal surface were made in cm, to one decimal place, using calipers. These measurements included the width (widest outer diameter), length (greatest length of each molar using a line parallel to the occlusal surface (Figure 2A), crown base length (CBL; Figure 2E) measurement, as used in this study, from the base of the crown mesially to the tip of the distal root, the full grinding length of tooth, the length of grinding surface distal to the foramena mentale (FM; Figure 2A) and the width of grinding surface (greatest enamel loop width). In addition, the total number of lamellae forming each molar, the number of lamellae in wear for each molar and the number remaining but unworn were recorded. Finally, the most distal lamellae both in wear and erupted and the most mesial lamellae in wear, as well as the lamellae present above the FM, were noted (Figure 2A). For M4, M5 and M6, when the mesial part of the molar was found to be eroded, the lamellae in wear were counted based on the finding that the fourth lamella marks the division between the mesial and distal root complexes (Sikes 1966). In M3 the roots are divided between the third and the fourth lamellae. Similar measurements have been made previously on both fossils and Elephas maximus (Maglio 1973; Roth 1982; Roth and Shoshani 1988; Todd 1997, 2005).

Possible sexually dimorphic characteristics of the mandible, molars and dental alveolus were examined when the sex of a mandible was known (n = 316) in order to determine if it might be possible to predict the sex of found jaws from anatomical criteria. These characteristics included anatomical measurements, a study of muscle attachments and the shapes and sizes of the mandibular condyles and symphysis.

Data were entered in an Excel spread-sheet and analysed using Stat Plus 2009. All data met the requirements for parametric tests, therefore a t-test was used to compare two groups and one-way ANOVA was used for 3 or more groups. Results are quoted as mean ± standard deviation and n = the number of observations. The null-hypothesis between classes was rejected at $p < 0.05$. Results where $p < 0.01$ were considered highly significant.

Results

Age groups

The mandibles were initially placed into age groups as determined by the presence of the most mesial molar type (Table 1). Except for Group 3 there was no significant difference between the estimated ages (Laws 1966; Lee et al. 2012) of males and females within a group. The difference in Group 3 [male

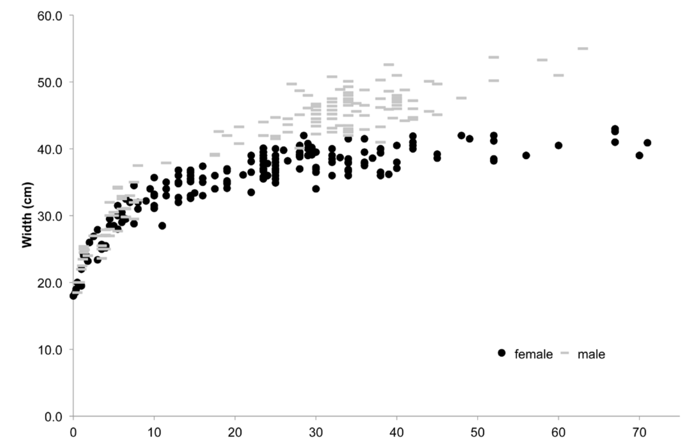


Figure 4. Width and length of African elephant molars
A: Width and length of male molars. B: width and length of female molars of the African elephant

mean = 6.8 y (range 5–8), female mean = 8.7 y (range 5–11.5)] was occasioned by the smaller number of older males in the group; many males of this age having a looser affiliation or having left the family groups but also being too young to be hunted as trophy animals.

Molar size and identification

The initial stage of ageing elephants involves the correct identification of the molars present. Only complete molars containing a full complement of lamellae were used in the comparison. No differences in length or width of the molars were found between the left and right sides of the mandible of an individual ($p > 0.05$; M1 n = 12, M2 n = 32, M3 n = 44, M4 n = 38, M5 n = 40, M6 n = 16). Whereas male elephants showed distinct differences in molar type size (Figure 4A) there was some overlap between M4, M5 and M6 in the females (Figure 4B). Male and female M1 and M2 were of similar size ($p > 0.05$; Table 2) M3 and M4 tended to have a similar width between sexes ($p =$ 0.05 and 0.9, respectively), but the male molars were significantly longer ($p = 0.01$). Male M5s were 4% longer ($p = 0.06$) and 12% wider ($p < 0.01$) than their female equivalent and male M6s were 16% longer ($p < 0.01$) and 12% wider ($p < 0.01$) than female M6s. Assessment of other biological data [e.g. shoulder height and back length (Le Bel et al. 2013)] from the elephants studied made it possible to positively identify the molars in use in all the individuals. Only four mandibles (1.2%) contained supernumerary molars.

Number of lamellae (L) per molar

The number of lamellae in M1s to M4s were similar for males and females, M1 being 5, M2 being 7 or 8, M3 and M4 being 9 or 10 (Table 2). Female M5s had 10, 11 or 12 lamellae with male M5s having 10 or 11. Female M6s had 11, 12 or 13 lamellae while male M6s had 12, 13 or 14 lamellae. Terminal lamellae were found to be small in all but M6. The impact of the number of lamellae per molar type was of interest due to the possible effect of this parameter on the longevity of the molar and thereby its impact on ageing techniques. To address such discrepancies the number of lamellae per molar type was compared with the dimensions of that molar in both males and females. For M2s and M3s the number of lamellae did not affect the length, width or CBL of the teeth (Table 2). Only in female M5s were molars with 11 lamellae significantly different in width to those with 10 lamellae, the latter surprisingly being wider. Significant differences in length were seen in female M4, M5 and M6 with differing number of lamellae, and male M4 and M6; curiously male M5s were all very similar. In female M6s, which had 11, 12 and 13 lamellae there was no significant difference in length between those with 12 and 13 lamellae (although there was between those with 11 and 13 lamellae). CBL is an important measurement owing to the forward and upward movement of the molars throughout their occlusal life (duration of wear); deeper teeth are less likely to be prematurely lost from the dental alveolus. Significant differences in the CBL of all molar types were found only in female M6s with 11 versus 13 lamellae. Data on molars of similar class with differing number of lamellae are given in Table 2.

Mandible size

No variations in mandible or molar sizes between animals of the same estimated age and sex were found between the two populations of elephants in ZV and SVC. Measurements on the few (n = 8) mandibles from the Hwange Park region, although not compared statistically, nevertheless fitted well within those from the other two populations. Accordingly, the 3 populations of jaws were combined for further analyses.

Table 2. Size of elephant inferior molars with differing numbers of lamellae

Molar & gender	No. of lamellae	Molar length (cm) length	sd	n	p	Molar width (cm) width	sd	n	p	Molar crown-base length (cm) CBL	sd	n	p
M1													
F	5	2.4	1.7										
M	5	2.4	1.5										
M2													
F	7	6.2	0.41	16		3.5	0.23	16		7.3	0.73	16	
F	8	5.9	0.38	16	0.06	3.5	0.51	16	0.65	7.7	0.82	16	0.23
M	7	6.1	0.29	18		3.5	0.26	18		7.3	0.65	16	
M	8	6.0	0.26	12	0.19	3.7	0.39	12	0.21	7.7	0.72	14	0.11
M3													
F	9	10.7	0.38	5		4.5	0.45	5		11.3	0.29	5	
F	10	11.3	0.98	34	0.19	4.8	0.39	34	0.18	12.6	1.33	23	0.05
M	9	11.5	0.33	11		5.0	0.31	12		13.1	1.65	9	
M	10	11.9	0.66	31	0.09	4.9	0.38	35	0.17	13.3	1.07	21	0.76
M4													
F	9	13.9	0.95	25		5.7	0.34	25		15.6	0.54	14	
F	10	14.9	1.95	34	0.03	5.7	0.50	39	0.80	16.1	0.83	19	0.07
M	9	14.6	0.89	8		6.0	0.23	7		16.9	1.07	5	
M	10	15.8	0.87	13	0.01	5.6	0.46	19	0.10	17.1	1.11	15	0.70
M5													
F	10	18.1	1.17	25		6.5	0.51	40		19.8	1.74	13	
F	11	19.6	1.50	42	<0.01	6.3	0.50	54	0.02	20.8	1.46	24	0.07
F	12	21.0		1		6.5		1		22.5		1	
M	10	19.6	1.53	24		7.4	0.49	28		20.8	1.16	12	
M	11	19.5	1.92	26	0.87	7.4	0.76	27	0.99	21.3	2.18	15	0.37
M6													
F	11	21.6	1.56	14		6.9	0.37	15		23.3b	1.16	12	
F	12	22.9a	1.35	14		6.8	0.74	20		24.2bc	1.37	12	
F	13	24.1a	0.87	11	<0.01	7.0	0.40	14	0.59	25.1c	1.33	10	0.01
M	12	26.6	1.53	18		7.7	0.59	31		28.7	1.58	18	
M	13	27.8	1.83	27	0.02	7.7	0.56	44	0.80	28.9	1.92	26	0.64
M	14	29.0		1		7.1		1		29.1		1	

F = female molars, M = male molars, p value = difference between the same molar types of the same sex with differing number of lamellae, sd = standard deviation, n = number.
For the 3 classes of female M6s the mean lengths with superscripts showed no significant difference using the Bonferroni Test p >0.05.

From all the measurements made on the mandibles that were described in Materials and Methods, the feature that correlated most closely to age was the distance between the mandibular rami. The mean mandible width for all 6 gender-neutral groups increased with age (Figure 5, see colour pages v) and although young males had wider jaws than females of similar age (Group 1, $p = 0.129$; Group 2, $p = 0.252$; Group 3, $p = 0.559$), this did not become highly significant ($p < 0.01$) until >12 years of age, i.e. after M3 had been lost. After age 20, the jaw width became indicative of sex with limited overlap between male and female data points.

The length of the dental alveolus was also examined with regard to sexual dimorphism (Figures 3 and 6). Males tended to have a longer mandibular body from the ARP to the mesial end of the alveolus than females, which showed borderline significance for Groups 1 and 2 ($p = 0.05$ for both) and became highly significant for Groups 4, 5 and 6 ($p = 0.002$ for G4 and $p < 0.001$ for G 5 and 6). Group 3 showed an inversion of this trend but this is most likely associated with the female Group 3 containing significantly older elephants than the male Group 3.

Other sexually dimorphic characteristics

Male mandibles >20 years were observed to have larger overall dimensions (length, width, height, length of dental alveolus, thickness of bone) and larger muscle attachments than female mandibles. The

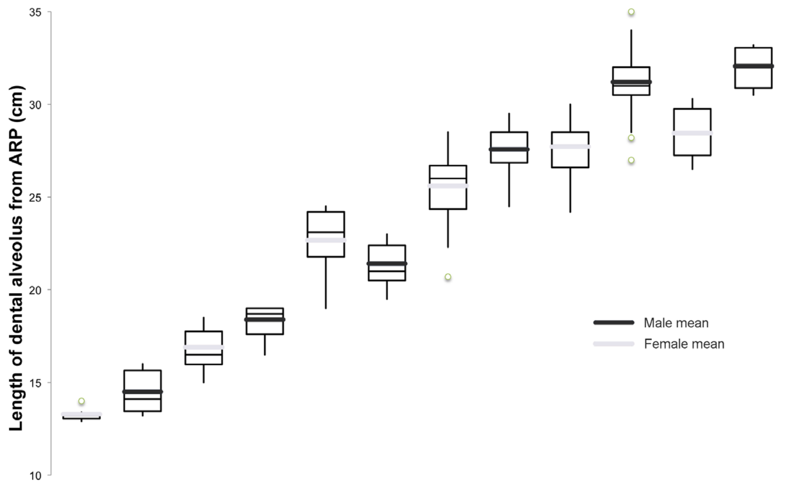


Figure 6. Boxplots for the length of the mandibular body from the 'age reference point' (ARP) Thick grey/black lines indicate means. Boxes are in pairs from left to right and represent the female (grey mean) and male (black mean) for each molar type ranging from M1s on the far left to M6s to the far right. Statistical comparison of the male and female groups; Group 1 p = 0.05; Group 2 p = 0.05; Group 3 p = 0.02; Group 4 p <0.01; Group 5, p <0.01; Group 6 <0.01. Note that the mean age of females in Group 3 was significantly greater than that of males due to the method of specimen collection.

Figure 7. Mandibular condyles from female elephants
The shape of mandibular condyles was not influenced by sex. Both male and female mandibles exhibited the flatter, latero-medial shape (left) and the round shaped condyle (right).

Figure 8. Association of shape of mandibular symphysis with sex in elephants.
Neither a pointed nor a rounded mandibular symphysis could be associated with male (A and B) or female (C and D) sex.

shape of the mandibular condyle was not influenced by gender. In a cohort of 56 jaws, 64% of females had round condyles, while the remainder exhibited a flatter, latero-medial shape to the condyle (Figure 7). In males, the equivalent figures were 73% and 27% respectively. Likewise visual appraisal was unable to relate 'pointiness of the chin' to either sex (Figure 8).

Discussion

This study presents, for the first time, an assessment and comparison of inferior molar teeth from the left and right sides of the jaw, and the mandibles of African elephants of both sexes from the same populations; the study observed mandibles from 3 discrete populations of elephants within Zimbabwe. The sizes of mandibles at a given age and sex were found to be similar between populations, as were the sizes of molar teeth. There was, as expected, within population variation in molar size, partly dependent on the number of lamellae present but this was assessed not to impact significantly on occlusal life and therefore estimates of age.

Molar size

In contrast with previous studies (Laws 1966; Krumrey and Buss 1968; Hanks 1979; Jachmann 1985; Lee et al. 2012) molars in the current study were separated according to sex. When plotting length against width of complete molars, quite discrete groups of points were obtained for each type of molar with the exception of female M5/M6. Laws (1966) suggested that this may have been the case with his collection of mandibles if he had been able to allocate sex. Furthermore Laws measured his elephant molars in situ whereas the molars in the current study were measured following extraction. This may account for the apparent differences in the plotted points in the graphs of the two studies, particularly in the length of M6s as maximum length and width of molars occurs below bone level.

Lee et al. (2012) also plotted length and width of molars, but as they measured any molar with ≥ 5 lamellae, it is difficult to make a comparison with other studies quoting complete molars.

When comparing male and female molars there were only significant differences in the length and width of the M6s. It can however be seen in Table 2 that male molar types M3 to M6 tend to have a longer CBL at a given number of lamellae than do female molars. Opening up the mandible to expose the roots of the molars in wear is therefore useful for molar identification and should be a recommended practice when aging elephant mandibles. Obviously complete molars are not always present in elephant mandibles but these results offer guidelines for comparison of partially eroded teeth.

Effect of number of lamellae on molar size

Assuming that animals of a similar age and sex masticate at a similar rate and that the forward progression of molars is intrinsic, it seems reasonable to assume that a molar of a certain type, for example a female M6 with 11 lamellae, would be eroded more quickly than an M6, with, say 12 or 13 lamellae. Table 3 compares the differing number of lamellae identified in previous elephant ageing studies with the data obtained in the present study. In the current study M4s, M6s and M5s in females, with a greater number of lamellae, were significantly longer than those with less lamellae (Table 2). However, this difference was not reflected in CBL (with the exception of female M6 with 11 or 13 lamellae). CBL is associated with molar longevity during the forward and upward progression throughout molar life, i.e. the occlusal life of a molar depends not just on its length, but also on its depth; therefore, as no significant difference in the CBL of most molar types were found (Table 2), it could be concluded that, within a molar type (with different number of lamellae), there is insufficient difference to impact significantly on the occlusal life of the tooth. Therefore, the number of lamellae present in each molar type should have little impact on ageing techniques of the elephants within the Zimbabwean populations studied. It will be interesting to note if this also occurs in other localized populations, as authors have recorded the differing number of lamellae per molar type since the seminal studies in the 1960s.

Sexual dimorphism in mandibles

Results indicated that both the inter-ramus width (see colour pages v)and the length of the dental alveolus (Figure 6) may be useful in aging and particularly for sexing elephant mandibles. The shape of the mandibular condyles has been previously noted to be sexually dimorphic (Yacobi et al. 2004) but this was not the case with the Zimbabwe populations studied. Neither was the length or sharpness of the point of the mandibular symphysis sexually dimorphic.

Table 3. Number of lamellae found in the inferior molars of African elephants during different studies

	Africa M-Scott	Uganda Laws	E Africa Sikes	Kenya Lee	Zambia Hanks	Botswana Craig	Zimbabwe (Current study)	Range
M1		3-4	5	4	4-5 (5)	5	5	3-5
M2		6-7	7	8	7-9 (7-8)	7	7-8	6-9
M3	8-10	8-10 (9-10)[1]	10	9	8-10 (9-10)	10	9-10	8-10
M4	8-11	7-10 (8-10)	10	10	8-10 (9)	9	9-10	7-10
M5	9-12	9-12 (9-11)	12	10	9-11	10	10-12 (10-11)	9-12
M6	9-14	10-14 (11-13)	13	11	10-13	12	11-14 (11-13)	9-14

[1] Most commonly found occurrences are in brackets.
References; Morrison-Scott (1947), Laws (1966), Sikes (1966), Lee et al. (2012), Craig and Peake (2011), Hanks (1972).

A limitation of this study was the small number of molars and mandibles examined in some age groups. Where some of the observed differences were quite close to significance, subsequent research employing a larger sample size could refute the null hypotheses, and in view of this, conclusions should be addressed with caution.

Conclusion

Mandible inter-rami width, length of the dental alveolus and molar CBL are all useful measurements which can contribute towards greater accuracy in ageing and sexing found elephant mandibles using existing ageing techniques. Male molar measurements fall into distinct groups and can be identified by their length and width. Widths of female M4, 5 and 6 are more problematic as they overlap; however, crown base lengths of these complete molars are distinct from each other. It is therefore important to open mandibles to fully expose the molars in wear for accurate identification. Partially eroded molars should be compared either directly with complete molars or with a table of their measurements.

The results of this study also suggest that the varying number of lamellae found in molars of the same type should not have any impact on their occlusal life and therefore on the ageing technique.

After the age of 20, the width of the mandible and of the M5 and M6 are indicative of gender. Mandible width may be indicative of gender down to the age of 10–12 but a greater sample number is required to confirm this. The length of the dental alveolus showed borderline significance in determining sex below the age of 5 and was highly significantly associated with sex after age 12.

These observations were accurate for the elephant populations studied within Zimbabwe. It is suggested that similar observations of other elephant populations within Africa should be made using the same guidelines.

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References

Craig GC, Peake D. 2011. The elephants of northern Botswana, age determinations, age and size of hunting trophies. *Conservation Trust Fund of the Ministry of Environment, Wildlife and Tourism,* Gabarone, p. 27.

Fatti LP, Smuts GL, Starfield AM, Spurdle AA. 1980. Age determination in African elephants. *Journal of Mammalogy* 61, 547–551.

Hanks J. 1972. Aspects of dentition of the African elephant. *Arnoldia Rhodesia* 5, 1-8.

Hanks J. 1979. *A Struggle for Survival. The Elephant Problem.* C Struik Publishers.

Haynes G. 1993. Appendix: Methods for determining age in proboscideans. Mammoths, mastodonts, and elephants; biology, behavior and the fossil record. Cambridge University Press, Cambridge, pp. 321-353.

Jachmann H. 1985. Estimating age in African elephants. *African Journal of Ecology* 23, 199-202.

Krumrey WA, Buss I. 1968. Age estimation, growth and relationships between body dimensions of the female African elephant. *Journal of Mammalogy* 49, 22–31.

Lark RM. 1984. A comparison between techniques for estimating the ages of African elephants (Loxodonta africana). *African Journal of Ecology* 22, 512-516.

Laws RM. 1966. Age criteria for the African elephant. *East African Wildlife Journal* 4, 1–37.

Le Bel S, Stansfield FJ, Perrotton A, Connear G, Muti G, La Grange M, Czudek R, Taylor R. 2013. Managing local overabundance of elephants through the supply of game meat: the case of Savé Valley Conservancy, Zimbabwe. *The Journal of Wildlife Management* 43, 103-119.

Lee PC, Sayialel S, Lindsay WK, Moss CJ. 2012. African elephant age determination from teeth: validation from known individuals. *African Journal of Ecology* 50, 9-20.

Maglio V. 1973. Origin and Evolution of the elephantidae. *Transactions of the American Philosophical Society* 63.

Morrison-Scott TCS. 1947. A revision of our knowledge of African elephants' teeth, with notes on forest and "pygmy" elephants. *Proceedings of the Zoological Society of London* 117, 505-527.

Rasmussen HB, Wittemyer G, Douglas-Hamiliton I. 2005. Estimating age immobilized elephants from teeth impressions using dental silicon. *African Journal of Ecology* 43, 215-219.

Roth VL. 1982. Quantitative variation in elephant dentitions: implications for the delimitation of fossil species. *Paleobiology* 18, 184-202.

Roth VL, Shoshani J. 1988. Dental identification and age determination in Elephas maximus. *Journal of Zoology* 214, 567-588.

Shrader AM, Ferreira SM, McElveen ME, Lee PC, Moss CJ, van Arde RJ. 2006. Growth and age determination of African savanna elephants. *Journal of Zoology* 270, 40-48.

Sikes SK. 1966. The African elephant, Loxodonta africana: a field method for the estimation of age. *Journal of Zoology London* 150, 279-295.

Stansfield FJ. 2015. A novel objective method of estimating the age of mandibles from African elephants (*Loxodonta africana*). *PLOS One* 10 e0124980.

Todd NE. 1997. Comparison of variation in cranial and dental morphology of Elephas recki and the extant elephants: implications for phylogeny and macroevolution. PhD. Dissertation. George Washington University, Washington DC.

Todd NE. 2005. Reanalysis of African Elephas recki: implications for time, space and taxonomy. *Quaternary International* 126-128, 65-72.

Yacobi Y, Shoshani J, Hagos Y, Debrom E. 2004. The elephants (*Loxodonta africana*) of Zoba Gash Barka, Eritrea: Part 3. Ecological and other data from tusks, teeth and carcasses. *Pachyderm* 37, 45-48.