RESEARCH

Tusk metrics and pair symmetry in savannah elephants

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Abstract

The right and left tusks and from both genders of five separately culled savannah elephant clans were measured, recording weight (n = 2453), overall length (n = 563), external length beyond the gingivae (n = 158), internal length within the alveolus (n = 158) and circumference at the lip (n = 158). The increase in tusk weights and lengths with age was reconfirmed as basically exponential in males and more linear in females up to their fifth decade. Between the right and left tusks, the five metrics were on average symmetrical (in the sense of being mirror images of one another), and predictive of both age and each other (i.e. from one the others can be deduced). Strikingly, however, pair length symmetry is less within alveoli, where growth takes place, than between their corresponding external parts, where tusks are essentially dead tissue. Such greater external symmetry can only occur if the shorter tusk grows faster to catch up with its partner or the longer tooth is reduced through wear towards parity with its partner, or both.

Résumé

Les défenses droite et gauche d'éléphants de savane (des deux sexes), abattus dans cinq clans différents, ont été mesurées selon des critères de poids (n = 2 453), de longueur totale (n = 563), de longueur externe après la gencive (n = 158), de longueur interne à l'intérieur de l'alvéole dentaire (n = 158) et de circonférence au niveau de la lèvre (n = 158). La croissance des défenses au fil des années, en poids et en dimensions, a été confirmée de nouveau comme étant essentiellement exponentielle chez les mâles et plus linéaire chez les femelles jusqu'à leurs 50 ans environ. Les cinq mesures sont en moyenne symétriques entre les défenses droites et gauches (en ce sens qu'elles sont des images miroirs l'une de l'autre), et s'avèrent prédictives de l'âge de l'individu et de comment serait constituée la deuxième défense (c'est-à-dire que l'on peut déduire l'une par rapport à l'autre). Il est toutefois frappant de constater que la symétrie des paires en longueur est moins importante à l'intérieur des alvéoles, où a lieu la croissance, qu'entre les parties externes correspondantes, où les défenses sont essentiellement constituées de tissus morts. Une telle symétrie externe ne peut se produire que si la défense la plus courte croît plus rapidement afin de rattraper sa semblable, ou si la plus longue des deux est réduite par l'usure, ou encore si les deux phénomènes coexistent.

Introduction

While using the term 'population' to infer genetic isolation, I use the term 'clan' to differentiate contiguous or separated groups of savannah elephants that are not necessarily genetically isolated (Parker 2023a). This paper statistically examines the tusk measurements from two populations: one in west-central Uganda and the other in the Nyika biome,

Table 1. The five populations sampled, showing regions, sampling areas, population designations (clan), sampling locations (coordinates), sample sizes, and date ranges when sampling occurred. NP = National Park

Region	Location	Clan	Coordinates	Sample Size	Dates
Murchison	Murchison Falls NP, Uganda	Murchison North	2°24'N, 31°42'E	1,197	Mar 1965–Jun 1967
		Murchison South	2°10'N, 31°50'E	798	Nov 1965–May 1967
Nyika	Tsavo NP, Kenya	Tsavo Koito	3°00'S, 38°42'E	298	Aug 1966
	Mkomazi NP, Tanzania	Mkomazi East	4°22'S, 38°35'E	299	Mar–Apr 1968
		Mkomazi Central	4°9'S, 38°14'E	295	Aug–Sept 1969

comprising coastal Kenya and north-easternmost Tanzania. Within them, five elephant clans were culled at different times and in separate places between 1965 and 1969, as described by Laws et al. (1975). Two were in the west-central part of Uganda's Murchison Falls National Park (Murchison), and three in the Nyika. The Murchison clans are referred to as Murchison North and Murchison South, located to the north and south of the Victoria Nile, respectively, and the Nyika clans as Tsavo Koito, Mkomazi East and Mkomazi Central (Table 1).

Materials and Methods

Field methods

The culling procedures and data collected are recorded in Laws et al. (1975). Elephants were aged using Laws' system (Laws 1966). Once the skulls were stripped of skin and flesh, the tusks were axed free, and the attached bone and tissue were removed. Where tusks were missing, the cause of absence was determined by dissecting the exposed skull.

All tusks were weighed to the nearest 0.25 kg on commercial scales (females: n = 1,343; males: n = 1,110). Measurements to the nearest 0.5 cm were taken from subsections of the culls as follows:

a. Total tusk length along the outer curves (n = 563)
b. Circumference at emergence from the gingiva (n =158)
c. External tusk length (n = 158)
d. Internal (i.e. within the alveolus) tusk length (n = 158) by subtracting (c) from (a).

All were identified as to gender and whether they were right or left[1].

Statistical analyses

The relationships between the dimensions of tusk pairs were examined for two-tusked elephants using one tusk per randomly selected elephant (i.e. rather than equating right against left or vice versa, comparison was randomly based). The relationships were effectively linearized, and the variances among y-values were homogenized for a range of x-values, by square-root transformation of circumference and cube-root transformation of weight. Linear regressions were used to test the independent values of total lengths and circumferences to predict weights, of circumferences to predict total lengths, and of internal lengths to predict external lengths.

Possible sources of variation in untransformed tusk weights while controlling for the effect of age were investigated using permutational ANOVAs. Only two-tusked elephants older than six years were included in the data analysis since below this age all tusks may not yet have erupted (Parker 2023a). The analysis was conducted with a random selection of either the left or right tusk, and exclusion of two individuals for which the selected tusk was broken and much smaller than the other. Possible explanatory variables considered were Gender and Age as fixed effects, and Region (Murchison and Nyika, Table 1) and Clan (nested in Region) as random effects, with all possible interactions included. Age was represented by five classes of approximately equal sample size, combining age year classes of 6.5–10.5, 11.5–16.5, 17.5–23.5, 24.5–30.5, and 31.5–60.5. Euclidean distance, Type III

[1]All the raw data from the five elephant clans cited in this paper are available at: http://ufdc.ufl.edu/AA00013409/0007

Table 2. Predictive relationships among tusk dimensions.

Relationship	r^2	p	n
$Weight^{1/3}$ = 0.0133 × length + 0.2287	0.939	<0.0001	553
$Weight^{1/3}$ = 0.6644 × $circumference^{1/2}$ – 1.5631	0.941	<0.0001	553
Total length = 45.5974 × $circumference^{1/2}$ – 114.2215	0.832	<0.0001	553
External length = 1.7842 × internal length – 24.8037	0.724	<0.0001	160

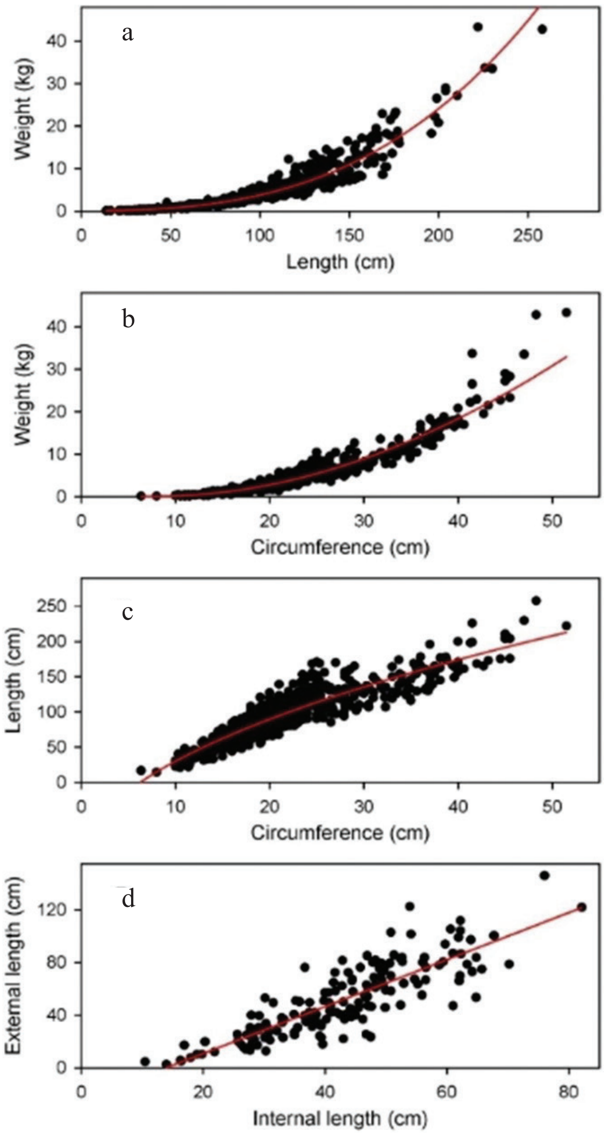

Figure 1. Relationships among the tusk dimensions of the savannah elephants' tusks. a) relates weight to length; b) weight to circumference; c) length to circumference and d) external length to internal (alveola) length.

(partial) sums of squares, fixed effects summing to zero for mixed terms, and 9,999 permutations of residuals under a reduced model were used.

The symmetry of three tusk measures (alveolar length, external length, circumference at lip) was investigated for two-tusked elephants as, for each measure: % dev = 100 × (right tusk– left tusk) / (left tusk + right tusk) where % dev is the percentage deviation from the mean, so that elephants with larger left tusks are represented by a negative percentage and those with larger right tusks by a positive percentage.

Effects on symmetry were investigated for each symmetry metric (as % dev) separately using permutational ANOVAs. Possible explanatory variables considered were Gender and Age as fixed effects and Clan as a random effect, with all possible interactions included. Except for weights, data were available for only three clans. Age was represented by five classes of approximately equal sample size, combining age year classes of 2.5–7.5, 8.5–14.5, 15.5–20.5, 21.5–27.5, and 28.5–57.5. Euclidean distance was used, Type III (partial) sums of squares, fixed effects summing to zero for mixed terms, and 9,999 permutations of residuals under a reduced model.

Table 3. Results of the permutational analysis of effects on tusk weight for elephants older than six years of age from five savannah elephant clans. Age was treated as categorical with five classes. Probabilities of significant terms at $p < 0.05$ are coloured red. df = degrees of freedom.

Terms	df	p
Age	4	**0.001**
Gender	1	0.16
Region	1	0.29
Region (Murchison or Nyika)	3	**0.001**
Age × Gender	4	**0.001**
Age × Clan (Region)	12	**0.001**
Age × Region	4	0.93
Gender × Clan (Region)	3	**0.002**
Gender × Region	1	0.66
Age × Gender × Clan (Region)	12	**0.001**
Age × Gender × Region	4	0.93
Residual	2,097	

Results

Tusk dimensions

Both length and circumference were strongly predictive of the weight of the tusk (Table 2; Fig. 1). Circumference also predicted total length, and internal length predicted external length, although less strongly and this applied to both sexes.

Tusk weight varied strongly with Age; it also varied with interactions between Age, Gender and Clan (nested in Region) (Table 3). Although Gender was not in itself a significant term in the model, interactions between Gender, Age and Clan (nested in Region) were highly significant, indicating that the gender effect on tusk weight is unevenly distributed. Neither the effect of Region nor any interactions including it were significant, but the effect of Clan (nested in Region), and interactions involving it, were all highly significant.

Overall, the weight of the female tusks showed a linear increase with age, although the small number of females older than 54 years may have had lighter tusks than predicted. The increase was exponential in males. The same patterns were identified for each clan examined separately with 70 to 91% of variance explained (Table 4; Fig. 2).

The effects of Age and Gender are highly significant, and differences between clans difficult to detect especially among females (Fig. 3). It is possible that the tusks of male elephants from Mkomazi Central are longer in comparison for age range than those from the other Tsavo ecosystem males, and that males from Murchison South have shorter tusks for age than those from Murchison North. It is also possible that the statistical effect of Clan (nested in Region) was exaggerated (especially through interactions) by poor representation of the oldest age class by males from the three Nyika clans.

Symmetry

As shown in Fig. 4, all four metrics for two-tusked elephants were on average quite strongly symmetrical, with the external length somewhat more symmetrical than the internal length, and circumference most strongly symmetrical but for a small number of outlying cases. For circumference, 89.5% of elephants were within 5% of the mean, whereas for external and internal tusk length the respective measures were 78.5% and 54.9%. For individuals with both metrics not prone to wear (internal length, circumference at

Table 4. Regressions of the relationship between tusk weight and age for each gender in elephants older than six years in five clans of savannah elephants. p < 0.0001 in all cases.

Gender	Clan	Relationship	r^2	n
M	Murchison North	Tusk weight$^{1/3}$ = 0.0581 × age + 0.7302	0.875	500
M	Murchison South	Tusk weight$^{1/3}$ = 0.0548 × age + 0.8068	0.886	377
M	Tsavo Koito	Tusk weight$^{1/3}$ = 0.0565 × age + 0.8414	0.909	108
M	Mkomazi East	Tusk weight$^{1/3}$ = 0.0569 × age + 0.8182	0.879	108
M	Mkomazi Central	Tusk weight$^{1/3}$ = 0.0615 × age + 0.7377	0.902	108
F	Murchison North	Tusk weight = 0.1498 × age – 0.2823	0.793	428
F	Murchison South	Tusk weight = 0.1625 × age – 0.289	0.733	266
F	Tsavo Koito	Tusk weight = 0.1684 × age + 0.0021	0.721	72
F	Mkomazi East	Tusk weight = 0.182 × age – 0.3473	0.698	97
F	Mkomazi Central	Tusk weight = 0.1746 × age – 0.4498	0.822	83

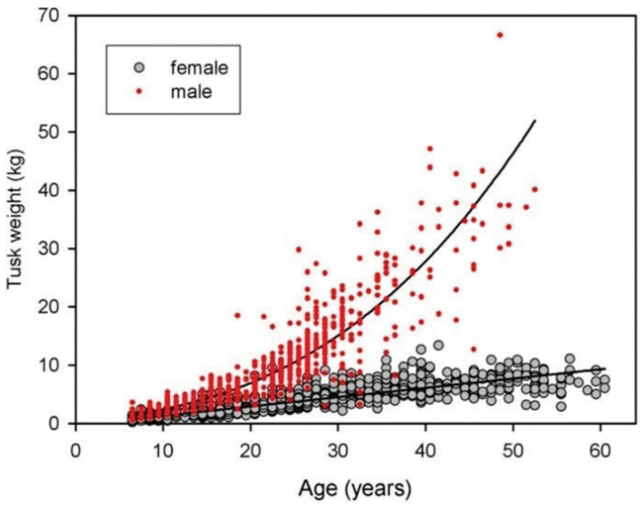

Figure 2. Relationship between tusk weight and age in five savannah elephant clans aged six years or older.
Females: tusk weight = 0.1594 × age – 0.2594; r^2 = 0.7509; p < 0.0001; n = 1,201
Males: tusk weight$^{1/3}$ = 0.0561 × age + 0.7864. r^2 = 0.8775; p < 0.0001; n = 946

lip), there was no relationship between them.

In all cases there were no significant effects of age or gender or their interaction on either the internal or external length symmetry scores (p > 0.4). For circumference, taking into account three clans, there were no significant effects of Age or Clan or of any of the interactions, but a weak effect of Gender (p = 0.050) that might imply that females are more left-biased than males. The difference, if real, is slight (mean symmetry scores of –0.68% and 0.26% for females and males, respectively).

There was no significant association between Tuskedness (left or right) and Gender (Fisher's Exact Test, p = 0.24). This was supported by recording serious transverse tusk breaks across the body of a tusk rather than minor breaks at and around the points. The two clans Murchison North and Murchison South provided the greatest volume of data, and in them transverse tusk breaks were recorded as occurring on 64 right-hand and 65 left-hand tusks, implying equal

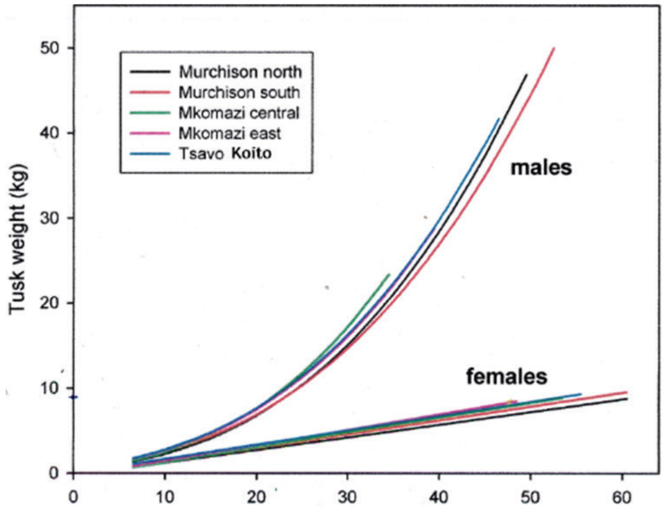

Figure 3. Modelled tusk weights with Age and Gender of savannah elephants aged six years or older from five clans. The model represents significant effects identified in the multivariate analysis (Table 3) and weight trends with Age for each Gender as demonstrated in Figure 2.

use, as shown in Table 5.

For individuals with both metrics not prone to wear (internal length, circumference), there was no relationship between the two (Fig. 5).

Discussion

The conclusion that male tusks are larger and heavier than female tusks at age and grow exponentially while female tusk growth is linear is not new. It was previously reported by Laws (1966); Laws and Parker (1968); Laws et al. (1975); Parker (1979) and Pilgram and Western (1986), all using the same data; and by Elder (1970). Whyte and Hall-Martin (2018) and Larramendi (2023) introduced lengths, circumferences, and in addition mass in describing tusk morphometrics. Here all these metrics—weight, total length, extruded and internal length, and tusk circumferences at lip—are analysed for symmetry between tusk pairs in East African savannah elephants.

From elephants viewed in the field as individuals, it may seem that shape variation infers low levels of symmetry between their two tusks. That perception is enhanced by knowledge that tusks may be broken and the belief that they are used preferentially and thus subject to differential wear. The data analysed here indicates otherwise, namely high levels of symmetry. The most obvious metric, external length, displayed a symmetry level of 78.5% between right and left. This highlights the caution necessary when using data from individuals as measures of population parameters. Fig. 6 visually illustrates tusk pair symmetry that is not readily apparent in the field in six families, bearing out the findings revealed by the metric analysis.

However, in both sexes, internally within the alveolus, symmetry is 23.6% less than what is visible externally. The fact that the pairs are less similar internally than externally seems counterintuitive, since outside the head, tusks are separated from the growth sources, and as ‘dead tissue’ can only be subject to reduction that is counterbalanced by extrusion from within the alveolus. Two possible causes may produce the greater tusk similarity outside the head. One would be differential growth between the tusks of a pair, in which the initially shorter one grows faster, catching up with its longer partner. The other, that elephants use the longer of their tusk pair preferentially, decreasing its length towards parity with the shorter. This levelling between external tusk lengths is the subject of a companion paper.

This study does not support the idea that elephants preferentially use one tusk more than the other as claimed by Whyte and Hall-Martin (2018) and others,

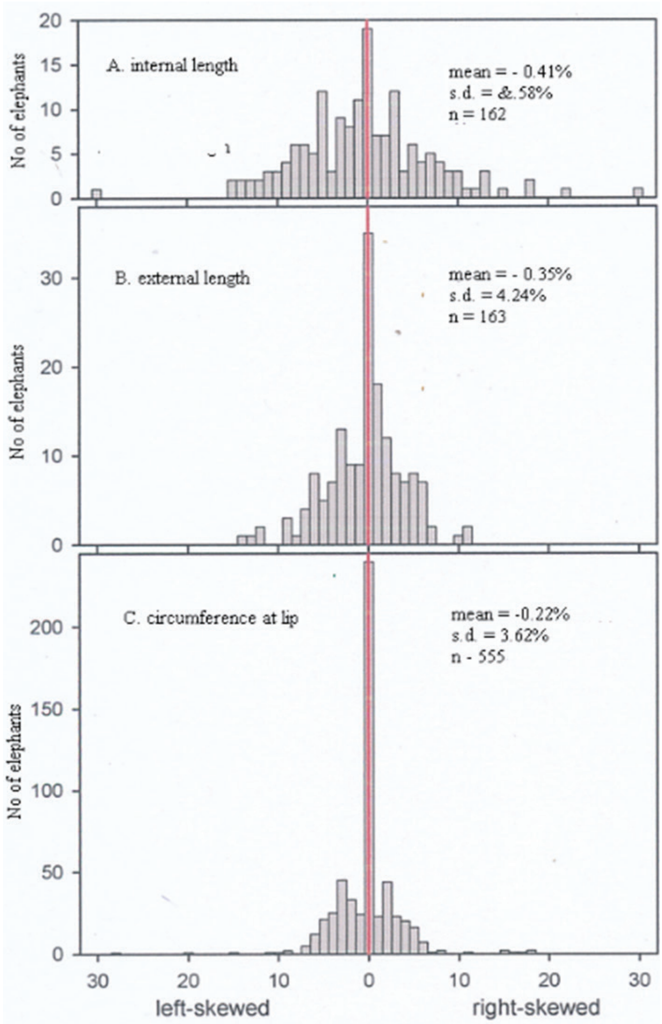

Figure 4. Percentage deviations from symmetry between pair of tusks of three tusk metrics in two-tusked savannah elephants. The red line indicates perfect symmetry. The numbers for data skewed left or right are shown as % deviation from the mean (% dev; see Materials and Methods).

Table 5. Broken tusks excluding tip loss, as occurred between right and left tusks.

Clan	Sample size	Right breaks	Left breaks
Murchison North	937	20	18
Murchison South	648	44	47
Combined	1,585	64	65

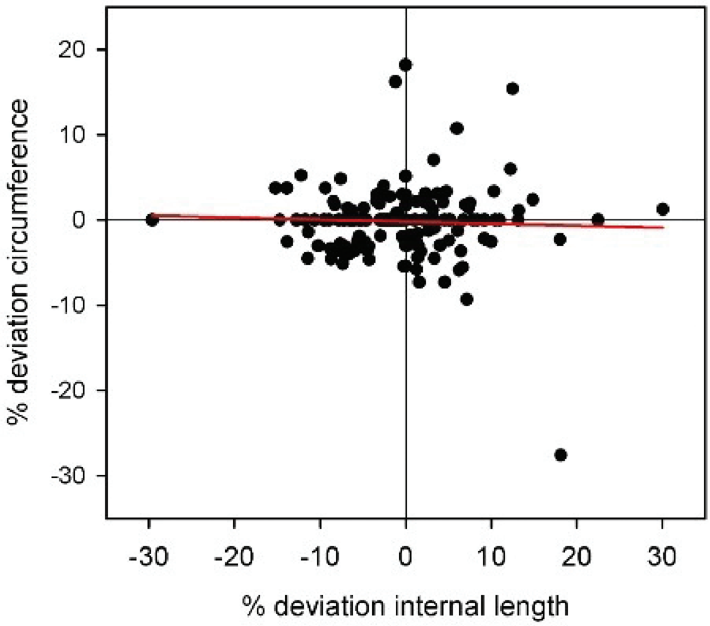

Figure 5. Relationship (r = –0.043, p = 0.59) between two measures of tusk symmetry not prone to wear (lip circumference and internal tusk length) for 161 two-tusked savannah elephants.

in the manner of human handedness. This will be examined further in the companion paper.

As an aside, given the finding by Steenkamp et al. (2007) that elephant tusk breakage in southern Africa was greater in dry seasons than when wet, it was reasonable to expect that tusk breakage in the semi-arid Nyika (rainfall <500 mm p.a.) would be greater than in humid Murchison (rainfall >1,000 mm p.a.). This finding is contradicted by the data here. In similar vein, elephants chiselling bark off *Terminalia glaucescens* (Planch. Ex Benth 1849) in Murchison North, where this tree was abundant, were stressing their tusks in a manner not occurring at the same time in Murchison South where the trees had been largely eliminated. The expectation that bark-chiselling would be reflected in different tusk lengths and breakage between the two clans was also not met. Furthermore, whatever the habitat differences between Murchison and Nyika may be, mean clan tusk weights at age (predictive of both lengths and circumferences (Figs. 1 and 3) were very close, suggesting that such environmental differences as may exist do not determine these metrics.

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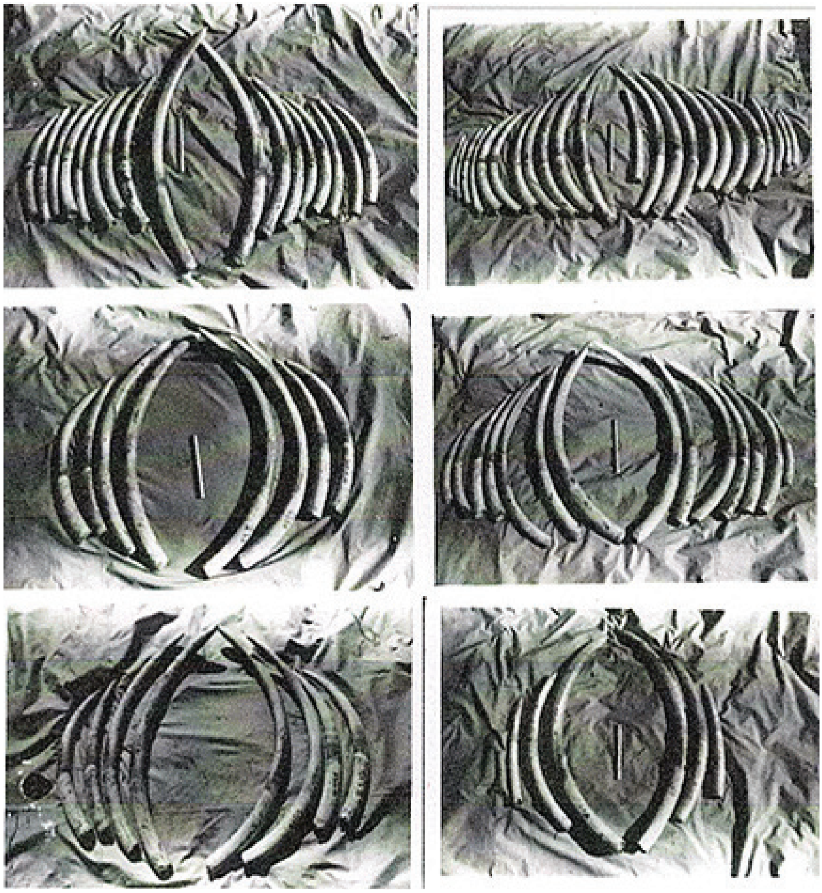

Figure 6. Pair symmetry of tusks in six family units. The oldest pair in the centre with age descending outward to youngest as the edge. Right tusks are on the left and left tusks on the right.

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