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Journal of Archaeological Science

journal homepage: <http://www.elsevier.com/locate/jas>

An experimental study of large mammal bone modification by crocodiles and its bearing on the interpretation of crocodile predation at FLK Zinj and FLK NN3

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ARTICLE INFO

Article history:

Received 10 November 2011

Received in revised form

7 January 2012

Accepted 10 January 2012

Keywords:

Taphonomy

Tooth mark

Bisected pits

Bisected scores

Microstriations

ABSTRACT

The taphonomic signature of crocodiles as agents of bone modification has been previously identified by specific tooth mark types (e.g., bisected pits) and by a conspicuous presence of these marks: more than 75% of bones modified by crocodiles bear at least one of these distinctive marks. Therefore, crocodile tooth-marking would be notably prevalent in bone assemblages resulting from crocodile predation and active scavenging. The present study contributes to refine this diagnosis by showing greater variability of these types of marks, a different degree of tooth-marking intensity, and a somewhat different distribution of tooth-marked elements according to skeletal parts from previous experiments with crocodiles. Some of these differences are due to different experimental variables and conditions and this highlights the need to understand behavioral variability in crocodile ecological settings. This variability in crocodile tooth-marking probably results from several as-yet-inadequately measured behavioral and ecological factors, such as intensity of feeding competition and differences between male and female crocodile feeding behaviors, among others. Furthermore, this study also contributes to a better definition of the microscopic criteria that can be used to distinguish crocodile-inflicted marks from other types of bone surface modifications. In light of these and previous experimental frameworks, we reevaluate the application of these analogs to modifications documented in hominin fossils from Olduvai Gorge (OH8 and OH35) and the resulting inferences about the hazard posed by crocodiles on the paleolandscape where FLK North North and FLK Zinj (Bed I) were formed. The taphonomic analysis also shows that Olduvai OH8 and OH35 were probably not preyed upon by crocodiles. It is concluded that no tangible evidence can be used to support the interpretation that OH35 was modified by crocodiles and that the overall presence of crocodiles in FLK North North and FLK Zinj was rather marginal, based on the virtual absence of crocodile-modified bones in both archaeofaunal assemblages.

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1. Introduction

Human and crocodile interactions have been variously interpreted in the past two centuries (Huxley, 1863; Dubois, 1927). The issue of who is the predator and who is the prey is still debated. Some argue that crocodiles were a serious hazard to hominins, who were frequently eaten by them (Njau and Blumenschine, *in press*), whereas others find evidence of the opposite in the archaeological record (Braun *et al.*, 2010).

Neo-taphonomic research is crucial when addressing this issue. Pioneering taphonomic studies of reptiles, and more specifically crocodiles, were carried out by Davidson and Solomon (1990) and West (1995). West (1995) suggested that in this relationship, hominins were predatory. By contrast, previous work by Davidson and Solomon (1990) supported predation of hominins by crocodiles at FLK NN, (Bed I, Olduvai Gorge). This has recently been supported and expanded by actualistic work with controlled experiments on crocodiles (Njau, 2006; Njau and Blumenschine, 2006, *in press*). These authors have provided a valuable experimentally-derived framework for understanding how bones are modified by crocodiles in captive settings. They have documented the frequencies of damage per skeletal part and the macro- and microscopic morphology of tooth marks, and have diagnosed new tooth mark types specifically made by these reptiles. Njau (2006) expanded

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this work to include a study of crocodile-damaged bone in modern habitats of the Serengeti. He demonstrated that in places where crocodiles are most active as predators, bones with crocodile damage could be identified in as much as 75% of the bone assemblage scattered around those places.

Experiments with mammalian carnivores indicate that their bone modification patterns are subject to variability according to a set of ecological and ethological variables (Haynes, 1983; Pobiner, 2007; Domínguez-Rodrigo and Pickering, 2010; Yravedra et al., 2011). Therefore, analogical interpretation is only epistemically supported when this variability is properly assessed. In the case of modern crocodile bone damage, only one systematic study exists (Njau, 2006; Njau and Blumenschine, 2006). The present study intends to broaden the known variability of crocodile bone-modifying behavior (Njau, 2006) by enlarging the sample of actualistic studies and providing different experimental conditions. The results show some important differences with the previous referential study. The behavioral variability documented is of utmost relevance, since a very common pattern of feeding behavior of crocodiles is not collective feeding through competition of dozens of individuals, but either solitary feeding or collective feeding with competition involving only a few individuals (Welman and Worthington, 1943; Guggisberg, 1972; Pooley, 1989; Coffron, 1993; Smet, 1999; Dinets, 2011). Even feeding cooperative behavior seems to be frequent in crocodiles and alligators (King, 1972; Schaller and Crawshaw, 1982). These results urge caution in the interpretation of hominin–crocodile interaction at the Olduvai Bed I sites when using the previous modern analog (Njau, 2006).

2. Method

Eight female crocodiles were used in the present experiment; one small (1.3 m in length from nose to end of tail), two medium-sized (1.8 m) and five large (2.3 m–3.10 m). They were fed in an enclosure in a zoo (Faunia, Madrid, Spain), where they are exposed to the public (Fig. 1). Crocodiles were fed once a week over a period of four months with a total of 19 partial carcasses. Carcass portions, comprising mostly articulated limbs of suids (pig and boar) and bovids (sheep and cow) were prepared by butchers, which resulted in the removal of most feet bones. Only in two instances in which suid limbs were used were feet attached to them. More specifically, the carcasses included four suid forelimbs and five suid hindlimbs, six sheep forelimbs and three cow hindlimbs. In all cases, sheep limbs were articulated to their respective scapulae. For the suid carcass sample, only in one case was the scapula attached to the limb. Four pelvises were articulated to some of the suid hindlimbs and two pelvises were articulated to two cow hindlimbs. Most feeding episodes were carried out by single individuals without undergoing competition from other crocodiles. Carcasses were retrieved after 15 h of exposure to crocodiles, although most of the feeding took place in the first hour. Feeding was monitored by us for the first 1.5 h, in order to attribute carcass modification to specific individuals. Monitoring by us stopped after carcass remains were abandoned by crocodiles. Zookeepers were afterwards monitoring crocodiles at regular intervals to document if carcass remains were further accessed by crocodiles. Every feeding episode was photographed and videotaped. A total of 198 elements were retrieved for analysis (Table 1). The end and shaft of each unfused bone from juvenile carcasses was counted as one element. Bones were frequently retrieved with flesh scraps adhering to them. These were mostly removed by an enzyme (Neutrase .8 L) in the laboratory. Only in a few cases, bones were disarticulated with the aid of surgical scalpels, in a controlled manner so as not to inflict marks on bone surfaces. Despite special care put into this operation, five marks were created, but they were easily identified because of the



Fig. 1. Crocodile from FAUNIA eating a juvenile cow limb.

controlled cleaning protocol and also because the morphology of these marks (extremely thin grooves) cannot be mistaken with any mark created by carnivore teeth. After the removal of the scraps, bones were cleaned with enzymes and then were submerged in a solution of water and hydrogen peroxide (H_2O_2) for one hour prior to drying.

Bone surfaces were analyzed using a 60W light and 15× hand lenses. Each mark was then microscopically analyzed using a binocular microscope (Motic) with magnifications of 20×–40× and an incorporated digital camera (MC V3), which transfers high-resolution images to a computer. Marks were also observed under a handheld digital microscope (Dinolite AM413FVT) with magnifications of 10×–200× and analyzed using the microscope's (Dino Capture 2.0) software.

For the study of mark frequency and morphology, tooth marks were analyzed using the following variables:

1. Mark type. Marks were identified using similar criteria to Njau and Blumenschine (2006). They were initially divided into four types: pits (with and without bisections), scores, punctures and hooks (Fig. 2). Bisected marks were particularly abundant (Fig. 3). Pits and scores showed two types of morphologies: some displayed similar characteristics to mammalian carnivore tooth pits and scores (U-sections with polished or crushed inner surfaces) (Fig. 4), while others showed a V-shaped section with a linear depression caused by the carinae of individual teeth (Fig. 5). Although Njau and Blumenschine (2006) only describe bisected pits, it would be accurate to

Table 1

Number of tooth-marked remains retrieved after carcass consumption by crocodiles. Numerator is for the number of tooth-marked specimens. Denominator is for the total number of specimens of each skeletal part. Percentages are in parenthesis.

	Ovine	Suid	Bovine
humerus	3/6(50)	3/4(75)	–
radius	0/6(0)	0/4(0)	–
ulna	1/6(16.6)	3/4(75)	–
femur	–	4/5(80)	2/3(66.6)
tibia	–	3/5(60)	1/4(25)
metapodials	–	1/11(9)	–
scapula	3/6(50)	1/1(100)	–
pelvis	–	1/4(25)	1/2(50)
vertebra	0/16(0)	–	1/4(25)
compact ^a	0/30(0)	1/67(1.4)	1/10(10)
total	7/70(10)	16/105(15.2)	5/23(21.7)

^a Carpals, tarsals, phalanges.



Fig. 2. One of the more heavily tooth-marked specimens in the experimental sample (juvenile suid femur) with several bisected marks.

also mention the presence of bisected scores (as opposed to those scores with same internal morphology as tooth scores made by mammalian carnivores, showing only crushing or polishing) (Figs. 4 and 5). These bisected scores can have the same type of linear depression dividing the score into two sides (Fig. 5A) and can occasionally be accompanied by microstriations (see below) (Fig. 5B). In tooth pits and punctures occurring on cancellous bone, frequently a single or a small double thin score (bisection) could be detected longitudinally on the rim of the mark as a by-product of the impact of the carinae as well as the tooth cusp on bone surface. The presence of the bisection in these marks has been argued to be distinctive of crocodiles (Njau and Blumenschine, 2006) (Fig. 3). Given the diversity of all these marks, they can be collectively referred to as carinated. In the present work, the term “carinated mark”

will be applied to both bisected pits and scores as well as punctures with bisections emanating from them.

2. Presence/absence of internal microstriations and their morphology (continuous, discontinuous). This was carried out with the aid of 15× hand lenses and confirmed under the microscope (at <50×).
3. Number of microstriations inside the groove. Although microstriations could be easily identified with 15× lenses, marks were observed under a digital microscope at 20×–50× and microstriations were counted under this magnification.
4. Trajectory of the microstriations (straight or curved) when present.
5. Element type and element portion where marks were documented.

Data were first used in raw format when comparing mark frequencies anatomically. Then, when comparing marks made on dense versus cancellous bone, they were modified using bootstrapping procedures. Randomized bootstrap methods were preferred over permutation approaches (e.g., Monte Carlo) because it was assumed, after examining the raw data, that differences of tooth mark types on cancellous and dense bone could be representative of different populations. Therefore, a non-parametric bootstrapping approach using an alternative model was carried out. Data were randomly resampled 1000 times because given the characteristics of the data, that number of replicates maximized accuracy in prediction of mean differences, standard error of mean difference and power (Pattengale et al., 2010). Mean values were established within adjusted bootstrap intervals using a bias-corrected-and-accelerated (BC_a) method (Efron, 1987). BC_a tends to produce good interval limits, more adjusted than typical studentized interval estimates (Zieffler et al., 2011). For the significance of the differences, both bootstrapped T tests were carried out and Cohen's δ values were obtained. Cohen's δ provides a value from 0 to 1 in which the mean difference is considered of small effect ($\delta = \sim .2$), medium effect ($\delta = \sim .5$ – 7), and large effect ($\delta = \sim .8$). All computations were made with the bootstrap functions of the “boot” R library.

3. Results

3.1. Anatomical distribution of tooth marks

The assemblage collected contained 28 tooth-marked bones (14.1%) (Tables 1 and 2). All bones but two were complete. The total number of tooth marks documented was 133, which averages 4.7 marks per each tooth-marked specimen; the minimum number of marks per tooth-marked specimen is 1 and the maximum is 20. This is less than one tenth of the maximum number of marks for each tooth-marked specimen reported by Njau and Blumenschine in their experimental assemblage (which shows an average of 50 marks per tooth-marked specimen). Our assemblage, despite comprising a few more elements than theirs, is substantially less tooth-marked, according to both NISP and number of marks in each tooth-marked specimen.

Pelvis and scapulae are the most tooth-marked elements in this experiment (Table 2). Tooth marks on the pelvis occurs mostly on the ilium. Marks on the scapula were documented on the proximal blade, along the blade and even on the neck. After the girdle, long bones were the second most tooth-marked elements, although substantially less than reported by Njau and Blumenschine (2006). Most marks on long bones were observed on shafts, with fewer marks occurring on ends. The mode is one mark per specimen and the median is two marks per specimen. Upper limb bones (humerus and femur) are more highly tooth-marked than

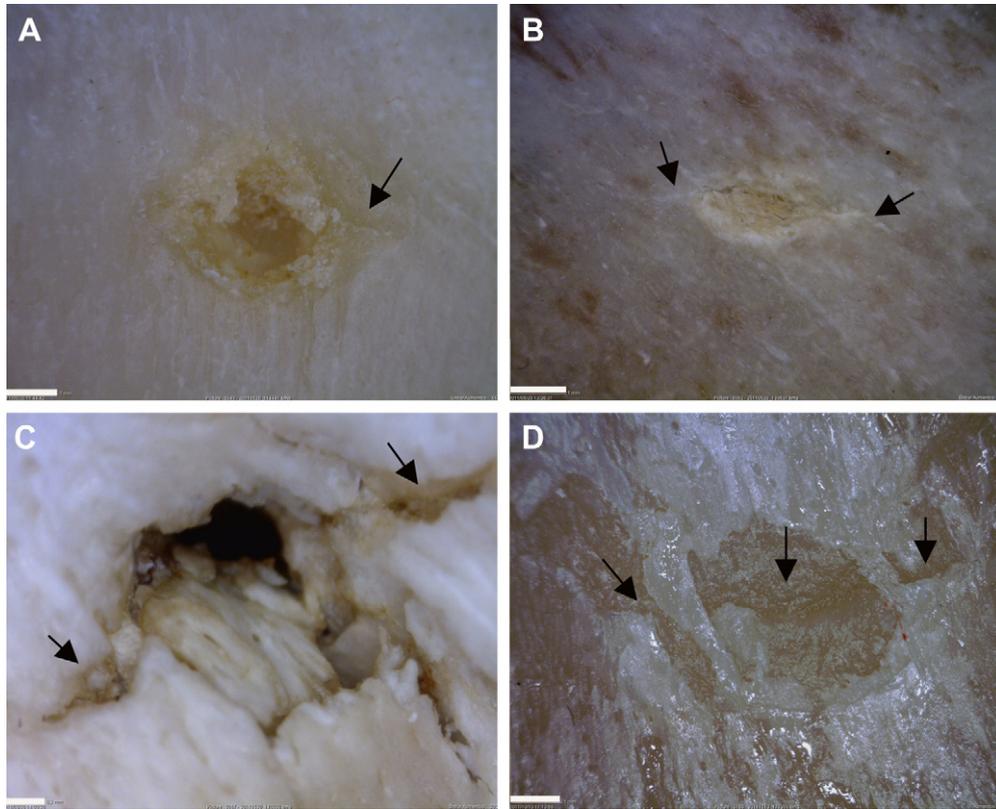


Fig. 3. Tooth pits (A, B, D) and puncture (C) with bisections made by crocodiles. In some cases, the bisection occurs on one side of the pit (A) and in other cases, on opposite sides (B, C, D). Scale for A, B, D = 1 mm. Scale for C = .2 mm.

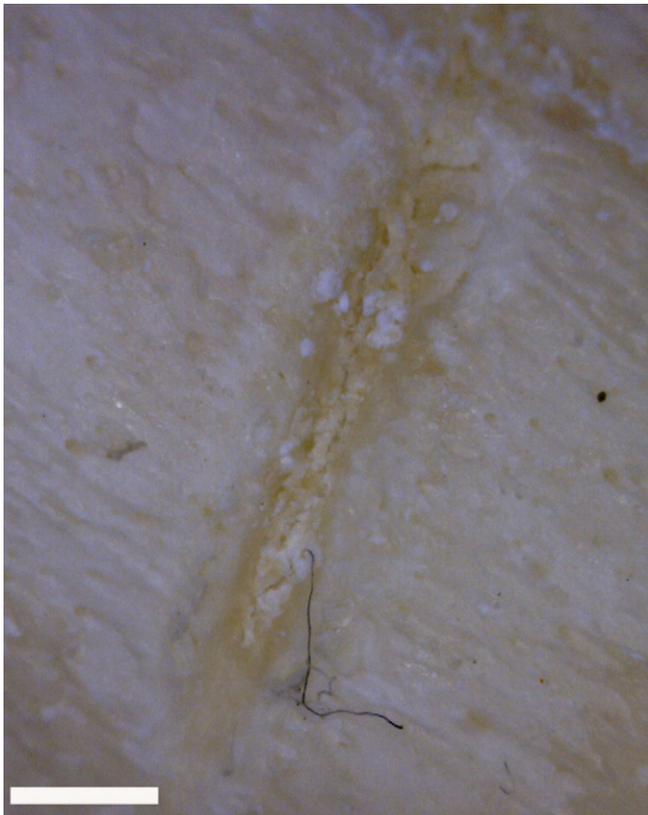


Fig. 4. Tooth score lacking microstriations, showing internal crushing and shoulder flaking made by crocodiles. Scale = 1 mm.

intermediate limb bones (radius-ulna and tibia). The radius is unmarked in our collection. In contrast, the olecranon of the ulna is more highly tooth-marked. Axial bones, namely vertebrae, were more tooth-marked than reported by Njau and Blumenschine (2006). In contrast, compact bones were substantially less tooth-marked than reported by these authors. The few examples documented in our assemblage occurred mainly on calcanea.

3.2. Tooth mark types and their frequencies

The 133 tooth marks documented include pits ($n = 56$), scores ($n = 65$) and punctures ($n = 11$) (Tables 3 and 4). Out of these, 57 marks bear a bisection: 33 bisected pits (24.8% of total tooth marks) and 24 bisected scores (18% of total tooth marks). Given that the presence of the bisection, imprinted on bone surface by the carinae of teeth, is the most diagnostic feature of crocodile bone damage (Njau and Blumenschine, 2006), 43% of the tooth marks in the experimental assemblage can be confidently identified as caused by crocodiles. This diagnosis contrasts with the other experimental analog available, in which it was claimed that “the majority of crocodile tooth marks (ca. 90%) cannot be distinguished from mammalian carnivore marks” (Njau, 2006: 114). The confidence in the identification of agent is even more solid when looking at the number of tooth-marked bones with the presence of at least one bisected pit or score. A total of 23 bones (82.1% of the tooth-marked specimen sample) bear at least one carinated mark. This overwhelming crocodile signal suggests that a crocodile-modified assemblage should be highly conspicuous and relatively easy to identify when analyzing bone surface modifications.

Most of these carinated marks occur on dense cortical bones (namely, long bone shafts) ($n = 51$; 89%) in contrast with cancellous and trabecular bone ($n = 6$; 11%) (Tables 3 and 4). Some marks bearing

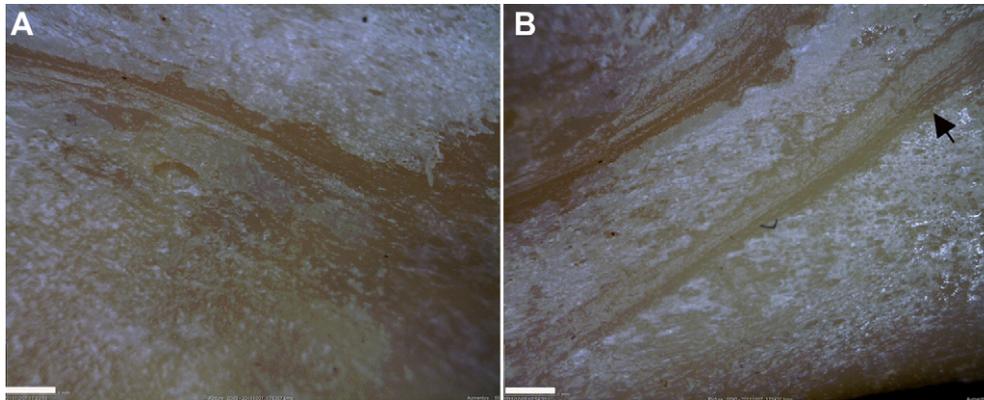


Fig. 5. Tooth scores made by crocodiles, showing three discontinuous microstriations (A) and more continuous microstriations (B). In both images it can be seen that scores are either curvy or, if they are generally straight, they have sections with a curved trajectory (arrow). Scale = 1 mm.

bisections also show internal microstriations. A total of 18 marks (13.5% of total mark sample; 31.5% of carinated marks) show microstriations. They occur more frequently on bisected scores ($n = 13$) than on bisected pits ($n = 5$). All these marks are located on dense cortical surfaces of long bone shafts. In addition, 30 marks lacking bisection bear microstriations. All of them also occur on long bone shafts. These microstriated marks are also more frequent on scores ($n = 22$) than on pits ($n = 8$). This shows that up to 36% of all tooth marks caused by crocodiles have internal microstriations, which is a trace that has the potential to be mistaken with those caused by either stone tool use or trampling (Domínguez-Rodrigo et al., 2009).

Some criteria can be used to aid in differentiating these marks from those inflicted with stone tools. A microscopic analysis of these microstriations shows that most of them occur in small numbers (mean = 3.6; median = 3 microstriations per mark). In contrast, microstriations are commonly more abundant in trampling and cut marks. It is very common that some microstriations in tooth marks made by crocodiles do not run the entire length of the score, but rather are interrupted. Frequently, they are sinuous trajectories, instead of straight ones as is typical of stone tool microstriations (Fig. 5). An additional diagnostic trait is that the bulk of scores with microstriations (76.6%) show curved or sinuous (but not straight) trajectories (Fig. 5). This feature has also been documented in two striae fields caused by crocodiles, which (in contrast with isolated striae fields made by hammerstone percussion) show curved trajectories instead of straight ones. However, two marks in our collection show a closer resemblance to marks traditionally interpreted as trampling marks (Fig. 6) (Domínguez-Rodrigo et al., 2009).

The differences in the distribution of marks according to structural bone type (dense cortical shafts versus cancellous/trabecular ends) have also been shown to be statistically significant. A bootstrapped group comparison of carinated marks on cancellous/trabecular and on dense cortical bone showed that there is a mean difference of 34.3% (adjusted bootstrap interval $\pm 2.1\%$) more carinated marks on the latter type of bone. This difference is of

medium effect (Cohen's $\delta = .56$). This difference was also supported by a bootstrapped T test ($t = 71.59$; $p = .000$). The same type of bootstrapped analysis for mark type (pits versus scores) showed that there is a mean difference of 28.3% (adjusted bootstrap interval $\pm 1.8\%$) more scores on dense bone compared to cancellous/trabecular bone. This difference is of great effect (Cohen's $\delta = .82$). This difference was also supported by a bootstrapped T test ($t = 59.55$; $p < .000$). Accordingly, this suggests that when analyzing assemblages with different proportions of marks distributed on cancellous/trabecular bone versus dense cortical bone, interpreting estimates of mark frequencies and distribution based on general analogical frameworks that do not differentiate structural bone types can be misleading. It also indicates that since microstriations (which occur more frequently on scores) and carinated marks (bisected pits and scores) are the landmark signatures of crocodile bone modification and they occur more frequently on dense cortical bone, there is a great potential to identify crocodile-modified assemblages given the better preservation of long bone shafts in paleontological and archaeological assemblages.

4. Discussion

This work intends to build upon the solid experimental work on crocodile modification of large mammal bones carried out by Njau and Blumenschine (2006). In their work, these authors stressed that crocodiles could be differentiated from mammal carnivores by the following factors:

1. Crocodile-created assemblages are composed of primarily complete elements, with minimal fragmentation.
2. These elements exhibit absence of gross gnawing.
3. Crocodile-made bone assemblages lack disarticulation of complete skeletal units, with the potential of abandoning a large portion of articulated specimens.
4. A proportion of the marks (bisected pits and punctures and hook scores) have a distinctive morphology not documented in tooth marks produced by mammalian carnivores.
5. Tooth-marked specimens usually bear dozens of marks.

Table 2

Distribution of the number of specimens for four postcranial anatomical regions and the frequency of tooth-marked specimens in raw numbers and percentages.

	Njau and Blumenschine (2006)			This study		
	NISP	TM-NISP	%	NISP	TM-NISP	%
axial	66	2	3	20	2	10
girdle	14	6	42.9	13	6	46.1
long bone	32	22	68.8	58	20	34.4
compact bone	74	10	13.5	107	2	1.8
total	191	40	20.9	198	28	14.1

Table 3

Distribution of tooth mark types (pits, scores and punctures) according to bone type (cancellous/trabecular and dense cortical).

	Cancellous bone	Dense bone
pits	10	45
scores	9	56
punctures	11	2
total	30	103

Table 4

Frequencies of carinated marks without microstriations, with microstriations and of marks lacking bisection but showing microstriations, according to tooth mark type (pits, score) and bone type (cancellous/trabecular versus dense cortical bone).

	<i>n</i>	Pits	Scores	Cancellous bone	Dense bone
carinated marks	57	33	24	6	51
carinated marks with microstriations	18	5	13	0	18
marks with microstriations	30	8	22	0	30

Our study confirms point 1. With the exception of a proximal tibia, a phalanx and a metatarsal of a suid, the remainder of bones were abandoned unbroken by crocodiles. NISP ($n = 198$) values are very close to MNE ($n = 196$) values. In our experimental sample, bones also lack gross gnawing, which confirms point 2. A few tooth pits were observed on some long bone ends, but gnawing and furrowing were not documented. Point 3 is also supported by our study. Crocodiles did not disarticulate most of the skeletal units that were fed to them. Only in one case, did crocodiles separate the femur from the tibia. Njau and Blumenschine (2006) also reported no disarticulation of humerus-radius and only one case of disarticulation of the femur-tibia joint.

Regarding point 4, not a single hook mark was observed in our sample, despite having documented a few instances of “death rolls” (Njau, 2006). This is not exceptional, since in their collection, Njau and Blumenschine only report 11 hook marks (out of more than 2000 tooth marks). Given the smaller number of tooth marks in our sample, the absence of hook marks is not surprising. The presence of carinated marks is indicative of crocodile bone modification only when they occur in certain frequencies. However, we believe that the categorical statement of bisected marks being caused *only* by crocodiles is unsupported. Galán et al. (2009: Fig. 6) reported bisected pits caused by modified hammerstones which were indistinguishable from those made by crocodiles. Furthermore, occasional bisected pits can also be observed on some bones modified by mammal carnivores. We have documented them on bones modified by lions and wolves (see Fig. 7). Some lion canines also have carinae (Fig. 8A), which can cause V-shaped marks with a bisection (Fig. 8B). Therefore, taphonomists have to be extremely cautious in attributing isolated bisected marks to specific agents. According to our experimentation with crocodiles, only when bisected marks occur in certain frequencies and in combination

with marks bearing microstriations can a safer attribution to crocodiles be made. Rather than seeing this as a drawback, it should be contemplated as an advantage, since the proportion of bisected marks in crocodile-modified assemblages can be as high as >40% of the whole tooth-marked assemblage; even higher when considering the number of specimens bearing at least one bisected mark (>80% in both Njau and Blumenschine’s study and ours). This makes crocodile bone modification potentially highly conspicuous on the landscape (Njau, 2006).

The most marked difference between our study and Njau and Blumenschine’s can be observed in the proportion of tooth-marked elements and in the intensity of tooth marking. Our sample shows overall a smaller frequency of tooth-marked specimens and their distribution is slightly different from that reported by Njau and Blumenschine (2006). This is especially relevant when comparing tooth marks on compact and axial bone. Long bones are tooth-marked at a frequency that is almost half of that reported by the other authors. This contrast is also documented in the frequencies of tooth marks per tooth-marked specimen. Njau and Blumenschine’s sample shows an average of tooth marks per tooth-marked specimen that is >10 times those documented in our study. This can be explained in part by the different number of crocodiles feeding on carcass parts in both experiments. In our experiment, we never documented the eight crocodiles feeding on the same carcass. Only one of the larger crocodiles (usually the one higher up in the hierarchy) would feed on a carcass at a time. Smaller crocodiles would also feed independently when the larger ones were distracted feeding on a different carcass or skeletal unit. In contrast, Njau (2006) reports that several of his experiments involved 20 (in some cases even up to 30) medium-sized crocodiles subjected to competition when consuming carcasses. This extreme competitive situation does not model what commonly occurs in crocodile carcass feeding in modern savannas (personal observations), but rather on locations exhibiting exceptional feeding bonanzas, such as river-crossing areas for migratory animals, where crocodiles congregate and can compete for carcasses (e.g., the Maasai Mara river crossing during the wildebeest and zebra migration).

We argue that the situations in the captive settings where crocodile experimentations have been carried out, which enabled a controlled collection of data, are highly influential on some of the results reported by Njau and Blumenschine (2006) and by ourselves. We question that either of them faithfully reproduce most of (or even the most common) crocodile behavior in natural savanna settings. For this reason, we present results on tooth mark frequencies and anatomical locations only to show variability within the spectrum of degrees of carcass modification reported in captivity and potentially documented in the wild. Neither Njau and Blumenschine’s study nor ours should be uncritically used to identify crocodile bone damage in natural settings when using frequency of tooth marks and intensity (number of tooth marks per tooth-marked specimen) of tooth marking.

In contrast, both studies can be analogically useful to document distribution of mark types, since these are mechanically produced and depend on the effector’s morphology instead of the conditions of the captive enclosure where experimentation was carried out. Our study further confirms the morphological diagnosis of crocodile tooth marks initially described by Njau and Blumenschine (2006) and expands it by including new microscopic criteria. Njau and Blumenschine (2006) did not elaborate on microscopic characteristics (>10 \times) beyond commenting that some marks had internal striae. In the present study, we have quantified such marks, which constitute a non-negligible portion of the tooth mark sample. We have shown that they usually display few internal microstriations, and interrupted microstriations with non-straight trajectories are not uncommon. However, we have also reported



Fig. 6. Crocodile tooth score showing straight trajectory and internal microstriations. Notice the uneven separation in between microstriations and the discontinuous (arrow) and curvy or sinuous nature of some of them. Scale = .2 mm.

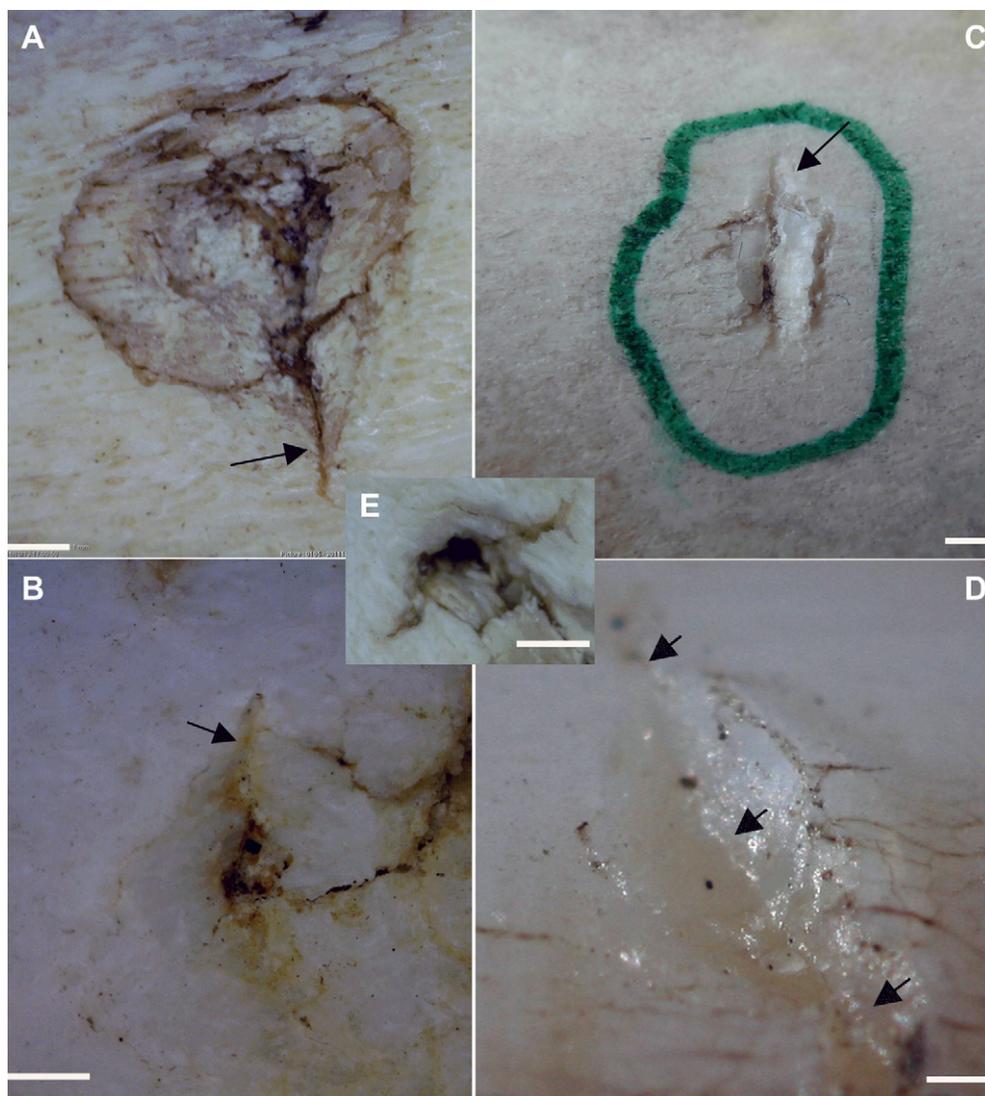


Fig. 7. Bisectioned pits documented on bones modified by wolves (A), lions (B), modified hammerstones (C, D) (Galán et al., 2009) and crocodiles (E). Arrows show the bisection made by dental carinae. Notice the resemblance between the pit with the bisection crossing the internal surface of D and a similar mark made by crocodiles. Scale = 1 mm.

a couple of cases in which it was more difficult to distinguish the marks from those created by trampling.

How does this new study contribute to the interpretation of hominin–crocodile interaction in the past? Recently, Njau and Blumenschine (in press) have argued that two separate hominins at FLK NN3 and FLK Zinj (Bed I, Olduvai Gorge) were preyed on by crocodiles, showing that the places were high-risk and not apt for behaviors typical of living floors (prolonged stay and food-sharing behaviors). The only empirical evidence for this interpretation is the presence of crocodile marks on the OH8 foot bones and on the OH35 tibia. We argue that empirical evidence supporting the following arguments is necessary to increase the heuristics of this interpretation:

1. A connection between the taxa to which these hominin fossils belong and the taxon responsible for the FLK Zinj and FLK NN3 archaeological sites is necessary. At the time these sites were created (ca 1.85 Ma), there were a minimum of four hominin taxa in East Africa (*Homo habilis*, *Homo rudolfensis*, *Homo erectus* and *Paranthropus boisei*). There is no evidence that the species to which OH8 and OH35 belonged were the agents responsible for these sites. It is commonly argued that one species of *Homo*

could be responsible for these sites. Some researchers even argue that OH8 may belong to a *Paranthropus* (Gebo and Schwartz, 2006). A predation hazard for one hominin type does not necessarily imply the same hazard for a different hominin species, so determining what OH8 and OH35 represent taxonomically and whether they were responsible for the archaeological records of FLK Zinj and FLK NN3 is crucial before asserting that the locations were dangerous for stone-tool-using hominins. Current evidence does not contradict that OH8 might have died naturally on the landscape (irrespective of whether or not it participated in the formation of the archaeological assemblage at FLK NN3) and a crocodile could have scavenged its remains. This could receive some support from a similar interpretation made by Njau and Blumenschine (in press) on OH35. The theoretical interaction of a leopard and a crocodile on the tibia and fibula suggests to Njau and Blumenschine (in press) that OH35 was probably preyed upon by a felid and then scavenged by a crocodile, since no example is known of a leopard scavenging from a crocodile. In this scenario crocodiles could not have been a major hazard agent to hominins.

2. If the setting where these archaeological sites formed were hazardous because of crocodile presence, a strong taphonomic

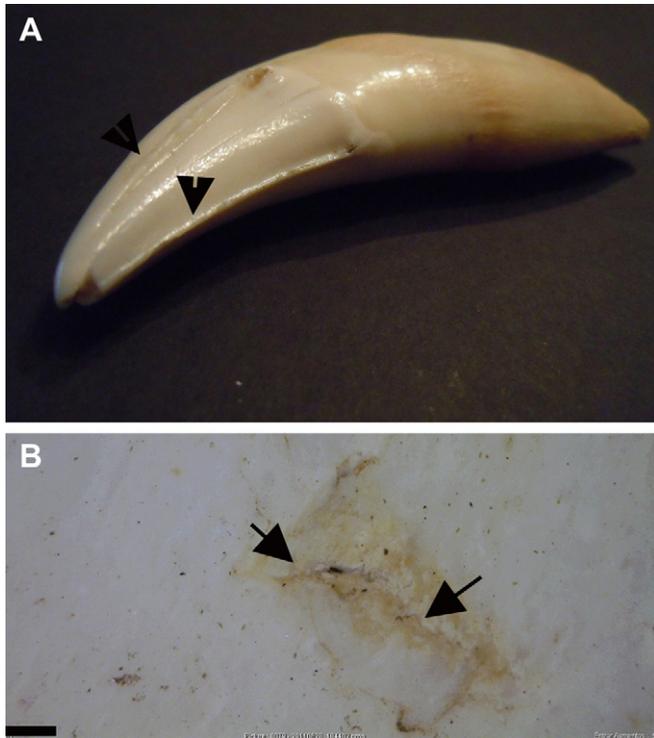


Fig. 8. A, canine of a lion showing dental carinae (arrows). B, V-shaped score made by a lion with presence of bissection, probably caused by a dental carina (arrows). Scale = 1 mm. The observation of more than one carina on some mammal carnivores invalidates Njau and Blumenschine's (2006: 149) assertion that "a lack of bicarinated teeth in any mammalian carnivore indicates that they cannot produce bisected pits".

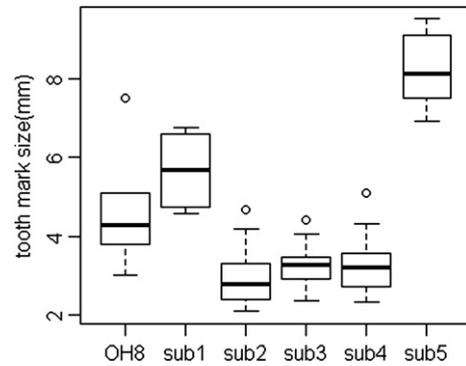


Fig. 9. Boxplot showing the sample distribution of tooth mark length documented in five subadult crocodiles (sub) and OH8. Sub 1 is 150 m long; sub 3 is 110 cm long; sub 4 is 104 cm long; sub 5 is 170 cm long. Sub 2 is incomplete but by the measurements of the head it is smaller than 1 m when compared to the other individuals.

to crocodiles is not well supported. The main argument used by our colleagues to interpret modifications on the distal end of OH35 as crocodile-made is the presence of one half bisected pit. In our analysis, we have not clearly identified any bisected mark on the specimen. Even if our identification were not accurate, the presence of a single bisected mark is not a definitive proof of crocodile intervention (see above). The sporadic presence of bisected marks made by mammalian carnivores means that we cannot rule out their involvement in the modification of OH35. Njau and Blumenschine (in press) argued that OH35 proximal end shows typical damage inflicted by leopards. Leopards usually deflesh their tree-stored carcasses before they fall to the ground (Cavallo, 1998). A defleshed bone would have been of no interest to any crocodile. The damage reported on the distal end of OH35 is similar to that inflicted by some mammalian carnivores which do not destroy dense epiphyses (e.g., foxes on ovicaprid remains) (Yravedra, 2006: 240). Similarly-sized carnivores, such as jackals, could have equally have been responsible for the type of damage documented on the distal end of the OH35 tibia. Therefore, if damage on OH35 cannot be definitely attributed to crocodiles, given that FLK NN3 and FLK Zinj were formed in different stratigraphic moments (Leakey, 1971), there is no empirical basis to the support the argument that during the formation of FLK Zinj, the place was a hazardous spot. It has been taphonomically shown that FLK NN3 was not a living floor but a natural palimpsest (Domínguez-Rodrigo et al., 2007). However, FLK Zinj is an anthropogenic assemblage that shows that hominins repeatedly butchered carcasses on the spot, more than 200 m away from the only place where a spring has been identified and where crocodiles could have potentially lived (FLK NN1) (Domínguez-Rodrigo et al., 2007, 2010). However, the surrounding landscape lacks crocodile-modified bones, indicating that if crocodiles were present, their impact on local mammals was rather marginal. This suggests that the place was not hazardous at the time FLK Zinj was being formed.

- Njau and Blumenschine (in press, Fig. 4) also attribute the modification of OH35 to crocodiles based on corresponding tooth marks on the distal articular surface of the tibia and the throclea of the talus. After having examined the original specimens, we can say that the corresponding mark on the talus shows a deep elongated pit, which can only have been produced by the apex of the effector perpendicular to the articular surface; that is, in the same direction as the axis of the tibia in the reconstructed image. In contrast, the "corresponding" mark on the articular edge of the tibia can only have been produced by an effector acting parallel or obliquely to the

signature of crocodile presence and activities would be expected on the bones accumulated at the sites and their surrounding landscape. The present study shows that bisected marks could represent >40% of marks inflicted by crocodiles. In a crocodile-infested environment, one would expect a high number of carcass remains accumulated and consumed by crocodiles, with more than 80% of their tooth-marked bones bearing at least one bisected mark. This is supported by actualistic studies of carcasses accumulated at ponds and riverine settings where crocodiles may have actively preyed them and modified them, with as many as 75% of bones showing carinated marks (Njau, 2006). In contrast, Njau (2006) argued that only 2 bones from FLK Zinj (1.1%) and 2 (4.6%) bones from FLK NN3 bore bisected marks. This is strongly supportive of a rather marginal presence of crocodiles in the paleolandscape and, thus, a low hazard risk scenario. The specimen numbers of the bones with bisected marks as identified by Njau (2006) were not reported, and cannot be contrasted by other researchers, but in another taphonomic study of these assemblages, no clear bisected mark attributed to crocodiles was identified (Domínguez-Rodrigo et al., 2007). In addition, in a recent landscape study of the FLK 22 paleolandscape, randomly testing more of 3000 m² of such a paleo-environment, not a single bone was retrieved showing any trace of crocodile-inflicted modifications (Domínguez-Rodrigo et al., 2010). This argues against the location being hazardous because of crocodile presence.

- We concur with Njau and Blumenschine (in press) that OH8 bears clear traces of modifications inflicted by a small reptile (probably a crocodile). The abundance of bisected pits on the talus is the best argument support to this interpretation (Fig. 9). However, we argue that attribution of the OH35 modifications

horizontal plane of the articular surface of the talus (See animation in [Supplementary online information](#)). This suggests that although there is apparent size correspondence between both marks, there is no functional correspondence. It also would explain why tooth marks on the distal tibia of OH35 are bigger than on the OH8 talus and, in contrast to these, they are round-shaped and lack bisections. These marks on the distal tibia are effectively indistinguishable from those inflicted by a small mammal carnivore. Furthermore, the remaining marks on the posterior proximal articular surface of the talus show that the effectors must have been oriented with their axes perpendicular to the surface, which implies that in the moment the tooth marks were imprinted on this surface, the talus must have been already disarticulated from the tibia. This could support the alternative interpretation that when the crocodile had access to OH8, the foot could have been already disarticulated from the leg, given that crocodiles rarely dismember limb skeletal units, as discussed above.

5. Tooth pit size of the marks documented on the OH8 talus suggest that a small reptile (crocodile) modified this element. Tooth mark casts taken from crocodiles of different ages and sizes, stored at the Museum of Comparative Anatomy of the Complutense University, support this interpretation (work in progress). Casts were made by making teeth penetrate the resin sufficiently for the carinae to create a bisected mark. This was done with several teeth from different sized individuals. Marks of the same morphology and size as documented on the OH8 talus were only obtained on crocodiles smaller than 1.5 m (Fig. 9). It could be argued to what extent such a small crocodile could constitute a predation hazard, but this shows that no hominin predation by a large or medium-sized crocodile is documented at FLK NN3. The only taphonomically-supported interpretation that can be made is that OH8 was modified by a small reptile, probably representing a small subadult crocodile, although whether this happened pre- or post-mortem is not known. Without knowing this, hazard risks at the site, based exclusively on crocodile bone damage, cannot be confidently evaluated.

5. Conclusions

Huxley (1863: 39) provided the first reference to the prey-predator relationship between primates and crocodiles: “*The only animal the Orang measures his strength with is the crocodile, who occasionally seizes him on his visits to the water side. But they say that the Orang is more than a match for his enemy, and beats him to death, or rips up his throat by pulling the jaws asunder!*”. Huxley’s (1863) description, irrespective of its veracity, stresses that apes have substantially more strength in their arms than modern humans. It is known that the upper limbs of Plio-Pleistocene hominins were more similarly built to them than to us in terms of strength. Therefore, they may have posed a bigger threat to crocodiles than inferred if considering only hominins’ overall smaller body size than modern humans. Fortunately, the available taphonomic studies allow identifying the potential traces of hominin–crocodile interactions.

The present experimental study supports previous assessments of the degree of bone damage inflicted by crocodiles while consuming carcasses. More than 80% of elements bear at least one diagnostic, easily identifiable crocodile-made mark. This is further supported by actualistic studies of bone damage in riverine settings where crocodiles feed, where a minimum of 75% of tooth-marked bones also bear specific crocodile-inflicted traces (Njau, 2006). This makes crocodile carcass-consumption activities potentially conspicuous on the landscape. Environments with an abundance of

crocodiles should be reflected in a high presence of crocodile-modified bones. In contrast, these are marginally represented in some Olduvai Bed I sites (FLK Zinj, FLK N and FLK NN) and their surrounding landscapes (Domínguez-Rodrigo et al., 2010), thus suggesting a low predation hazard for hominins and granting more support to the alternative interpretation of the crocodile-modified hominin OH8 remains as post-mortem access to the carcass by crocodiles.

The intensity of tooth-marking varies between both experimental sets (Njau & Blumenschine’s and ours) suggesting that this is highly affected by the experimental conditions of the captive crocodiles used. The larger sample used by Njau and Blumenschine, probably containing a higher number of males, which are highly competitive, contrasts with the much smaller sample used by us. Our sample also contains only females, which may explain minimal competition over carcasses; most feeding episodes were carried out by single individuals without interference from others. This impacts the intensity of bone damage and the presence or absence of hook-shaped tooth marks.

Our study has expanded the interpretation of crocodile tooth marks by showing different proportions of mark types according to long bone portion. It has also elaborated on the microscopic definition of crocodile-inflicted marks by analyzing the proportion of traces of carinae, including microstriations. The results contribute to a diagnosis of these microscopic features in crocodile tooth marks, which can help differentiate them from other bio-stratigraphic processes, although in a couple of instances, similarities with trampling marks were strong.

Future studies on crocodiles are encouraged by these results. Given that bone modifications by some mammalian carnivores vary according to whether they are carried out in captivity or in the wild, the next logical step would be to experiment with crocodiles in their natural environments. Until that is made, both experimental scenarios have a limited applicability to the past.

Acknowledgments

We thank the Tanzanian Commission for Science and Technology and the National Museum and House of Culture at Dar es Salaam for their permission to conduct research. We are also indebted to Mariano Padilla and the Complutense Comparative Anatomy Museum for their assistance in providing access to their crocodile collection to elaborate tooth mark casts. We also thank the following people and institutions for their help and collaboration in this project: FAUNIA (Parques Reunidos), the Regional Archaeological Museum of Madrid, the Foundation of the University of Alcalá de Henares, the Department of Zoology of the University of Alcalá de Henares, Diego Sanjuán Benito (Madrid City Council), Gonzalo Ruiz Liso, Juan Antonio Espinosa and José Luis Martínez. We also thank two anonymous reviewers for their comments on an earlier draft of this paper.

Appendix. Supplementary material

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.jas.2012.01.010](https://doi.org/10.1016/j.jas.2012.01.010).

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