Reassessing the role of carnivores in the formation of FLK North 3 (Olduvai Gorge, Tanzania): A pilot taphonomic analysis using Artificial Intelligence tools

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ABSTRACT

FLK North (FLK N) (Bed I, Olduvai Gorge, Tanzania) is one of the best examples of a palimpsest where felids, hyenids and hominins made use of the same space without or with minimal interaction between hominins and the other two carnivores. Felids have been interpreted as the main accumulators and carcass consumers followed by frequent hyenid intervention. The presence of hominins at this site has been documented through the discovery of stone tools. Here, we test previous taphonomic interpretations of this site through the application of Artificial Intelligence (AI) tools (computer vision applied to bidimensional images of tooth pits) to taxonomically discriminate carnivore-made tooth marks. The bones we analyzed constitute a small sample, being a preliminary study of bone surface modifications (BSM) through the application of AI to a sample of the FLK N archaeofaunal assemblage (mostly to Level 3 fossils), pending access to the larger excavated collections. The results obtained in the present study show that the marks analyzed have been generated both by hyenids and felids. The slight predominance of hyena tooth marks is expected, since the bone sample used is dominated by long limb bones, and hyenas are the most likely agent causing long bone breakage, although felids also break bones of carcasses smaller than 150 kg as documented in the site. Felid impact, in at least three cases, is documented with tooth marks imprinted by felids and hyenas occurring on the same specimens. Felid-hyenid interaction is, thus, documented though the deep learning methods applied. The limited number of specimens where both agents are documented suggest that both hyenids and felids were independently breaking a substantial part of the bones at FLK N. This preliminarily modifies previous interpretations that attributed most long bone fragmentation exclusively to hyenas.

1. Introduction

Multiple studies have been carried out to reconstruct the behavior of the early Pleistocene hominins of Olduvai Gorge (Tanzania) (Leakey, 1971; Bunn, 1981; Domínguez-Rodrigo et al., 2007a, 2014), and to understand carnivore and hominin interactions at these sites (e.g.,

Blumenschine, 1986; Capaldo, 1997, 1998; Domínguez-Rodrigo et al., 2007a; Pante et al., 2012; Domínguez-Rodrigo et al., 2014). There are several sites in Bed I in which hominins are the main taphonomic agent responsible for the accumulation and modification of the archaeofaunal assemblages, such as FLK Zinj, DS and PTK (Domínguez-Rodrigo & Cobo-Sánchez, 2017; Cobo-Sánchez, 2020). There, hominins had early

access to carcasses and were targeting flesh bulk defleshing (Domínguez-Rodrigo & Barba, 2007b; Domínguez-Rodrigo et al., 2010a, 2014; Domínguez-Rodrigo & Cobo-Sánchez, 2017; Cobo-Sánchez, 2020), but at other sites, hominin roles remain unknown, because what they did in those locations remains unknown. The latter type of sites are palimpsests, in which hominin agency is one among other agent types, and it is even marginal when it comes to the creation of faunal accumulations (Domínguez-Rodrigo et al., 2007a). FLK North (FLK N) is probably-one of the best examples of carnivore-accumulated assemblages with marginal hominin input, despite hominin intervention being attested by the continuous presence of stone artefacts throughout the deep vertical deposit. Hominin and carnivore redundant use of the same location has been argued to have occurred without or with minimal interdependence (Domínguez-Rodrigo & Barba, 2007a; Domínguez-Rodrigo et al., 2007b, 2010b). Felids have been identified as the main accumulators and carcass consumers at the site, followed by frequent but intermittent hyenid intervention across this vast time-averaged deposit. The site has major relevance for the understanding of potential kleptoparasitism by early hominins, since they were exposed to felid-accumulated remains during prolonged periods of time, but they did not exploit them, thus questioning the often debated hominin opportunistic behavior at these early sites (Blumenschine, 1987; Domínguez-Rodrigo et al., 2010b; Pante et al., 2012; Domínguez-Rodrigo et al., 2014, 2021a).

From previous taphonomic work using traditional techniques, it is known that both felids and hyenids modified bones at FLK N site across Levels 1–6 (Domínguez-Rodrigo & Barba, 2007a; Domínguez-Rodrigo et al., 2007b, 2007c; Egeland, 2007). In the present study, the real impact of each of these agents at FLK N is re-evaluated through the application of Artificial Intelligence (AI) tools. We intend to test previous interpretations and asses if both felids and hyenids participated in the bone assemblage modification documented at the site, with special emphasis on Level 3.

Leakey excavated six archaeological levels at FLK N: Levels 1–5 were interpreted as hominin living floors and Level 6 as an elephant butchery site where hominins modified a proboscidean carcass (Leakey, 1971). Binford´s (1981) interpretation of FLK N 6 was that the stone tools found next to the *Elephas recki* bones were not functionally associated with it, but could be correlated with non-*Elephas* bones belonging to smaller fauna. Bunn (1982, 1986) also studied FLK N 1–2, which was interpreted as a central foraging place. Domínguez-Rodrigo et al. (2007a) subsequently reviewed the interpretation of the Olduvai Bed I sites and concluded that: FLK N 1–4 was a palimpsest where carnivores (namely, felids) and hominins contributed independently to the accumulation of the archaeological record (Domínguez-Rodrigo & Barba, 2007a; Domínguez-Rodrigo et al., 2007b). FLK N 5 was also the result of carnivore´s accumulation and modification (Egeland, 2007), and FLK N 6 was interpreted as a natural death place of an elephant without any taphonomically-reliable evidence of hominin exploitation, and in association with a natural background scatter of bones from smaller mammals, some of them with visible felid-induced damage (Domínguez-Rodrigo et al., 2007c).

During their more recent work, The Olduvai Paleoanthropology and Paleoecology Project (TOPPP) excavated FLK N systematically exposing new levels (7–9) in one trench, and providing new data to this debate. This recent work provided further evidence of the taphonomically-predominant carnivore signal in these underlying archaeological levels, and also evidence that hominins occasionally modified large faunal remains amplifying the knowledge that we had about the site and the agents implicated in the formation and modification of the assemblage (Domínguez-Rodrigo et al., 2010b).

Hyenids and felids modify bones differently (Parkinson et al., 2015; Domínguez-Rodrigo et al., 2021b). This allows us to identify which carnivore agent generates or modifies any given bone accumulation and their order of intervention. Usually, hyenids modify long bones until they are substantially or completely fragmented, with intensive deletion

of spongy trabecular portions, while felids usually leave long bones complete or modified to a substantially lesser extent (Domínguez-Rodrigo et al., 2007a; Parkinson et al., 2015). However, it is known that under stress conditions, felids can fracture bones from small and the smaller range of medium-sized carcasses to the point that the pattern may overlap partially with hyenids (Gidna et al., 2015). The information contained in the morphology of tooth marks becomes, thus, extremely relevant to overcome potential ambiguities in the identification of carnivore agents. Recently, AI tools deployed to analyze bidimensional images of bone surface modifications (BSM) have yielded accurate results in discriminating different types of BSM (Cifuentes-Alcobendas & Domínguez-Rodrigo, 2019; Domínguez-Rodrigo et al., 2020; Jiménez-García et al., 2020a, 2020b; Abellán et al., 2021). The application of these methods to the analysis of tooth marks has also been a major improvement over the subjective identification by human experts. The resolution has been as high as to differentiate tooth scores made by jaguars and lions with 89 % of accuracy (Jiménez-García et al., 2020a, 2020b). AI methods applied to a limited array of different carnivores have also succeeded in providing good discrimination among taxa; especially when comparing meat-eating carnivores (like felids) and durophagous carnivores (like hyenids) (Abellán et al., 2021). The machine has shown an accuracy > 90 % in correctly identifying tooth marks made by hyenas and those from lions (Abellán et al., 2021). It is precisely because of this high accuracy in differentiating both carnivore types that we intend to apply these AI methods to the fossils record of FLK N, with the goal of detecting the hyenid and felid taphonomic signatures that were previously inferred from the damage patterning documented in the sequence of archaeofaunal assemblages at the site.

Here, we will analyze through some of the most successful transfer learning architectures the tooth marks found on bone surfaces from a randomly selected sample of fossils from FLK N, to identify carcass modifying agent(s). This will enable us to test the felid-hyenid predominant agencies at FLK N 3 as inferred in previous taphonomic analysis of the site (Domínguez-Rodrigo et al., 2007a), and detect the interactions (if any) that took place between carnivores and hominins at the site. The implications for the understanding of hominin behavior are of utmost relevance.

2. Materials and method

2.1. Materials

FLK N site is one of the best examples of a palimpsest where both hominins and carnivores used the place repeatedly over several years (probably centuries or millennia) and where carnivores were the main agent responsible of the bone accumulation (Domínguez-Rodrigo et al., 2010b). FLK N is situated in the top of Bed I and < 100 m to the north of FLK 22 *Zinjanthropus* (FLK Zinj) site, and it is "the thickest early Pleistocene archaeological deposit currently known" (Domínguez-Rodrigo et al., 2010b: 2), spanning a continuous vertical sequence. The site was discovered in 1960 and the sequence of the deposits include Bed I and the lower part of Bed II (Leakey, 1971). The initial excavations uncovered three archaeological levels overlying Tuff IF and six more under the tuff (Leakey, 1971). Later, TOPPP discovered and excavated additional underlying levels (7–9) (Domínguez-Rodrigo et al., 2010b). A geological description of the levels can be seen in Leakey (1971) and in Domínguez-Rodrigo et al. (2010b), and here we present an updated geological description of the levels at FLK N (Fig. 1).

The bones we analyzed constitute a small sample from that excavated at the site. This small sample is intended as a pilot study of the whole collection, which is currently stored at the National Museums of Tanzania. The current pandemic situation prevented us from having access to the complete collection and this has delayed its study. The sample used was accessible because it was mostly excavated at a geo-trench, and is not stored at the National Museums of Tanzania with the exception of one specimen bearing two marks documented during a
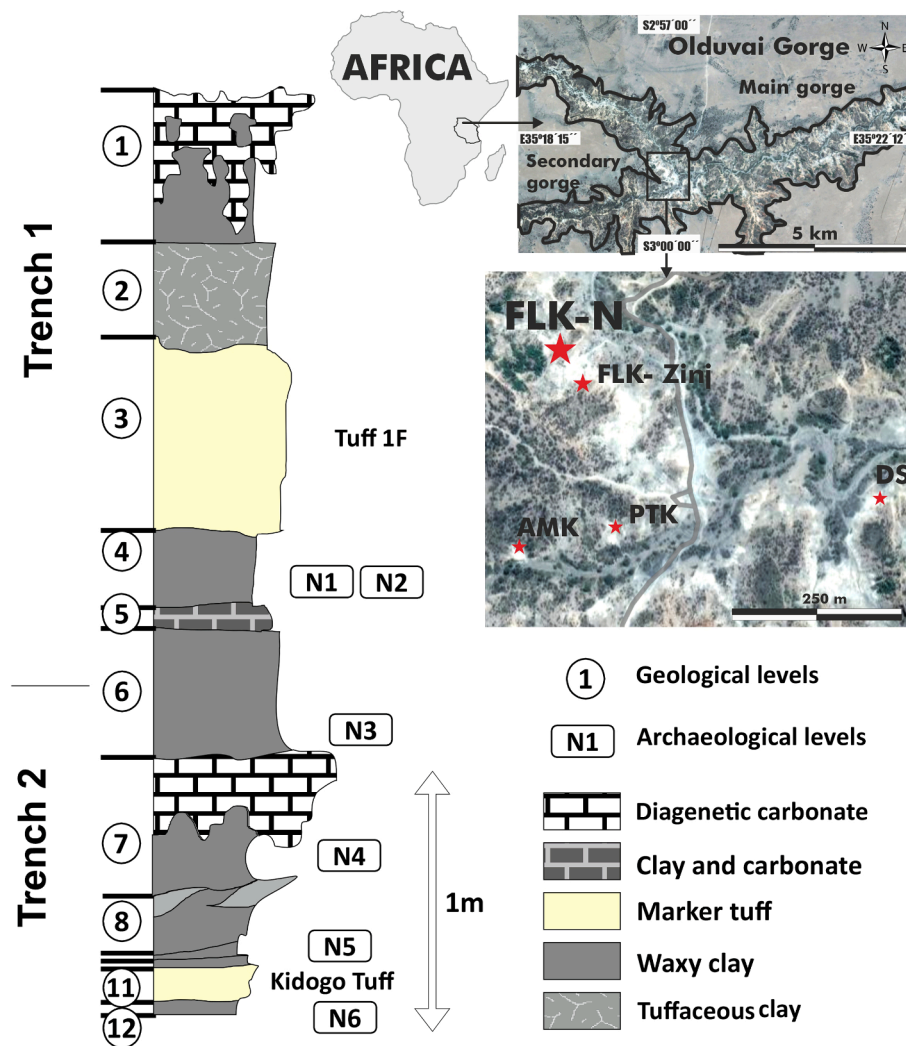
Fig. 1. Geological description of levels at FLK N.

short stay at the National Museum of Dar es Salaam. All the bones, except three of them, come from the geo-Trench 3, situated at the margin of the main bone accumulation, in the transition of the elevated terrain and the wetland margin (Domínguez-Rodrigo et al., 2010). FLKN 410 and FLKN 811 were found at geo-Trench 1 and FLKN 354 at Trench 6. A total of 53 tooth pits have been examined in the present study. The 53 images can be found at: https://dataverse.harvard.edu/dataset.xhtml?persistentId = https://doi.org/10.7910/DVN/1OGN32. All the bones analyzed come from Level 3 except FLKN 354 that came from Level 1–2, FLKN 410 that was collected from Level 7 and FLKN 811 that came from Levels 4–5.

Bones at FLK North display good cortical preservation. This enables the analysis of bone surfaces with confidence. Despite this, frequent bioturbation in the form of bioerosive marking by plant roots is common in the archaeofaunal assemblage of this site. We only used the tooth mark data set that was well preserved, discarding those marks that presented some modifications introduced by diagenesis. Almost all the bones used belong to green-broken long bone shafts (Table 1), since all our experimental data sets for computer vision were made on long bones only.

2.2. Method

Tooth pits were documented and photographed with a microscope Leica S9i, except the 2 pits documented at the National Museum of Dar es Salaam, that were taken with a binocular Optika microscope. All of them were taken with a magnification of 30x, except five of the marks (numbers 30, 31, 40, 41 and 52 in Table 1), that were documented with magnifications of 20x because of their substantially bigger size.

The experimental image data bank utilized in the present study was documented with a binocular microscope (Optika) with magnifications of 30x and it was generated by members of the TOPPP research team and is already published (Cobo-Sánchez et al., 2022; see below). Previous interpretations of FLK N posited that felids accumulated the bulk of the assemblage and hyenas intermittently had access to carcasses (Domínguez-Rodrigo et al., 2007a). Although it was argued that given the *Antidorcas-Parmularius* specialized taxonomic profile in the FLK N assemblage, a medium-sized felid specialist was the best candidate, this could be the action of leopards, *Dinofelis*, *Megantereon* or other felids. Given that presently there are deep learning data sets for lions and jaguars (but not leopards or any of the extinct sabertooth taxa), we selected lions as the closest proxy available, given that felid tooth morphology is inter-taxonomically more similar than any felid is to a durophagous carnivore like hyenas. It has also been debated if referential frameworks on carcass consumption and the resulting bone breaking carried out with carnivores in captivity could reflect what the same carnivores do in the wild (Domínguez-Rodrigo et al., 2012; Gidna et al., 2013). Carcass modification (i.e., bone breakage and destruction) is widely different when felids are wild, semi-captive or captive (Brain, 1981) with the latter showing the most marked diversion by displaying

Table 1

Classification of BSM through ensemble learning, using transfer learning algorithms. ID number = Identification number; GF = Green fracture. In column ID number appears the name of the site, the number of each bone and a letter that indicate the number of marks that have been recorded from the same bone for the present study.

Mark	ID number	Agent	GF	Element	Portion
1	FLKN 43A	Felid	Yes	Femur	Diaphysis
2	FLKN 45A	Hyenid	Yes	Tibia	Diaphysis
3	FLKN 45B	Hyenid	Yes	Tibia	Diaphysis
4	FLKN 46A	Hyenid	Yes	Skull	Skull
5	FLKN 47A	Hyenid	Yes	Radius	Diaphysis
6	FLKN 49A	Felid	No	Metatarsal	Diaphysis
7	FLKN 49B	Hyenid	No	Metatarsal	Diaphysis
8	FLKN 49C	Hyenid	No	Metatarsal	Diaphysis
9	FLKN 49D	Hyenid	No	Metatarsal	Proximal epiphysis
10	FLKN 49E	Hyenid	No	Metatarsal	Diaphysis
11	FLKN 49F	Felid	No	Metatarsal	Proximal epiphysis
12	FLKN 50A	Felid	Yes	Humerus	Diaphysis
13	FLKN 50B	Felid	Yes	Humerus	Diaphysis
14	FLKN 52A	Felid	Yes	Metacarpal	Diaphysis
15	FLKN 54A	Hyenid	Yes	Radius	Diaphysis
16	FLKN 56A	Hyenid	Yes	Tibia	Diaphysis
17	FLKN 60A	Hyenid	Yes	Vertebrae	Arch
18	FLKN 62A	Felid	Yes	Metapodial	Diaphysis
19	FLKN 68A	Hyenid	Yes	Tibia	Diaphysis
20	FLKN 68B	Hyenid	Yes	Tibia	Diaphysis
21	FLKN 72A	Felid	Yes	Metacarpal	Diaphysis
22	FLKN 99A	Hyenid	Yes	Mandible	Body
23	FLKN 105A	Hyenid	Yes	Metatarsal	Proximal epiphysis
24	FLKN 113A	Hyenid	Yes	Tibia	Diaphysis
25	FLKN 128A	Hyenid	Yes	Metacarpal	Diaphysis
26	FLKN 133A	Hyenid	Yes	Tibia	Diaphysis
27	FLKN 138A	Felid	Yes	ULB	Diaphysis
28	FLKN 144A	Felid	Yes	Atlas vertebrae	Apophysis
29	FLKN 172A	Hyenid	Yes	Metatarsal	Proximal epiphysis
30	FLKN 354A	Felid	Yes	Vertebrae	Body
31	FLKN 354B	Felid	Yes	Vertebrae	Body
32	FLKN 410A	Felid	Yes	Metacarpal	Distal diaphysis
33	FLKN 410B	Hyenid	Yes	Metacarpal	Distal diaphysis
34	FLKN 410C	Felid	Yes	Metacarpal	Distal diaphysis
35	FLKN 410D	Hyenid	Yes	Metacarpal	Proximal epiphysis
36	FLKN 410E	Felid	Yes	Metacarpal	Proximal epiphysis
37	FLKN 410F	Felid	Yes	Metacarpal	Proximal epiphysis
38	FLKN 811A	Hyenid	Yes	Metacarpal	Diaphysis
39	FLKN 811B	Felid	Yes	Metacarpal	Proximal epiphysis
40	FLKN 811C	Felid	Yes	Metacarpal	Proximal diaphysis
41	FLKN 811D	Felid	Yes	Metacarpal	Proximal diaphysis
42	FLKN 811E	Hyenid	Yes	Metacarpal	Proximal diaphysis
43	FLKN 811F	Felid	Yes	Metacarpal	Proximal diaphysis
44	FLKN 811G	Hyenid	Yes	Metacarpal	Proximal diaphysis
45	FLKN 811H	Hyenid	Yes	Metacarpal	Proximal diaphysis
46	FLKN 811I	Felid	Yes	Metacarpal	Proximal diaphysis
47	FLKN 811J	Hyenid	Yes	Metacarpal	Proximal diaphysis
48	FLKN 811K	Felid	Yes	Metacarpal	Proximal diaphysis
49	FLKN 811L	Felid	Yes	Metacarpal	Proximal diaphysis
50	FLKN 811M	Hyenid	Yes	Metacarpal	Proximal diaphysis
51	FLKN 811N	Hyenid	Yes	Metacarpal	Proximal diaphysis
52	FLKN 811O	Felid	Yes	Metacarpal	Proximal epiphysis
53	FLKN 811P	Hyenid	Yes	Metacarpal	Proximal epiphysis

long bone elements survived (almost) complete carcass consumption. If broken, they should bear tooth marks imparted by a durophagous carnivore having secondary access to carcasses.

2. Felids and hyenids participated at different stages of carcass consumption at FLK N. This should be reflected in the identification of tooth marks by both agents. Given the sequential interaction (felid transporting and consuming carcasses and hyenid ravaging post-depositionally the abandoned kills), there should even be mixed signals of agent interaction in some bone specimens.

3. A felid consumption of carcasses at FLK N followed by hyenas should result in long bone green-broken specimens displaying overwhelmingly a hyenid signal over the felid one, unless the felid consumed and modified carcasses as documented in the stereotypic behaviors reported in captivity.

2.2.1. The experimental sample

In order to model durophagous carnivory, we used experiments of bones modified by spotted hyenas. The reason is that these are the most common durophagous carnivores in Africa savanna ecosystems. Additionally, the hyenid taphonomic signal has been previously identified in all levels at FLK N (Domínguez-Rodrigo et al., 2007a). In contrast, strict carnivores do not modify the bones from the carcasses they eat as intensively as durophagous carnivores. We selected lions as representative of felids, which typify strict carnivores. Both tooth samples were obtained from experiments carried out with semi-captive carnivores at the reserve of Cabárceno (Cantabria, Spain). At Cabárceno, carnivores live in open spaces, and they do not undergo the stereotypic behaviors that carnivores have been documented to display in small enclosures (Gidna et al., 2015). Carcass parts consumed by lions at Cabárceno were collected after a few days of exposure (when they were completely defleshed and unattended, which usually spanned 1–4 days). With hyenas, the protocol was modified, because when bones were exposed for more than one day, they tended to be completely consumed. Thus, bones in their enclosure were collected earlier, usually on the same day, after a few hours of consumption. The lion tooth mark sample consisted of 60 limb bones from 9 older juvenile and prime adult horses consumed by 11 lions. A total of 209 scores and 80 pits were identified in this sample. The spotted hyena sample was composed of 67 long bones from 23 carcasses from adult horses consumed by a variable number of hyenas. A total of 83 scores and 82 pits were selected. In total, 451 tooth marks were used for the transfer learning models used for pairwise and multiple carnivore identifications (Abellán et al., 2021; Cobo-Sánchez et al., 2022). Given that in the present analysis all the tooth marks identified were tooth pits, we used the models derived from the use of the 80 and 82 tooth pits from lions and hyenas respectively. We insist that we intend to use this information as preliminary awaiting the analysis of a sample of marks more substantial than that contained in this pilot study.

2.2.2. Deep learning analysis

The present study uses the models elaborated in previous studies for classification of tooth pits (Cobo-Sánchez et al., 2022). For a detailed information of the experimental samples used, we refer to this work. A summary of the methods for these models follows.

For the present study, convolutional neural networks (CNN) from transfer learning (i.e., pre-trained architectures on thousands of diverse objects) were applied. For the analysis of tooth marks, up to five different architectures and CNN types were used: DenseNet 201, ResNet 50, InceptionResnetV2, EfficientNetB7 and VGG19. They were used with image augmentation. Samples were augmented via random transformations of the original images involving shifts in width and height (20 %), in shear and zoom range (20 %), and also including horizontal flipping, as well as a rotation range of 40°.

Given that we did not have leopard-specific libraries, we used a binary classifications trying to determine the carnivorous (felid) or durophagous (hyenid) nature of BSM. Therefore, lion-hyena pairwise

stereotypic behaviors that are commonly not documented in the wild (Gidna et al., 2013). An example of this is the intense modification and bone breakage (overlapping with that resulting from spotted hyenas) in carcasses consumed by leopards in captivity (Gidna et al., 2015). Although wild and captive carnivores can generate different frequencies of bone damage, this does not affect the present study which focuses on tooth mark morphology only. Here, we present the following hypotheses to be tested by agency identification through the analysis of tooth mark morphology:

1. Felids in the past were modifying carcasses more similarly to modern wild felids than to other types of carnivores. This implies that their tooth mark frequencies on bones should be low. It also implies that

comparisons were carried out using an ensemble learning approach. For such an analysis, we used stacking as an ensemble learning method. Stacking is built upon a series of base learners (model listed above) and then their weights are reused through a second layer *meta*-learner. In this case, we applied a Random Forest, tuned with 100 trees and a minimum sample split of 2.

The base models were fine-tuned using transfer learning approaches (highest accuracy and lowest loss with moderate to high balanced classification). In each of the models used, the activation function for every layer was a rectified linear unit (ReLU). The last fully connected layer of the network used a "sigmoid" activation for the binary comparison between lions and spotted hyenas. The loss function selected was binary cross-entropy. Cross-entropy measures distances between probability distributions and predictions. The optimizer used was Stochastic Gradient Descend (SGD) with a learning rate of 0.001 and a momentum of 0.9. Accuracy was the metric selected for the compilation process.

The models were trained on about 70 % of the original image dataset. The resulting models were subsequently tested against the 30 % remaining sample, which was not used during the training. Training was performed through mini-batch kernels (size = 20). Testing was made

also using mini-batch kernels of size 20. Weight update was made using a backpropagation process for 100 epochs. All images were transformed into black and white during image processing in the Keras Application Programming Interface (API), by using bidimensional matrices for standardization and centering. Each image was then reshaped so that they share the same dimensions (60 × 60 pixels). The Keras library was used with the TensorFlow backend. The original data set can be found at: https://dataverse.harvard.edu/dataset.xhtml?persistentId = https ://doi.org/10.7910/DVN/BQTKBA and the ensemble analysis code can be found at: https://dataverse.harvard.edu/dataset.xhtml? persistentId = https://doi.org/10.7910/DVN/1OGN32.

3. Results

The ensemble analysis applied to the testing experimental set yielded an accuracy of 95.7 % of correct classification. Of the total of the 53 marks analyzed using AI tools, 29 of them have been classified by the stacked ensemble model as made by hyenas, while 24 BSM have been classified as felid-made (Table 1). Every single individual model yielded very balanced classifications (See Supplementary data).

All the bones analyzed in the present study showed evidence of

Fig. 2. Bones with tooth pits. SQ. A & B: cranial and caudal view of FLKN 410 respectively; SQ. C: the vertebrae FLKN 354 with two pits, both of them are located on the body.

intensive green breakage, except one of them that only presents dry fractures (FLKN 49) (Table 1). It should be emphasized that almost all the bones analyzed belong to long bone shaft fragments. Before running the BSM through the machine, we had uncertainty as to the agency of long bone breakage. However, we suspected of a felid agency in the modification of one vertebral specimen, which was preserved almost complete (Fig. 2). This specimen displayed two tooth pits on the vertebral body, which was otherwise unaltered. This type of damage had been previously documented among felid-modified bones (Domínguez-Rodrigo & Barba, 2007a). When we showed these marks to the ensemble learners, all of them classified them as felid-made tooth marks.

The results displayed here (Table 1) show that both felids and hyenids modified the FLK N assemblage (Figs. 3 and 4), as interpreted previously from the application from other taphonomic techniques (Domínguez-Rodrigo et al., 2007a).

4. Discussion

In the early Pleistocene archaeological record, two types of sites can be found in uneven distributions: anthropogenic assemblages and palimpsests. The first ones are marginal in these chronologies, but palimpsests are commonly found. A palimpsest is an assemblage formed by the accumulation and modification of carcasses through the activity of various agents (Binford, 1978, 1981). They may or may not have a strong hominin component. FLK N site is one of the best examples of a palimpsests in Bed I times, where felids and hyenids took part in the accumulation and modification of bones (Domínguez-Rodrigo et al., 2007a).

There has been some debate about the definition of the term palimpsest and its archaeological categorization (Bailey, 2007). The most common definition is "the aggregated result of numerous small independent events" (Binford, 1981: 204), regardless of the nature or number of actors involved. This refers to the number of depositional events, but also to the number of modifying events. A leopard bringing a carcass to a spot, followed by hyena modification of those remains indicates one single depositional event, but two successive modifying events, in which taphonomic information has been changed. Even if we were dealing with the same agent (e.g., one leopard bringing the carcass and partially consuming it, followed by another leopard further consuming it and modifying the bones) we would still be dealing with a palimpsestic situation in which one depositional event is articulated around two independent carcass modifying events. In our opinion, taphonomists should be targeting the bone modifying accretion of the process, because it is there that taphonomic information morphs. This could fit Bailey's (2007) accumulative palimpsest definition (versus true palimpsest). However, in the present work, we want to go back to the second definition of palimpsest provided by Binford (1981: 9) where a palimpsest was a deposit of archaeological materials "deriving from a
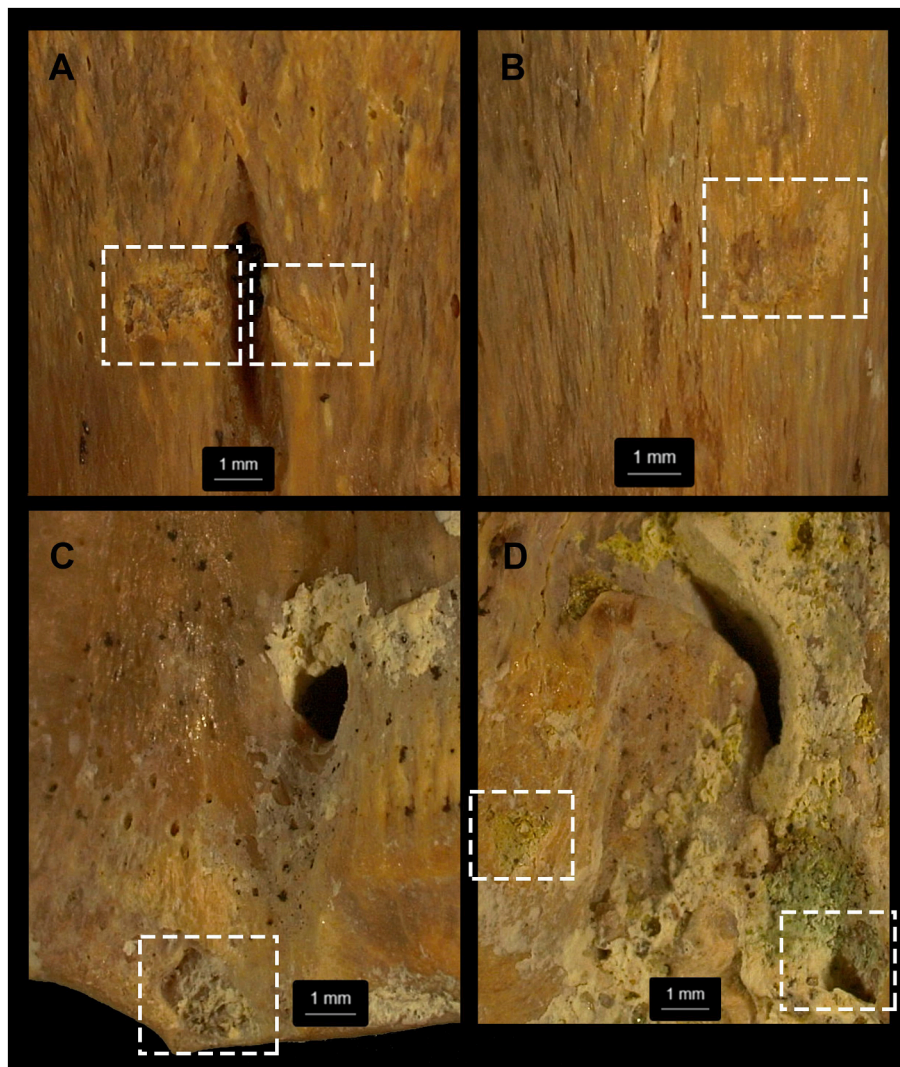

Fig. 3. Pits analyzed at FLKN 410 metacarpal (0.6x): SQ. A: FLKN 410A & FLKN 410B; SQ. B: FLKN 410C; SQ. C: FLKN 410D & SQ. D: FLKN 410E & FLKN 410F.
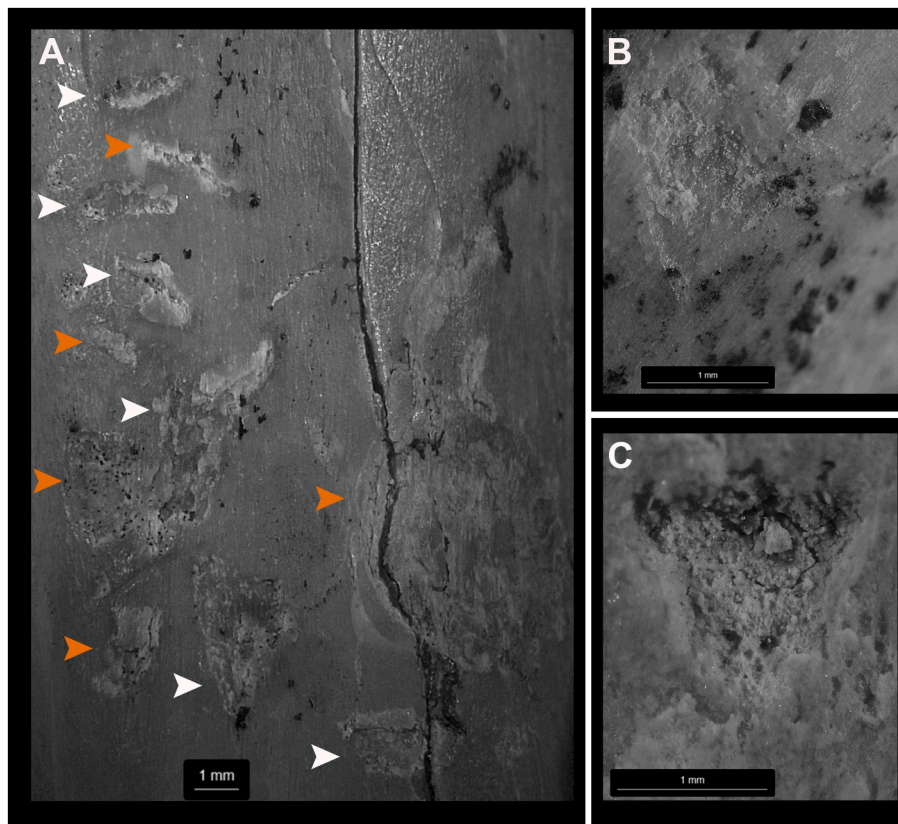
Fig. 4. SQ. A: Tooth pits at FLKN 811 metacarpal (0.6x). White arrows point to the tooth pits made by hyenids and orange arrows point to the pits made by felids; SQ. B: tooth pit (FLKN 99A) made by hyena (30x) & SQ. C: tooth pit (FLKN 410E) made by felid (30x). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

variety of events or actions of both man and animals" (Lyman, 1994). It is because of this second version of palimpsest that Binford (1981) created the terms "integrity" and "resolution" to refer to archaeological sites. Integrity referred to the number of agents contributing to a deposit, and resolution indicated the number of successive activities performed in the deposit́s locus. It is resolution that relates directly to the first definition of palimpsest. Here, we adopt Binford́s (1981) broader concept to include agency as well as event accretion.

The results obtained in the present study show that there is a slightly greater percentage of FLK N marks generated by hyenas. Felid input has been detected in almost half a sample of the tooth mark sample. This association of tooth marks with green breakage planes supports previous interpretations of a felid-hyenid interaction at the site (Domínguez-Rodrigo et al., 2010b). Two of the marks classified as felid-made are located on the body of a vertebrae that also presents green fractures on the apophyses; both are typical in vertebral felid damage. The abundance of hyena tooth marks is expected since hyenas are the most likely agent causing long bone breakage, and these bones are the ones that compose most of the sample analyzed. When hyenas have access to long bones, they usually generate a large amount of shaft fragments (Domínguez-Rodrigo et al., 2010b), and they leave multiple tooth marks on their surfaces (Domínguez-Rodrigo & Pickering, 2010). We selected two of the most accurate models to test probability in fossil mark classification. Given that the experimental sample contained true hyena tooth marks, the individual models were very confident (with probabilities > 90 %) in the identification of hyena tooth pits in the FLK North assemblage. In contrast, the felid tooth marks were identified with lower confidence, probably because the experimental dataset used for training did not contain leopard tooth marks, but lion tooth marks. If those marks were indeed made by leopards or other similarly-sized felids, the classification as felid is weakened by the potential differences between the

experimental lion tooth marks and the fossil tooth marks, which were most likely made by a different type of felid. We are currently working on experiments with leopards, which are extremely time consuming, to create a library of marks made by this felid. This is one of the reasons why the present study provides only preliminary results.

The preliminary testing of the three hypothesis outlined in the Method section shows that: a) the felid input detected agrees with the frequencies of tooth marks found in modern wild felid-consumed carcasses that have undergone subsequent fragmentation by other agents (Organista et al., 2016); b) felids must have broken a substantial part of long bones at FLK N, leaving the unbroken elements to be subsequently broken and consumed by hyenas, and c) this shows that there was a felid-hyenid interaction at the site. This pilot study preliminary seems to confirm the three initial hypotheses. This reinforces previous taphonomic interpretations of the site (Domínguez-Rodrigo & Barba, 2007a; Domínguez-Rodrigo et al., 2007b, 2007c, 2010b; Egeland, 2007), as well as the validity of modern experimental analogs derived from behaviors that can be used as proxies for prehistoric versions of similar carnivores.

Future comprehensive analyses of the complete assemblage must test the results and interpretations described in the present work using more complete experimental libraries and a more extensive sample from the fossils assemblage.

5. Conclusion

We have presented here the results of a taphonomic analysis of BSM of a small sample of remains from the FLK N (mostly from Level 3) site using AI tools. The site is one of the best examples of a palimpsest in which felids were the main agent responsible for the bone accumulation followed by hyenas who did most of the bone breakage.

Here, with some of the most successful transfer learning architectures applied to experimental data sets, it has been confirmed that both felids and hyenids participated in the modification of bones documented at FLK N 3, and that such interaction (by the presence of both felid and hyenid agency in the modification of the assemblage) can be detected through the different levels documented at the site if using traditional taphonomic analyses, and at least in Levels 3, 4–5 and 7 if using the present AI approach. This has preliminarily confirmed the previous interpretation using traditional taphonomic techniques (Domínguez-Rodrigo et al., 2007a, 2010b), underscoring the intensive damage of hyenas and the more discrete modification created by felids. This would be expected since hyenas modify bones much more intensively than felids, and also, given that most bones are limb shafts, the breaking of these elements is in essence attributed to hyenas and not felids. Future work with the complete collection of tooth marks from this extremely large faunal assemblage should further confirm or refine the preliminary interpretations displayed in the present work. Future research should also include experimental leopard (instead of lion) tooth marks as a library with which the AI models should be trained again and tested against the FLK N ichnological fossil record.

Data availability

The following information was supplied regarding data availability. The data is available at Harvard Dataverse: Cobo Sanchez, L., 2021. Replication Data for: Computer vision indicates primary access to meat by early Homo 1.84 million years ago. Harvard Dataverse, V6. https://doi.org/10.7910/DVN/BQTKBA.

Vegara Riquelme, M., 2022. Data for: Reassessing the role of carnivores in the formation of FLK North 3 (Olduvai Gorge, Tanzania): A pilot taphonomic analysis using Artificial Intelligence tools. Harvard Dataverse, V1. https://doi.org/10.7910/DVN/1OGN32.

CRediT authorship contribution statement

Marina Vegara-Riquelme: Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Agness Gidna:** Investigation. **David Uribelarrea del Val:** Investigation, Writing – original draft, Writing – review & editing. **Enrique Baquedano:** Validation, Investigation, Writing – review & editing, Project administration, Funding acquisition. **Manuel Domínguez-Rodrigo:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jasrep.2022.103736.

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