The hunted or the scavenged? Australopith accumulation by brown hyenas at Sterkfontein (South Africa)

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ABSTRACT

In the present study, we report brown hyena tooth marks on australopiths from Sterkfontein's Plio-Pleistocene-age Member 4 (South Africa). Classic taphonomic analyses and the implementation of new techniques, including Geometric Morphometrics and Machine Learning, are combined to identify the modifying agent and provide the first direct evidence of hyenid scavenging on australopiths. This hypothesis adds a new perspective to the relationships between carnivores and hominins in the Cradle by expanding on previous hypotheses proposing that leopards were the primary predator and bone accumulator of early hominin remains at South African palaeocaves.

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1. Introduction

Australopiths have long been considered key in understanding early hominin evolution. Generally, research has focused on taxonomic diversity, chronology, palaeobiology and paleoenvironmental reconstructions of the ecosystems in which australopiths evolved (e.g., Vrba, 1975; Partridge, 1978; Reed et al., 2013). Dart's osteodontokeratic culture hypothesis described australopiths as hunters capable of transporting prey bones to caves such as Makapansgat (South Africa) which, after consumption, were used as weapons and tools (Dart, 1957). Subsequently, Brain (1981) showed that the bone assemblage from Makapansgat was rather the product of carnivore activity. The taphonomic study of

australopith specimens from the Cradle of Humankind caves (Swartkrans, Sterkfontein and Kromdraai) in South Africa revealed the presence of tooth marks on hominin remains (Brain, 1981). These discoveries prompted hypotheses that large felids (e.g., leopards; *Panthera pardus*) were responsible for accumulating hominin skeletal remains in the caves. The leopard hypothesis is strongly supported by the renowned cranium of a juvenile *Paranthropus robustus* (SK 54), which bears tooth marks that match the lower canines of a leopard mandible (SK 349) from the same deposit (Brain, 1981). This evidence suggests that leopards preyed on australopiths at least at Swartkrans. Brain pointed out that leopards could have preyed on hominins at the caves of Kromdraai and Sterkfontein too (Brain, 1981). This stimulated a sharp change in perception of early hominin behaviour, since australopiths could no longer be assumed to be primarily hunters. Further taphonomic research re-examined australopith remains from Sterkfontein to test Brain's Swartkrans hypothesis. The study mainly corroborated the hypothesis that large carnivores played a role in its

accumulation; though no further inferences on the predator taxa involved could be drawn (Pickering et al., 2004a). Other taphonomic processes, such as natural deaths, could have also been involved in the hominin accumulation at Sterkfontein (Pickering et al., 2004a). Despite numerous taphonomic studies focusing on early hominin remains (e.g., Brain, 1981; Pickering, 1999; Pickering et al., 2004a; Val et al., 2015, 2018; Aramendi et al., 2017, 2019) significant potential remains for testing established hominin accumulation hypotheses. Thus, The Leopard Swartkrans Hypothesis, as proposed by Brain, is worth testing at Sterkfontein through the application of new methodologies that have recently addressed equifinality problems regarding tooth mark morphology (Aramendi et al. 2017, 2019; Arriaza et al. 2018, 2021; Courtenay et al. 2019, 2021; Yravedra et al., 2019). In this work, we present taphonomic evidence of brown hyena tooth marks on australopith remains from Sterkfontein Member 4. This is the first direct evidence of hyena-inflicted modifications on australopith remains. Here we present "The Brown Hyena Sterkfontein Hypothesis" and discuss its implications for early hominin palaeobiology.

2. Materials and methods

Sterkfontein Cave is located in dolomitic limestone hills approximately 50 km northwest of Johannesburg (Gauteng, South Africa) (Stratford et al., 2016). Its deposits are grouped into six principal stratigraphic units: Member 1 to Member 6 (Partridge, 1978; Clarke, 2006) (Fig. 1 and Fig. S1). Excavation of Sterkfontein Member 4 has yielded a large assemblage of australopith specimens together with antelope, primate and carnivore remains, and is dated to the Plio-Pleistocene (Vrba, 1975; Clarke and Partridge, 2002; Pickering and Herries, 2020). Sterkfontein Member 4 is one of the richest *Australopithecus*-bearing deposits worldwide and has a long tradition of paleoanthropological research spanning more than eight decades. The study of the australopiths, associated fauna and fossil plant remains has provided detailed evidence of the morphology, diversity, and palaeobiology of the hominins and their relationship with the paleoenvironment in a key moment for human evolution (Vrba, 1975; Brain, 1981; Pickering, 1999; Kibii, 2004; Bamford, 1999; Reynolds and Kibii, 2011; Zipfel et al., 2020).
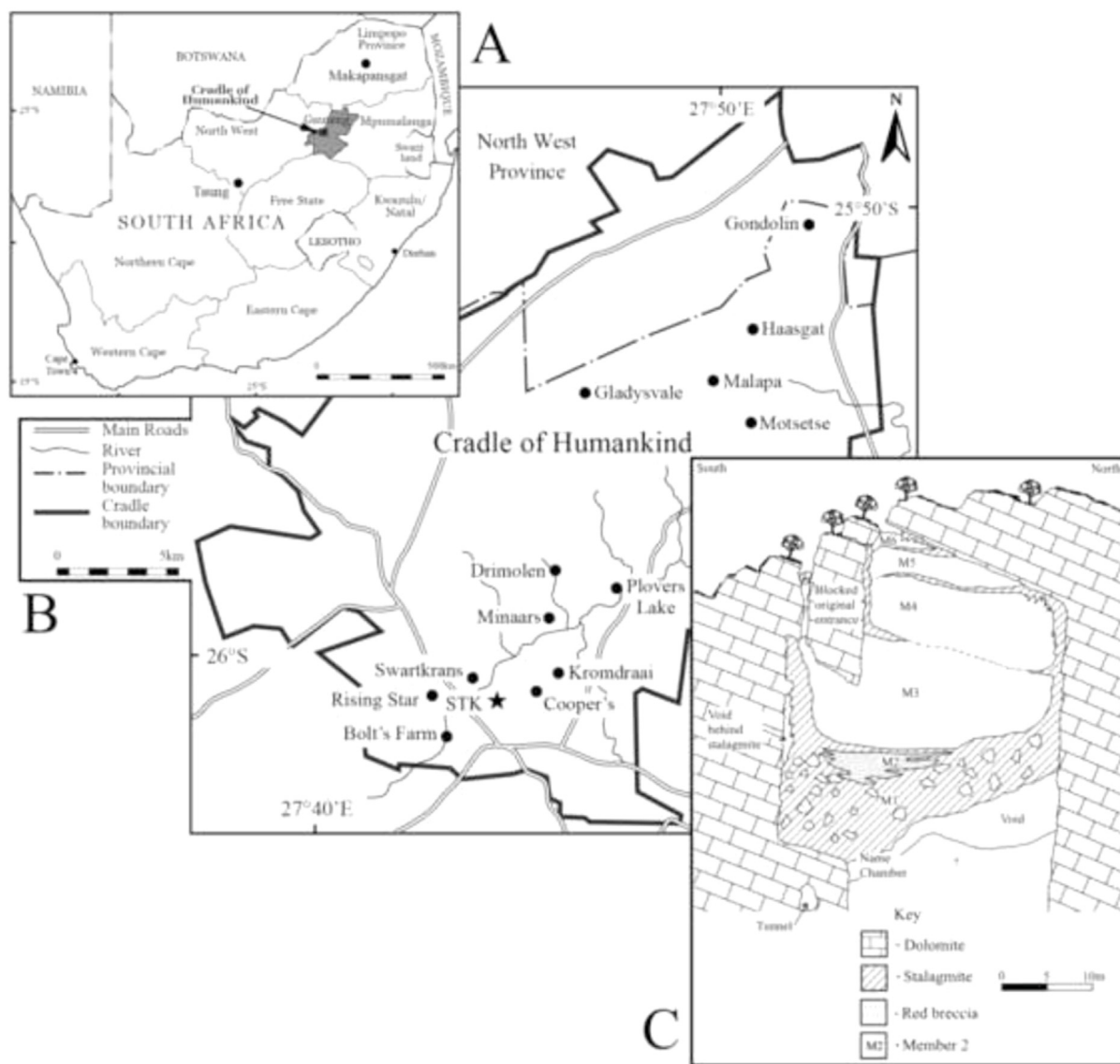

Fig. 1. Geographic and stratigraphic context of the Sterkfontein Caves and Member 4 of the Sterkfontein Formation. (**A**) Map of South Africa with location of the Cradle of Humankind; (**B**) Map of the Cradle of Humankind with location of the Sterkfontein Caves, labelled 'STK' (Inserts A and B modified from Stratford et al., 2016); (**C**) The Sterkfontein Formation (*2*) with relative stratigraphic position of Member 4 (Modified from Clarke, 2006).
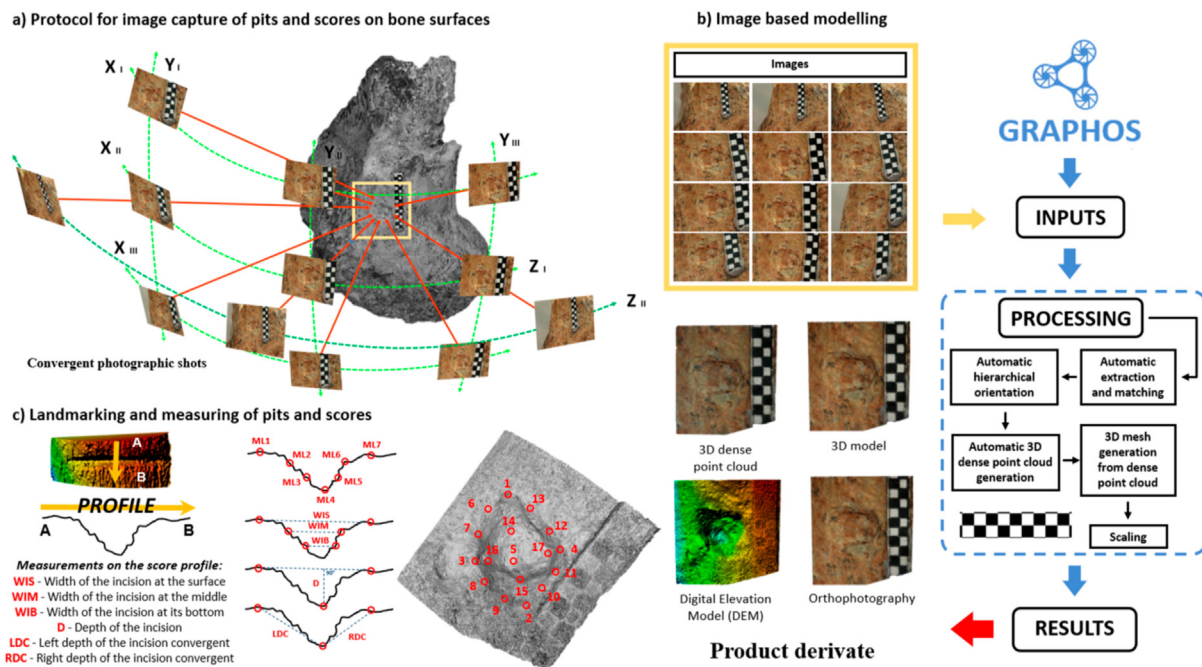
Fig. 2. Visual summary of the data collection process. (**A**) procurement of the images, (**B**) processing for 3D reconstruction, (**C**) acquisition of the landmark data and measurements from the tooth pits and scores.

The hominin sample studied here consists of the Sterkfontein Type Site/Transvaal Museum (Sts/TM) hominin specimen series, which are permanently curated at the Ditsong Museum (Pretoria, South Africa), and the Sterkfontein Witwatersrand (StW) hominin specimen series, housed at the Evolutionary Studies Institute, University of the Witwatersrand (Johannesburg, South Africa). The StW series examined here consists of material recovered from Sterkfontein excavations between 1968 and 2003, under the direction of Phillip Tobias and then Ron Clarke. For further detail on the hominin sample see Brain (1981), Pickering (1999), Clarke (2013), Pickering et al. (2004a, 2019), Pickering and Herries, 2020 and Zipfel et al. (2020).

Following the criteria summarised by Blumenschine et al. (1996), the bone surfaces of the australopith specimens were examined with the aid of a 20x hand lens. All conspicuous and inconspicuous tooth marks were identified. The tooth mark sample was classified according to bone density: cancellous bone (from epiphyseal sections) and dense cortical bone (from diaphyseal sections). Tooth marks were also classified according to form: pits (tooth marks that contain bowl-shaped interiors) and scores (characterised by U-shaped cross-sections) (Binford, 1981; Blumenschine et al., 1996). Carnivore modification can also be distinguished in the redundant consumption of long bones, which leaves a regular pattern called furrowing, or digestion (Haynes, 1983). The different carnivore modifications were also recorded according to hominin skeletal part.

Some of the tooth marks found on the Sterkfontein australopiths were digitised and compared with tooth marks generated by modern carnivores (table S1), including tooth pits and scores generated by spotted (*Crocuta crocuta*) and brown hyenas (*Parahyena brunnea*), leopards and lions (*Panthera leo*). Tooth marks were selected on the basis of their preservation and their location (long bone shafts). The taphonomic study revealed that the best-preserved tooth marks were those from StW 38, StW 124, StW 339, StW 577 and StW 182. 3D models of the tooth pits and scores were obtained by means of photogrammetry, a technique capable of extracting information on the geometric properties of an object based on the capture of several images (see supplementary file).

The 3D models of the pits were studied by means of Geometric Morphometrics (GMM). The study of the tooth scores entailed an intermediate stage consisting of the extraction of 2D cross-sections from the 3D models as representations of the overall score morphology (Maté-González et al., 2015; Arriaza et al., 2017; Yravedra et al., 2017; Courtenay et al., 2019). In addition to the GMM approach based on the location of seven 2D landmarks on the score cross-sections, seven linear measurements were taken to capture size information (Fig. 2).

Linear measurements and morphological information captured by the landmark configurations were statistically analysed following the requirements imposed by the different approaches (see supplementary file). Statistical analyses were performed on the free software R (www.rproject.org, Core-Team, 2015). Analyses (described in detail in SI) include principal component analyses (PCA) to reduce data dimensionality and observe sample variance, and classification tests that generally achieve high accuracy rates, such as linear discriminant analysis (LDA), and those based on machine learning (ML) techniques and neural networks (NN). Differences in size of the tooth marks were observed either by the investigation of raw linear measurements (scores) or centroid size (pits), commonly used size measure in GMM studies calculated as the square root of the sum of all the square distances between the landmark configuration and their centroid (Klingenberg, 2016).

3. Results

A total of 23 australopith specimens could be identified as bearing carnivore modification (Table 1, Figs. S2 and S3). Of these, three specimens are cranial skeletal parts and 20 are appendicular bones (Table 1). No non-cranial axial elements showed any carnivore modification. Tooth mark frequency (including pits, scores, furrowing, and digestion) is very low, only 3.3% specimens of the hominin sample showed any kind of carnivore modification. The

Table 1
Carnivore modifications in the Member 4 hominin assemblage. * Please note that StW 99 is usually attributed to *Australopithecus*, but it has been hypothesized that it could rather be allocated to *Paranthropus* (Kuman and Clarke, 2000; Pickering et al., 2021).

Specimen number	Element	Grid information	Carnivore modification
StW 99*a,b	femur	X44 (5′9″–6′9″) and W46 (6′11″–7′11″)	Furrowing
StW 121	femur	W46 (9′11″–10′11″)	Furrowing
StW 124	humerus	T49 (14′8″–15′8″)	1 pit/1 score
StW125	radius	T49 (16′8″–17′8″)	Furrowing
StW 129	femur	T50 (18′10″–19′10″)	Furrowing/2 pits
StW 150	humerus	O45 (13′3–14′3″)	Furrowing
StW 182	humerus	R46 (13′11″–14′11″)	Furrowing/1 pit
StW 252	skull	W46 (24′10″–25′10″)	Digestion
StW 338	skull	T49 (14′8″–15′8″)	1 score
StW 339	humerus	V43 (6′7″–7′7″)	Furrowing/3 scores
StW 347	talus	R43 (11′2″– 2′3″)	1 pit
StW 348	radius	W42 (8′7″–9′7″)	1 score
StW 349	ulna	W42 (8′7″–9′7″)	Furrowing/1 possible pit
StW 357	mandible	P44 (13′5″–14′5″)	Digestion/green fracture
StW 367	femur	R43 (16′0″–17′0″)	Furrowing
StW398b	ulnae	P44 (18′11″–19′10″)	Digestion
StW 577	ulna	R41 (14′7″–15′4″)	4 Scores/1 pit
StW 613	ulna	P45 (27′1″–28′1″)	Digestion
StW 626a	ulna	N48 (15′0″–16′0″)	Furrowing/2 scores
StW 626 b	radius	N48 (15′0″–16′0″)	More than 10 scores
StW 628	metatarsal	N48 (19′0″–20′0″)	Digestion
StW 634	metatarsal	N49 (22′0″–24′0″)	Digestion
StW 38	humerus	Dump 18	2 Scores

number of tooth marks per specimen is also low. Only one specimen showed more than ten scores, the radius StW 626 b (Table 1). As previously pointed out by Pickering et al. (2004a), two partial skeletons (StW 431 and Sts 14) did not show any carnivore modification. Both the low tooth mark frequency of the complete hominin sample and the absence of carnivore modification on partial skeletons suggest at least parts of the hominin carcasses were accumulated after natural deaths instead of by biotic taphonomic agents. Fifteen australopith remains showed possible carnivore action, but the bone surface preservation did not allow confirmation of carnivore-inflicted modifications. These specimens were: StW299 (skull), StW316 (skull), StW411 (skull), StW521 (skull), StW302 (skull), StW326c (ulna), StW403 (femur), StW501 (femur), StW479 (femur), StW522 (femur), StW88 (talus), StW102 (talus), StW366 (scapula), StW14 (mandible) and StW25 (femur). Even if these hominin specimens were included in the analysis, the frequency of carnivore action would remain low. During the taphonomic study other kinds of bone surface modification were identified, such as biochemical marks or modifications produced by insects. These taphonomic modifications not produced by carnivores will be discussed elsewhere.

According to the results obtained on the tooth mark digital models, the four modern carnivore groups studied here can be distinguished to a lesser or greater extent based on the morphology and size of the traces they leave on long bones after consumption. The more classical statistical analyses (PCA, LDA) conducted for the present study show different success rates on separating the carnivore groups based on the morphological trends observed among the pits and scores generated by lions, leopards, and spotted and brown hyenas. However, the implementation of highly accurate ML models, such as gradient boosted machines (GBM) and decision trees with the C5.0 algorithm (DT C5.0), along with NN provides very efficient ways of distinguishing among the four carnivore groups on the basis of the tooth pits and scores they generate (tables S2 and S3).

Comparisons between the carnivore modern sample and the tooth marks identified on the Sterkfontein australopithś long bones highlight the morphological affinities between the marks on the Sterkfontein hominins and the traces left by brown hyenas

(Table 2). Classifications are, however, not fully consistent, as some degree of overlap is still observed between the modern carnivore sample.

PCAs in shape space (Fig. S4) do not offer a clear association between the Sterkfontein scores and any of the modern carnivore groups, though they tend to be better associated with all carnivores except leopards. When size is accounted for, the association of the Sterkfontein scores with a single carnivore group, namely brown hyenas, is more significant (Fig. S4), though there is still certain overlap with other carnivore groups in 2D space. The predictions provided by the LDAs (table S4) reflect the distribution observed in the PCAs. Shape data do not accomplish a clear, singular association of the Sterkfontein marks, but emphasise that no score could be associated with the action of leopards. On the other hand, size data highlight the similarities between the Sterkfontein score morphology and the data observed among brown hyena scores. ML models (Table 2) emphasise the association of the Sterkfontein scores with the brown hyena group. The predominant association of the scores identified on the South African australopiths is clearer when size features are accounted for. Nevertheless, ML models find stronger shape similarities between the brown hyena scores and those registered on the Sterkfontein fossil hominins.

Similarly, the PCA graphs generated for the Sterkfontein pits against the modern carnivore sample suggest a more straightforward discrimination when size is considered in the analysis (Fig. S5). The outstanding differentiation between the group formed by leopards and brown hyenas and the group formed by lions and spotted hyenas on the basis of form features clearly locates the Sterkfontein pits in the former group. The boxplot (Fig. S6) comparing the centroid sizes calculated for the Sterkfontein pits with those generated by leopards and brown hyenas, stresses that the similarities in size between both carnivore species are relevant enough to raise doubts about the association of the Sterkfontein pits with any of the groups. However, brown hyenas seem to be capable of generating larger pits than leopards (Fig. S6). This is particularly important considering that one of the pits identified on the australopith specimens seems to be larger than both the pits recorded for brown hyenas and leopards. The morphological equifinality produced by the shape and form of pit features is also

Table 2
Results for the machine learning most accurate models. Summary of the classifications provided by the most accurate machine learning models for the most conspicuous pits and scores identified on the long bones of the Sterkfontein australopiths included in the present study.

Model	Accuracy	Kappa	95% CI	Scores on StW hominins								Pits on StW hominins	
				StW 124a	StW 339a	StW 339 b	StW 339c	StW 38a	StW 38 b	StW 577a	StW 577 b	StW 182a	StW 577c
Shape													
GBM	1	1	0.96−1	b hyena	s hyena	b hyena	b hyena	lion	s hyena	s hyena	b hyena		
DT C5.0	1	1	0.91−1	b hyena	b hyena	b hyena	b hyena	b hyena	b hyena	b hyena	b hyena		
NN	0.79	0.72	0.7−0.87	b hyena	b hyena	b hyena	b hyena	lion	lion	b hyena	b hyena		
NN	1	1	0.95−1									b hyena	b hyena
GBM	1	1	0.95−1									s hyena	b hyena
DT C5.0	1	1	0.88−1									b hyena	b hyena
Form													
DT C5.0	1	1	0.88−1									b hyena	b hyena
GBM	1	1	0.95−1									leopard	b hyena
NN	0.93	0.9	0.83−0.98									leopard	b hyena
Biometric data													
GBM	1	1	0.95−1	b hyena	b hyena	b hyena	b hyena	b hyena	b hyena	b hyena	b hyena		
DT C5.0	1	1	0.91−1	b hyena	b hyena	b hyena	b hyena	b hyena	b hyena	b hyena	b hyena		
NN	0.97	0.96	0.91−0.99	b hyena	b hyena	b hyena	b hyena	b hyena	b hyena	b hyena	b hyena		

reflected in the LDA results, where the Sterkfontein pits appear indistinctively associated with leopards and brown hyenas (table S4). This comes as no surprise since the LDA accuracy reached for the modern carnivore pit sample was not particularly high and similarities in size between the leopard and brown hyenas pits did not allow proper distinction of both groups based on form data (table S5).

Classification problems observed in the LDAs could be overcome by more powerful techniques. ML models (Table 2) do not only achieve higher accuracy rates when classifying the modern sample, but they also are more suggestive of a strong association between the Sterkfontein pit sample and brown hyenas. In this particular case, the ML prediction based on shape features seems to be more significant due to the great overlap in size of the pits inflicted by leopards and brown hyenas. The discrimination provided by tooth mark size features acts as filter and highlights a preliminary association of the Sterkfontein scores with brown hyenas and of the Sterkfontein pits with the group formed by brown hyenas and leopards. Consideration of shape features alone or in combination with size, generally highlights the association of the Sterkfontein tooth marks with those generated by brown hyenas, leading to the idea that those australopiths were only modified by brown hyenas.

4. Discussion

Several taphonomic variables such as skeletal part representation and tooth mark frequency, among others, have previously been used by researchers to analyse the carnivore taxa involved in hominin modification in Sterkfontein Member 4. However, these taphonomic variables exhibited issues of equifinality and prohibited identification of the carnivore species involved beyond suggestion of its large size (Brain, 1981; Pickering et al., 2004a). Recently, new hominin fossils have been recovered from Sterkfontein Member 4 (Pickering et al., 2019), stimulating a re-examination of the complete hominin collection. The re-analysis confirms that carnivore modifications are infrequent on Sterkfontein australopiths (Table 1). The presence of two partial skeletons (Sts 14 and StW 431) with no biotic modification indicates that hominin skeletons were partly accumulated through natural deaths. The same scenario is found in Sterkfontein Member 2, where the almost complete australopith skeleton (StW 573) was found without any carnivore modification (Pickering et al., 2004b). Thus, it seems that australopiths have died naturally in the vicinity of, and/or inside the Sterkfontein Cave since Member 2 times. On

the other hand, the identification of a few tooth marks on some hominin remains demonstrated that carnivores also modified australopiths (Table 1). Previous research observed that carnivore collecting behaviour (felids and hyenids) usually results in higher tooth mark frequencies (Pickering et al., 2004a). It has been argued that tooth mark scarcity may be due to preparation damage, post-depositional processes, or the action of extinct carnivore species with unknown taphonomic behaviour (Pickering et al., 2004a). However, hyenid scavenging may also produce low tooth mark frequencies (Blumenschine, 1988) and can be considered a potentially relevant accumulation hypothesis. In addition to a low tooth mark frequency, there is a lack of long bone epiphyses and smaller compact bones such as carpals/tarsals in the hominin assemblage (Pickering et al., 2004a; Clarke, 2013). It has been suggested that selective transport by carnivores from kill sites, slope wash processes, or identification bias of long bone fragments may have affected skeletal part frequency (Pickering et al., 2004a). Nevertheless, neotaphonomic experiments have shown that hyenid scavenging preferentially removes ends of long bones and compact bones (Marean and Spencer, 1991). Both low tooth mark frequency and biased skeletal part representation may be explained by secondary access to australopith carcasses by hyenas. Additionally, the application of new methodological approaches such as micro-photogrammetric 3D reconstruction of tooth marks (Fig. 2) and geometric morphometric analyses provides sufficient morphological data to distinguish between African carnivores (e.g., lion, brown hyena, spotted hyena and leopard) based on the traces they generate - overcoming some of the equifinality problems hindering previous taphonomic studies. Multivariate statistics, as well as powerful models based on artificial intelligence algorithms, suggest that the tooth marks found on the Sterkfontein australopiths and those inflicted by brown hyenas are morphologically similar (Table 2).

Brown hyenas are primarily scavengers, and only a small proportion of their diet derives from hunting. They mainly scavenge from large predator kills and natural deaths (Mills, 1990) and bones of extant primates have been found at modern brown hyena dens and scats (Brain, 1981; Skinner, 1976; Kuhn et al., 2008). This research suggests that it is likely that brown hyenas scavenged australopith carcasses after natural deaths. It is not clear whether australopiths may have naturally died inside the cave, assuming that the upper chambers could have been used as a retreat in a similar way to chacma baboons (Brain, 1981; Val et al., 2014; Nel et al., 2021), or in the vicinity of the cave and were then

accumulated in the inside of the upper chambers by hyenas. The earliest evidence of the brown hyena in South Africa is found in Sterkfontein Member 4 (Turner, 1987) and the proximity and stratigraphic association of the specimen to australopith remains bearing tooth marks (table S6) supports the proposal that the brown hyena was the taxon that modified the australopith body parts. It has been argued that the entrances to the caves during the time of australopiths were vertical shafts and the upper chambers of the caves were accessible only when the talus infill had nearly reached the roof (Clarke, 2013). The recorded depth information from the brown hyena specimen from Sterkfontein Member 4 is consistent with the scenario where the upper surface of the sedimentary infill would have reached close to the roof of the chamber, enabling use of the upper area as den (table S6). Furthermore, taphonomic analyses conducted on bovid material from Sterkfontein Member 4 and 5 indicated that hyenas may have used the cave as a den (Pickering, 1999; Kibii, 2004). Further, the Sterkfontein Member 5 bovid assemblage has been interpreted as a brown hyena den due to the presence of coprolites and brown hyena skeletal parts (Pickering, 1999). The same accumulation scenario is plausible for australopiths during the formation of Sterkfontein Member 4, at least in the later periods of the sedimentation process. It is important to note that it has been suggested that the non-hominin primate sub-assemblage from Swartkrans Hanging Remnant Member 1 may have been modified by hyenas (Carlson and Pickering, 2003). Further, a taphonomic study of non-hominin primates and seven *Paranthropus robustus* remains from Cooper's D, a palaeocave situated less than two miles east of Sterkfontein, showed that both leopards and brown hyenas could have modified/accumulated primate remains. Equifinality problems of taphonomic variables prohibited distinction of the carnivore taxa involved at Cooper's D (Val et al., 2014). Altogether, these results emphasise that brown hyenas should be considered a potential taphonomic agent for hominin modification and accumulation in South African karstic systems.

Australopiths from Sterkfontein Member 4 being accumulated mainly by natural deaths and brown hyena scavenging should be considered for the reconstruction of hominin palaeobiology. It has been proposed that differential sex ratios in the australopith record from Swartkrans and Sterkfontein reflected different hominin social structures, if both populations were preyed upon by leopards practicing selective predation (Lockwood, 1999; Lockwood et al. 2007). Sex attribution of australopiths at Sterkfontein has been demonstrated to be problematic (e.g., Grine, 2013) and further complicated by proposed taxonomic heterogeneity (for discussions see Clarke, 1988, 1994, 2008, 2013; Grine, 2013, 2019; Grine et al., 2013; Clarke and Kuman, 2019; Zipfel et al., 2020; Ward and Zipfel, 2020). It is clear from this research that predator activity at Sterkfontein (at least) is more complicated than has been proposed previously and the action of scavengers such as the brown hyena can result in balanced sex ratios that do not reflect dissimilar social structure between australopiths. While leopard hunting may produce sex ratios biased to *Paranthropus* males at Swartkrans due to predator sex preferences, hyena scavenging and natural deaths may reflect the natural population proportions of *Australopithecus* at Sterkfontein. We believe that it is important to conduct taphonomic studies to better comprehend the nature of the accumulations of australopiths and the carnivore predation rate. Carnivore predation on australopiths has also been used to explain the retention of certain anatomical features and locomotor capacities in early hominins. It has been posited that australopiths were committed terrestrial bipeds but their locomotor system retained significant adaptations to arboreality (Jungers, 1982; Green, 2020). There is a debate concerning whether these anatomical features were retained because they granted fitness to australopiths or

because of neutral selection (Ward, 2013). The retention of arboreal capabilities could have been advantageous to avoid carnivore predation, find shelter to sleep or get access to fruits, ultimately improving individual fitness (Ward, 2013; Lieberman, 2015). Results presented here demonstrate that taphonomic histories of archaeopaleontological sites are complex due to the intervention of multiple agents in bone assemblage accumulation. Furthermore, it has been shown that the presence of tooth marks on hominin remains per se does not ensure that hominins were predated rather than scavenged. Thus, carnivore predation rate on early hominins should be considered with caution when constructing palaeobiological hypotheses, even if tooth marks are found on hominin remains.

Declaration of competing interest

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Author contributions

Taphonomic Sterkfontein analysis, brown hyena and leopard modern dens analysis and project conceptualization: M.C.A. Geometric morphometric analyses: J.A. Virtual reconstruction of tooth marks and Fig. 2: M.A.M.G. Spotted hyena and lion modern sample analysis: J.Y. Sterkfontein excavations, project management and Fig. 1: D.S. Writing: M.C.A. with contributions from J.A. and D.S. J.A. and D.S edited the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2021.107252.

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