The macrovertebrate fossil assemblage from the Name Chamber, Sterkfontein: taxonomy, taphonomy and implications for site formation processes

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The Name Chamber contains some of the deepest fossiliferous deposits in the Sterkfontein Caves, at ~20 metres below the surface deposits of Members 4 and 5. Recent excavations complemented by detailed studies of the geological context, as well as of the microfaunal and lithic (i.e. Oldowan artefacts) assemblages, have shed some light on the complex history of sediment accumulation in that part of the Sterkfontein karstic system. The Name Chamber has a long and intricate history of deposition that is of particular value for understanding the redistribution of Oldowan-bearing sediments from Member 5 into the deep chamber below. Recognizing sediment movement and sources through multidisciplinary investigations is of key importance to reconstructing primary lithic assemblages and ultimately the behavioural proxies associated with them. Here, we present the results of a taxonomic and taphonomic analysis of the macrofaunal assemblage recovered during excavations of the decalcified sediments of the Western Talus in the Name Chamber. The taxonomic composition of the faunal spectrum is similar to that of Member 5 East Oldowan, with an overrepresentation of medium-sized bovids and the occurrence of taxa associated with grasslands. The taphonomic features of the fossil remains are characteristic of a mixed assemblage with indications of contributions by carnivores, slope wash and gravity collecting bones from the catchment surface (including carnivore-gnawed and butchery-marked specimens). The results independently corroborate lithic and microfaunal analyses and support the hypothesis of multiple origins for the sediments of the Name Chamber, with a main contribution from Member 5 East Oldowan (notably illustrated in the Name Chamber assemblage by the identification of several cut-marked remains and a bone tool), shortly after it accumulated at about 2.18 Ma. There is also indication of a minor contribution from Member 4 but no evidence for a noticeable contribution from Post-Member 6 (L/63 Infill).

Keywords: Sterkfontein Caves, Name Chamber, cave taphonomy, faunal analysis, Plio-Pleistocene, early hominins.

INTRODUCTION

Continuous work for more than 75 years in the Sterkfontein Caves, in the UNESCO World Heritage Site of the Cradle of Humankind, South Africa (Fig. 1), has led to the recovery of abundant fossils of early hominins and associated fauna, dating back from 3.67 ± 0.16 Ma to the mid-late Pleistocene (Broom 1936; Brain 1981; Kuman 1994a; Reynolds & Kibii 2011; Granger *et al.* 2015). Detailed studies of these fossils have greatly contributed to document the modalities of human evolution in the southern part of the African continent. Member 4 of the Sterkfontein Formation (Partridge 1978) especially has produced the most prolific assemblage of australopithecine remains in the world, found in association with large macro- and microfaunal assemblages. Member 5 has yielded the largest and most complete Oldowan sample in southern Africa associated with *Paranthropus robustus*, and an early Acheulean industry associated with *Homo ergaster* (Brain 1981; Pickering 1999; Kibii 2004; Kuman 1994a,b; Kuman & Clarke 2000; Reynolds & Kibii 2011). As expected in karstic systems, the history of sediment accumulation is complex. The lower subterranean parts of the caves, namely the Silberberg Grotto, Milner Hall, Jacovec Cavern, and Name Chamber contain deposits that represent intricate and long infilling sequences that have only recently been the focus of dedicated stratigraphic studies (e.g. Clarke 1994; Stratford 2011; Stratford *et al*. 2012, 2014; Bruxelles *et al.* 2014). One of the questions still debated concerns the exact nature of the relationship between the sediments and fossil assemblages recovered from the subterranean chambers (Members 2 and 3 in the Silberberg Grotto) with those found in the exposed deposits of the Sterkfontein main excavation area (Members 4 and 5) (Fig. 1) (Robinson 1962; Wilkinson 1983; Partridge & Watt 1991; Pickering & Kramers 2010; Stratford *et al*. 2014). This research contributes further to the multidisciplinary study of the Name Chamber faunal and archaeological assemblages and their stratigraphic histories in order to help clarify these relationships in this part of the caves.

The Name Chamber is one of the most recent parts of the Sterkfontein Caves to have undergone excavations and received comprehensive geological attention (Avery *et al*. 2010; Stratford 2011; Stratford *et al*. 2012). Early pilot excavations were conducted in 2000, before more extensive

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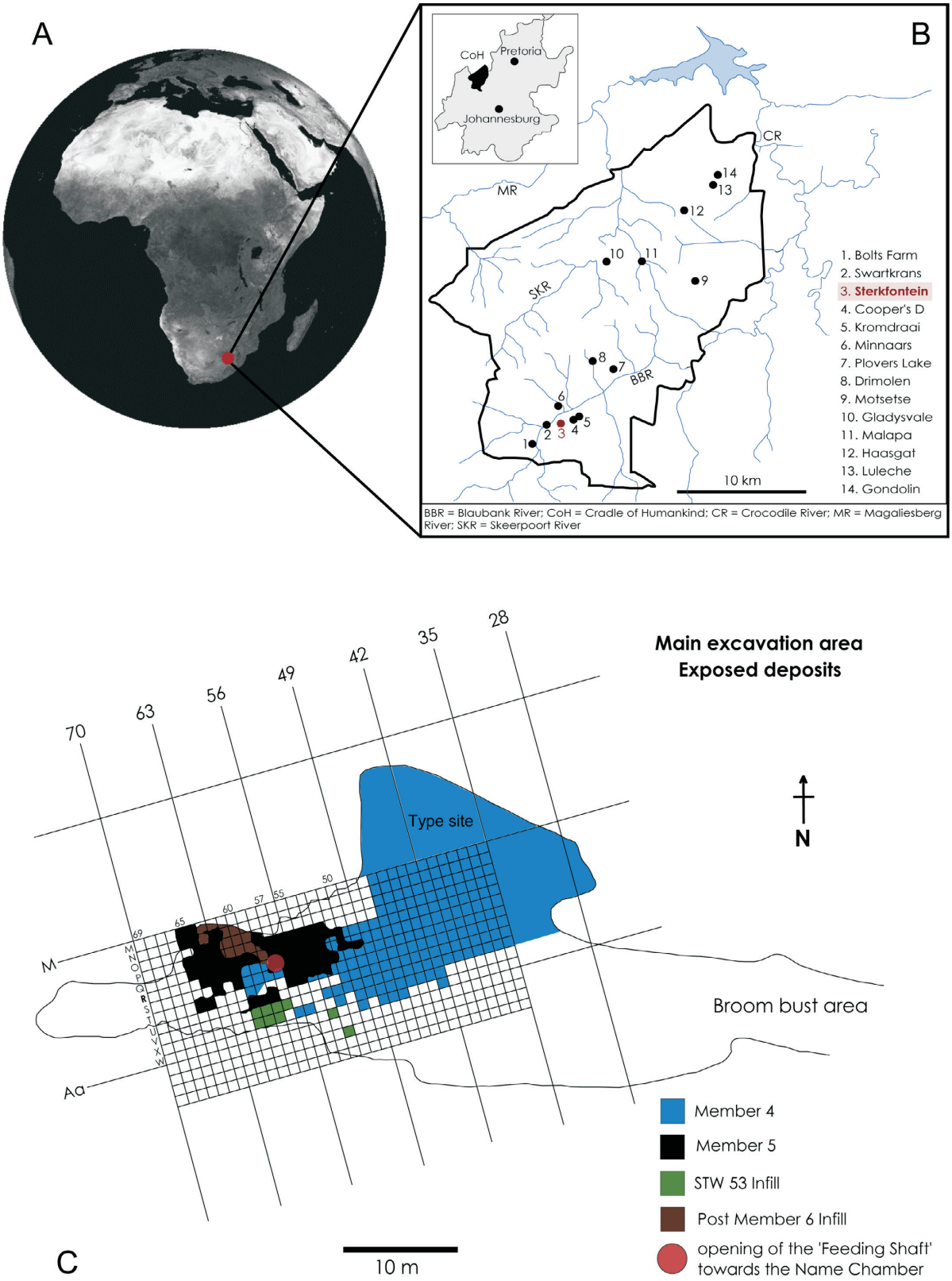

Figure 1. Geographical situation of the Sterkfontein Caves inside the Cradle of Humankind in South Africa (**A** & **B**) and location of the Name Chamber (**C**), from Kuman & Clarke (2000), modified.

excavations took place between 2007 and 2009, under the direction of Clarke and Stratford. The Name Chamber lies directly below the exposed deposits of Member 5 about 20 metres below the landscape surface (Robinson 1962; Clarke 1994). More precisely, the shaft (referred to as the 'Feeding Shaft'), through which most of the sediments from the Name Chamber are thought to originate, opens directly to the excavated Member 5 deposit in square R57 in the main excavation area, on the western fringe of Member 5 East (Clarke 1994; Figs 1 & 2). The deposits of the Name Chamber consist of calcified and decalcified sediments that have accumulated from the deposits exposed on the surface through the 'Feeding Shaft'. Within the Name Chamber itself, the infills are divided

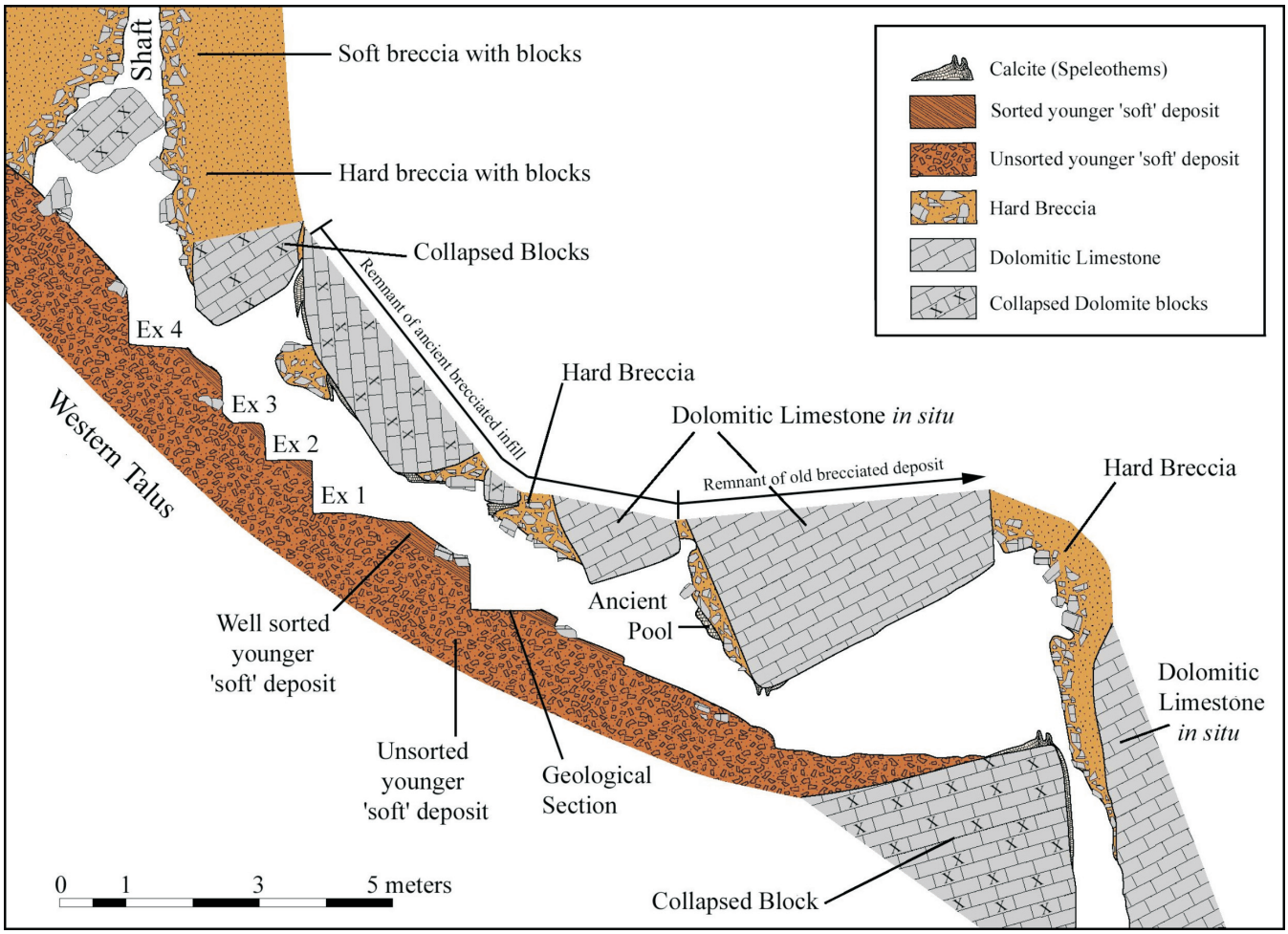

Figure 2. Stratigraphic profile of the Name Chamber.

into two steep talus cone deposits, the Eastern and Western talus deposits, which are separated by a large collapsed dolomite roof block (Fig. 2). Three stratigraphic units have been identified, consistent with successive events of sediments being introduced into the cave. The two first units (the Ancient and Old Brecciated Deposits) have not yet been excavated and are largely represented by calcified remnants preserved on the walls of the chamber. The fossil assemblage presented here comes exclusively from the third unit, called the Younger 'Soft Deposit', and was excavated from decalcified sediments of the Western Talus. The areas focused on for the excavations were chosen based on accessibility and were placed at medial and distal portions of the talus. The Eastern Talus was not excavated because it is significantly steeper and less accessible than the Western Talus. Based on the occurrence, in the Western Talus, of more than a thousand artefacts typologically attributed to the Sterkfontein Oldowan industry, an overrepresentation of the <2 cm fraction in the lithic assemblage (Stratford *et al*. 2012), and the taxonomic composition of the microfaunal assemblage (Avery *et al*. 2010), it has been hypothesized that the sediments from this soft deposit mostly come from Member 5 East Oldowan. Nevertheless, contribution from other parts of the cave system, especially Member 4 and Post-Member 6 (L/63 Infill), cannot be excluded. As identified by Moen and Keyser (Clarke 1994), the 'Feeding Shaft' transects at least parts of the Member 4 deposit.

The aim of this paper is to describe the taxonomic composition of the macrofaunal assemblage recovered from the Western Talus and to propose a thorough analysis of its taphonomic features. Results are compared with taxonomic and taphonomical characteristics of the fauna from Member 5 East Oldowan, Member 4 and Post-member 6 (L/63 Infill), in order to further test the hypothesis that the dominant sediment source is Member 5 East Oldowan and assess the possible degree of contribution of the overlying deposits that are found in close proximity to the 'Feeding Shaft' opening in the Sterkfontein surface excavation (Fig. 1). A brief description of the potential contributing deposits and their macrofaunal assemblages is provided below (see also: Table S1).

Member 4

Member 4 represents the largest deposit exposed on the landscape surface and has been the focus of most excavations at Sterkfontein. It is generally located in the central and eastern areas of the surface excavation site and contains the important 'Type Site' from which the first hominin specimen was discovered in 1936 (Broom 1936). Various dating methods including biochronology, palaeomagnetism, Electon Spin Resonance (ESR), Uranium-Lead and Uranium-Thorium isotopes (Vrba 1976, 1980; Delson 1984, 1988; Schwarcz *et al*. 1994; Partridge 2005; Pickering & Kramers 2010; Herries & Shaw 2011) suggest an age between 2.0 and 2.8 Ma for this large

deposit. Member 4 has yielded over 750 australopithecine specimens representing a minimum number of 87 individuals (Pickering *et al*. 2004a), attributed to *Australopithecus africanus* and *Au. prometheus* (Clarke 2006, 2013). The hominin remains were found in association with abundant faunal remains. The fauna recovered from Member 4 was first studied by Brain (1981) and more recently re-examined by Kibii (2004), who analysed the non-hominin remains, and Pickering and colleagues (2004a), who focused on the taphonomy of the hominin assemblage. Other extensive and diverse studies have been conducted on macrofaunal assemblages yielded from Member 4 (e.g. Broom *et al*. 1950; Ewer 1956; Vrba 1976, 1980; Brain 1981; Delson 1984; Clarke 1988, 1994; Turner 1987, 1997; Pickering 1999; Lockwood & Tobias 2002; de Ruiter 2004; Kibii 2004; Curnoe & Tobias 2006; Moggi-Cecchi *et al*. 2006; O'Regan & Reynolds 2009). The occurrence in the fossil assemblage of the large extinct caprid species *Makapania broomi*, as well as fossilized lianas that require large trees for support (*Dichapetalum mombuttense*; Bamford 1999), indicates moister and more wooded habitats around the site at that time, while species associated with grassland and drier conditions such as *Equus*, *Pedetes* and *Struthio* are absent (Brain 1981; Kuman & Clarke 2000; Reynolds & Kibii 2011). These results are mostly corroborated by analyses of stable carbon isotopes from fossil tooth enamel (see for instance: van der Merwe *et al*. 2003; Codron *et al.* 2005; Lee-Thorp *et al*. 2007).

The taphonomy of the Member 4 assemblage is complex, largely because of the lack of stratigraphic resolution and the enormous 600 000 year time frame represented by the deposit, which is generally analysed as a single entity. The accumulation of the faunal remains inside the deposit is better explained by the combined action of several biotic and abiotic agents; the possible existence of several entrances to the cave; and the repeated introduction of animal remains over a long period of time rather than as a single event (Brain 1981; Kibii 2004; Pickering *et al*. 2004a; Reynolds & Kibii 2011). Large carnivores using the cave as a den combined with a natural death trap scenario seem to explain the origin of most carnivore and bovid remains, while a few individuals might also have been introduced by slope wash (Brain 1981; Kibii 2004). The majority of bone surface modifications observed on the bovid remains are due to carnivore chewing and numerous large carnivore cranial elements together with spotted hyaena coprolites were identified in the assemblage. However, the presence of low-density elements such as ribs and vertebrae, including those of juveniles, which lack any evidence of carnivore activity, indicates that some animals entered the cave via a natural death trap. This is confirmed by the presence of two partial australopithecine skeletons, Sts 14 and Stw 431 (Toussaint *et al.* 2003 and references therein). The carnivore-collecting hypothesis was postulated by Brain (1981) and is supported by more recent studies (Pickering *et al*. 2004) to explain the abundance of hominin remains in Member 4. There seems to have been a predator selection towards smaller individuals that is, females and juveniles. The overrepresentation of cranial material and underrepresentation of postcranial material is interpreted as a consequence of feeding on the hominin carcasses by large carnivores (felids and/or hyaenids). There is no evidence that the cave was used by the hominins: stone artefacts, burnt or cut-marked bones are absent from the assemblage (Brain 1981).

Member 5 East Oldowan

Member 5 formed on the irregular erosional surface of the Member 4 deposit and is found in the western areas of the surface exposed breccias. The basal part of Member 5 has yielded a large and informative Oldowan industry (Kuman 1994a,b; Kuman & Field 2009) and is mainly restricted to the eastern part of the Member 5 deposit. Based on biostratigraphy, lithic industry, ESR, isotopic analyses and palaeomagnetism, Member 5 East Oldowan deposits have been dated to 2.0–1.1 Ma (Kuman & Clarke 2000; Herries *et al.* 2009; Herries & Shaw 2011). A recent study proposes an earlier age for the deposits, with a new cosmogenic date at 2.18 ± 0.21 Ma (Granger *et al.* 2015). The faunal assemblage, largely dominated by bovids, and especially medium-sized bovids (i.e. class II), comprises 28 274 remains. The occurrence of *Equus*, *Pedetes* and *Struthio* is consistent with grassland habitats and drier conditions in the vicinity of the site (Brain 1981; Kuman & Clarke 2000; Lee-Thorp *et al.* 2007). Five hominin specimens were recovered, including at least three attributed to *P. robustus* (Pickering 1999; Kuman & Clarke 2000).

A detailed taphonomic study of the fauna was conducted by Pickering (1999), who proposed the accumulation of animals falling inside the cave via a natural death trap, complemented by a few individuals and/or bones being washed directly from the landscape. This hypothesis is supported by the extremely low percentage of carnivore-modified material, representing only 0.6% of the faunal assemblage, as well as by skeletal survival patterns for bovids consistent with a natural death trap scenario rather than accumulation by mammalian predators. The presence of one cut-marked bovid scapula fragment is consistent with the practice of butchery activities by hominins in the cave catchment area. The abundant Oldowan stone tools ($n = 3245$) recovered from Member 5 East are also considered by Kuman (1994a,b; Kuman & Field 2009) to have been washed into the cave from the surface. Member 5 has yielded the only bone tool documented at Sterkfontein so far.

Post-Member 6 (L/63 Infill)

The L/63 Infill of Post-Member 6 is one of the recent deposits of the Sterkfontein Formation. Biochronological data and some of the artefacts recovered (i.e. Middle Stone Age stone tools) point towards a mid- to late Pleistocene deposit (Reynolds *et al*. 2007), while ESR dating proposes an age between 0.5 and 0.3 Ma (Herries & Shaw 2011). The sediments from Post-Member 6, similar to those of Lincoln Cave, are poorly calcified. Large carnivores are absent from the faunal assemblage ($n = 5584$), which comprises mostly ungulates and small to medium-sized carnivores, associated with a few remains of archaic *H. sapiens* (Reynolds *et al*. 2007). The faunal spectrum also includes *Equus* and *Pedetes*, generally associated with open habitats.

Compared to other deposits from Sterkfontein, the faunal sample is characterized by a relatively high percentage of remains gnawed by porcupines, with 1.86% of the assemblage modified by this rodent. A few hyaena coprolites were collected from the deposits but the absence of large carnivore remains together with the very low incidence of carnivore damage suggest a negligible carnivore contribution to the assemblage. No anthropogenic modifications, whether in the form of cut-marks, percussion marks or burning, were observed (Reynolds & Kibii 2011).

MATERIALS AND METHODS

The faunal sample analysed here was recovered during excavations conducted between July 2000 and September 2001 of an initial two-square-metre test pit inside the Young 'Soft Deposit' of the Western Talus (i.e. decalcified sediments) of the Name Chamber (Ex1 in Fig.2). Sediments excavated were systematically wet- and dry-sieved using 2 mm screen-meshes (Stratford *et al*. 2012). Results of the study of the mammalian microfaunal remains from this sample and further excavations (Ex 2, 3 & 4; Fig. 2) have been published elsewhere (Avery *et al.* 2010). The present work focuses therefore on the complete mammalian macrofauna and bird assemblage, with the exception of the dental remains, which could not be located. The impossibility to include teeth in the analysis has several limitations both in terms of degree of taxonomic identification and understanding of the fossil assemblage taphonomy. For instance, taxonomic attribution of bovid remains to species level relies almost exclusively on dental material, given the high degree of morphological similarities of postcranial elements between the various bovid species. Furthermore, the absence of dental material can mean the loss of potentially informative elements, such as carnivore deciduous teeth, typically associated with the use of the cave by carnivores as a denning site, especially in the case of hyaenids.

Preliminary taxonomic attributions, anatomical descriptions, and macroscopic bone surface analyses on the macrofaunal material have been conducted by several people (i.e. T.R. Pickering, S. Reynolds & K. Fatherley), but the results of these various ongoing studies were never published. Existing bone identifications were verified using the comparative collections of modern and extinct mammals hosted at the Evolutionary Studies Institute, as well as modern bird skeletons from the Ditsong Museum in Pretoria. Bone surfaces of all identifiable elements and all non-identifiable elements larger than 2 cm were systematically inspected using an Olympus SZ61 microscope (magnification up to ×45). For the non-identifiable elements smaller than 2 cm, a gross inspection of bone surface damage using a hand lens was conducted. Although this type of inspection may not always allow for superficial cut mark or insect damage identification, it is sufficient to recognize acid etched remains through digestion as well as bone percussion flakes. Breakage patterns have been described for long bone fragments, using criteria proposed by Villa & Mahieu (1991) for human long bones. The influence of abiotic processes potentially removing or limiting the visibility of informative animal and human-induced modifications on bones (e.g. cut marks and tooth marks) were quantified. These include: degree of manganese invasion, weathering stage (following Behrensmeyer 1978), water abrasion, chemical dissolution, presence/absence of matrix concretions, and decalcification. Five stages in the extent of precipitated manganese dioxide on the bone surface were recognized, from none, slight (only a few spots), slight to moderate (abundant spots covering less than 50% of the surface), moderate (>50% the surface of the specimen is covered) to heavy (whole surface of the specimen is covered). Various types of damage caused by biotic agents (root etching, carnivore and rodent gnawing, bird of prey beak and talon impacts, mammalian and/or avian digestion, insect boring and gnawing, animal trampling and hominin butchery) were recorded. The criteria used to distinguish between stone tool, carnivore tooth and trampling marks are based on the definitions proposed by Shipman & Rose (1983), Domínguez-Rodrigo and colleagues (2009) and others (Binford 1981; Behrensmeyer *et al.* 1986; Lyman 1994a). Data available in the literature concerning carnivore (e.g. Maguire *et al*. 1980; Binford 1981; Brain 1981; Shipman & Rose 1983; Lyman 1994a), rodent (Maguire *et al*. 1980; Binford 1981; Brain 1981; Shipman & Rose 1983), insect (Lyman 1994a; Britt *et al*. 2008; Backwell *et al*. 2012) and bird of prey (Andrews 1990; Bocheñski & Tomek 1997; Bocheñski *et al.* 1997, 1998; Laroulandie 2000, 2002; Bocheñski & Tornberg 2003) damage were used for comparative purposes. Definitions of the quantitative units used (i.e. NISP, MNE, MNI and percentage of survival) are those found in Lyman (1994b and references therein).

Due to the absence of dental material and the high degree of fragmentation, the majority of ungulate remains were only attributed a class size (following Brain 1974). Reconstitution of mortality profiles relies on age estimates of the individuals present in the faunal assemblage. In our case, given the absence of dental material, age estimates could rely only on the degree of fusion of long bones and phalanges, with three identifiable distinct stages: juveniles (epiphyses not fused at all), young adults (epiphyses fusing), and adults (epiphyses completely fused).

RESULTS

The total sample comprises 5828 bone fragments. Of this sample, 63 tooth fragments that had been mixed with non-identifiable long bone shaft fragments (small fragments of enamel of molar and premolars of ungulates) are excluded for the analysis since the rest of the tooth sample is missing. Another 27 remains of small rodents are also excluded from the analysis as the majority of the small rodent specimens have already benefitted from thorough descriptions (Avery *et al*. 2010). The sample studied here comprises therefore 5738 bone remains, including 554 specimens identified at least to the family level, 1973 non-identifiable fragments smaller than 4 cm and 3211 non-identifiable fragments smaller than 2 cm.

Composition of the faunal spectrum

The faunal assemblage is largely dominated by bovids, which compose 83% of the identified bone assemblage,

Table 1. *Composition of the faunal assemblage from the Name Chamber.*

ORDER	FAMILY	SPECIES	NISP	MNE	MNI
PRIMATES	Cercopithecidae	*Cercopithecoides williamsi*	1	1	1
		Papio sp.	7	7	1
		Large *Papio*	2	2	1
		Total primates	10	10	3
CARNIVORES	Felidae	*Panthera pardus*	6	5	1
		Felis sp. (size wild cat)	3	2	1
		Felids indet.	2	2	–
	Canidae	*Canis* sp. (size black-backed jackal)	2	2	1
		Canis sp. (size wild dog)	5	5	1
		Canids indet.	1	1	–
	Hyaenidae	*cf. Parahyaena brunnea*	1	1	1
		Hyaenids indet.	1	1	–
	Herpestidae	Herpestids indet. (size marsh mongoose)	2	2	1
		Carnivores indet.	9	9	–
		Total carnivores	32	30	6
ARTIODACTYLAE	Bovidae	*Connochaetes* sp.	7	7	1
		Damaliscus cf. dorcas	1	1	1
		Alcelaphus sp.	2	2	1
		Tragelaphus strepsiceros	1	1	1
		Bovids indet. Class I	7	7	2
		Bovids indet. Class II	317	134	5
		Bovids indet. Class III	115	56	5
		Bovids indet. Class IV	4	4	1
		Total bovids	454	212	13
	Suidae	Suid indet.	2	2	2
PERISSODACTYLAE	Equidae	*Equus* sp.	6	6	3
		Total ungulate indet.	94	–	–
RODENTS	Pedetidae	*Pedetes capensis*	3	3	1
	Leporidae	*Lepus* sp.	1	1	1
HYRACOIDS	Procaviidae	*Procavia transvalensis*	2	2	1
		Procavia sp.	1	1	1
BIRDS	Galliformes	*Numida meleagris*	1	1	1
	Colombiformes	*Columba* sp.	2	2	1
	Strigiformes	*Tyto alba*	7	7	2
	Charadriiformes	Indet.	1	1	1
	Falconiformes	Small kite/goshawk	1	1	1
	Passeriformes	*Corvus* sp.	1	1	1
		Passeriformes indet.	6	6	3
		Birds indet.	18	18	–
		Total birds	37	37	10
TOTALS		Total identifiable remains	554	304	41
		Total non-identifiable remains	5184	–	–
		GRAND TOTAL	5738	–	41

with class II bovids being the most numerous (69.3% of the bovid assemblage). Birds are also abundant in the assemblage with the second most numerous NISP and MNI. Carnivores and primates, even though relatively abundant in terms of MNI (with a carnivore/ungulate ratio of 33.3%), are only represented by a few remains and characterized by low taxonomical diversity (Table 1). Taxa consistent with open and dry conditions (i.e. *Equus* sp. and *Pedetes capensis*) occur in the faunal sample alongside taxa usually associated with woodland and more humid conditions (i.e. *Tragelaphus strepsiceros*) (Sponheimer *et al*. 2003; Skinner & Chimimba 2005) (Table 1). *Cercopithecoides williamsi* is represented in the assemblage by one tooth; based on morphological analyses and isotopic data, this cercopithecoid is regarded as an 'open mixed' species, practising terrestrial locomotion and including a significant amount of savanna-based C_4 resources in its diet (Elton 2000, 2001; Codron *et al*. 2005).

General preservation

The vast majority of the faunal sample is composed of non-identifiable remains (90.3%). The material is highly fragmented, with complete elements (n = 85) representing only 1.5% of the assemblage and including exclusively short compact bones, namely phalanges, sesamoids, carpals and tarsals. Despite the presence of large taxa (ungulates such as equids and bovids class III and IV), there is a clear overrepresentation of the small fraction

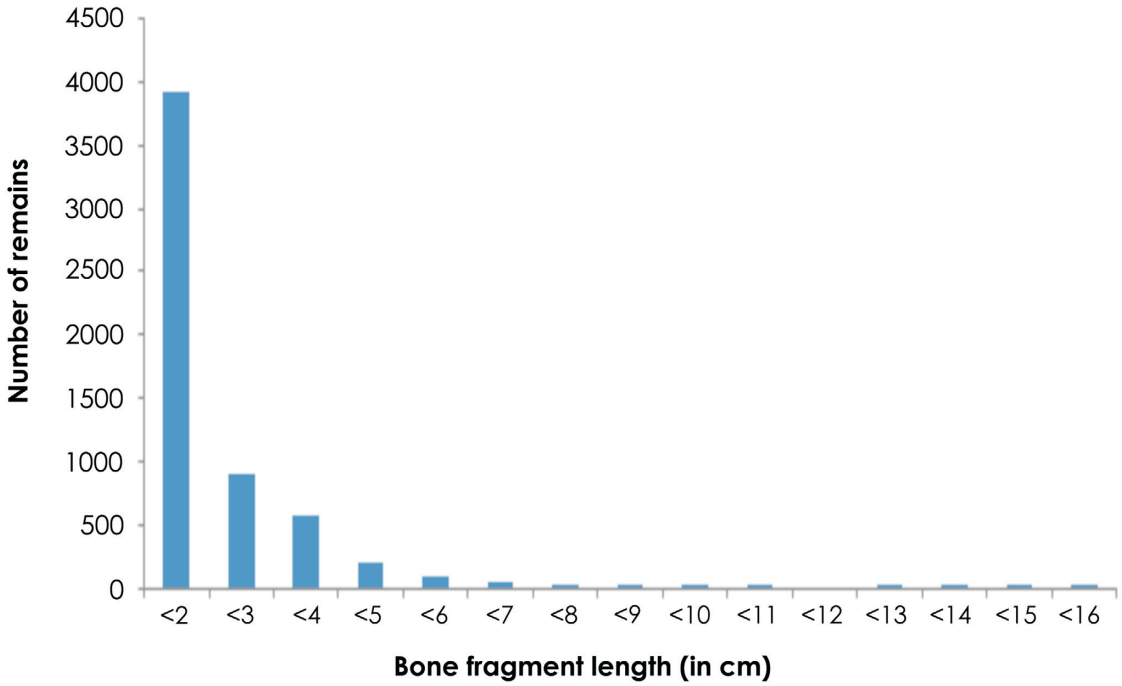

Figure 3. Distribution of the faunal remains from the Name Chamber according to their length.

with elements smaller than 2 cm constituting 56% of the assemblage and the existence of a dramatic decrease in size above 4 cm (Fig. 3). Elements preserved in articulation as well as antimeric bones are absent from the assemblage. No refitting between broken specimens was possible.

Breakage patterns could be observed on 1780 long bone fragment edges and are mostly consistent with dry fractures (n = 1524 or 85.6%). Green breakages were observed in 233 cases (13.7%), while 23 edges (1.3%) show evidence for recent breakage, probably occurring during excavations and/or curation of the material. Bone cylinders (i.e. long bones preserving most of the shaft but lacking the epiphyses), typical of carnivore-accumulated assemblages (Cruz-Uribe 1991; Pickering 2002; Kuhn *et al*. 2010) are absent from the assemblage.

32.2% of the elements for which this information was recorded (n = 2013) have undergone a decalcification process whereby the calcium initially present in the bone has disappeared, leading to a white chalky aspect of the fossils (Fig. 4). Manganese coating is present on the majority of the remains, from only a few dots (stage 1) to complete covering (stage 4), obscuring in the last case previous bone surface modifications (Table 2). The majority of the remains falls within stage 1 of weathering, with only superficial cracks visible on the surface of the cortical bone, but specimens characterized with deeper cracks, flaking and removal of the cortical bone consistent with stages 2 and 3 are also present (Table 3).

Fluvial action has produced rounding on 40 specimens, including 39 non-identifiable bone fragments, and one small fragment of bovid metapodial (Fig. 4).

Table 2. Distribution of bone remains according to the degree of manganese coating.

Manganese cover	0	1	2	3	4	Total
NR	62	425	936	527	56	2006
%	3.1%	21.2%	46.6%	26.3%	2.8%	100%

Table 3. Distribution of bone remains according to their degree of weathering (following Behrensmeyer 1978).

Weathering stage	1	2	3	4	Total
NR	1116	324	249	117	1806
%	61.8%	17.9%	13.8%	6.5%	100%

Body part representation

Most skeletal parts (limb, axial, cranial and distal elements) are present in the assemblage, with the exception of the sacrum. The general pattern of body-part representation seems to be slightly density mediated. Hence, in the bovid sample (Table 4), compact elements such as long bones,

Table 4. Bovid skeletal part frequencies in the Name Chamber assemblage.

Element	NISP	MNE	% Survival
Skull	66	7	53.8
Mandible	10	5	19.2
Scapula	4	1	3.8
Pelvis	3	3	11.5
Humerus	14	5	19.2
Radius	13	5	19.2
Ulna	16	4	15.4
Femur	7	3	11.5
Tibia	18	7	26.9
Metacarpal	21	6	23.1
Metatarsal	20	5	19.2
Patella	2	2	7.7
Carpal	8	8	5.1
Tarsal	19	15	11.5
Phalanx	72	59	18.9
Rib	31	11	3.2
Cervical	16	4	4.4
Thoracic	21	4	2.4
Lumbar	7	4	4.4
Vertebra tot.	46	14	2.4
Sacrum	0	0	0

Figure 4. General state of preservation of the Name Chamber faunal assemblage: **A & B**, superior and inferior views of specimen BP/3/29064, metatarsal shaft fragment, bovid class II, showing abrasion by water; **C & D**, closed up views of the abraded surface; **E–J**. superior and inferior views of non-identifiable bone fragments abraded by water; **K**, specimens BP/3/25618–25641, typical non-identifiable bone fragments smaller than 2 cm; **L & M**, different types of manganese coating; **O–R**, highly weathered remains (**O**, long bone shaft fragment; **P & Q**, superior and inferior views of specimen BP/3/27968, metatarsal shaft fragment, bovid class II; **R**, specimen BP/3/28833, proximal right ulna, bovid class II); **S & T**, specimen BP/3/25917, complete proximal phalanx, bovid class II, completely covered by sedimentary concretions; **U & V**, posterior and lateral views of specimen BP/3/29033, near complete talus, bovid class II, showing decalcification.

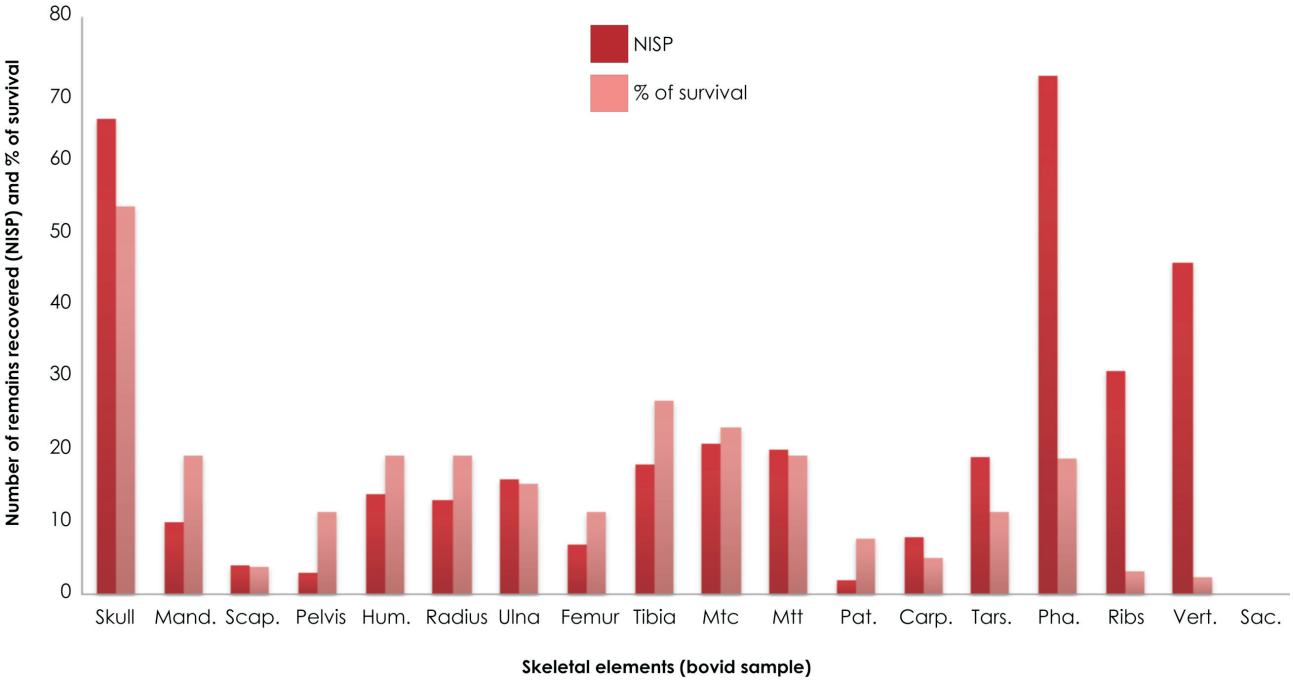

Figure 5. Body part representation pattern for the bovid sample (Mand: mandible; Scap: scapula; Hum: humerus; Mtc: metacarpal; Mtt: metatarsal; Pat: patella; Carp: carpals; Tars: tarsals; Pha: phalanges; Vert: vertebra; Sac: sacrum).

and especially long bone diaphyses, as well as short bones (phalanges, tarsals, carpals and sesamoids) (Lyman 1984; Kreutzer 1992; Lam *et al.* 1999) are the most abundant elements, just after cranial elements. However, low-density skeletal parts, namely ribs, vertebrae and patellae are also present (Table 4; Fig. 5), together with fragile and spongy bones such as non-fused long bone epiphyses of juveniles. Elements from the skull dominate, but this is largely due to the relative abundance of horn core fragments.

Mortality profile

As pointed out previously, age estimates are limited by the absence of dental specimens. Based on postcranial material, carnivores and primates seem to be represented only by adult individuals. The minimum number of 13 individuals composing the bovid sample is distributed as follows: two juveniles (one from class II and one from class III), three young adults (one from class I, one from class II and one from class III) and eight adults. The equid sample contains six remains, two of which belong to juvenile individuals and four to adults.

Bone surface modifications caused by biotic agents

Carnivore damage

There is clear indication of carnivore damage (Fig. 6; Table 5) in the assemblage (n = 94 or 1.6% of the whole assemblage). Specimens affected by pits, punctures and furrows include bovid, carnivore (one canid pelvis fragment and one felid humerus fragment), equid (one phalanx of a juvenile) and non-identifiable remains (Table 5). These modifications occur on various parts of the skeleton: long bones, phalanges, scapula, pelvis, ribs and tarsals. The majority of the digested remains are small fragments (<3 cm) of non-identifiable bones, with the exception of one caudal vertebra and an intermediate phalanx attributed to *Papio* sp. (Fig. 6; Table 5).

Other biotic damage

Only two specimens (both non-identifiable bone fragments) show evidence for porcupine gnawing. Bird of

Table 5. Bone surface modifications caused by biotic and abiotic agents observed in the Name Chamber assemblage.

Modification		Ungulate	Carnivore	Primate	Birds	Non-ident.	Total
Decalcification		161	9	1	–	478	649
Fluvial rounding		1	–	–	–	39	40
Trampling	striae	58	9	2	2	92	163
Root	etching	21	1	–	–	21	43
Carnivore	pits	20	2	–	–	30	52
	punctures	–	–	–	–	1	1
	scores	10	–	–	–	15	25
	crenulated edges	3	–	–	–	–	3
	digested remains	4	–	2	–	48	54
Porcupine	gnawing	–	–	–	–	2	2
Bird of prey	beak/talon impact	–	–	–	–	–	–
Insect damage		18	1	–	–	12	31
Anthropogenic	cut marks	10	0	0	–	6	16

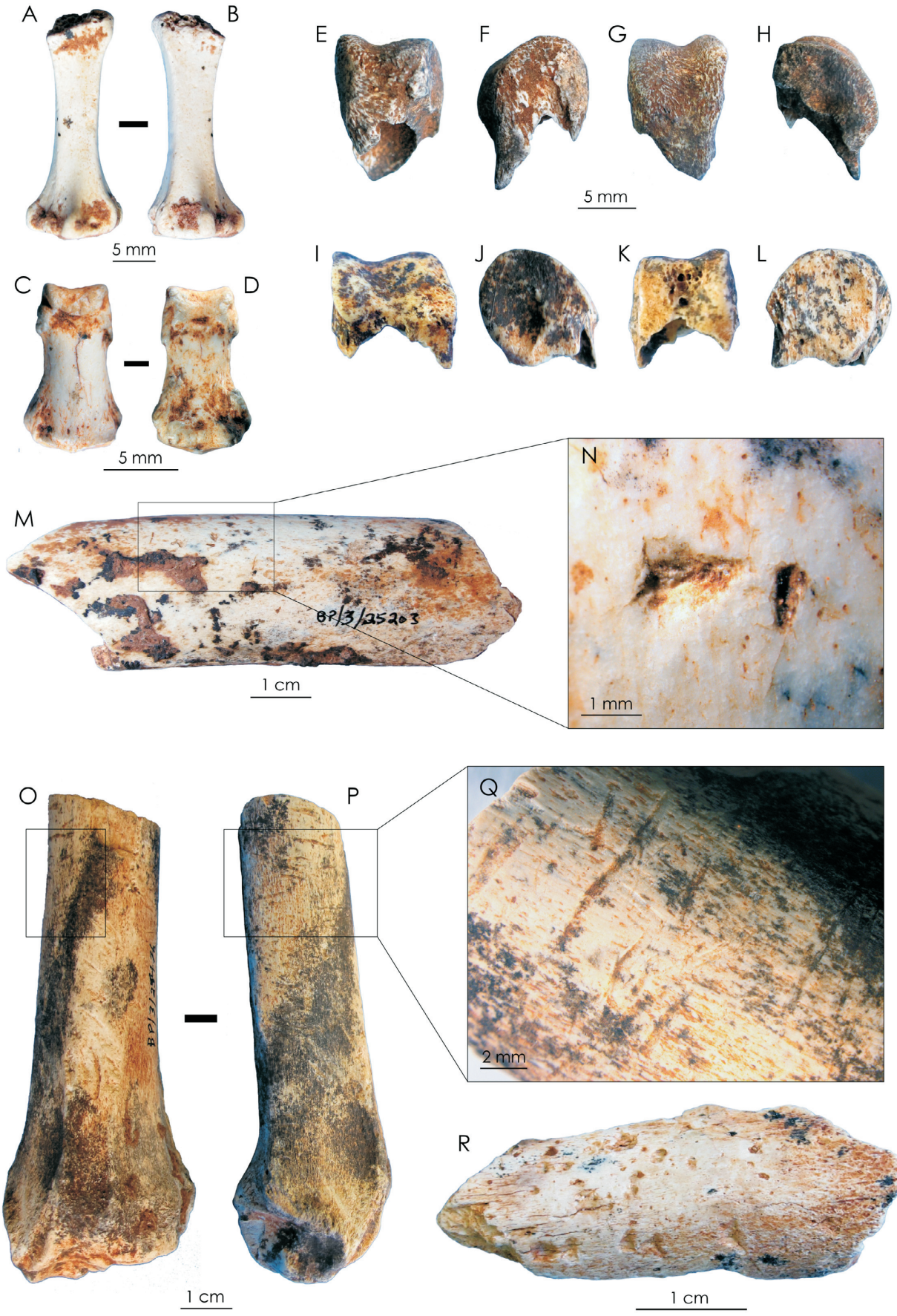

Figure 6. Bone fragments showing evidence of carnivore damage. **A–L**, examples of digested bones: **A & B**, specimen BP/3/31160, caudal vertebra, *Papio* sp.; **C & D**, specimen BP/3/31156, intermediate phalanx, *Papio* sp.; **E–H**, specimen BP/3/28239, proximal phalanx, bovid class I; **I–L**, specimen BP/3/29927, proximal phalanx, bovid class I; **M**, specimen BP/3/25203, femur shaft fragment, non-identifiable mammal, with carnivore pits and scores; **N**, close-up of the carnivore pits; **O & P**, anterior and lateral views of specimen BP/3/25476, distal radius, bovid class II, with carnivore scores; **Q**, close-up of the carnivore scoring; **R**, specimen BP/3/29436, long bone shaft fragment, non-identifiable mammal, with carnivore tooth pits and scores.

prey damage is not documented in the assemblage. Modifications produced by insects in the form of star pits, boreholes, parallel and intersecting striae are observed on 31 specimens. While it is not possible to determine with certainty the identity of the species at the origin of these modifications, it is possible to point out similarities between these modifications and those experimentally-created for termites (Backwell *et al*. 2012).

Anthropogenic modifications

Bone surface modifications linked to hominin butchery are visible in the assemblage in the form of 16 cut-marked bones (Fig. 7; Table 5). Unsurprisingly, no burnt bone was identified. The cut marks occur on bovid (class II and III) phalanges, metatarsal, tibia shafts, lumbar vertebra, ribs and taxonomically non-identifiable long bone shaft fragments. One distal fragment of a bovid tibia bears evidence both for carnivore (pitting) and anthropogenic damage (cut marks) (Fig. 7). As the modifications do not intersect, it is difficult to estimate the chronology of events in terms of carcass consumption by carnivores and hominins.

One non-disputable bone tool (specimen BP/3/28232) was identified in the assemblage. It is a 9 cm long, 3 cm wide fragment of non-identifiable flat bone of a large mammal (most likely class III/IV ungulate), which has been appointed on one end. Detailed descriptions of this specimen and other bone fragments modified during butchery by hominins will be presented elsewhere (Val *et al*., in prep.).

DISCUSSION

Taphonomy of the Name Chamber fauna: accumulation agents

The characteristics of the Name Chamber fauna (1) indicate contribution by and impact from multiple biotic and abiotic taphonomic agents, and (2) confirm the mixed origin of the sediments from which the material was recovered – in other words, the secondary depository location of these sediments. Both carnivore and anthropogenic modifications are present in the assemblage, as well as indication of fluvial rounding. High (>20%) carnivore/ungulate ratio, using the MNI, is one of the criteria considered as indicative of bone assemblages accumulated by hyaenids (Cruz-Uribe 1991; Pickering 2002; de Ruiter *et al.* 2009). The high ratio (33.3%) observed in the Name Chamber could reflect hyaenid contribution, even though carnivore-modified bones (i.e. digested and gnawed remains) only account for a small percentage of the assemblage. Besides, elements usually associated with cave use by hyaenids (e.g. Brain 1981; Cruz-Uribe 1991; Pickering 2002; Kuhn *et al*. 2010) such as presence of juvenile carnivore remains and coprolites are lacking. The occurrence of bone cylinders, a consequence of carnivores feeding preferably on long bone epiphyses rather than shafts, can be used to distinguish carnivore-accumulated assemblages from hominin-accumulated ones (Binford 1981; Brain 1981; Cruz-Uribe 1991; Pickering 2002; Kuhn *et al.* 2010). In the Name Chamber assemblage, bone cylin-

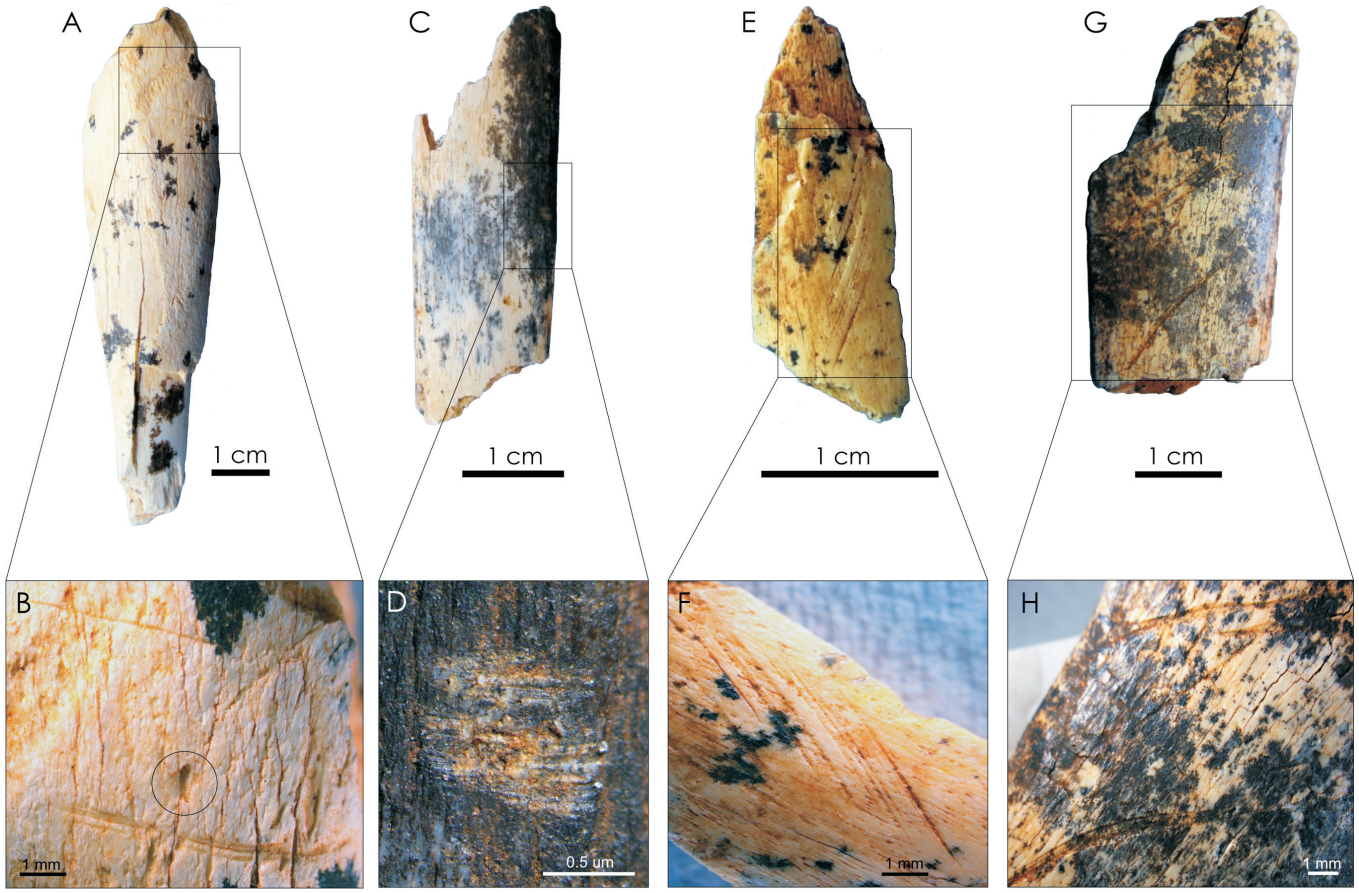

Figure 7. Examples of cut-marked bones: **A & B**, specimen BP/3/28485: tibia shaft fragment, bovid class II (note the co-occurrence of butchery marks and carnivore tooth pit); **C & D**, specimen BP/3/28455: rib fragment, non-identifiable mammal; **E & F**, specimen BP/3/28689: long bone shaft fragment, non-identifiable mammal; **G & H**, specimen BP/3/29062: long bone shaft fragment, non-identifiable mammal.

ders are absent and/or could not be identified given the high degree of fragmentation. Interestingly, the fact that some of the digested remains are carnivore bones could indicate a situation whereby carnivores trapped in the cave practiced scavenging. This is more consistent with a natural death trap scenario. The high carnivore/ungulate ratio has been questioned by some as not necessarily characteristic of hyaenid accumulations (Kuhn *et al.* 2010) and carnivore remains are also found in abundance in natural death trap assemblages, alongside other animals with good climbing proclivities such as primates (see for instance Cooke 1991; Wang & Martin 1993; Costamagno 1999; Pickering *et al.* 2004b; Val *et al*. 2015). The presence of low-density parts also supports a natural death trap scenario where it is expected to find at least some animals entering the cave as complete individuals. Evidence for water abrasion on some specimens suggests the introduction of some fossils from the surface by slope wash.

The occurrence of specimens showing different stages of weathering can suggest either different times of exposure on the surface before the introduction of the remains inside the cave or small variations inside the cave chamber in terms of air circulation or light exposition. However, as the Name Chamber is one of the lowest chambers at Sterkfontein, it seems more likely that conditions in that part of the karstic system will be stable (same degree of humidity, temperature, and constant darkness). Consequently, the lack of homogeneity in terms of weathering can probably be attributed to the introduction into the cave of different types of bones (from fresh carcasses/bones to isolated weathered elements). A similar process has been proposed for the introduction of the stone tools by slope wash (Kuman 1994a,b; Kuman & Field 2009). The high degree of fragmentation of the fossils together with the overrepresentation of the small fraction (<2 cm) can be explained firstly by the methods of recovery chosen, namely excavations of decalcified sediments and systematic sieving using small meshes. Secondly, it also most likely indicates a selective bias during transport of sediments from the exposed deposits into the Name Chamber via the 'Feeding Shaft', a phenomenon already described for the lithic assemblage (Stratford *et al*. 2012).

Comparisons with fauna from Member 4, Member 5 East Oldowan and Post Member 6

The majority of the faunal material known from Member 4 was recovered during excavations conducted by Hughes between 1982 and 1991 (Clarke 2012) in a decalcified area in the centre of the deposit; the fauna from Member 5 East was collected during excavations of both calcified and decalcified sediments (Tobias & Hughes 1969; Kuman 1994a; Clarke 2012). Direct quantitative comparisons with the material from the Name Chamber might not be relevant since systematic taphonomic analysis of the small fraction was not conducted and focus was most likely given to larger, readily identifiable remains (Brain 1981). For instance, in the Name Chamber, the water-abraded, digested and some of the cut-marked remains might be overrepresented as they are generally associated with small non-identifiable bone fragments. In the L/63 Infill, fossils were recovered from loose sediments. Unfortunately, limited data on the characteristics of the faunal assemblage is available and does not allow in-depth comparisons with our results. Differences in sample sizes (e.g. MNI for Member 5 East is 67, while it is 546 for Member 4) and quantitative units used in the literature (e.g. both NISP and MNI are available for the Name Chamber and Member 5 East, while only the MNI is provided for Member 4 and post-Member 6) prevent testing the statistical significance of differences and similarities observed between the four samples considered. Nevertheless, several lines of data can be compared, in particular: (1) the general composition of the faunal spectrum; and (2) main taphonomic characteristics of the three samples (Table 6; Table S1)

Taxonomic composition

The composition of the faunal assemblage from the Name Chamber is most similar to Member 5 East. In the two assemblages, bovids, and especially class II bovids, largely dominate the faunal sample both in terms of number of remains and minimum number of individuals (Fig. 8), while non-hominin primates and carnivores are much more poorly represented (Fig. 8). Hominin remains from Member 5 East are very few; they are absent from the Name Chamber. This is greatly contrasting with the fauna from Member 4, characterized by a significant overrepresentation of australopithecines and non-hominin primates. Furthermore, in this deposit, the most abundant bovids belong to classes III and IV (76% of the bovid sample in number of remains: Kibii 2004) rather than class II. Regarding palaeohabitat associations indicated by the taxa present in the different fossil assemblages, the Name Chamber is also most similar to Member 5 East. Hence, grassland species recovered from Member 5 East and absent from Member 4 are also present in the Name Chamber (*Pedetes* and *Equus*). Yet, it is worth noticing the occurrence of *C. williamsi* ($n = 1$) and *T. strepsiceros* ($n = 1$) in the Name Chamber, two taxa only found in Member 4. In Member 4, carnivores are represented by a wide range of species (at least 14 different taxa, including various large felid and hyaenid, as well as several canid species), some of them being considered to have made use of the cave as a den, while Member 5 East has only yielded a few carnivore taxa, and their contribution to the faunal assemblage is limited. In that regard, the carnivore sample from the Name Chamber is more similar to what is observed in Member 5 East (Table 6).

Taphonomy

While the faunal assemblage from Member 4 seems to be completely non-anthropogenic (i.e. no stone tools recovered and no butchery damage) with a significant contribution by large carnivores combined with the introduction of some animals via a natural death trap, the sample from Member 5 East has yielded more anthropogenic elements (i.e. lithic assemblages and presence of one cut-marked bone) with a limited contribution by carnivores. The main taphonomic features from post-member 6 (L/63 Infill) are

Table 6. Taxonomic composition of the faunal assemblages recovered from Member 4, Member 5 East Oldowan, post-Member 6 (L/63 Infill) and the Name Chamber at Sterkfontein (data from: Brain 1981; Pickering 1999; Kuman & Clarke 2000; Kibii 2004; Reynolds & Kibii 2011; this paper).

FAMILY	Taxon	M4	M5 East	Post-M6	Name Chamber
HOMINIDAE	*Homo* sp.	–	–	X	–
	Australopithecus. sp.	X	–	–	–
	Australopithecus africanus	X	–	–	–
	Paranthropus robustus	–	X	–	–
CERCOPITHECIDAE	*Theropithecus oswaldi*	–	X	–	–
	cf. *Cercopithecoides williamsi*	X	–	–	X
	Parapapio jonesi	X	–	–	–
	Parapapio whitei	X	–	–	–
	Parapapio broomi	X	–	–	–
	Parapapio sp.	X	–	–	–
	Papio izodi	X	–	–	–
	Papio cynocephalus	–	–	X	–
	Papio sp.	–	–	–	X
FELIDAE	*Dinofelis barlowi*	X	–	–	–
	Dinofelis sp.	–	–	–	X*
	Megantereon cultridens	X	–	–	–
	Homotherium latidens	X	–	–	–
	Panthera leo	X	X	–	–
	Panthera pardus	X	–	–	X
	Felis indet.	X	X	X	X
CANIDAE	*Canis* sp.	X	X	–	X
	Canis mesomelas	X	–	X	–
	Canis brevirostris	X	–	–	–
	Canis antiquus	X	–	–	–
HYAENIDAE	*Chasmaporthetes nitidula*	X	–	–	–
	Chasmaporthetes silberbergi	X	–	–	–
	Pachycrocuta brevirostris	X	X	–	–
	Crocuta crocuta	X	–	–	–
	Parahyaena brunnea	X	–	–	X
	Hyaenidae indet.	X	X	X	X
HERPESTIDAE	cf. *Mungos* sp.	–	X	–	–
	Suricata sp.	–	X	X	–
	Herpestes ichneumon	–	–	X	–
	Herpestidae indet.	–	X	–	X
BOVIDAE	Alcelaphini indet.	–	X	X	X
	Connochaetes sp.	X	–	–	X
	Damaliscus parmularius	X	–	–	–
	Damaliscus cf. *dorcas*	–	–	–	X
	Damaliscus sp.	–	X	X	–
	Antidorcas bondi	X	–	–	–
	Antidorcas recki	X	–	–	–
	Antidorcas sp.	–	X	X	X*
	Tragelaphus strepsiceros	X	–	–	X
SUIDAE	*Phacochoerus africanus*	–	–	–	X*
	Metridiochoerus modestus	–	X	–	–
	Suidae indet.	X	–	–	X
EQUIDAE	*Hipparion lybicum*	X	–	–	–
	Equus sp.	X[1]	X	X	X
HYRACOIDAE	*Procavia transvaalensis*	X	X	–	X
	Procavia capensis	–	–	X	X
RODENTIA	*Hystrix africaeaustralis*	X	–	X	X*
	Pedetes capensis	–	X	X	X
	Lepus sp.	X	–	X	X
BIRDS	*Struthio camelus*	–	X	–	–

*Identified only by S. Reynolds and K. Fatherley (most probably based on dental material).
[1]The presence of *Equus* sp. in Member 4 is mentioned by Brain (1981) but Kuman & Clarke (2000) suggested that the provenance of the equid remains was not clear; they argued that these remains are more likely to have come from Member 5 instead. However, the study conducted by Kibii (2004) on more recently excavated material confirms the occurrence of *Equus* sp. in Member 4 (two remains identified with secure provenance).

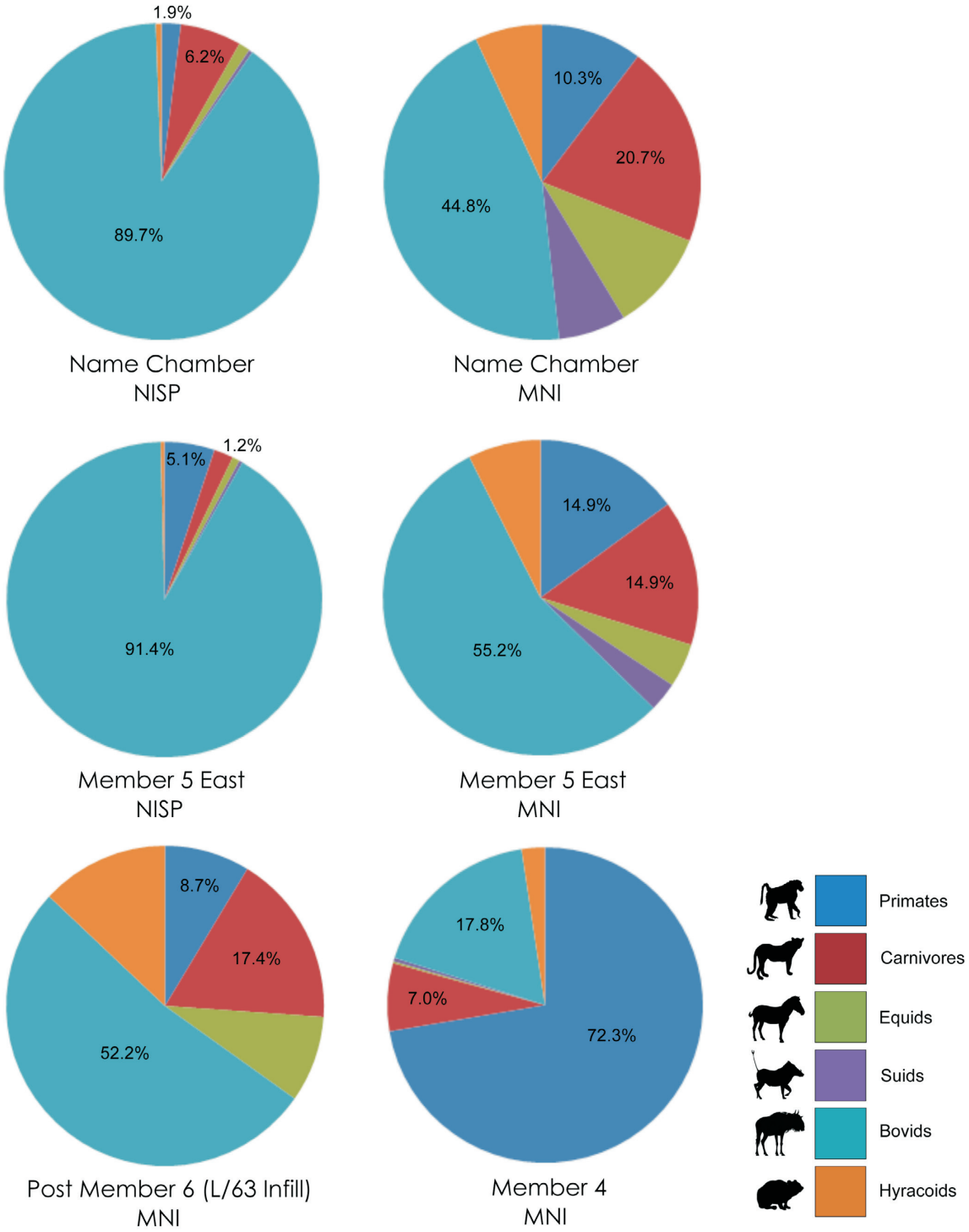

Figure 8. Taxonomic composition of the faunal assemblages from the Name Chamber, Member 4 (data from Brain 1981; Kibii 2004; Pickering *et al*. 2004a), Member 5 East Oldowan (data from Pickering 1999) and the L/63 Infill, Post-Member 6 (data from Reynolds *et al*. 2007).

the notable degree of porcupine damage on the one hand and the low incidence of carnivore damage on the other hand. Evidence for human occupation of the cave at that time is absent. We argue that the mixed taphonomic features of the fauna from the Name Chamber are consistent both with Member 5 East and Member 4, combining carnivore damage, hominin butchery modifications and indications for slope wash. Interestingly, the Name Chamber sample has a higher percentage of both carnivore-damaged remains and butchery modified bones than what is observed for Member 4 and Member 5 East, which is mostly due to sampling biases. Porcupine damage at the Name Chamber is only illustrated by the presence of one single gnawed bone.

Finally, the identification of a bone tool in the Name Chamber assemblage is worth noting since it supports Robinson's find (1959) and confirms the presence of such implements at Sterkfontein, a presence that is debated by Kuman (2005).

Comparisons with existing studies on the Name Chamber

Previous research on material recovered from the Name Chamber (artefacts and microfaunal remains) combined

with stratigraphic analyses have suggested a scenario whereby the sediments present today in the cave accumulated from exposed deposits via a 12.5-metre-deep vertical shaft (i.e. the 'Feeding Shaft') located just below square R57 in the surface excavation and associated with Member 5 East Oldowan deposit. The presence of numerous blocks of dolomite along this shaft would have led to the filtering of larger elements and the selection of the small fraction (>2 cm) of the lithic assemblage (Stratford *et al.* 2012). Similar observations were made for the macrofaunal assemblage, largely dominated by highly fragmented, small elements (95% of the remains are smaller than 4 cm and 56% are smaller than 2 cm). The taxonomic composition of the microfaunal assemblage from the Name Chamber points out towards a major contribution from Member 5 East, while the identification of a few taxa also suggests contributions from both Member 4 (transected by the 'Feeding Shaft'; Stratford *et al*. 2012) and post-Member 6 (Avery *et al*. 2010). Taxonomical attributions and taphonomic analysis of the macrofauna confirm that the sediments of the Name Chamber mostly come from the Member 5 East Oldowan deposits. Contribution from post-Member 6 was suggested by the presence of *Crocidura*, *Saccostomus* and *Thallomys* in the Name Chamber sample (Avery *et al*. 2010) but this is not supported by clear indication in the macrofaunal assemblage. Some features of the large faunal sample, however, suggest the introduction of sediments and associated fossil material from Member 4, as illustrated by the relatively high incidence of carnivore damage and the presence of *C. williamsi*.

CONCLUSION

Taxonomic and taphonomic analysis of the faunal assemblage recovered during excavations of the soft sediments from the Western Talus in the Name Chamber at Sterkfontein highlights evidence for a mixed assemblage, in a secondary depositional context. The fossil sample, characterized by a generally poor degree of cortical surface preservation and a high level of fragmentation, comprises a significant percentage of small (>2 cm) non-identifiable fragments. Some of these features might easily be explained by the excavation procedures employed, namely the use of a small mesh during sieving, and the type of sediments excavated (i.e. decalcified), leading to the recovery of abundant small elements. The assemblage is characterized by various taphonomic signals, including carnivore damage and water abrasion. Systematic microscopic investigation of bone surfaces also revealed the presence of several butchery marks, which are of special interest since this type of modification is rarely recorded in Plio-Pleistocene faunal assemblages from the Bloubank Valley cave deposits. The taxonomic composition and taphonomic characteristics of the faunal sample are in favour of a major contribution to the sediments of the Name Chamber from Member 5 East Oldowan, and to a much lesser degree from Member 4. The results of this study confirm results of previous studies on the lithics and microfaunal remains and support the initial stratigraphic connection between the Member 5 area initially proposed by Robinson (1962), further explored by Clarke (1994) and refined by Stratford and colleagues (2012).

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REFERENCES

ANDREWS, P. 1990. *Owls, Caves and Fossils*. Chicago, University of Chicago Press.

AVERY, D.M., STRATFORD, D.J. & SÉNÉGAS, F. 2010. Micromammals and the formation of the Name Chamber at Sterkfontein, South Africa. *Geobios* **43**, 379–387.

BACKWELL, L.R., PARKINSON, A.H., ROBERTS, E.M., D'ERRICO, F. & HUCHET, J-B. 2012. Criteria for identifying bone modification by termites in the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology* **337-338**, 72–87.

BAMFORD, M. 1999. Pliocene fossil woods from an early hominid cave deposit, Sterkfontein, South Africa. *South African Journal of Science* **95**, 231–237.

BEHRENSMEYER, A.K. 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* **4**(2), 150–162.

BEHRENSMEYER, A.K., GORDON, K.D. & YANAGI, G.T. 1986. Trampling as a cause of bone surface damage and pseudo-cutmarks. *Nature* **319**, 768–771.

BINFORD, L.R. 1981. *Bones. Ancient Men and Modern Myths*. London, Academic Press.

BOCHEŃSKI, Z.M. & TOMEK, T. 1997. Preservation of bird bones: erosion versus digestion by owls. *International Journal of Osteoarchaeology* **7**, 372–387.

BOCHEŃSKI, Z.M. & TORNBERG, R. 2003. Fragmentation and preservation of bird bones in uneaten food remains of the gyrfalcon *Falco rusticolus*. *Journal of Archaeological Science* **30**, 1665–1671.

BOCHEŃSKI, Z.M., KOROVIN, V.A., NEKRASOV, A.E. & TOMEK, T. 1997. Fragmentation of bird bones in food remains of imperial eagles (*Aquila heliacal*). *International Journal of Osteoarchaeology* **7**, 165–171.

BOCHEŃSKI, Z.M., HUHTALA, K., JUSSILA, P., PULLIAINEN, E., TORNBERG, R. & TUNKKARI, P.S. 1998. Damage to bird bones in pellets of gyrfalcon *Falco rusticolus*. *Journal of Archaeological Science* **25**, 425–433.

BRAIN, C.K. 1974. Some suggested procedures in the analysis of bone accumulation from southern African Quaternary sites. *Annals of the Transvaal Museum* **29**(1), 1–8.

BRAIN, C.K. 1981. *The Hunters or the Hunted? An Introduction to South African Cave Taphonomy*. Chicago, University of Chicago Press.

BRITT, B.B., SCHEETZ, R.D. & DANGERFIELD, A. 2008. A suite of dermestid beetle traces on dinosaur bone from the Upper Jurassic Morrison Formation, Wyoming, USA. *Ichnos: An International Journal for Plant and Animal Traces* **15**(2), 59–71.

BROOM, R. 1936. New fossil anthropoid skull from South Africa. *Nature* **138**, 486–488.

BROOM, R., ROBINSON, J.T. & SCHEPERS, G.W.H. 1950. Sterkfontein ape-man *Plesianthropus*. *Transvaal Museum Memoir* **4**. Pretoria, Transvaal Museum.

BRUXELLES, L., CLARKE, R.J., MAIRE, R., ORTEGA, R. & STRATFORD, D. 2014. Stratigraphic analysis of the Sterkfontein StW 573 *Australopithecus* skeleton and implications for its age. *Journal of Human Evolution* **70**, 36–48.

CLARKE, R.J. 1988. A new *Australopithecus* cranium from Sterkfontein and its bearing on the ancestry of *Paranthropus*. **In**: Grine, F. (ed.), *Evolutionary History of the 'Robust' Australopithecines*, 287–292. New York, Aldine de Gruyter.

CLARKE, R.J. 1994. On some new interpretations of Sterkfontein stratigraphy. *South African Journal of Science* **90**, 211–214.

CLARKE, R.J. 2006. A deeper understanding of the stratigraphy of Sterkfontein fossil hominid site. *Transactions of the Royal Society of South Africa* **61**(2), 111–120.

CLARKE, R.J. 2012. A brief review of history and results of 40 years of Sterkfontein excavations. **In**: Reynolds, S.C. & Gallagher, A. (eds), *Perspectives on Hominin Evolution*, 120–142. Cambridge University Press.

CLARKE, R.J. 2013. *Australopithecus* from Sterkfontein Caves, South Africa. **In**: Reed, K.E., Fleagle, J.G. & Leakey, R.E. (eds), *The Paleobiology of* Australopithecus, *Vertebrate Palaeobiology and Palaeoanthropology*, 105–123. Springer, Dordrecht.

CODRON, D., LUYT, J., LEE-THORP, J.A., SPONHEIMER, M., DE

RUITER, D. & CODRON, J. 2005. Utilization of savanna-based resources by Plio-Pleistocene baboons. *South African Journal of Science* **101**, 245–248.
COOKE, H.B.S. 1991. *Dinofelis barlowi* (Mammalia, Carnivora, Felidae) cranial material from Bolt's Farm, collected by the University of California African expedition. *Palaeontologia africana* **28**, 9–21.
COSTAMAGNO, S. 1999. Coudoulous II: taphonomie d'un aven-piège. Contribution des accumulations d'origine naturelle à l'interprétation des archéofaunes du Paléolithique moyen. *Anthropozoologica* **29**, 13–31.
CRUZ-URIBE, K. 1991. Distinguishing hyena from hominid bone accumulations. *Journal of Field Archaeology* **18**, 467–486.
CURNOE, D. & TOBIAS, P.V. 2006. Description, new reconstruction, comparative anatomy, and classification of the Sterkfontein Stw 53 cranium, with discussions about the taxonomy of other southern African early *Homo* remains. *Journal of Human Evolution* **50**, 36–77.
DELSON, E. 1984. Cercopithecid biochronology of the African Plio-Pleistocene: correlation among eastern and southern hominid-bearing localities. *Courier Forschungsinstitut Senckenberg* **69**, 199–218.
DELSON, E. 1988. Chronology of South African australopith site units. **In**: Grine, F.E. (ed.), *Evolutionary History of the 'Robust' Australopithecines*, 317–324. New York, Aldine de Gruyter.
DE RUITER, D.J. 2004. Undescribed hominin fossils from the Transvaal Museum faunal collections. *Annals of the Transvaal Museum* **41**, 29–40.
DE RUITER, D.J., PICKERING, R., STEININGER, C.M., KRAMERS, J.D., HANCOX, P.J., CHURCHILL, S.E., BERGER, L.R. & BACKWELL, L.R. 2009. New *Australopithecus robustus* fossils and associated U-Pb dates from Cooper's Cave (Gauteng, South Africa). *Journal of Human Evolution* **56**, 497–513.
DOMÍNGUEZ-RODRIGO, M., DE JUANA, S., GALÁN, A.B. & RODRÍGUEZ, M. 2009. A new protocol to differentiate trampling marks from butchery cut marks. *Journal of Archaeological Science* **36**, 2643–2654.
ELTON, S. 2000. *Ecomorphology and evolutionary biology of African cercopithecoids: providing an ecological context for hominin evolution*. Unpublished Ph.D. thesis, University of Cambridge, Cambridge.
ELTON, S. 2001. Locomotor and habitat classifications of cercopithecoid postcranial material from Sterkfontein Member 4, Bolt's Farm and Swartkrans Member 1 and 2, South Africa. *Palaeontologia africana* **31**, 115–126.
EWER, R.F. 1956. The fossil carnivores of the Transvaal Caves: Canidae. *Proceedings of the Zoological Society*, London **126**(1), 97–100.
GRANGER, D.E., GIBBON, R.J., KUMAN, K., CLARKE, R.J., BRUXELLES, L. & CAFFEE, M.W. 2015. New cosmogenic burial ages for Sterkfontein Member 2 *Australopithecus* and Member 5 Oldowan. *Nature* **522**, 85–88.
HERRIES, A.I.R. & SHAW, J. 2011. Palaeomagnetic analysis of the Sterkfontein palaeocave deposits: implications for the age of the hominin fossils and stone tool industries. *Journal of Human Evolution* **60**, 523–539.
HERRIES, A.I.R., CURNOE, D. & ADAMS, J.W. 2009. A multi-disciplinary seriation of early *Homo* and *Paranthropus* bearing palaeocaves in southern Africa. *Quaternary International* **202**, 14–28.
KIBII, J.M. 2004. *Comparative taxonomic, taphonomic and palaeoenvironmental analysis of 4–2.3 million year old australopithecine cave infills at Sterkfontein*. Unpublished Ph.D. thesis, University of the Witwatersrand, Johannesburg.
KREUTZER, L.A. 1992. Bison and deer bone mineral densities: comparisons and implications for the interpretation of archaeological faunas. *Journal of Archaeological Science* **19**, 271–294.
KUHN, B., BERGER, L.R. & SKINNER, J.D. 2010. Examining criteria for identifying and differentiating fossil faunal assemblages accumulated by hyenas and hominins using extant hyenid accumulations. *International Journal of Osteoarchaeology* **20**, 15–35.
KUMAN, K. 1994a. The archaeology of Sterkfontein – past and present. *Journal of Human Evolution* **27**, 471–495.
KUMAN, K. 1994b. The archaeology of Sterkfontein: preliminary findings on site formation and cultural change. *South African Journal of Science* **90**, 215–219.
KUMAN, K. 2005. Bone tool mimics from an early hominin site in South Africa. **In**: *Congress of the Pan African Association for Archaeology and Related Studies*, 12th, July 3–10, Gaborone, Abstract 20 pp.
KUMAN, K. & CLARKE, R.J. 2000. Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5. *Journal of Human Evolution* **38**, 827–847.
KUMAN, K. & FIELD, A.S. 2009. The Oldowan industry from Sterkfontein caves, South Africa. **In**: Schick, K. & Toth, N. (eds), *The Cutting Edge: Approaches to the Earliest Stone Age*, 151–170. Stone Age Institute Press, Bloomington, Indiana.
LAM, Y.M., CHEN, X. & PEARSON, O.M. 1999. Intertaxonomic variability in patterns of bone density and the differential representation of bovid, cervid, and equid elements in the archaeological record. *American Antiquity* **64**, 343–362.
LAROULANDIE, V. 2000. *Taphonomie et archéozoologie des oiseaux en grotte: applications aux sites paléolithiques du Bois-Ragot (Vienne), de Combe Saunière (Dordogne) et de La Vache, (Ariège)*. Unpublished Ph.D. thesis, University of Bordeaux, France.
LAROULANDIE, V. 2002. Damage to pigeon long bones in pellets of the eagle owl *Bubo bubo* and food remains of peregrine falcon *Falco peregrinus*: zooarchaeological implications. *Acta zoologica cracoviensia* **45** (special issue), 331–339.
LEE-THORP, J.A., SPONHEIMER, M. & LUYT, J. 2007. Tracking changing environments using stable carbon isotopes in fossil tooth enamel: an example from the South African hominin sites. *Journal of Human Evolution* **53**, 595–601.
LOCKWOOD, C.A. & TOBIAS, P.V. 2002. Morphology and affinities of new hominin cranial remains from Member 4 of the Sterkfontein Formation, Gauteng Province, South Africa. *Journal of Human Evolution* **42**, 389–450.
LYMAN, R.L. 1984. Bone density and differential survivorship of fossil classes. *Journal of Anthropological Archaeology* **3**, 259–299.
LYMAN, R.L. 1994a. *Vertebrate Taphonomy*. Cambridge University Press.
LYMAN, R.L. 1994b. Quantitative units and terminology in zooarchaeology. *American Antiquity* **59**(1), 36–71.
MAGUIRE, J.M., PEMBERTON, D. & COLLETT, M.H. 1980. The Makapansgat limeworks grey breccias: hominids, hyaenas, hystricids or hillwash? *Palaeontologia africana* **23**, 75–98.
MOGGI-CECCHI, J., GRINE, F.E. & TOBIAS, P.V. 2006. Early hominid dental remains from Members 4 and 5 of the Sterkfontein Formation (1966–1996 excavations): catalogue, individual associations, morphological descriptions and initial metrical analysis. *Journal of Human Evolution* **50**, 239–328.
O'REGAN, H.J. & REYNOLDS, S.C. 2009. An ecological reassessment of the southern African carnivore guild: a case study from Member 4, Sterkfontein, South Africa. *Journal of Human Evolution* **57**, 212–222.
PARTRIDGE, T.C. 1978. Re-appraisal of lithostratigraphy of Sterkfontein hominid site. *Nature* **275**, 282–287.
PARTRIDGE, T.C. 2005. Dating of the Sterkfontein hominids: progress and possibilities. *Transactions of the Royal Society of South Africa* **60**(2), 107–109.
PARTRIDGE, T.C. & WATT, I.B. 1991. The stratigraphy of the Sterkfontein hominid deposit and its relationship to the underground system. *Palaeontologia africana* **28**, 35–40.
PICKERING, R. & KRAMERS, J.D. 2010. Re-appraisal of the stratigraphy and determination of new U-Pb dates for the Sterkfontein hominin site, South Africa. *Journal of Human Evolution* **59**, 70–86.
PICKERING, T.R. 1999. *Taphonomic interpretations of the Sterkfontein early hominid site (Gauteng, South Africa) reconsidered in the light of recent evidence*. Unpublished Ph.D. thesis, University of Wisconsin, Madison.
PICKERING, T.R. 2002. Reconsideration of criteria for differentiating faunal assemblages accumulated by hyenas and hominids. *International Journal of Osteoarchaeology* **12**, 127–141.
PICKERING, T.R., CLARKE, R.J. & MOGGI-CECCHI, J. 2004a. Role of carnivores in the accumulation of the Sterkfontein Member 4 hominid assemblage: a taphonomic reassessment of the complete hominid fossil sample. *American Journal of Physical Anthropology* **125**, 1–15.
PICKERING, T.R., CLARKE, R.J. & HEATON, J.L. 2004b. The context of Stw 573, an early hominid skull and skeleton from Sterkfontein Member 2: taphonomy and paleoenvironment. *Journal of Human Evolution* **46**, 279–297.
REYNOLDS, S.C. & KIBII, J.M. 2011. Sterkfontein at 75: review of palaeoenvironments, fauna and archaeology from the hominin site of Sterkfontein (Gauteng Province, South Africa). *Palaeontologia africana* **46**, 59–88.
REYNOLDS, S.C., CLARKE, R.J. & KUMAN, K.A. 2007. The view from Lincoln Cave: mid- to late Pleistocene fossil deposits from Sterkfontein hominid site, South Africa. *Journal of Human Evolution* **53**, 260–271.
ROBINSON, J.T. 1959. A bone implement from Sterkfontein. *Nature* **184**, 583–585.
ROBINSON, J.T. 1962. Sterkfontein stratigraphy and the significance of the Extension Site. *South African Archaeological Bulletin* **17**(66), 87–107.
SCHWARCZ, H.P., GRÜN, R. & TOBIAS, P.V. 1994. ESR dating studies of the australopithecine site of Sterkfontein, South Africa. *Journal of Human Evolution* **26**, 175–181.
SHIPMAN, P. & ROSE, J. 1983. Early hominid hunting, butchering, and carcass-processing behaviours: approaches to the fossil record. *Journal of Anthropological Archaeology* **2**, 57–98.
SKINNER, J.D. & CHIMIMBA, C.T., 2005. *The Mammals of the Southern African Subregion*. Cambridge, Cambridge University Press.

SPONHEIMER, M., LEE-THORP, J.A., DE RUITER, D.J., SMITH, J.M., VAN DER MERWE, N.J., REED, K., GRANT, C.C., AYLIFFE, L.K., ROBINSON, T.F., HEIDELBERGER, C. & MARCUS, W. 2003. Diets of southern African Bovidae: stable isotope evidence. *Journal of Mammalogy* **84**(2), 471–479.

STRATFORD, D.J. 2011. *The underground central deposits of the Sterkfontein caves, South Africa.* Unpublished Ph.D. thesis, University of the Witwatersrand, Johannesburg.

STRATFORD, D.J., BRUXELLES, L., CLARKE, R.J. & KUMAN, K. 2012. New stratigraphic interpretations of the fossil and artefact-bearing deposits of the Name Chamber, Sterkfontein. *South African Archaeological Bulletin* **67**(196), 159–167.

STRATFORD, D., GRAB, S. & PICKERING, T.R. 2014. The stratigraphy and formation history of fossil- and artefact-bearing sediments in the Milner Hall, Sterkfontein Cave, South Africa: new interpretations and implications for palaeoanthropology and archaeology. *Journal of African Earth Sciences* **96**, 155–167.

TOBIAS, P.V. & HUGHES, A.R. 1969. The new Witwatersrand University excavation at Sterkfontein: progress report, some problems and first results. *South African Archaeological Bulletin* **24**(95/96), 158–169.

TOUSSAINT, M., MACHO, G.A., TOBIAS, P.V., PARTRIDGE, T.C. & HUGHES, A.R. 2003 The third partial skeleton of a late Pliocene hominin (Stw 431) from Sterkfontein, South Africa. *South African Journal of Science* **99**, 215–223.

TURNER, A. 1987. New fossil carnivore remains from the Sterkfontein hominid site (Mammalia: Carnivora). *Annals of the Transvaal Museum* **34**, 319–347.

TURNER, A. 1997. Further remains of Carnivora (Mammalia) from the Sterkfontein hominid site. *Palaeontologia africana* **34**, 115–126.

VAN DER MERWE, N.J., THACKERAY, J.F., LEE-THORP, J.A. & LUYT, J. 2003. The carbon isotope ecology and diet of *Australopithecus africanus* at Sterkfontein, South Africa. *Journal of Human Evolution* **44**, 581–597.

VAL, A., DIRKS, P.H.G.M., BACKWELL, L.R., D'ERRICO, F. & BERGER, L.R. 2015. Taphonomic analysis of the faunal assemblage associated with the hominins (*Australopithecus sediba*) from the early Pleistocene deposits of Malapa, South Africa. *PLOS ONE* **10**(6), e0126904.

VILLA, P. & MAHIEU, E. 1991. Breakage patterns of human long bones. *Journal of Human Evolution* **21**, 27–48.

VRBA, E.S. 1976. The fossil Bovidae of Sterkfontein, Swartkrans and Kromdraai. *Transvaal Museum Memoir* **21**. Pretoria, Transvaal Museum.

VRBA, E.S. 1980. The significance of bovid remains as indicators of environment and predation patterns. **In**: Behrensmeyer, A.K. & Hill, A.P. (eds), *Fossils in the Making*, 247–271. Chicago, University of Chicago Press.

WANG, X. & MARTIN, L.D. 1993. Late Pleistocene, paleoecology and large mammal taphonomy, natural Trap Cave, Wyoming. *National Geographic Research & Exploration* **9**(4), 422–435.

WILKINSON, M.J. 1983. Geomorphic perspectives on the Sterkfontein australopithecine breccias. *Journal of Archaeological Science* **10**, 515–529.