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Fossil micromammals and the palaeoenvironments of the *Paranthropus robustus* site of Cooper's Cave

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ABSTRACT

The Cradle of Humankind (Gauteng, South Africa) provides an important fossil record of the evolutionary history of PlioPleistocene hominins. Cooper's Cave deposits have yielded a rich fossil faunal assemblage, as well as six remains attributed to *Paranthropus robustus*. This study provides the first taxonomic, taphonomic and palaeoecological description of the micromammal material from the 1.4 Ma assemblage of Cooper's D. The taphonomic signature of the assemblage indicates an accumulation by tytonid owls (probably *Tyto alba*) and advanced postdepositional disturbance probably related to trampling by the occupants of the cave, sorting of the bones along slope, and burying. The taxonomic analysis undertaken here at genus level describes at least 22 taxa of small mammals, including one extinct genus *Proodontomys*. This assemblage is dominated by *Mystromys* and *Otomys*, two rodent genera adapted to grassland habitats which are among the most common among pliopleistocene micromammal faunas from the region. The palaeoecological analysis suggests an open landscape with a predominance of grassland and savanna vegetation, and the proximity of rocky outcrops and a perennial river. These results support previous indications of a shift in the African climate and vegetation towards more open habitats during the Early Pleistocene.

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Introduction

Nearly a hundred years after the discovery of the first remains of *Australopithecus africanus* in Taung (Dart 1925), South Africa is still regarded as a key region for shedding light on hominin evolutionary history. In the Gauteng Province, a series of PlioPleistocene deposits of the Cradle of Humankind (COH) has provided one of the richest fossil records of hominin remains, which comprises three genera: *Australopithecus, Paranthropus* and early *Homo* representatives. The hominin remains are found within the same deposits as bone and stone tools, and numerous fossils of fauna, which shed light on site formation processes, hominin behaviours, and environmental conditions in the region during the PlioPleistocene.

The effects of climate change on African ecosystems are acknowledged to have affected and shaped human evolution (e.g. Vrba 1974, 1985; Reed 1997; Maslin and Christensen 2007; Herries et al. 2010; DeMenocal 2011; Caley et al. 2018), but the nature and the extent of this relationship are still unclear. Many authors have attempted to answer this question by looking at the abundant and well-documented mammalian fossil record in order to determine whether climatic and environmental changes exerted selective pressures, leading to speciation, extinction, or migration events (e.g. Vrba 1974; Behrensmeyer 1984; Alemseged 2003; Bobe and Behrensmeyer 2004). Small mammals, notably rodents, have proved to be very useful in this respect: they are accurate local palaeoenvironmental indicators as they have limited home ranges, and some have precise ecological requirements; they constitute the most taxonomically diverse mammalian group comprising numerous species associated with specific habitat types (Andrews 1990; Avery 2007a); as primary consumers, they are directly dependent on vegetation and its fluctuations, and may therefore be sensitive to slight variations in climate. However, fossils of micromammals remain relatively understudied. Of the roughly 200 Pleistocene sites from Southern Africa listed by Avery (2019), only about 30 have produced microfaunal assemblages with more than 10 taxa identified, and this number is even smaller for South Africa alone (Figure 1). Yet, micromammals have the potential to provide considerable information on climatic and environmental conditions at the time of deposition and throughout the Plio-Pleistocene – a key period for hominin evolution and diversification.

Except for Wonderwerk Cave, all the Early Pleistocene micromammalian assemblages were recovered from the dolomitic cave sites of the Cradle of Humankind: Sterkfontein (Broom 1948; De Graaff 1961a; Pocock 1987; Denys 1990; Avery 2000, 2001; Avery et al. 2010), Swartkrans (Pocock 1987; Denys 1990; Brain 1993; Avery 1998, 2001), Drimolen (Sénégas et al. 2005), Gondolin (Sénégas et al. 2005), Kromdraai (Broom 1948; De Graaff 1961b; Pocock 1987; Denys 1990) and Gladysvale (Avery 1995) are the best known.

Our current understanding of rodent taxonomy has advanced since these faunal lists were published due to advanced molecular genetics and palaeontological research. New records with a taxonomically updated list of fossil micromammals are necessary for accurate palaeoenvironmental reconstructions. In this study, we provide the first detailed description of the fossil micromammal

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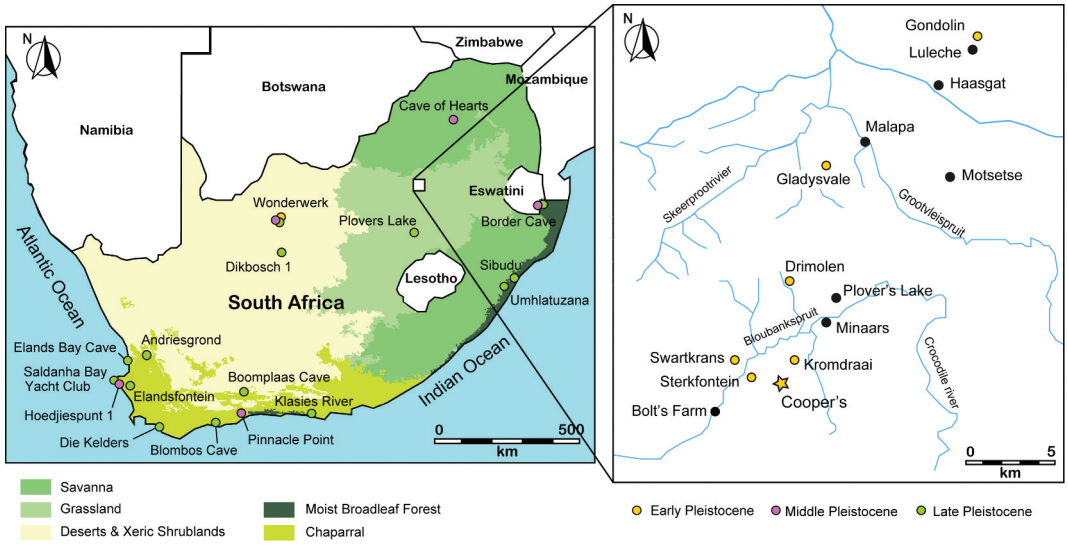

Figure 1. Map of South Africa superimposed on the biomes of South Africa, with a zoom on the Cradle of Humankind (right panel). The coloured dots indicate Pleistocene fossil sites for which at least ten micromammal taxa have been identified: Early Pleistocene sites are indicated in yellow, Middle Pleistocene sites in purple, Late Pleistocene in green. The star shows the position of the site of Cooper's D. This map was modified from .Hanon et al. (2022a)

remains retrieved from Cooper's D. We investigate taphonomic processes at the site to elucidate the origins of the fossil micromammals and the taphonomic history of the deposit. Identifying the predator(s) responsible for the fossil accumulations and incorporating their trophic and hunting preferences into the analysis is essential for an accurate palaeoecological interpretation of the fossil assemblages. Likewise, taphonomy provides information on the post-depositional processes and agents which may have affected and biased the assemblage.

The site of Cooper's D

Cooper's Cave is one of the Plio-Pleistocene fossil cave systems in the Cradle of Humankind World Heritage Site (Figure 1), located approximately 1.5 km northeast of Sterkfontein. Like the surrounding sites, Cooper's Cave is in the Monte Cristo Formation (Malmani Subgroup, Transvaal Supergroup) that forms a dolomitic karst landscape in which numerous soil-filled depressions have developed (Eriksson et al. 2006). The Cooper's Cave karst system corresponds to an area of 303 × 198 metres in which three spatially distinct infills have been identified: Cooper's A, B, and D (Berger et al. 2003). Most of the excavation work has been focused on Cooper's D (COD), which has offered the greatest concentration of fossils. The excavation area at Cooper's D rests along an east–west-trenching of approximately 3 m wide x 20 m long that corresponds to the location of an ancient de-roofed cave, filled with calcified and decalcified sediments (de Ruiter et al. 2009; Val et al. 2014).

Cooper's D has yielded a vast quantity of fossils (n > 100 000) associated with stone tools (n = 49) and bone tool (n = at least 1), as well as six hominin remains attributed to *Paranthropus robustus*, and one identified as Indeterminate Hominidae (Berger et al. 2003; de Ruiter et al. 2009; Val et al. 2014; Sutton et al. 2017; Hanon et al. 2021, 2022a). Uranium-lead dating provided an age of 1.526 ± 0.088 Ma for the basal speleothem and ca. 1.4 Ma for a flowstone layer intercalated with fossil-bearing clastic sediments (de Ruiter et al. 2009). More recently, new uranium-lead dating of the basal flowstone suggested an age of 1.375 ± 0.113 Ma (Pickering et al. 2019), which makes the fossiliferous deposit slightly younger. Recently, Hanon et al. (2022b) proposed an age comprised between 1.4 and 1.0 Ma based on both previous U-Pb dates and large mammal biochronology. Following this scenario, the Cooper's D fauna is, therefore, most likely contemporary with that of Swartkrans Member 2 dated to 1.36 ± 0.29 Ma (de Ruiter 2003; Balter et al. 2008). However, a biochronological age estimate using cercopithecids dentition suggested Cooper's D fossils could be as old as 2.0–1.6 Ma (Frost et al. 2022). This incongruence is likely attributable to the cave accumulation representing a chronological palimpsest with unclear bounds.

Cooper's Cave faunal remains represent one of the most extensively studied assemblages. Taxa studied and published include hominins (Berger et al. 1995; Steininger et al. 2008; de Ruiter et al. 2009), non-human primates (DeSilva et al. 2013; Folinsbee and Reisz 2013; Val et al. 2014), small and larger carnivores (Hartstone-Rose et al. 2007, 2010; O'Regan et al. 2013; Kuhn et al. 2016; O'Regan and Steininger 2017; Cohen et al. 2019), equids (Badenhorst and Steininger 2019), bovids (Hanon et al. 2022b) and birds (Pavia et al. 2022). These faunal studies are listed in Table 1. In a recent paper, Hanon et al. (2022a) published an updated list of mammalian specimens from Cooper's D, listing more than 80 taxa from 12 families and six orders. To complete this already detailed panorama, the micromammalian fauna was studied.

Cradle of Humankind landscape today

Today's landscape in the Cradle of Humankind is dominated by the Rocky Highveld Grassland vegetation unit (Mucina and Rutherford 2006), an area of rolling grassland dissected by prominent rocky ridges and small streams (Figure 2). The Cooper's D cave is located in the Carletonville Dolomite Grassland vegetation type and is bound by the Egoli Granite Grassland to the East (Mucina and Rutherford 2006). Mean annual precipitations are approximately 700 mm, and mean annual temperature ca. 16.5°C, with records showing the highest temperature of 36.3°C in January and the lowest temperature of −6°C in June. Due to the high altitude (ca. 1500 m), some episodes of severe frost occur in winter, which can kill the seedlings of woody species and block colonisation by indigenous trees from the savanna or forest biomes (Bredenkamp et al.

2002). The species-rich vegetation forms a complex mosaic pattern favoured by the sloping topography. It is dominated by grasses (Poaceae) that are tolerant to some extent to grazing, fire and drought, including *Aristida congesta, Loudetia simplex and Eragrostis chloromelas*. It includes scattered low shrubs such as *Searsia magalismontana* (Anacardiaceae), Diospyros lycioides (Ebenaceae) or Zanthoxylum capense (Rutaceae). Some trees, such as *Celtis africana* (Cannabaceae) and *Olea europaea* (Oleaceae), also take advantage of underground cavities and alkaline soil to house their roots, making them helpful indicators of the potential presence of a fossiliferous cave.

Fossil samples

Micromammal fossils from Cooper's D were collected during field seasons from 2001 to 2018. Decalcified sediments from the excavation were dry-sieved using a 1 mm mesh to recover micromammalian-sized fossils. The material is currently housed at the Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg. The successive excavations yielded impressively large microfossil assemblage, with an estimated >100,000 remains collected. Since it was impossible to examine all the material, the choice was made to subsample a part of the total collection. As



Figure 2. Photograph of the Cradle of Humankind landscape taken in April 2022 (photo P. Linchamps).

Table 1. Review of faunal analysis undertaken on Cooper's D fossils with a summary of the palaeoenvironmental indications.

Study	Taxonomic group	Palaeoenvironmental indication	Approach
Badenhorst and Steininger (2019)	equids	grassland with a water component	actualistic ecology
Berger et al. (2003)	large mammals	/	/
Cohen et al. (2019)	mongooses	grassland with a strong woody component near a permanent water source	actualistic ecology
de Ruiter et al. (2009)	large mammals	grassland environment, with localised dense riverine underbrush and presence of a permanent water source	actualistic ecology
DeSilva et al. (2013)	cercopithecoid primates	/	/
Folinsbee and Reisz (2013)	papionin monkeys	mix of C3 and C4 plants	stable carbon isotopes
Hanon et al. (2019)	large mammals	open savanna with wooded areas and riverine vegetation	faunal associations, multivariate analysis
Hanon et al. (2021)	large mammals	/	/
Hanon et al. (2022c)	carnivores	/	/
Hanon et al. (2022b)	bovids	landscape dominated by grassland with the presence of sparse covered habitat and a probable water source in the vicinity	actualistic ecology, multivariate analysis
Hartstone-Rose et al. (2007)	sabre-tooth felid	/	/
Kuhn et al. (2016)	hyenids	complex habitat structure with multiple vegetation units	actualistic ecology
O'Regan and Steininger (2017)	felids	/	/
O'Regan et al. (2013)	mustelids and viverrids	/	/
Parkinson (2016)	insects	/	/
Pavia et al. (2022)	birds	open grassland with a wooded component and rocky outcrops	actualistic ecology
Steininger (2011)	bovids	mosaic environment with C3 and C4 feeders	stable carbon isotopes, dental microwear analysis
Val et al. (2014)	primates	/	/

a first step, we randomly selected ca. 7,000 fossils for a full taphonomic analysis, including cranial and postcranial remains. This number was considered sufficient to reflect the representational proportions of the different skeletal elements. To expedite matters, as the taxonomic and ecological analyses do not take postcranial remains into account, we then extracted the craniodental remains from the entire micromammalian assemblage, corresponding to 2,380 craniodental elements. Each fossil has a specific inventory number and associated geographic x, y, z coordinates, as well as date of collection.

Methods

Taxonomic identifications

Fossils from Cooper's D are identified to genus level using the modern and fossil collections of the ESI, the Ditsong National Museum of Natural History (Pretoria, South Africa) and the Muséum national d'Histoire naturelle (Paris, France). Taxonomic identifications were also undertaken with pictures and keys from published literature (De Graaff 1981; Sénégas 2000; Avery 2007b; Happold 2013; Monadjem et al. 2015; Wilson et al. 2016, 2017). The maximum length and width of the teeth were taken with a Mitutoyo digital calliper and were reported to be 0.01 mm. The photographs were captured using LC30 digital colour camera for microscopy (3.1 Mpixel) and NIKON D3300 digital camera (24.2Mpixel) with a macro lens and extension rings.

Rodent taxonomic classification follows here Wilson et al. (2016, 2017). For other micromammal taxa, such as bats, shrews and golden moles, we refer to Happold (2013). Identifications were based on the jaw anatomy (maxillae, mandibles and isolated teeth). We opted for a conservative approach and chose not to take identifications below the genus level in order to avoid risks of false identifications for sibling species. Even then, the identification of some genera based on dental pattern can be challenging due to fragmentation of material, a weak morphological divergence between some taxa and lack of comparative material. Possible confusions are summarised here.

Thallomys and *Grammomys* are morphologically closely related. However, they can be identified with well-preserved craniodental elements (using cusp configuration and molar width and length, for instance). The task is more complicated when the remains are fragmented and/or encrusted with manganese like those from Coopers' D.

The molar pattern of the tribe Praomyini is very conservative in its occlusal morphology, which can lead to a difficult distinction between the genera *Zelotomys* and *Mastomys*: they share the same alveolar and molar cusp patterns and differ mainly in size, with *Mastomys* being slightly smaller than *Zelotomys*.

Teeth of the three genera *Aethomys, Micaelamys* and *Lemniscomys* from the tribe Arvicanthini are not easily distinguished when the molar series is incomplete, given the partial overlap in size range of the toothrows. The third upper molar is of diagnostic importance, but this tooth is rarely represented in the fossil assemblages or associated with the second and third molars. The first lower molar of *Micaelamys* is very distinctive, but this tooth lacks good criteria for distinguishing *Lemniscomys* from *Aethomys*.

Fossil soricids display other sources of morphological confusion. Multiple taxa belonging to the genera *Myosorex, Suncus*, and *Crocidura* have been identified in the COH assemblages. These genera were traditionally distinguished based on various criteria such as size, number of unicuspid teeth, the configuration of the palatal foramina and anatomy of the tooth crown. Unfortunately, soricid maxillae are always scarce in fossil assemblages due to their fragile structure, so attempts to separate the genera are most often made on the lower dentition only, which is seldom fully preserved. Furthermore, recent craniometric descriptions of modern material showed overlap between the features cited above, as well as phenotypic variability for some species and genera of shrews (Hutterer 2005; Taylor et al. 2013; Voet et al. 2022). While *Myosorex* can be easily identified, the distinction between *Suncus* and *Crocidura*, which are morphologically close, is less straightforward. Without a further accurate understanding of their taxonomy and biogeography, identifying fossil shrews from remote periods may thus be over-ambitious. Morphometric geometrics can provide some useful insights into the differentiation of fossil specimens (e.g. Matthews and Stynder 2011).

For the taxonomic survey, the relative abundance of the micromammal taxa was based on craniodental material only, using the number of identified specimens (NISP) and the minimum number of individuals (MNI) described in Lyman (1994), Lyman (2008). The MNI was calculated by counting the most frequent lateralised anatomical element for each taxon.

Taphonomic analyses

The taphonomic analysis follows the standard methodology described by Andrews (1990) and Fernández-Jalvo et al. (2016). It includes calculation of skeletal representation, analysis of faunal fragmentation patterns and analysis of surface modification of bones (including evidence of digestion).

Skeletal representation describes the percentage of representation (PR) of the different skeletal elements from the assemblage. The PR is calculated by following the formula:

$$PR = [MNE/(TF \times MNI)] \times 100$$

where MNE is the minimum number of elements, established by identifying the most abundant segment (proximal part, proximal part + shaft, shaft, shaft + distal part, distal part) of a skeletal element,

TF is the theoretical frequency of elements from a prey skeleton; for example, for mice: 1 cranium, 2 hemi-mandibles, 2 maxillaries, 2 scapulae, 2 humeri, 2 radii, 2 hemipelves, 2 femurs, 2 tibiae, 54 vertebrae, 4 incisors, 12 molars, 20 metapodials, 54 phalangias, 24 ribs.

We used Voorhies categories (Voorhies 1969) based on the size, weight, and density of each bone, to determine whether water or wind transportation could have affected the micromammal assemblage. There are differences in transport capacities between different bones, and between taxa. Values for micromammal bones published in various works are summarised in Fernández-Jalvo and Andrews (2003).

The fragmentation rates were recorded for the four longest limb bones, *i.e.* the humerus, the radius, the femur and the tibia. Here we report two fragmentation categories: complete bones versus incomplete, fragmented bones. We obtained the number of fragmented bones by subtracting the number of complete bones to the MNE value of each specific limb bone element.

The analysis of bone surface modification focused on observing digestion marks on isolated incisors. The manganese coating of variable thickness on the fossils greatly complicated this task. We gently rinsed 250 isolated, relatively well preserved, incisors with water, in order to remove manganese infiltration and record potential evidence of acid etching (digestion). To this end, the degree and percentage of digested elements were evaluated, following the methods of Andrews (1990) and Fernández-Jalvo et al. (2016). The following categories and criteria were used to estimate the degree of digestion: (a) none = no visible etching; (b)

light = light pitting of the enamel at the tip of the incisor, dentine unaffected; (c) moderate = light etching and removal of upper layers of enamel and/or dentine, (d) heavy = total removal of enamel and underlying dentine in some areas; (e) extreme = total removal of enamel all along the incisor with only a dentine core remaining.

Skeletal representation and breakage intensity can be used to distinguish between different predator types (Andrews 1990; Matthews 2002, 2006; Denys and Cochard 2017), but the interpretation of these results must be tempered in fossil bone accumulations where post-depositional processes, unrelated to the taphonomic signature produced by the predator, may alter the assemblage. Such processes include trampling, soil compaction, collapse of the ceiling or walls of the cave or excavation and sorting practices. Nonetheless, they provide useful information on the state of preservation of a bone assemblage. The study of digestion patterns on teeth and bone surfaces offers direct evidence of predation, and may enable the identification of the predator(s) responsible for the fossil micromammal accumulation. Many works have been devoted to the preservation of bones in modern coprocenoses (Raczyński and Ruprecht 1974; Dodson and Wexlar 1979; Denys et al. 1992; Fernandez-Jalvo and Andrews 1992; Matthews 2002, 2006), resulting in the allocation of predators to distinct categories based on the patterns of digestion. In this work, we used Andrews's (1990) five categories of predators; Category 1: digestion absent or minimal digestion, 5–13% digested isolated incisors (e.g. *Tyto alba, Asio flammeus, Bubo scandiacus*); Category 2: light or moderate digestion, 25–38% digested isolated incisors (e.g. *Asio otus, Bubo lacteus, Strix nebulosa*); Category 3: heavy digestion, 48–73% digested isolated incisors (e.g. *Strix aluco, Bubo bubo, Bubo africanus, Athene noctua*); Category 4: extreme digestion, 60–80% digested isolated incisors (e.g. *Falco tinnunculus, Falco peregrinus*); Category 5: extreme digestion, 100% digested isolated incisors (e.g. *Circus cyaneus, Buteo* buteo, mammalian carnivores)

Palaeoecological study

We compared microfaunal data from Cooper's D with eight Pleistocene micromammal assemblages from the Cradle of Humankind (Table 2) studied by Pocock (1987) and Avery (2001). Some other studied fossil deposits which also yielded micromammal remains were not included because the provenance of the material is unclear or the number of identified remains is lower.

We first used the Jaccard coefficient of similarity (Jaccard 1901; Marcon 2015) to measure COD rodents' proximity in presence-absence data with modern communities in South Africa. The composition of these communities was obtained by gathering distributional data published in Monadjem et al. (2015), Wilson et al. (2016, 2017) and data from the IUCN (*International Union for Conservation of Nature*) red list database (https://www.iucnredlist.org/). We then compared COD with other micromammalian assemblages from the Sterkfontein valley listed in Table 2 based on the presence-absence of micromammalian taxa (bats were not included), using the unweighted pair group method with arithmetic mean (UPGMA) hierarchical cluster analysis and Jaccard index. Ultimately, we compared the taxonomic relative abundance of these assemblages (expressed as the percentage of the MNI) by performing a correspondence analysis (CA), with individuals (rows) represented by the percentage of the MNI for each rodent taxa from the various assemblages (columns) listed in Table 2. We analysed the relationships between each variable using Spearman's rank correlation coefficients. All statistical analyses were performed with the software R 4.1.2 using 'factoextra' and 'FactoMineR' packages.

Results

Taphonomy

The micromammalian assemblage from the decalcified sediments of Cooper's D is heavily fragmented (60–91.4%; Table 3). All elements of the skeleton were recovered, but no postcranial element was found in anatomical connection.

Table 2. Micromammal assemblages from various deposits of the Cradle of Humankind, with estimated ages and associated references.

Deposit	Abbrev.	Age	Study	Dating method	Dating references
Swartkrans member 1 Lower Bank	SK1	2.22 ± 0.05–1.71 ± 0.07	Avery (2001)	U-Pb, isochron Cosmogenic (26Al/10Be)	Pickering et al. (2011); Kuman et al. (2021)
Sterkfontein member 5 East-Oldowan	St5EO	2.18 ± 0.21	Avery (2001)	Cosmogenic (26Al/10Be)	Granger et al. (2015)
Kromdraai B	KB	2.0–1.8	Pocock (1987)	Palaeomagnetism, Biochronology	Brain (1981); Thackeray et al. (2002); Bruxelles et al. (2017)
Kromdraai A	KA	1.8–1.6	Pocock (1987)	Biochronology	Brain (1981); Pickford (2013); Bruxelles et al. (2017)
Swartkrans member 2	SK2	1.36 ± 0.29	Avery (2001)	U-Pb	Balter et al. (2008)
Cooper's D	COD	< 1.38	This study	U-Pb	de Ruiter et al. (2009); Pickering et al. (2019)
Sterkfontein member 5 East-Acheulean	St5EA	1.3–1.1	Avery (2001)	Palaeomagnetism, ESR	Herries and Shaw 2011
Swartkrans member 3	SK3	0.96 ± 0.09	Avery (2001)	Cosmogenic (26Al/10Be)	Gibbon et al. (2014)
Sterkfontein post-member 6	StP6	*c.* 0.1	Avery (2001)	Archaeostratigraphy	Kuman and Clarke (2000)

Table 3. Numbers and percentages of fragmented long bones.

	MNE	%		MNE	%
Humerus			**Femur**		
complete	66	30.1	complete	47	14.5
fragmented	153	69.9	fragmented	278	85.5
total	219	100	total	325	100
Radius			**Tibia**		
complete	22	40	complete	28	8.6
fragmented	33	60	fragmented	297	91.4
total	55	100	total	325	100

Similarly, mandibles and maxillaries display a high degree of breakage: the persistence of the posterior part of the mandible, including coronoid, condylar and angular processes, is very rare (<1% of the specimens). Incisors remained rooted in the mandibular alveolus in 59.2% of the specimens. The percentage of representations of molars from the upper and lower identifiable toothrows varies according to the type of molar and the taxon (Figure 3). Variations between taxa can be partly explained by the difference in the number of molar roots, with increasing resistance to loss when the number of roots is higher. Fragmentary jaws from which all or some of the teeth have been lost are not always easily identifiable, for example, the morphology of the upper third molar is discriminating for identifying some Muridae taxa, yet this tooth is present in less than 50% of the specimens (Figure 3).

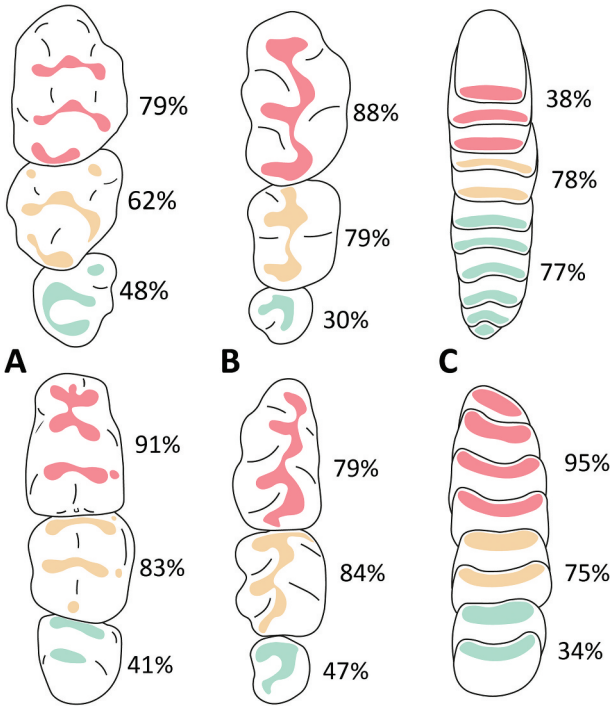

Figure 3. Percentages of retention of the upper (up) and lower (below) molars in the identified specimens from Cooper's D (expressed as percentages of NISP for each taxonomic group; first molar of the row in red, second in Orange, third in green. A) Murinae spp. (except *Otomys*); B) genus *Mystromys*; C) genus *Otomys*.

The profile of skeletal representation was calculated and compared to neotaphonomic data from pellet assemblages produced by three owl species collected in Southern Africa (Figure 4). With a total of 1048 remains, hemi-mandibles are the most represented skeletal element of the Cooper's D assemblage (PR = 100%), substantially exceeding the second most present element, *i.e.* the maxillaries, with 289 remains (PR = 26.7%). The over-representation of jaw bones from Cooper's D differentiates it from the three modern predator profiles, as do the relatively low representation of postcranial bones. Smaller, thinner bones such as ribs (PR = 0.1%), phalanges (PR = 0.7%) and metapodials (PR = 0.1) are largely under-represented in the Cooper's D micromammal assemblage. The lack of small skeletal elements and the loss of the small teeth may partly result from a sampling bias related to the relatively large 1 mm sieve mesh size and the sorting process.

As with other fossils from the Cradle of Humankind (Cukrowska et al. 2005), the micromammal remains from Cooper's D are covered by a brownish coating of manganese dioxide (Figure 5), whose nature (infiltration or encrustation), thickness (up to a millimetre thick), and colour (from reddish-brown to ebony-black) are variable.

We were able to examine the digestion on a subsample of 250 isolated incisors (cleaned with water). Study of the material showed low percentages of digestion (12.4% of isolated incisors), and the majority of these fell into the 'light' digestion category 1 (Table 4). Other surface alterations were observed on the fossils, such as root and weathering marks (Behrensmeyer 1984; Andrews 1990; Fernández-Jalvo and Andrews 2016), but these alterations were not quantified. We detected no sign of water abrasion, but no specific attempt was made to identify this as the manganese coating on bones and teeth complicated inspection.

Faunal list

Among the 4,116 craniodental remains analysed in the present study, 3,303 were identified at the family or genus level, representing a minimum number of 1,365 individuals. The assemblage of Cooper's D is taxonomically rich, with at least 22 genera belonging to seven families and five orders (Table 5). Rodents represent the most abundant micromammalian order (80.2% of the NISP, 74.8% of the MNI), followed by the elephant-shrews of the order Macroscelidea (10.6% of the NISP, 13.3% of the MNI), and the shrews of the order Eulipotyphla (9% of the MNI, 11.5% of the MNI). The remaining two orders are much less well represented: these include the bats (order Chiroptera, 0.1% of the NISP, 0.1% of the MNI) and the golden-moles of the order Afrosoricida (<0.1% of the NISP, 0.1% of the MNI).

Among rodents (Figure 6), Murinae are the most diversified rodents, with nine genera represented at Cooper's D, versus three Dendromurinae, two Gerbillinae and two Mystromyinae. Two Murinae genera remain indeterminate (Murinae indet. sp.1, NISP = 2; Murinae indet. sp. 2, NISP = 1), differing from other known fossil and modern forms, pending thus further systematic investigation. The micromammalian assemblage is numerically dominated by *Mystromys* (48.7% of the NISP, 41.7% of the MNI) and by *Otomys* (16.2% NISP, 16.6% MNI), which together account for 64.9% of the NISP and 58.3% of the MNI.

The majority of micromammals from Cooper's D can be attributed to genera that still occur today in South Africa, with the exception of the unique rodent fossil genus *Proodontomys* (Subfamily Mystomyinae). Only two genera present in the fossil assemblage are now locally extinct from the region of the Cradle of Humankind: *Zelotomys*, which is found further west in the North West and Northern Cape provinces, and *Dasymys*, whose presence in Gauteng today is restricted to its extreme North border.

The comparison of the micromammalian composition of Cooper's D with modern inventory data indicates that this fauna, although having no analogue, is similar in its composition to the modern micromammal communities occurring in the montane grassland areas of the Gauteng and the Free State provinces (Figure 7). This is not surprising as various works have already pointed out the great uniformity in the faunal composition of the COH cave site assemblages through the Pleistocene (De Graaff 1961a; Denys 1990; Leichliter 2018), with a high generic α-diversity and few fossil forms.

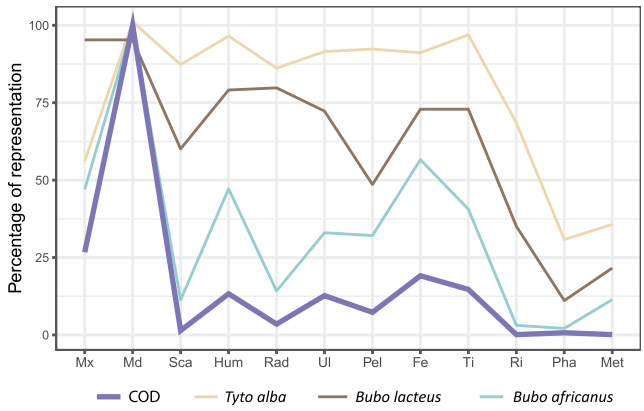

Figure 4. Profiles of skeletal representation for the micromammal remains from Cooper's D (COD), compared to percentages of representation for three owls currently present in South Africa. Mx: maxilla; Md: mandible, Sca: scapula; Hum: humerus; Rad: radius; Ul: ulna; Pel: hemi-pelvis; Fe: femur; Ti: tibia; Ri: rib; Pha: phalanx; Met: metapod. Values for *T. alba* are summarised from Linchamps et al. (2021) and from Andrews (1990) for *B. lacteus* and *B. africanus*.

Palaeoecological interpretation

Presence-absence data from Cooper's D was combined with data published by Avery (2001) for Swartkrans and Sterkfontein and by Pocock (1987) for Kromdraai (Table 6). An attempt has been made to discover whether the taxonomic composition of the various micromammalian assemblages from the Sterkfontein valley could reflect some chronological or ecological similarities between these deposits.

The unweighted pair group method with arithmetic mean (UPGMA) hierarchical cluster analysis aimed at interpreting relationships among the fossil assemblages based on the presence or absence of genera (we excluded the bats from this analysis). The COD micromammal community is grouped with that of Kromdraai B (Figure 8), for they share a significant number of common taxa. However, the cluster analysis suggests that the grouping of the sites may be more related to the author who led the study rather than being based on chronological provenience or ecological significance.

Rather than using presence-absence data, methods based on the relative abundance of taxa may thus prove more effective for disentangling ecological signals from inter-operator identification biases. A correspondence analysis was then performed to plot the different micromammal assemblages from the Cradle of Humankind. For counting the percentages of occurrence of each taxon, we grouped genera for which identification is challenging: *Mastomys* and *Zelotomys* are grouped in the 'Praomyini' group, *Elephantulus* and *Macroscelides* in the 'Macroscelididae' group, *Micaelamys, Lemniscomys* and *Aethomys* in the 'Arvicanthini' group and all genera of golden moles in the 'Chrysochloridae' group.

Representation of the variables in Figure 9 shows no clear segregation along axes driven by taxa with a strongly opposed ecological signal. Surprisingly, there is a negative correlation between the abundance of *Mystromys* and that of *Otomys* (r = – 0.72, p-value = 0.02), despite being both considered strongly indicative of grassland habitat. As they are generally the two most abundant taxa in Pleistocene deposits from the Sterkfontein Valley, it would be of special interest to consider this matter further. Less counterintuitive is the positive correlation between the abundance of *Desmodillus* and macroscelids (r = 0.94, p-value = 0.002), which both favour open arid environments. SK1, SK2 and SK3 are grouped, sharing very similar faunal composition, with the same species represented in equally similar proportions. They have more woodland and water adapted taxa in common with KB. SK1, SK2 and SK3 are also the only sites with StP6 to have yielded the remains of *Thallomys*. StP6 is the youngest of the COH sites studied here and is unique in having yielded the remains of *Saccostomus*, but no remains of the extinct genus *Proodontomys*. KA is isolated in the plane, having yielded a distinctively high number of remains of *Dendromus* and *Mus*. The deposits St5EO and St5EA are similar in having a high proportion of shrews, as well as more than 10% of their MNI constituted by the tribe Praomyini, as well as the lowest values for *Mystromys* abundance. COD shows intermediate trends in taxonomic abundances. It first stands out from the other sites by being the only one not to have yielded remains of *Graphiurus*. COD also has the highest proportion of macroscelid specimens and the second-highest rate of soricids after the contemporaneous site St5EA.



Figure 5. Photograph of the general aspect of micromammal fossil bones from Cooper's D that illustrate the brownish coating attributed to manganese dioxide on the bone surface.

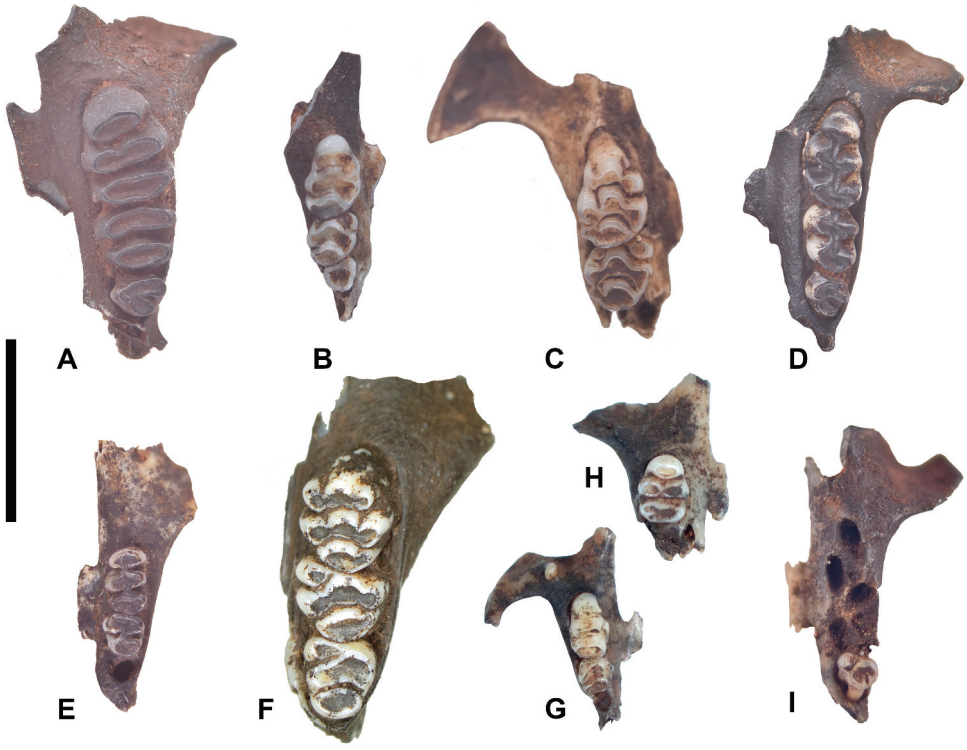

Figure 6. Some rodent upper toothrows from Cooper's D. A) CD124: left maxilla of *Gerbilliscus;* B) CD1862: right maxilla of *Mastomys*; C) CD1859: right maxilla of *Aethomys*; D) CD1431: left maxilla of Mystromys; E) CD1980: left maxilla of *Proodontomys*; F) CD34: left maxilla of *Dasymys*; G) CD3235: right maxilla of *Steatomys*; H) CD2108: right maxilla of *Desmodillus*; I) CD2614: left maxilla of *Zelotomys*. Scale bar = 5 mm.

Table 4. Percentages and stages of digestion of rodent isolated incisors. NR: number of remains, PD: percentage of digestion.

	None	Light	Moderate	Heavy	Extreme	Total
NR	219	27	4	0	0	250
PD	87.6	10.8	1.6	0	0	100

Discussion

Origin of the micromammal accumulation

The taxonomic composition of the micromammals from Cooper's D suggests an allochtonous origin of the bone remains, as the rodents identified usually do not frequent rocky habitats or caves. Various avian and small mammalian predators whose diet includes rodents and other small mammals occur today in South Africa. The taphonomy, namely the low percentages and grades of digestion, have enabled us to exclude small carnivores and diurnal birds of prey (including those identified by Pavia et al. (2022) at Cooper's D such as *Accipiter melanoleucos* and *Falco* sp.) as potential accumulators at the site.

The taphonomy indicates the involvement of a digestion category one predator in the accumulation of the studied remains. One potential objection to this conclusion could be that only incisors which were not coated with manganese were observed, and it cannot be ruled out that manganese may adhere preferentially to the enamel surfaces which have undergone digestion. Although this phenomenon may be negligible, it warrants further examination. Several owl species can be ruled out based on their habits and habitat preferences (Table 7). Potential predators remaining are the Barn owl, *Tyto alba*, the Cape eagle-owl, *Bubo capensis*, and the Verreaux's eagle-owl, *Bubo lacteus*.

Evidence of *T. alba* involvement was found by Pavia et al. (2022), who attributed 54 bone remains from Cooper's D to *Tyto* cf. *alba*, and identified the remains of young individuals, indicating that the cave was used as a breeding site. They report that the bones are morphologically similar to the extant *Tyto alba* but are smaller and show some morphological differences in the tarsometatarsus. Barn owl remains are quite common in the fossil record of the Cradle of Humankind, and *Tyto* sp. and *T. alba* have been identified at Sterkfontein (Pocock 1969; Val and Stratford 2015; Kruger and Badenhorst 2018) and *Tyto* cf. *alba* at Kromdraai (Pavia 2020). Furthermore, this species still nests nowadays in caves in the area.

B. lacteus is the largest owl in Africa. It typically nests and roosts in trees (König et al. 2009), and it is unlikely that it would roost in a cave for long periods. Furthermore, it is placed in modification categories one and two based on the breakage of skulls and loss of teeth, but in digestion category two based on both the percentage and degree of digested incisors (Andrews 1990). We have thus excluded it as a potential candidate for accumulation. The last candidate, *B. capensis*, inhabits rocky areas and is sometimes reported as a specialist hunter relying on the presence of hyrax (*Procavia*) in the previous literature (Sessions 1972). However, a recent analysis of pellet assemblages found that small rodents such as *Otomys* sp. constituted most of its diet (Rödel et al. 2002). No detailed information has been found on patterns of digestion for

Table 5. Faunal list of the micromammals from Cooper's D.

Order	Family	Sub-Family	Genus	NISP	%NISP	MNI	%MNI
RODENTIA	Bathyergidae	Bathyerginae	*Cryptomys/Fukomys*	20	0.6	13	1
	Muridae	Deomyinae	*Acomys*	8	0.2	4	0.3
		Gerbillinae	*Desmodillus*	4	0.1	2	0.1
			Gerbilliscus	18	0.5	6	0.4
		Murinae	*Aethomys*	51	1.5	19	1.4
			Dasymys	71	2.1	25	1.9
			Mastomys	65	2.0	28	2.1
			Mus	10	0.3	5	0.4
			Otomys	534	16.2	224	16.6
			Rhabdomys	25	0.8	11	0.8
			Zelotomys	4	0.1	2	0.1
			Murinae indet. gen. 1	1	<0.1	1	0.1
			Murinae indet. gen. 2	2	0.1	2	0.1
	Nesomyidae	Dendromurinae	*Dendromus*	61	1.8	30	2.2
			Malacothrix	10	0.3	5	0.4
			Steatomys	102	3.1	44	3.3
		Mystromyinae	*Mystromys*	1610	48.7	564	41.7
			†*Proodontomys*	52	1.6	25	1.9
Total identified rodents				**2648**	**80.2**	**1010**	**74.8**
AFROSORICIDA	Chrysochloridae	Amblysomyinae	*Neamblysomus*	3	0.1	3	0.2
		Chrysochloryinae	*Chrysospalax*	1	<0.1	1	0.1
CHIROPTERA	Rhinolophidae		*Rhinolophus*	3	0.1	2	0.1
EULIPOTYPHLA	Soricidae		Soricidae indet.	297	9.0	155	11.5
MACROSCELIDEA	Macroscelididae		*Elephantulus*	347	10.5	177	13.1
			cf. *Macroscelides*	4	0.1	3	0.2
Total identified micromammals				**3303**	**100**	**1351**	**100**
Indeterminate rodents				813		308	
Total rodents				**4116**		**1659**	

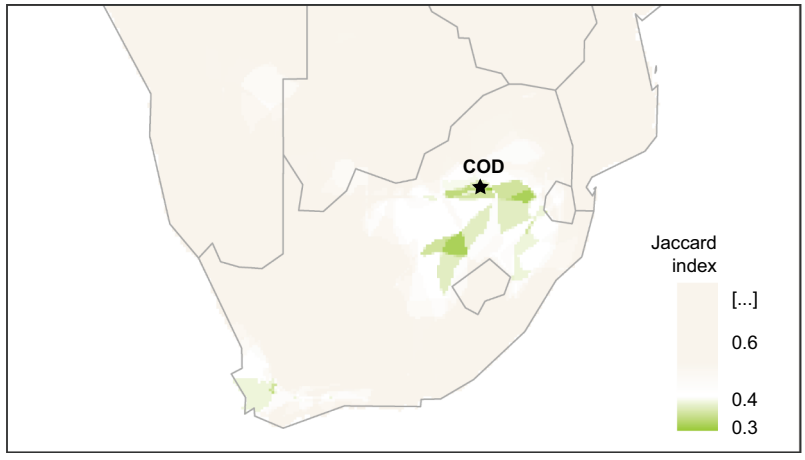

Figure 7. Similarity map using Jaccard index for comparing Cooper's D (COD) rodent assemblage with modern communities at the genus level.

B. capensis. However, Nel and Henshilwood (2016) indicate that digestive etching on incisors is close to that of the small-spotted genet (*Genetta genetta*), which is placed in category 5 (Andrews 1990). Further neotaphonomic analyses of *B. capensis* pellet assemblages are critically needed.

Given the persistent presence of *T. alba* from the Early Pleistocene to the present in the caves of the Sterkfontein Valley, the agent of accumulation appears more likely to be the Barn owl, but the Verreaux's eagle-owl (*B. lacteus*) cannot be entirely ruled out.

The bulk of the micromammal material from Cooper's D is thus interpreted as fossilised owl pellet assemblage. This implies that a suitable nesting site existed close to the cave entrance before it was eroded. Barn owls usually swallow small prey items whole and regurgitate the undigested fur, teeth and bones; these bones are characterised by minor breakage and low digestion damages, and articulation of body parts is not uncommon (e.g. Andrews 1990; Fernández-Jalvo and Andrews 2016; Linchamps et al. 2021).

The high proportion of fragmentation found in Cooper's D material is unlikely to have been produced by the category one predator and is thus interpreted as resulting from post-depositional modifications. We suggest that trampling and burying may have played a role in the taphonomic modification of the assemblage. Marks of trampling were observed on the remains of large mammals from Cooper's D, with the potential implication of carnivores and (to a lesser extent) hominins that contributed to the accumulation of the bones (Hanon et al. 2022c). Micromammals bones exposed on the cave ground before burial may have been similarly affected by trampling. Furthermore, de Ruiter et al. (2009) highlighted several episodes of large dolomitic roof block collapse throughout the formation, as well as infilling and erosion of the Cooper's D deposit – all of which could have resulted in post-depositional breakage. In addition, dry-sieving and transport of the material during and after excavations may also have impacted taphonomic modification, but this is considered to have a minor

Table 6. Micromammal genera (except Chiroptera, Afrotheria, Soricidae and *Rattus*) are found in various fossil sites and today in the Cradle of Humankind, with modern habitat preferences. Abbreviations and information for each site are listed in Table 2. Habitat preferences are taken from Happold (2013), Monadjem et al. (2015) and Wilson et al. (2016, 2017) and relate to the representatives from the southern African region only. 0 = absence, 1 = presence.

Genus	Favoured habitat	St5EO	SK1	KB	KA	SK2	COD	St5EA	SK3	StP6	Modern
Acomys	fynbos /dry open savanna	1	1	1	0	1	1	0	1	0	1
Aethomys	grassl./open-wooded savanna	1	1	1	0	1	1	1	1	1	1
Cryptomys/Fukomys	varied if sandy/friable soils	1	1	1	1	1	1	1	1	1	1
Dasymys	marsh/moist grassland	1	1	1	1	1	1	1	1	1	0
Dendromus	moist grassl./moist savanna	1	1	1	1	1	1	1	1	1	1
Desmodillus	semi-desert	0	1	1	0	1	1	0	1	0	1
Georychus	fynbos/grassland/forest	1	1	0	0	1	0	0	1	1	1
Gerbilliscus	savanna/semi-desert	1	1	1	1	1	1	1	1	1	1
Graphiurus	arid-moist sav./woodland/forest	1	1	1	1	1	0	1	1	1	1
Lemniscomys	grassland/savanna	0	0	1	0	0	0	0	0	0	1
Malacothrix	dry savanna	1	1	1	1	1	1	0	1	1	0
Mastomys	grassland/savanna	1	1	0	1	1	1	1	1	1	1
Micaelamys	mesic-arid savanna	0	0	1	1	0	0	0	0	0	1
Mus	ubiquitous	1	1	1	1	1	1	1	1	1	1
Mystromys	grassland	1	1	1	1	1	1	1	1	1	1
Otomys	grassland	1	1	1	1	1	1	1	1	1	1
Proodontomys	?	1	1	1	1	1	1	1	1	0	0
Rhabdomys	fynbos/ grassland/ savanna	1	1	1	1	1	1	1	1	1	1
Saccostomus	savanna	0	0	0	0	0	0	0	0	1	1
Steatomys	grassland/open savanna	1	1	1	1	1	1	1	1	1	1
Thallomys	mesic savanna	0	1	0	0	1	0	0	1	1	1
Zelotomys	arid-mesic savanna	1	0	1	1	0	1	1	0	1	0
Elephantulus	grassland/savanna	1	1	1	1	1	1	1	1	1	1
Macroscelides	desert/semi-desert	0	1	1	1	1	cf.	0	1	1	0
Amblysomus	sandy/friable soils	1	1	0	0	1	0	1	1	1	1
Chlorotalpa	sandy soils in grassland/forest	1	0	1	1	0	0	0	0	0	0
Chrysospalax	dense grassl./savanna/forest	0	1	1	0	1	1	0	1	0	1
Neamblysomus	sandy/friable soils	0	0	0	0	0	1	0	0	0	1
Richness in genera		**20**	**22**	**22**	**18**	**22**	**20**	**16**	**22**	**20**	**22**

impact as almost all observed fracture zones are covered by brownish-black coatings of manganese – arguing in favour of ancient breakage. These coatings of manganese dioxide and smaller amounts of iron oxide are commonly observed in fossil assemblages from the dolomitic caves in the Cradle of Humankind (see Cukrowska et al. 2005). An additional potential explanation may relate to the geomorphological characteristics of the site. Based on the distribution and description of the sedimentary facies, de Ruiter et al. (2009) state that fossils may have accumulated as two depositional cones located beneath ancient vertical or subvertical roof openings. If owls sought out fissures and cavities above the sloping ground, the bones could have been transported by sliding down slopes (due to the action of run-off water or gravity), resulting in differential movement of materials within the cave and post-depositional sorting. This is supported by the fact that the most represented bones from Cooper's D micromammal assemblage fall into Voorhies groups four and five (Voorhies 1969), which correspond to disarticulated skeletal elements that are least likely to be carried by water or wind action. Although no evidence of water abrasion was found, likely, percolating water or new external infilling would then have flowed along the cones, washing further the lighter and less dense skeletal elements. A pocket of micromammal-bearing material composed of reddish-brown calcified sediments is visible in the western zone of the deposit, which contains thin, highly layered strips of micromammal bones oriented in the same direction, suggesting they could have been deposited through water activity.

Micromammalian composition as reflection of the surrounding habitats

Identifying *T. alba* as the principal predator has some significant palaeoecological implications. Barn owls are generally considered generalist (*i.e.* non-selective) predators, with the consequence that the species captured as prey should properly reflect the surrounding micromammalian diversity (Avenant 2005; Terry 2010; Andrade et al. 2015), but this is only partially true. The rapor's preferences for small preys between 5 g and 30 g (König et al. 2009), its nocturnal/crepuscular habits, and the limited length of its home range that varies from 400 m to 5 km (Andrews 1990; Taylor 1994) must also be taken into consideration when making palaeoenvironmental inferences using the micromammalian composition. Furthermore, although the taxonomic representation is related to the relative availability of prey, common species are usually favoured, while less common species are captured well below their abundance level (Andrews 1990); in some cases, half or more of the assemblage may be composed of a single taxon (Vernon 1972; Andrews 1990). Lastly, the barn owl also hunts preferentially in open areas (König et al. 2009), so species that inhabit forests are likely to be less represented in the assemblage. Vernon's (1972) extensive analysis of *T. alba* pellet collection from 22 South African localities revealed that myomorph rodents constitute approximately 83% of the raptor diet, while shrews and birds both represent about 6%. Other faunal groups (including arthropods, afrosoricids, amphibians, reptiles and bats) make up the remaining 5%.

This mixed vegetation provides suitable habitats for many rodent species. Studies of faunal remains found in modern barn owl pellets from roosts located within the Cradle of Humankind show a species composition dominated by *Mastomys, Gerbilliscus, Otomys* and representatives of the Dendromurinae sub-family (Brain 1981; Laudet et al. 2002). These lists offer valuable comparative data for interpreting the percentages of occurrence of each taxonomic group within the fossil and modern assemblages. However, anthropogenic surface activities in the area, including intensive cattle farming, have most certainly influenced the status and distribution of both the small mammal and the vegetation communities (e.g. by favouring the presence of commensal species such as *Mastomys, Rattus* and *Mus*), so these modern inventory

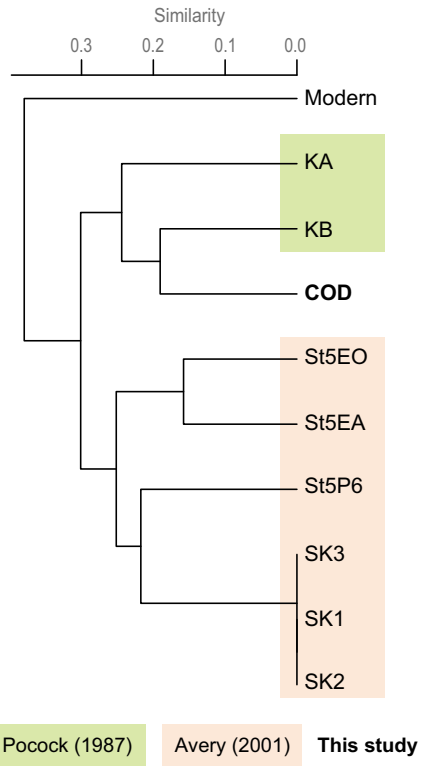

Figure 8. Hierarchical clustering analysis of various micromammal deposits by UPGMA using Jaccard similarity index based on the presence-absence of genera. Abbreviations and information for each site are listed in .Table 2

data cannot be considered as an accurate reflection of the original composition of the ecosystem. Faunal lists based on trapping data from protected areas may be more representative of the region's environment. Still, they are prone to the same bias of representation (e.g. lower occurrence of rare or hard-to-catch species) than pellet-derived data. Ultimately, distribution data compiled from the literature (e.g. Happold 2013; Monadjem et al. 2015) provide a comprehensive inventory of wildlife diversity within a region. In the vicinity of the Cradle, a total of 22 genera of micromammals (with the exclusion of bats) are listed (see Table 6).

The taxonomic uniformitarian hypothesis has been used frequently in environmental reconstruction based on fossil micromammals (e.g. Avery 1982; Wesselman 1984; Denys 1990; Reed 2003). In this approach, one assumes that a fossil taxon had similar ecological strategies to its close living relatives; some conclusions may thus be deduced about the environment in which the fossil rodents lived. This approach is more applicable to fossil assemblages from recent periods: for rodents of Southern Africa, it is best applied for assemblages from the Plio-Pleistocene or younger periods, during which almost all the extant genera can be found (Winkler et al. 2010). However, taxonomic uniformitarism is undermined by various limitations. For example, Matthews et al. 2020) noted that the fossil micromammal communities at Pinnacle Point (South Africa) indicated that many murid taxa had different or more extensive ranges in the past, and these would have incorporated different habitats to those they currently inhabit. Taxonomic uniformitarianism also ignores the adaptability and plasticity shown by modern micromammals, which may have enabled fossil taxa to adapt to environmental change, while retaining their morphological stability (Kowaleski 1999; Matthews et al. 2020). With these reservations, useful information can still be obtained by looking at the environmental interpretations for the community as a whole: the use of multiple taxa in the reconstruction of the environments can help to mitigate the possibility of error resulting from differences in ecological tolerances of one or a few species.

The predominance of herbivorous rodents occurring in open grasslands suggests that this was the main habitat around Cooper's D cave. The two most abundant taxa, *Mystromys* and *Otomys*, comprise 58.3% of the MNI. These two genera indicate highveld and middle to high altitude grasslands, showing adaptation to herbivory and grass consumption. Elephant shrews (*Elephantulus*) constitute the third most abundant taxa from the micromammal fossil assemblage of Cooper's D. They are adapted to arid environments and live in various habitats (Happold 2013). Besides shrews, which account for 11.5% of the MNI, all other taxa are represented by less than 4% of the number of individuals. The remaining taxa suggest that the landscape was predominantly open (*Steatomys*), with a succession of sandy plains (*Cryptomys/Fukomys, Neamblysomus*) with semi-arid vegetation (*Desmodillus, Malacothrix*) and patches of savanna (*Aethomys, Gerbilliscus*) with denser vegetation (*Chrysospalax*), interspersed between rocky hills (*Acomys*) with bushes and shrubs and open woodlands. The presence of *Dasymys* in relatively high proportion also provides evidence for proximity to a stream or a permanent waterhole.

These environmental indications are consistent with information provided by other groups of fauna. Most of the previous faunal analyses at Cooper's D indicated a predominance of grassland and open savannah environment, with a constant water source and woodland areas in the vicinity of the site (see Table 1 for a synthesis). The proximity of a perennial river, with associated riverine vegetation, was evidenced by the presence of several water-dependent taxa, including mongooses from the genera *Atilax* and *Ichneumia* (Cohen et al. 2019), bovids (Hanon et al. 2022b) and other ungulates (de Ruiter et al. 2009). As mentioned above, the micromammal fauna supports this palaeoenvironmental interpretation, as testified by the relative abundance of *Dasymys*, which is associated with rivers and marshy habitats in southern African savannas. Using fossil birds, Pavia et al. (2022) highlighted for the first time the importance of rocky outcrops at Cooper's D. This interpretation is supported by the presence of *Acomys* in the rodent fauna. In contrast, the micromammalian fauna of Cooper's D does not support previous indications of neighbouring dense woody environment obtained by avian fauna and other mammals (Steininger 2011; Cohen et al. 2019; Pavia et al. 2022). Among South African rodents, this type of environment could be indicated by the presence of the genus *Thallomys* (which live and feed almost exclusively on *Acacia* trees) and secondarily by *Graphiurus* and *Grammomys* but none of these taxa was identified among the studied assemblage. However, it is hard to say whether these genera were absent from the surrounding habitat of Cooper's D or if it may be attributed to an incomplete fossil record or a bias related to the hunting strategy of the predator.

Overall, no marked environmental trend seems to emerge from the faunal composition of Cooper's D when compared with other micromammal assemblages from the Sterkfontein Valley. Examination of the relationships among these assemblages using UPGMA cluster analysis (Figure 8) showed that interobserver differences in identification can partly drive palaeoecological interpretations. This situation raises concerns about the ability of palaeoenvironmental methods using generic presence-absence data, such as the taxonomic habitat index (Evans et al. 1981; Andrews 1990; Andrews and Hixson 2014) for tracing environmental and habitat changes through time. One probable explanation is the difficulty of identifying the various genera on fragmented remains with little diagnostic features in the context of an ever-

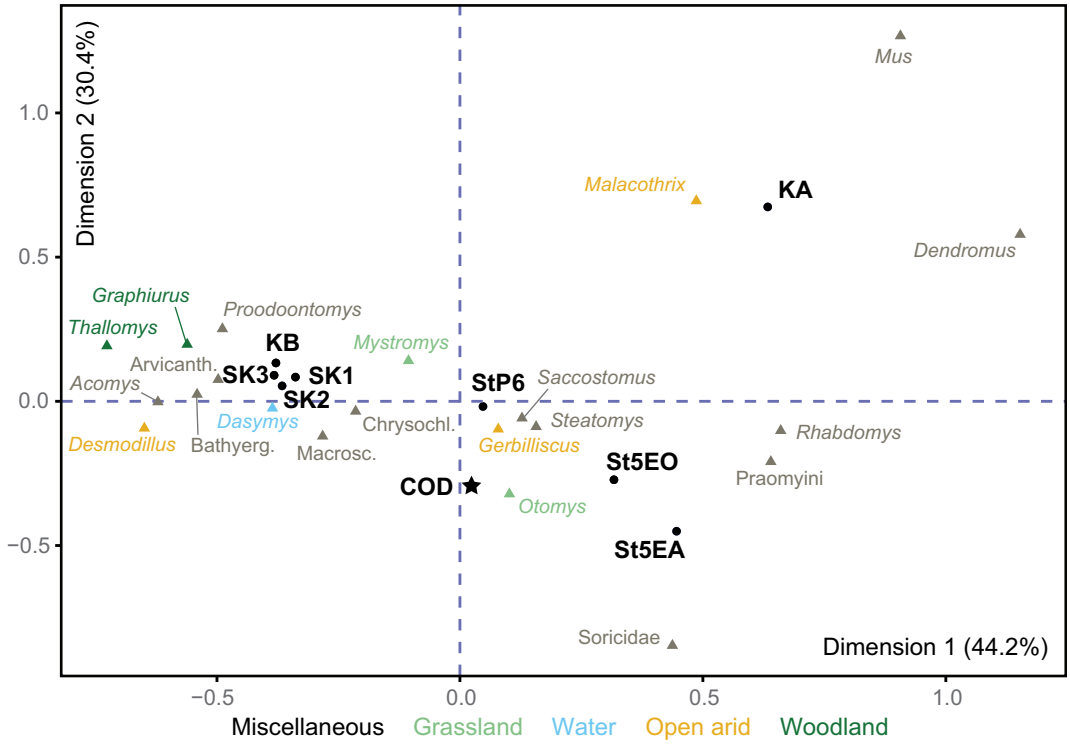

Figure 9. Correspondence analysis showing the divergence of faunal composition based on percentages of taxa between the different micromammalian assemblages from the COH. The term Praomyini includes the genera *Mastomys* and *Zelotomys* (the genus *Rhabdomys* is treated separately); the term *Arvicanthini* includes the genera *Aethomys, Micaelamys* and *Lemniscomys* (the genus *Dasymys* is treated separately). Abbreviations and information for each site are listed in .Table 2

Table 7. Owls occurring in South Africa, with predation category based on Andrews (1990) and Fernández-Jalvo et al. (2016), and arguments against their implication in the accumulation of Cooper's D micrommamalian assemblage. No information has been found on patterns of digestion for most of the species. Ethological data from König et al. (2009).

Species	Digestion category	Modification category	Contraindications
Tyto alba	1	1	
Tyto capensis	?	?	Always roost on the ground in tall grass
Bubo africanus	2–3	2	
Bubo capensis	?	?	
Bubo lacteus	2	1–2	
Otus senegalensis	?	?	Roost in dense foliage, unlikely to inhabit a cave
Ptilopsis granti	?	?	Roost in trees, unlikely to inhabit a cave
Strix woodfordii	?	?	Roost in dense cover, high in trees, unlikely to inhabit a cave
Glaucidium capense	?	?	Mostly diurnal, unlikely to inhabit a cave, hunts smaller preys
Glaucidium perlatum	?	?	Mostly crepuscular or diurnal, unlikely to inhabit a cave, hunts smaller preys

changing rodent taxonomy and classification. South Africa is a country of high biodiversity with more than 70 species of extant rodents identified (Monadjem et al. 2015; Wilson et al. 2016, 2017), of which a large portion can hardly be distinguished using morphological criteria (i.e. cryptic species). In this respect, publications devoted to the description of taxonomically diagnostic criteria for African rodent genera (e.g. Avery 1998) offer valuable support for identifying fossil faunal remains. Principal component analysis conducted on the relative abundance data makes the Cooper-D assemblage quite isolated from other micromammalian assemblages from the Cradle. This result does not relate to differences in taxonomic composition, as most of the taxa are equally found in other sites, but rather to species abundance. For example, Cooper's D also has the highest proportion of macroscelids and the second highest rate of soricids (followed by contemporaneous site St5EA). Reed (2003) successfully used a taxonomic ratio of Murinae to Soricidae as an indicator of closed habitat for discriminating East African environments, based on the assumption that Murinae are more closely associated with dense vegetation and shrews with open habitats. However, this ratio is hardly transferable to South Africa, where the soricid community is distributed between crociduran (*Crocidura, Suncus*) and myosorican (*Myosorex*) shrews. A better identification of the Soricidae material from Cooper's D should provide interesting results.

In general, micromammals have not provided useful indications to construct detailed chronologies in the deposits from the Gauteng (Denys 1990; Sénégas 2000; Avery 2021). At the genus level, two taxa may help estimate the relative age of the South African deposits: *Saccostomus* and the extinct *Proodontomys*. In South Africa, *Saccostomus* appears only at the end of the Middle Pleistocene or at the beginning of the Upper Pleistocene, with a scarce occurrence in the fossil record: it was recorded at Wonderwerk in stratum 11 and stratum 12 (Avery 2007b; Fernández-Jalvo and Avery 2015), Border Cave (Avery 1992),

Cave of Hearths (De Graaff 1961a), Gladysvale (Avery 1995), Sterkfontein StP6 (Avery 2001), Pinnacle Point (Matthews et al. 2011, 2020) and ultimately at Apollo 11 (Vogelsang et al. 2010). On the other hand, the presence of the fossil genus *Proodontomys* circumscribes a time between ca. 3.7 Ma and approximately 0.96 Ma, with its oldest occurrence at Makapansgat EXQR, MRCIS and MLWD (Matthews et al. 2007) and the latest appearance at Swartkrans Member 3 (Avery 1998, 2001). During this interval, it is listed by Pocock (1987) at Sterkfontein, Kromdraai A and B and Makapansgat, by Cooke (1990) at Taung, Makapansgat Member 3, Sterkfontein Member 4, Bolt's Farm, Swartkrans Member 1, Kromdraai A and B, by Avery (1998, 2001) at Swartkrans Member 1, 2 and 3, by Denys (1990) at Swartkrans 1, by Sénégas (Sénégas 2000; Sénégas et al. 2005) at Bolt's Farm Quarry 7 and Quarry 9, Makapansgat Beehive Loc, Kromdraai A, GPS168, Gladysvale, Gondolin and Drimolen. Its presence at Cooper's D thus likely indicates that the deposit is at least equal in age or older than Swartkrans Member 3.

Questions remain relating to the probable climate- and time-averaged nature of Cooper's palaeo-assemblage, and it has been alleged that the deposit may be the result of the mixing of fossils of different ages and/or environmental conditions between 1.4 and 1.0 Ma (Hanon 2019; Hanon et al. 2022b). Unfortunately, undertaking this study at the genus level provides too little evidence to resolve this question.

Perspectives for future micromammal studies in South Africa

This first study of the micromammals from Cooper's D raises many questions about the palaeoecological interpretation of the assemblage and opens new avenues of research. The faunal assemblage of Cooper's D is one of the most extensively studied in recent years, allowing detailed reconstruction of the ecosystem of *Paranthropus robutus* at the time of deposition. The contribution of micromammals adds further information on the vegetation and structure of the surrounding environment, yet some palaeoenvironmental interpretations could be improved in the future.

First, the genus-level unit of investigation used here provides necessarily limited information. It has been said that all Early Pleistocene sites from South Africa share very similar micromammalian taxonomic composition, which results in the interpretation of a low-contrast global scenario with few or no marked environmental signatures. Identification at the genus level also prevents documenting anatomical trends through time to provide chronometric tools such as those used with larger mammals (e.g. Vrba 1974; McKee et al. 1995; Frost et al. 2022). Unfortunately, with the prevalence of molecular systematics, identification at the species level turned out to be far more complicated than previously thought; some species lack distinctive craniodental features and cannot be identified based on their morphology. In addition, the systematics of many southern African taxa remain unresolved (e.g. Matthews and Nel 2021). Several approaches can help to resolve this issue. Computer assisted methods in taxonomic identification, such as geometric morphometric techniques (e.g. Matthews and Stynder 2011; Cornette et al. 2015), Deep learning methods (e.g. Miele et al. 2020) or a combination of both (Moclán et al. 2023) offer promising tools for accurate identification of modern and fossil material. Morpho-functional analyses that minimise our dependence on taxonomy are another solution to extracting ecological information from unidentified fossil specimens (Paine et al. 2019; Terray et al. 2021).

The palaeoecological interpretation also stressed the importance of biological and ecological studies for extrapolating environmental information from fossil and modern taxa, such as distribution, habitat, diet, population structure, predators, etc. This issue was already discussed by Avery (2007a) in an article taking stock of the micromammal studies in South Africa. Although many ecological traits may remain beyond reach for fossil specimens, stable isotope analyses provide a useful tool for tackling questions related to food sources or predator–prey relationships, for instance. An example was provided by Leichliter et al. (2017) who demonstrated that fossil Gerbillinae from Gladysvale Fossil Site (~700 Ka, Sterkfontein Valley) consumed more C4-derived carbon plants than their modern counterparts. Local inventories from live-trapping and owl pellet counts also provide valuable information regarding abundance and habitat use, and frequently increase the known current distributions of taxa, a fact which highlights the gaps in our current understanding of the existing biogeography of many micromammal taxa (Matthews et al. 2020).

Conclusion

The present study expands the faunal list of Cooper's D with 22 taxa of micromammals belonging to five orders and seven families. The taphonomic analysis suggests that these remains were accumulated by owls, probably *Tyto alba* that still occupies the surrounding caves today. Nowadays, the entirety of the deposit is exposed to the surface, but at the time of the accumulation of fossils, the cave consisted of a vertical or sub-vertical fissure continuously occupied by hyenas and/or primates, with a suitable nesting site close to the cave entrance.

The surroundings of the cave must have consisted of an undulating open landscape divided into hills and plains with some prominent rocky ridges and a river running nearby. A complex mosaic vegetation prevailed, dominated by grassland and open savanna species, including prominent grasses, and encompassing intrazonal shrubland, open sandy zones with scarce vegetation and minor patches of woodland. The micromammalian composition of Cooper's D appears rather distinct from that observed in other fossil sites of the Cradle of Humankind, with the absence of arboreal species and a high proportion of macroscelids and soricids. It is likely that time averaging and predation have influenced the faunal composition; further investigation using finer taxonomic resolution and novel computer-assisted methods should provide more information to address this issue. The high diversity of rodents and their abundant fossil record render them an indispensable ally for palaeoenvironmental reconstructions.

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References

Alemseged Z. 2003. An integrated approach to taphonomy and faunal change in Shungura formation (Ethiopia) and its implication for hominid evolution. J Hum Evol. 44:451-478. doi:10.1016/S0047-2484(03)00012-5
Andrade A, Menezes J, Monjeau A. 2015. Are owl pellets good estimators of prey abundance? J King Saud Univ Sci. 28:239–244.
Andrews P. 1990. Owls, caves and fossils : predation, preservation and accumulation of small mammal bones in caves, with an analysis of the pleistocene cave faunas from westbury-sub-mendip, somerset. London: Natural History Museum Publications.
Andrews P, Hixson S. 2014. Taxon-free methods of palaeoecology. Ann Zool Fennici. 51:269-284. doi:10.5735/086.051.0225
Avenant N. 2005. Barn owl pellets : a useful tool for monitoring small mammal communities? Belg J Zool. 135.
Avery DM. 1982. Micromammals as palaeoenvironmental indicators and an interpretation of the late quarternary in the Southern Cape province, South Africa. AnnS Afr Mus. 85:183-374.
Avery DM. 1992. The environment of early modern humans at border Cave, South Africa : micromammalian evidence. Palaeogeogr Palaeoclimatol Palaeoecol. 91:71-87. doi:10.1016/0031-0182(92)90033-2
Avery DM. 1995. A preliminary assessment of the micromammalian remains from Gladysvale Cave, South Africa. Palaeontol Afr. 32:1-10.
Avery DM. 1998. An assessment of the lower pleistocene micromammalian fauna from Swartkrans members 1–3, Gauteng, South Africa. Geobios. 31 (3):393-414. doi:10.1016/S0016-6995(98)80022-3.
Avery DM. 2000. Notes on the systematics of micromammals from Sterkfontein, Gauteng, South Africa. Palaeontol Afr. 36:83-90.
Avery DM. 2001. The Plio-Pleistocene vegetation and climate of Sterkfontein and Swartkrans, South Africa, based on micromammals. J Hum Evol. 41 (2):113–132. doi:10.1006/jhev.2001.0483.
Avery DM. 2007a. Micromammals as palaeoenvironmental indicators of the Southern African quaternary. Transactions of the Royal Society of South Africa. 62(1):17–23. doi:10.1080/00359190709519193.
Avery DM. 2007b. Pleistocene micromammals from Wonderwerk Cave, South Africa : practical issues. J Archaeol Sci. 34:613–625.
Avery DM. 2019. A Fossil History of Southern African Land Mammals. Cambridge: Cambridge University Press. doi:10.1017/9781108647243.
Avery DM. 2021. Micromammals and the late quaternary of Southern Africa | south African Journal of Geology | geoScienceWorld. South Afr J Geol. 124 (4):1073-1082.
Avery DM, Stratford DJ, Sénégas F. 2010. Micromammals and the formation of the name chamber at Sterkfontein, South Africa. Geobios. 43(4):379-387. doi:10.1016/j.geobios.2010.01.002.
Badenhorst S, Steininger C. 2019. The equidae from Cooper's D, an early Pleistocene fossil locality in Gauteng, South Africa. PeerJ. 7:e6909. doi:10.7717/peerj.6909
Balter V, Blichert-Toft J, Braga J, Telouk P, Thackeray F, Albarède F. 2008. U–Pb dating of fossil enamel from the Swartkrans Pleistocene hominid site, South Africa. Earth Planet Sci Lett. 267:236-246. doi:10.1016/j.epsl.2007.11.039
Behrensmeyer AK. 1984. Taphonomy and the fossil record : the complex processes that preserve organic remains in rocks also leave their own traces, adding another dimension of information to fossil samples. Am Sci. 72 (6):558-566.
Berger LR, de Ruiter DJ, Steininger CM, Hancox J. 2003. Preliminary results of excava- tions at the newly investigated Coopers D deposit, Gauteng, South Africa. S Afr J Sci. 99:276–278.
Berger LR, Pickford M, Thackeray F. 1995. A Plio-Pleistocene hominid upper central incisor from the Cooper's site, South Africa. S Afr J Sci. 91:541-542.
Bobe R, Behrensmeyer A. 2004. The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus Homo. Palaeogeogr Palaeoclimatol Palaeoecol. 207:399-420. doi:10.1016/j.palaeo.2003.09.033
Brain CK (1981). *The hunters or the hunted? : an introduction to African Cave Taphonomy*. Chicago, IL: University of Chicago Press.
Brain CK. 1993. Swartkrans : a cave's chronicle of early man. Pretoria: Transvaal Museum Monograph.
Bredenkamp GJ, Spada F, Kazmierczak E. 2002. On the origin of Northern and Southern Hemisphere grasslands. Plant Ecol. 163:209-229. doi:10.1023/A:1020957807971
Broom R. 1948. Some South African pliocene and pleistocene mammals. Annals of the Transvaal Museum. 21(1):1-38. doi:10.10520/AJA00411752_457.
Bruxelles L, Maire R, Couzens R, Thackeray F, Braga J. 2017. A revised stratigraphy of Kromdraai. Braga J, Thackeray F editors. Kromdraai. A Birthplace of Paranthropus in the Cradle of Humankind. Johannesburg: African Sun Media; p. 31–47.
Caley T, Extier T, Collins J, Schefuß E, Dupont L, Malaizé B, Rossignol L, Souron A, McClymont E, Jiménez-Espejo F, et al. 2018. A two-million-year-long hydroclimatic context for hominin evolution in southEastern Africa. Nature. 560: doi:10.1038/s41586-018-0309-6.
Cohen B, O'regan H, Steininger C. 2019. Mongoose manor : herpestidae remains from the early pleistocene Cooper's D locality in the Cradle of Humankind, Gauteng, South Africa. Palaeontol Afr. 53:97-113.
Cooke HBS. 1990. Taung fossils in the university of California collections. In: Sperber G, Tobias V, editors. Apes to Angels: Essays in Anthropology in Honour of Phillip V. Tobias. New York: Wiley-Liss; p. 119–134.
Cornette R, Stoetzel E, Baylac M, Moulin S, Hutterer R, Nespoulet R, Hajraoui M, Denys C, Herrel A. 2015. Shrews of the genus Crocidura from El Harhoura 2 (Témara, Morocco) : the contribution of broken specimens to the understanding of Late Pleistocene–Holocene palaeoenvironments in North Africa. Palaeogeogr Palaeoclimatol Palaeoecol. 436:1-8. doi:10.1016/j.palaeo.2015.06.020
Cukrowska EM, McCarthy TS, Pole S, Backwell L, Steininger C. 2005. The chemical removal of manganese dioxide coatings from fossil bones from the Cradle of Humankind, South Africa. S Afr J Sci. 101.
Dart RA. 1925. Australopithecus africanus The Man-Ape of South Africa. Nature. 115(2884):195-199. doi:10.1038/115195a0.
De Graaff G. 1961a. A preliminary investigation of the mammalian microfauna in Pleistocene deposits of caves in the Transvaal system. Palaeontol Afr. 7:79-118.
De Graaff G. 1961b. On the fossil mammalian microfauna collected at Kromdraai by draper in 1895. S Afr J Sci. 57(9):259-260. doi:10.10520/AJA00382353_886.
De Graaff G. 1981. The rodents of Southern Africa : notes on their identification, distribution, ecology and taxonomy. Durban: Butterworths.
DeMenocal P. 2011. Climate and Human Evolution. Science. 331:540–542. doi:10.1126/science.1190683
Denys C. 1990. Implications paléoécologiques et paléobiogéographiques de l'étude de rongeurs plio-plaistocènes d'Afrique orientale et Australe [Thèse de 3e cycle]. Université Pierre et Marie Curie.
Denys C, Cochard D. 2017. Taphonomie des restes ingérés par les petits carnivores. In TaphonomieS. (éditions des archives contemporaines, p. 369-387) 10.17184/eac.3761
Denys C, Kowalski K, Dauphin Y. 1992. Mechanical and chemical alterations of skeletal tissues in a recent Saharian accumulation of faeces from Vulpes rueppelli (Carnivora, Mammalia). Acta Zool Cracov. 35:265–283.
de Ruiter DJ. 2003. Revised faunal lists for Members 1-3 of Swartkrans, South Africa. Annals of the Transvaal Museum. 40:29–41.
de Ruiter DJ, Pickering R, Steininger C, Kramers J, Hancox J, Churchill S, Berger L, Backwell L. 2009. New Australopithecus robustus fossils and associated U–Pb Dates from Cooper's Cave (Gauteng, South Africa). J Hum Evol. 56:497–513. doi:10.1016/j.jhevol.2009.01.009
DeSilva J, Steininger C, Patel B. 2013. Cercopithecoid primate postcranial fossils from Cooper's D, South Africa. Geobios. 46:381–394. doi:10.1016/j.geobios.2013.07.001
Dodson P, Wexlar D. 1979. Taphonomic investigations of owl pellets. Paleobiology. 5(3):275–284.
Eriksson PG, Altermann W, Hartzer FJ (2006). The Transvaal Supergroup and its precursors. In *The geology of South Africa* , (Johnson MR, Anhaeusser CR, Thomas RJ editors, 237–260).
Evans EMN, Van Couvering JAH, Andrews P. 1981. Palaeoecology of miocene sites in Western Kenya. J Hum Evol. 10(1):99–116. doi:10.1016/S0047-2484(81)80027-9.
Fernandez-Jalvo Y, Andrews P. 1992. Small mammal taphonomy of Gran Dolina, Atapuerca (Burgos), Spain. J Archaeol Sci. 19(4):407–428. doi:10.1016/0305-4403(92)90058-B.
Fernández-Jalvo Y, Andrews P. 2003. Experimental effects of water abrasion on bone fragments. J Taphonomy. 1:147–163.
Fernández-Jalvo Y, Andrews P (2016). *Atlas of Taphonomic Identifications : 1001 + Images of Fossil and Recent Mammal Bone Modification*. 10.1007/978-94-017-7432-1
Fernández-Jalvo Y, Andrews P, Denys C, Sesé C, Stoetzel E, Marin-Monfort D, Pesquero D. 2016. Taphonomy for taxonomists : implications of predation in small mammal studies. Quat Sci Rev. 139:138–157. doi:10.1016/j.quascirev.2016.03.016

Fernández-Jalvo Y, Avery DM. 2015. Pleistocene micromammals and their predators at wonderwerk cave, South Africa. J Afr Archaeol. 32(4):751–791. doi:10.1007/s10437-015-9206-7.
Folinsbee K, Reisz R. 2013. New craniodental fossils of papionin monkeys from Cooper's D, South Africa. Am J Phys Anthropol. 151:613–629. doi:10.1002/ajpa.22317
Frost SR, White FJ, Reda HG, Gilbert CC. 2022. Biochronology of South African hominin-bearing sites : a reassessment using cercopithecid primates. Proc Natl Acad Sci. 119(45):e2210627119. doi:10.1073/pnas.2210627119.
Gibbon R, Pickering T, Sutton M, Heaton J, Kuman K, Clarke R, Brain CK, Granger D. 2014. Comogenic nuclide burial dating of hominin-bearing Pleistocene cave deposits at Swartkrans, South Africa. Quat Geochronol. 24: doi:10.1016/j.quageo.2014.07.004.
Granger DE, Gibbon RJ, Kuman K, Clarke RJ, Bruxelles L, Caffee MW. 2015. New cosmogenic burial ages for Sterkfontein Member 2 Australopithecus and Member 5 Oldowan. Nature. 522(7554):85-88. doi:10.1038/nature14268.
Hanon R (2019). *Comportements de subsistance des hominines du Pléistocène inférieur d'Afrique du Sud : analyse archéozoologique du site de Cooper's D (Bloubank Valley)*. [Thesis for the degree of Doctor of Philosophy]. Muséum national d'Histoire naturelle. https://hal.archives-ouvertes.fr/hal–01744746
Hanon R, d'Errico F, Backwell L, Prat S, Péan S, Patou-Mathis M. 2021. New evidence of bone tool use by Early Pleistocene hominins from Cooper's D, Bloubank Valley, South Africa. J Archaeol Sci Rep. 39:103129. doi:10.1016/j.jasrep.2021.103129
Hanon R, Fourvel J-B, Steininger C. 2022c. Carnivores and hominins contributions to the early pleistocene bone accumulation of Cooper's D, South Africa. Quat Sci Rev. 291:107660. doi:10.1016/j.quascirev.2022.107660
Hanon R, Patou-Mathis M, Péan S, Prat S. 2019. Paleobiodiversity and large mammal associations during the late pliocene and the early pleistocene in South Africa. Quaternaire Revue de l'Association Française Pour l'étude Du Quaternaire. 30:30/3. doi:10.4000/quaternaire.12131
Hanon R, Patou-Mathis M, Péan S, Prat S, Cohen B, Steininger C. 2022a. Early Pleistocene hominin subsistence behaviors in *South Africa* : evidence from the hominin-bearing deposit of Cooper's D (Bloubank Valley, *South Africa*). J Hum Evol. 162:103116. doi:10.1016/j.jhevol.2021.103116
Hanon R, Péan S, Patou-Mathis M, Prat S, Rector A, Steininger C. 2022b. Fossil Bovidae from the Hominini-bearing site of Cooper's D (Bloubank Valley, South Africa) : implications for Paranthropus robustus Broom, 1938 and early Homo Linnaeus, 1758 habitat preferences. Comptes Rendus Palevol. 21(21):431-450.
Happold DCD, Éd. 2013. *Mammals of Africa. Vol. III: rodents, Hares and Rabbits*. London: Bloomsbury Publishing.
Hartstone-Rose A, Ruiter D, Berger L, Churchill S. 2007. A sabre-tooth felid from Coopers Cave (Gauteng, South Africa) and its implications for megantereon (Felidae : Machairodontinae) taxonomy. Palaeontol Afr. 42:99–108.
Hartstone-Rose A, Werdelin L, Ruiter D, Berger L, Churchill S. 2010. The plio-pleistocene ancestor of wild dogs, lycaon sekowei n. Sp. J Paleontol. 84:299-308. doi:10.1666/09-124.1
Herries AIR, Hopley PJ, Adams JW, Curnoe D, Maslin MA. 2010. Letter to the editor : geochronology and palaeoenvironments of Southern African hominin-bearing localities—A reply to Wrangham et al., 2009. "Shallow-water habitats as sources of fallback foods for hominins". Am J Phys Anthropol. 143 (4):640-646. doi:10.1002/ajpa.21389.
Herries A, Shaw J. 2011. Paleomagnetic analysis of the sterkfontein paleocave deposits : implications for the age of the hominin fossils and stone tool industries. J Hum Evol. 60:523-539. doi:10.1016/j.jhevol.2010.09.001
Hutterer R. 2005. Homology of unicuspids and tooth nomenclature in shrews. In: In JF, Churchfield MS, Hutterer B, Sheftel BI, editors. Advances in the biology of shrews II. Special Publication of the International Society of Shrew Biologists 1, New York; p. 397-404.
Jaccard P. 1901. Étude comparative de la distribution florale dans une portion des Alpes et du Jura. Bulletin de la Société Vaudoise des Sciences Naturelles. 37:547-579.
König C, Weick F, Becking J-H (2009). *Owls of the World* (Yale University Press).
Kowaleski M. 1999. Actuopaleontology : the strength of its limitations. Acta Palaeontologica Polanica. 44:452-454.
Kruger A, Badenhorst S. 2018. Remains of a barn owl (*Tyto alba*) from the Dinaledi Chamber, rising star Cave, South Africa. S Afr J Sci. 114:1-5. doi:10.17159/sajs.2018/5152
Kuhn B, Werdelin L, Steininger C. 2016. Fossil hyaenidae from Cooper's Cave, South Africa, and the palaeoenvironmental implications. PALAEOBIO PALAEOENV. doi:10.1007/s12549-016-0247-y
Kuman K, Clarke R. 2000. Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5. J Hum Evol. 38:827-847. doi:10.1006/jhev.1999.0392
Kuman K, Granger DE, Gibbon RJ, Pickering TR, Caruana MV, Bruxelles L, Clarke RJ, Heaton JL, Stratford D, Brain CK. 2021. A new absolute date from Swartkrans Cave for the oldest occurrences of Paranthropus robustus and Oldowan stone tools in South Africa. J Hum Evol. 156:103000. doi:10.1016/j.jhevol.2021.103000
Laudet F, Denys C, Senegas F (2002). *Owls, multirejection and completeness of prey remains : Implications for small mammal taphonomy*.
Leichliter JN (2018). Early Hominin environments in Southern Africa : a Micromammalian Perspective. [Thesis for the degree of Doctor of Philosophy]. University of Colorado Boulder.
Leichliter J, Sandberg P, Passey B, Codron D, Avenant NL, Paine OCC, Codron J, de Ruiter D, Sponheimer M. 2017. Stable carbon isotope ecology of small mammals from the Sterkfontein Valley : implications for habitat reconstruction. Palaeogeogr Palaeoclimatol Palaeoecol. 485:57-67. doi:10.1016/j.palaeo.2017.06.003
Linchamps P, Stoetzel E, Hanon R, Denys C. 2021. Neotaphonomic study of two *Tyto alba* assemblages from Botswana : palaeoecological implications. J Archaeol Sci Rep. 38: doi:10.1016/j.jasrep.2021.103085.
Lyman R (1994). *Vertebr Taphonomy*. 10.1017/CBO9781139878302
Lyman RL (2008). *Quantitative Paleozoology*. Cambridge University Press. 10.1017/CBO9780511813863
Marcon E (2015). *Mesures de la Biodiversité. Master*. Kourou.
Maslin M, Christensen B. 2007. Tectonics, orbital forcing, global climate change, and human evolution in *Africa* : introduction to the African paleoclimate special volume. J Hum Evol. 53:443-464. doi:10.1016/j.jhevol.2007.06.005
Matthews T. 2002. South African micromammals and predators : some comparative results. Archaeometry. 44:363-370. doi:10.1111/1475-4754.00069
Matthews T. 2006. Taphonomic characteristics of micromammals predated by small mammalian carnivores in South Africa : application to fossil accumulations. J Taphonomy. 4:143-160.
Matthews T, Denys C, Parkington JE. 2007. Community evolution of Neogene micromammals from Langebaanweg 'E' Quarry and other west coast fossil sites, south-western Cape, South Africa. Palaeogeogr Palaeoclimatol Palaeoecol. 245(3-4):332-352. doi:10.1016/j.palaeo.2006.08.015.
Matthews T, Marean CW, Cleghorn N. 2020. Past and present distributions and community evolution of Muridae and Soricidae from MIS 9 to MIS 1 on the edge of the Palaeo-Agulhas Plain (south coast, South Africa). Quat Sci Rev. 235:105774. doi:10.1016/j.quascirev.2019.05.026
Matthews T, Nel TH. 2021. The cryptic case of Otomys sloggetti (Sloggett's vlei rat) : interpreting murid molar morphology in the fossil record. S Afr J Sci. 117(1-2):1-8. doi:10.17159/sajs.2021/7137.
Matthews T, Rector A, Jacobs Z, Herries AIR, Marean CW. 2011. Environmental implications of micromammals accumulated close to the MIS 6 to MIS 5 transition at Pinnacle Point Cave 9 (Mossel Bay, Western Cape Province, South Africa). Palaeogeogr Palaeoclimatol Palaeoecol. 302(3-4):213-229. doi:10.1016/j.palaeo.2011.01.014.
Matthews T, Stynder DD. 2011. An analysis of two Myosorex species (Soricidae) from the early pliocene site of Langebaanweg (West coast, South Africa) using geometric morphometrics and linear measurements. Geobios. 44:87-99.
McKee JK, Thackeray JF, Berger LR. 1995. Faunal assemblage seriation of Southern African Pliocene and Pleistocene fossil deposits. Am J Phys Anthropol. 96(3):235-250. doi:10.1002/ajpa.1330960303.
Miele V, Dussert G, Cucchi T, Renaud S (2020). *Deep learning for species identification of modern and fossil rodent molars [En ligne]* [PrePrint]. HAL Archives Ouvertes. 10.1101/2020.08.20.259176
Moclán A, Domínguez-García ÁC, Stoetzel E, Cucchi T, Sevilla P, Laplana C. 2023. Machine Learning interspecific identification of mouse first lower molars (genus Mus Linnaeus, 1758) and application to fossil remains from the Estrecho Cave (Spain). Quat Sci Rev. 299:107877. doi:10.1016/j.quascirev.2022.107877
Monadjem A, Taylor PJ, Denys C, Cotterill FPD. 2015. Rodents of Sub-Saharan Africa: A biogeographic and taxonomic synthesis. De Gruyter; p. 1092.
Mucina L, Rutherford MC, Éds. 2006. The vegetation of South Africa, *Lesotho* and *Swaziland*. Pretoria: South African National Biodiversity Institute.
Nel TH, Henshilwood CS. 2016. The Small Mammal Sequence from the c. 76 – 72 ka Still Bay Levels at Blombos Cave, South Africa – taphonomic and Palaeoecological Implications for Human Behaviour. PLOS ONE. 11(8): Art. 8 10.1371/journal.pone.0159817
O'Regan H, Cohen B, Steininger C. 2013. Mustelid and viverrid remains from the Pleistocene site of Cooper's D, Gauteng, South Africa. Palaeontol. Afr 48:19-23.
O'Regan H, Steininger C. 2017. Felidae from Cooper's Cave, South Africa (Mammalia : Carnivora). Geodiversitas. 39:315-332. doi:10.5252/g2017n2a8
Paine OCC, Leichliter JN, Avenant N, Codron D, Lawrence A, Sponheimer M. 2019. The ecomorphology of Southern African rodent incisors : potential applications to the hominin fossil record. PLoS ONE. 14(2):e0205476. doi:10.1371/journal.pone.0205476.

Parkinson AH. 2016. Traces of Insect Activity at Cooper's D Fossil Site (Cradle of Humankind, South Africa). Ichnos. 23(3-4):322-339. doi:10.1080/10420940.2016.1202685.
Pavia M. 2020. Palaeoenvironmental reconstruction of the Cradle of Humankind during the Plio-Pleistocene transition, inferred from the analysis of fossil birds from Member 2 of the hominin-bearing site of Kromdraai (Gauteng, South Africa). Quat Sci Rev. 248:106532. doi:10.1016/j.quascirev.2020.106532
Pavia M, Val A, Carrera L, Steininger C. 2022. Fossil birds from Cooper's D aid in reconstructing the early pleistocene paleoenvironment in the cradle of Humankind (Gauteng, South Africa). J Hum Evol. 167:103185. doi:10.1016/j.jhevol.2022.103185
Pickering R, Herries A, Woodhead J, Hellstrom J, Green H, Paul B, Ritzman T, Strait D, Schoville B, Hancox J. 2019. U–Pb-dated flowstones restrict South African early hominin record to dry climate phases. Nature. 565: doi:10.1038/s41586-018-0711-0.
Pickering R, Kramers JD, Hancox PJ, de Ruiter DJ, Woodhead JD. 2011. Contemporary flowstone development links early hominin bearing cave deposits in South Africa. Earth Planet Sci Lett. 306(1):23-32. doi:10.1016/j.epsl.2011.03.019.
Pickford M. 2013. The diversity, age, biogeographic and phylogenic relationships of Plio-Pleistocene suids from Kromdraai, South Africa. Ann Dits Natl Mus Nat Hist. 3:11-32.
Pocock TN. 1969. Pleistocene Bird Fossils from Kromdraai and Sterkfontein. Ostrich. 40(1):1-6. doi:10.1080/00306525.1969.9639100.
Pocock TN. 1987. Plio-Pleistocene fossil mammalian microfauna of Southern Africa—A preliminary report including description of two new fossil muroid genera (Mammalia : Rodentia). Palaeontol Afr. 26(7):70-91.
Raczyński J, Ruprecht AL. 1974. The effect of digestion on the osteological composition of owl pellets. Acta Ornithologica. 14(2).
Reed KE. 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. J Hum Evol. 32(2-3):289-322. doi:10.1006/jhev.1996.0106.
Reed DN (2003). *Micromammal paleoecology : past and present relationships between African small mammals and their habitats* [Thesis for the degree of Doctor of Philosophy]. Stony Brook University.
Rödel HG, Scholze W, Kock D. 2002. Diet of Mackinder's eagle owl Bubo capensis mackinderi in the alpine zone of Mount Kenya. Afr J Ecol. 40:283-288. doi:10.1046/j.1365-2028.2002.00374.x
Sénégas F (2000). *Les faunes de rongeurs (Mammalia) plio-pléistocènes de la province de Gauteng (Afrique du Sud) : mises au point et apports systématiques, biochronologiques et précisions paléoenvironnementales* [Thèse de Doctorat]. Université de Montpellier 2.
Sénégas F, Paradis E, Michaux J. 2005. Homogeneity of fossil assemblages extracted from mine dumps : an analysis of Plio-Pleistocene fauna from South African caves. Lethaia. 38:315-322. doi:10.1080/00241160500355103
Sessions PHB. 1972. Observations on MacKinder's Eagle Owl Bubo capensis MacKinderi Sharpe on a Kenya farm. J East Afr Nat Hist. 1972(138):1-20. doi:10.10520/AJA00128317_329.
Steininger C (2011). *The Dietary behaviour of early Pleistocene Bovids from Cooper's Cave and Swartkrans, South Africa*. [Thesis for the degree of Doctor of Philosophy, University of the Witwatersrand].
Steininger C, Berger L, Kuhn B. 2008. A partial skull of Paranthropus robustus from Cooper's Cave, South Africa. S Afr J Sci. 104:143-146.
Sutton MB, Kuman K, Steininger C. 2017. Early pleistocene stone artefacts from Coopers Cave, South Africa. South African Archaeol Bull. 72:156-161.
Taylor I (1994). *Barn Owls. predator-prey relationships and conservation*. Cambridge University Press.
Taylor PJ, Kearney TC, Kerbis Peterhans JC, Baxter RM, Willows-Munro S. 2013. Cryptic diversity in forest shrews of the genus Myosorex from Southern Africa, with the description of a new species and comments on Myosorex tenuis. Zool J Linn Soc. 169(4):881-902. doi:10.1111/zoj.12083.
Terray L, Stoetzel E, Herrel A, Cornette R. 2021. The contribution of functional traits to the understanding of palaeoenvironmental changes. Biol J Linn Soc. 133: doi:10.1093/biolinnean/blab057.
Terry R. 2010. On raptors and rodents : testing the ecological fidelity and spatiotemporal resolution of cave death assemblages. Paleobiology. 36: doi:10.1666/0094-8373-36.1.137.
Thackeray F, Kirschvink J, Raub T. 2002. Palaeomagnetic analyses of calcified deposits from the Plio-Pleistocene hominid site of Kromdraai, South Africa. S Afr J Sci. 98:537-540.
Val A, Stratford DJ. 2015. The macrovertebrate fossil assemblage from the name chamber, sterkfontein : taxonomy, taphonomy and implications for site formation processes. Palaeontol Afr. 50:1-17.
Val A, Taru P, Steininger C. 2014. New taphonomic analysis of large-bodied primate assemblage from Cooper's D, Bloubank Valley, South Africa. South African Archaeol Bull. 69:49-58. doi:10.13140/2.1.4554.3042
Vernon C. 1972. An Analysis of owl pellets collected in Southern Africa. Ostrich. 43:109-124.
Voet I, Denys C, Colyn M, Lalis A, Konečný A, Delapré A, Nicolas V, Cornette R. 2022. Incongruences between morphology and molecular phylogeny provide an insight into the diversification of the Crocidura poensis species complex. Sci Rep. 12: doi:10.1038/s41598-022-12615-5.
Vogelsang R, Richter J, Jacobs Z, Eichhorn B, Linseele V, Roberts R. 2010. New excavations of middle stone age deposits at Apollo 11 rockshelter, Namibia : stratigraphy, archaeology, chronology and past environments. J Afr Archaeol. 8: doi:10.3213/1612-1651-10170.
Voorhies MR (1969). *Taphonomy and population dynamics of an early pliocene vertebrate Fauna, Knox County, Nebraska*. 10.2113/gsrocky.8.special_paper_1.1
Vrba E. 1974. Chronological and ecological implications of the fossil Bovidae at the Sterkfontein Australopithecine site. Nature. 250:19-23. doi:10.1038/250019a0
Vrba ES. 1985. Ecological and adaptive changes associated with early hominid evolution. Delson E, editor. Ancestors : the hard evidence. New York: Alan R. Liss, Inc; p. 63-71.
Wesselman HB. 1984. The Omo micromammals. Contributions to Vertebrate Evolution (Karger: In M. K. Hecht & F. S. Szalay.
Wilson DE, Lacher TE, Mittermeier RA (2016). *Handbook of the Mammals of the World – Vol. 6, Lagomorphs and Rodents I*. Barcelona: Lynx Edicions.
Wilson DE, Lacher TE, Mittermeier RA (2017). *Handbook of the Mammals of the World – Vol. 7, Rodents II*. Barcelona: Lynx Edicions. https://www.lynxeds.com/product/handbook-of-the-mammals-of-the-world-volume–7/
Winkler AJ, Denys C, Avery DM. 2010. Fossil rodents of Africa. Werdelin L, Sanders W editors. Cenozoic mammals of Africa. United States: California University Press.