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New modern and Pleistocene fossil micromammal assemblages from Swartkrans, South Africa: Paleobiodiversity, taphonomic, and environmental context

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ABSTRACT

The oldest deposit at the hominin-bearing cave of Swartkrans, South Africa, is the Lower Bank of Member 1, dated to ca. 2.2 million years ago. Excavations of this unit have produced a diverse and extensive mammalian fossil record, including *Paranthropus robustus* and early *Homo* fossils, along with numerous Oldowan stone tools. The present study focuses on the taxonomic analysis of the micromammalian fossil assemblage obtained from recent excavations of the Lower Bank, conducted between 2005 and 2010, as part of the Swartkrans Paleoanthropological Research Project. The taxonomic composition of this assemblage is dominated by *Mystromys*, a rodent indicative of grassland environments. Taphonomic analysis indicates an accumulation of prey by *Tyto alba* (Barn owl) or a related species. Environments inferred from this evidence reflect an open landscape primarily covered by grassland vegetation, but they also feature components of wooded areas, rocky outcrops, and the proximity of a river. The Swartkrans fossil assemblage is compared with Cooper's D (dated to ca. 1.4 Ma) and a modern coprocoenosis of *Bubo africanus* (spotted eagle-owl) collected within the Swartkrans cave for taxonomic, taphonomic, and paleoecological perspectives. Contrasting fossil and modern micromammalian data provide a better understanding of accumulation processes and facilitate a diachronic reconstruction of changes in climate and landscape evolution. Issues regarding paleoenvironmental reconstruction methodologies based on micromammals are also discussed.

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1. Introduction

The cave of Swartkrans is an emblematic paleoanthropological site within the Cradle of Humankind (COH) in Gauteng Province, South Africa, boasting a rich history of paleontological and archeological research dating back to 1948 when Robert Broom first discovered *Paranthropus* fossils at the site. Over the years, a significant collection of faunal remains has been accumulated, encompassing, among other taxa, numerous remains of micromammals (mammals of less than 500 g live weight). As early as 1955, Davis drew up an inventory of the fossil microfauna from Member 1, which he never published but was referred to in Brain (1981). This faunal list was later complemented by the works of Levinson (1985), Denys (1990), and Avery (1998) who published further descriptions of the small vertebrates from various stratigraphic units.

The study of fossil micromammalian assemblages can provide an excellent opportunity for reconstructing landscapes and climates of the past, especially in cave contexts, where remains of small vertebrates often accumulate in great abundance (e.g., Andrews, 1990; Avery, 2007). Due to their narrow home ranges, short lifespans, limited dispersal abilities, and the fact that many taxa are restricted to a particular type of habitat (Happold, 2013),

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micromammals are sensitive to slight changes in climate and vegetation at a local scale and are considered as spatiotemporally well-constrained indicator taxa (Avery, 1982; Andrews, 1990; Fernández-Jalvo et al., 1998; Stoetzel et al., 2011). Microfaunal studies thus offer the opportunity to track climate changes and landscape dynamics over time in the COH. This area of approximately 47,000 hectares has yielded numerous hominin-bearing Plio-Pleistocene deposits, with ages ranging from ca. 4 to 1 million years. This span represents a critical juncture in human evolution, marked by a series of significant anatomical and behavioral adaptations that led to the emergence of the genus *Homo* (Bobe and Behrensmeyer, 2004; Antón and Snodgrass, 2012; Clarke, 2017).

Despite these high stakes, the turn of the 21st century represents an important milestone in microfaunal studies of the COH fossils, with few works published after the major contributions of Pocock (1987), Denys (e.g., 1990, 1992), Avery (e.g., 1995, 1998, 1999, 2001), and Sénégas (2000). Avery (2007) described this situation in hindsight, emphasizing that recent progress in ecology, paleoecology, taphonomy, and systematics has shown the oversimplicity of several paleoenvironmental interpretations. Today, there is anticipation for a renewed interest in micromammal studies, which could be facilitated by an improved understanding of the often complex geological and stratigraphic context of Pleistocene fossil deposits (e.g., Bruxelles, 2022; Dirks and Berger, 2013), along with the increase in available neotaphonomic referentials for studying the origin and formation history of fossil assemblages (e.g., Matthews, 2006; Cohen and Kibii, 2015, 2019; Linchamps et al., 2021), and a rise in taxonomic and systematic research providing significant advancements in the delineation of rodent species and enhanced knowledge of their ecology and distribution (see, for instance, synthesis handbooks such as Monadjem et al., 2015; Wilson et al., 2016, 2017). Methodological progress also enables a more cautious paleoenvironmental interpretation of the fossil communities. With the development of increasingly refined paleo-data analysis methods, a central challenge now lies in having access to more faunal lists with accurate identification in light of current taxonomic knowledge and well-contextualized understanding of the stratigraphy and chronology.

In this study, we describe and analyze a new micromammalian fossil assemblage from the Lower Bank of Member 1 at the Swartkrans cave site. This material originates from new excavations by the Swartkrans Paleoanthropological Research Project (SPRP) conducted between 2005 and 2010 and dating largely to ca. 2.2 Ma (Kuman et al., 2021). The analysis includes the identification of the fossils, an examination of the mode of accumulation through taphonomic investigation, and a preliminary reconstruction of past environmental conditions and habitats surrounding the cave through paleoecological analysis. A pellet accumulation produced by the spotted eagle-owl (*Bubo africanus*), which currently nests in the cave, was also collected and analyzed. This coprocoenosis provides a comparative modern-day micromammal inventory and further neotaphonomic referential for the interpretation of the Swartkrans fossils. Throughout this study, the fossil assemblage from Swartkrans is compared to that of the ca. 1.4-Myr-old assemblage of Cooper's D, recently documented by Linchamps et al. (2023a), along with the contemporary pellet-derived assemblage. One objective is to ascertain whether it is possible or not to detect distinct environmental signals over time by analyzing the faunal content of each assemblage, using methodologies from microfaunal analyses. This will enable a discussion of the possibilities and expected research avenues for microfaunal studies in the COH.

1.1. Stratigraphy, chronology, and paleoanthropological significance of Swartkrans Member 1

The fossil site of Swartkrans (25°55′45″S, 27°47′20″E; altitude: 1480 m) lies within South Africa's Cradle of Humankind World Heritage Site (Fig. 1), about 30 km northwest of Johannesburg and 1 km northwest of Sterkfontein. It was identified as a hominin site in

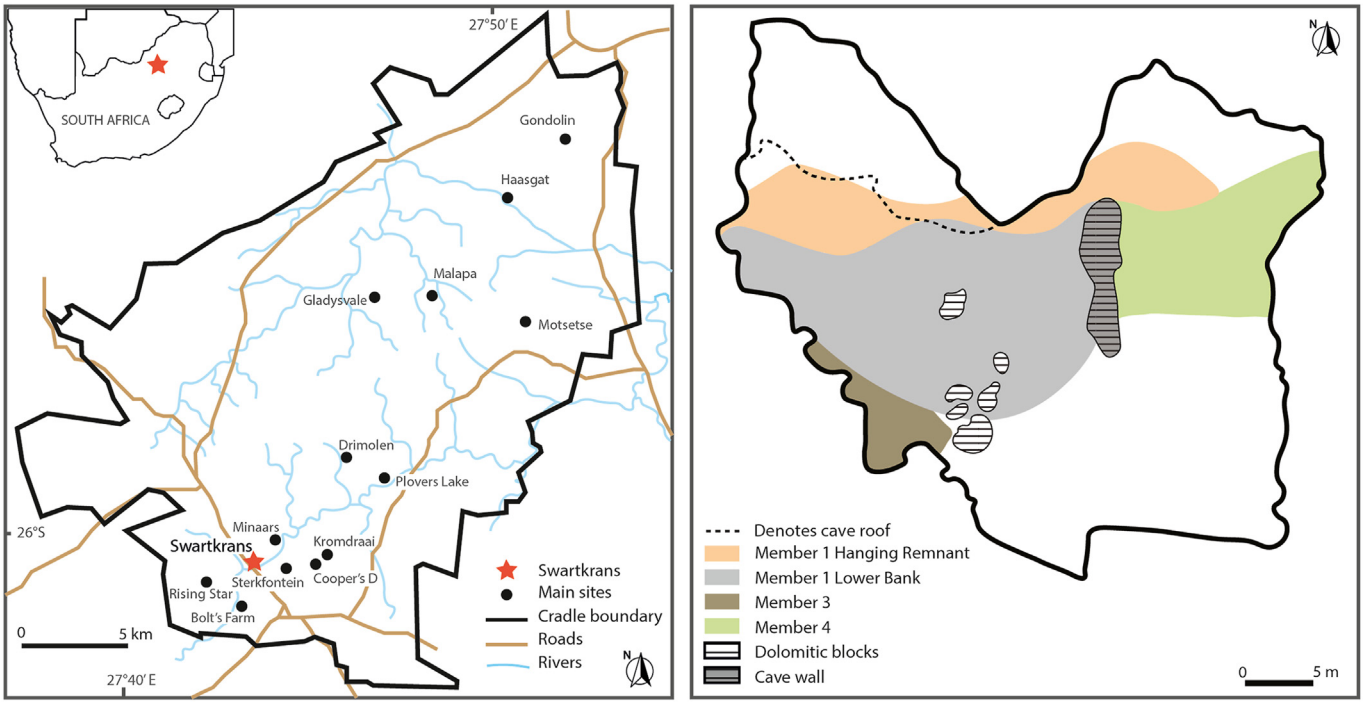

Figure 1. Location of Swartkrans in relation to other fossil sites of the Cradle of Humankind in South Africa, with plan of the Members 1, 3, and 4 deposits that have been excavated as part of the Swartkrans Paleoanthropological Research Project. Plan modified from Kuman et al. (2021). (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article.)

1948, with investigations carried out by Robert Broom and John Robinson. They soon found a partial hominin mandible and some isolated teeth for which Broom named a new species *Paranthropus crassidens* (Broom, 1949), generally today grouped with *Paranthropus robustus* (Broom, 1938). In 1949, John Robinson discovered a mandible that he and Broom designated as a humanlike form, naming it *Telanthropus capensis* (Broom and Robinson, 1949)—since transferred to *Homo* by Robinson (1961) but discussed by Clarke (2017) as a possible *Australopithecus africanus*. Broom and Robinson continued collecting fossils at Swartkrans until Broom's death in 1951, and excavations continued under the direction of Robinson until 1953. The site was then abandoned until 1965, when fieldwork resumed under C.K. (Bob) Brain for over 21 years. Brain's work at the site provided a detailed hypothesis outlining stratigraphy and taphonomy of the site and considerably augmented the faunal and lithic artefact collections (e.g., Brain, 1970, 1981, 1993; Brain and Sillen, 1988). He designated five distinct members (Table 1).

In 2005, the SPRP carried out a new program of excavations under the direction of T.R.P., focusing mostly on Member 1 Lower Bank (SWT1/LB), Member 3 (SWT3), and parts of Member 4 (SWT4) (Fig. 1). Several micromammal samples were collected during this fieldwork, but only the fossils from the Member 1 Lower Bank correspond to in situ material, recovered from squares 1N5E, 1N6E, 1N8E, 2N6E, 2N7E, 3N6E, and 3N7E. Member 1 is the oldest deposit currently recognized in Swartkrans. It is divided into two subunits: the Lower Bank (SWT1/LB) and the Hanging Remnant (SWT1/HR) (Brain, 1993). Most of the discoveries made by Broom and Robinson between 1948 and 1953 derive from what today is designated as the HR. The SWT1/LB infill was recognized by Brain in the 1970s as a distinct sedimentary subunit of Member 1, which he thought formed prior to SWT1/HR. It consists of orange-/brown-colored, poorly calcified or decalcified sediments. The Lower Bank unit excavated by Brain and later by Pickering has yielded many Oldowan stone tools (Clark, 1993; Kuman et al., 2018) and a large mammalian fossil record, including 28 craniodental remains attributed to *P. robustus*, one mandible attributed to *Homo* sp., one molar to cf. *Homo* sp., six craniodental remains assigned to Hominidae gen. and sp. indet., as well as 23 additional postcranial hominin remains not assigned to a specific taxon (Kuman et al., 2021). The entire Member 1 sequence was originally estimated by Vrba (1985) to be between 1.8 and 1.5 Ma based on her analysis of the bovids. Several researchers have since attempted to provide more precise ages using radiometric dating methods, which showed that the whole member was much older. Using cosmogenic nuclide burial dating, Gibbon et al. (2014) reviewed these efforts and published two nonoverlapping preliminary cosmogenic dates of 2.19 ± 0.08 and 1.80 ± 0.09 Ma for the Member 1 Lower Bank, which could not be reconciled at the time. More recently, Kuman et al. (2021) used the isochron cosmogenic nuclide burial dating method and provided an absolute age of 2.22 ± 0.09 Ma for a large portion of the Lower Bank. SWT1/LB thus represents, together with Sterkfontein (Kuman and Clarke, 2000; Granger et al., 2015) and Kromdraai (Bruxelles et al., 2017), one of the earliest appearances of *P. robustus* fossils.

1.2. Environmental setting

The karst system of Swartkrans lies on the north side of the small Bloubank River at an elevation of 1480 m. The excavated area is situated 30 m above the current river level, which today is located 140 m below the south side of the site (Kuman et al., 2018). Similar to the surroundings of the fossil sites of Cooper's D, Sterkfontein, and Kromdraai, the actual landscape is dominated by the rocky Highveld grassland made up of grassy plains, shrubs, and dolomite outcrops, with some trees thriving in the loose sediments of cleared excavation areas and cave surroundings (Fig. 2A). However, the proximity to the Bloubank River results in the presence of a riverine woodland corridor nearby (Fig. 2B), which is not present in some other fossil sites. Today, the Bloubank consists of a small-sized perennial river. During the rainy season, from November to March in summer, the river reaches its maximum flow and can expand to a width of 4 to 5 m between its banks (Sutton, 2012). Mapping of the terrace gravel indicates that it was much wider in the past (Kuman, 1996; Kuman et al., 2018) and played a major role in the incision of the surrounding valley (Dirks and Berger, 2013). The importance of the paleoriver is also reflected in the fossil fauna recovered from SWT1/LB, which yielded remains of African clawless otter (*Aonyx capensis*) and hippopotamus (*Hippopotamus* sp.) (Watson, 1993). Today, the landscape's vegetation around Swartkrans is heavily degraded by human activities. These include cattle farming, introduction of invasive species, use of pesticides and fertilizers, gravel and tar roads, and commercial and industrial ventures, among others, which have altered original natural habitats.

1.3. Previous micromammal studies at Swartkrans and what has changed since then

Several researchers have examined the micromammalian fauna of the Swartkrans assemblages (Table 2). In about 1960, Davis analyzed the Robinson collection and compiled a faunal list for Member 1, which, although never published, is referenced in the study by Brain (1981). Brain later disaggregated and examined additional breccia blocks, with Levinson (1985) identifying the rodent genera present within them. Denys (1990) later published a list of fossil rodents from the 'rodent section East End' of Member 1. She interpreted the abundance of *Mystromys* and *Otomys* as evidence of a relatively arid grassland steppe environment, with the presence of *Dasymys* suggesting a nearby water source. However, it was Avery (1998, 2001) who made the most significant contributions to the study of micromammalian fauna from Swartkrans. She studied material from Members 1 to 3 excavated by Brain between 1979 and 1986. Examining taphonomy, she identified the barn owl *Tyto alba* as the most likely accumulation agent (Avery, 2001). She found no difference in taxonomic composition between the three members, which was also observed by Brain (1993) with large mammals. These three members are numerically dominated by *Mystromys albicaudatus*, whose frequency varies from 45.80% of the minimum number of individuals (MNI) in Member 2 to 53.84% in Member 1

Table 1
The different deposits at Swartkrans, with latest estimated chronology.

Deposits	Estimated ages (in Ma)	Dating methods	Dating references
Member 1 Lower Bank	2.22 ± 0.09−>1.8/1.7	Isochron cosmogenic ($^{26}Al/^{10}Be$)	Kuman et al. (2021)
Member 1 Hanging Remnant	2.248 ± 0.052−1.8 ± 0.005	U-Pb	Pickering et al. (2019)
Member 2	Intermediate between the M1 and M3; ca. 1.5	U-Pb; relative stratigraphy; faunal content	Balter et al. (2008) Pickering et al. (2016)
Member 3	0.96 ± 0.09	Cosmogenic ($^{26}Al/^{10}Be$)	Gibbon et al. (2014)
Member 4	Middle Stone Age, with underlying flowstone dated to 0.11 ± 0.02	Stone tool typology; U-Th	Sutton et al. (2009)
Member 5	0.011	C^{14}	Brain (1993)

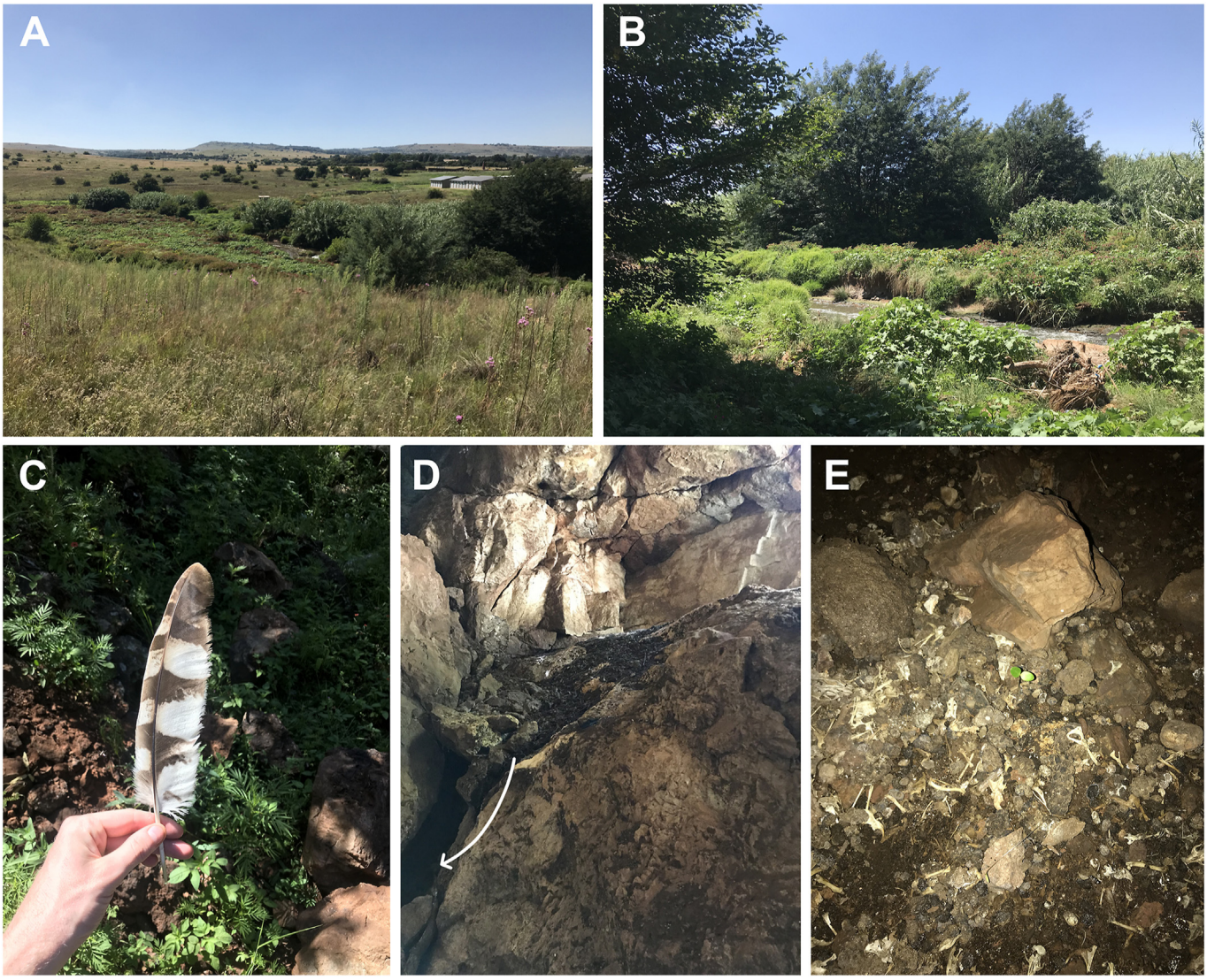

Figure 2. View of the landscape around Swartkrans and details of the modern micromammal bone assemblage accumulated by the spotted eagle-owl *Bubo africanus*. A) Looking southeast from the hill on which the Swartkrans cave is located, the course of the Bloubank is visible in the center of the photograph, along with storage buildings and settlements to the right; B) a closer look at the Bloubank river and its riverine vegetation; C) feather of *B. africanus* found near the bone assemblage; D) bones accumulated on the inclined floor and slid by gravity into the cavity below (indicated by the white arrow); E) the floor of the cavity consists of a mixture of sediments, micromammal bones, and rock hyrax feces. All pictures were taken in February 2023. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

and 54.53% in Member 3. The two other most abundant species are *Otomys saundersiae* and *Fukomys damarensis*. Avery (2001) interpreted the three samples as representative of interglacial conditions with similar environment, comprising "a vegetational succession from riverine grassland, sometimes with *Acacia* trees, through hillsides with bush, grass, and some trees, to plains with open savannah woodland" (p. 130). She suggested that conditions were more arid than today, with lower mean annual rainfall (285–333 mm as opposed to about 650 mm today) and higher mean minimum monthly temperatures (5.7–9.4 °C vs. ±1 °C today). It is important to highlight that the number of fossils examined by Avery is notably higher than those investigated in this study, with a minimum of 6107 identified micromammal individuals for Member 1 'SKX1' alone (compared to 721 in this study).

Table 2 summarizes the various published rodent inventories for the fossil material from Swartkrans. These faunal lists are valuable not only for their taxonomic complementarity and the paleoecological insights they offer but also for tracking and discussing the evolution of identification practices for South African microfauna, particularly in light of advancements in systematic and taxonomic research. The classification of rodents in South Africa has a relatively unstable history (see Monadjem et al., 2015), which has impacted the identification of key diagnostic features used for identifying both fossil and modern craniodental material. Today, we have far more comprehensive comparative anatomical data than before, allowing for a better understanding of interspecific variability. Thanks to the taxonomic revision work on rodents by Denys (1990), Avery (1998), and Sénégas (2000), several taxa originally described by Broom between 1937 and 1948 have been discarded, either because they fell within the known variation of modern species or due to the lack of explicit anatomical descriptions. This is the case for *Dendromus antiquus*, *Tatera robinsoni*, and likely *Cryptomys robertsi*, which can be considered, with the benefit of current insights, as nomina dubia. Phylogenetic analyses have also reassigned several species from South Africa to distinct genera. For instance, the *Tatera* species were transferred to the genus

Table 2
Previously published rodent inventories for Member 1 of Swartkrans.

Davis, in Brain (1981)	Levinson (1985)	Denys (1990)	Avery (2001)
	Acomys	*Acomys* sp.	*Acomys spinosissimus*
	Aethomys	*Aethomys* cf. *chrysophilus*	*Aethomys chrysophilus*
Cryptomys robertsii	*Cryptomys*	*Cryptomys* sp.	*Cryptomys damarensis*
Dasymys bolti	*Dasymys*	*Dasymys* cf. *bolti*	*Dasymys* spp.
Dendromus antiquus	*Dendromus*	*Dendromus* sp.	*Dendromus melanotis*
			Desmodillus auricularis
			Georychus capensis
		Grammomys sp.	
	Graphiurus		*Graphiurus murinus*
Lemniscomys sp.	*Lemniscomys*	*Lemniscomys* sp.	
Malacothrix cf. *typica*	*Malacothrix*	*Malacothrix* cf. *makapani*	*Malacothrix typica*
	Mastomys		*Mastomys* sp.
Mus cf. *minutoides*	*Mus*	*Mus* sp.	*Mus* spp.
Mus cf. *triton*			
Mystromys hausleitneri	*Mystromys*	*Mystromys hausleitneri*	*Mystromys albicaudatus*
Otomys gracilis	*Otomys*	*Otomys gracilis*	*Otomys saundersiae*
		Praomys sp.	
	Proodontomys	*Proodontomys cookei*	*Proodontomys cookei*
	Rhabdomys		*Rhabdomys pumilio*
Steatomys cf. *pratensis*	*Steatomys*	*Steatomys* sp.	*Steatomys pratensis*
Tatera robinsoni	*Tatera*	*Tatera* sp.	*Tatera leucogaster*
			Thallomys sp.
	Thamnomys		
	Zelotomys	*Zelotomys* sp.	

Gerbilliscus, the *Praomys* species to the genus *Mastomys*, the *Thamnomys* species to the genus *Thallomys,* and some species of *Dendromus* to the genus *Poemys* (Monadjem et al., 2015; Wilson et al., 2016, 2017). Recently, further advancements in molecular systematics have revealed a significant level of cryptic diversity, characterized by minimal morphological differences but high genetic disparity, resulting in a rise in the number of species described in South Africa (58 species listed in De Graaff, 1981 vs. 76 species in Linchamps et al., 2023b). Some previously published species, such as *Mus* cf. *triton*, *Acomys spinosissimus*, *Cryptomys damarensis* (today reassigned to *Fukomys damarensis*), or *Rhabdomys pumilio*, could therefore be more parsimoniously reallocated to other anatomically similar species based on current distribution data. Finally, we now know that in South Africa, some genera, such as *Otomys*, *Gerbilliscus* (formerly *Tatera*), and *Aethomys*, are particularly challenging, if not impractical, to identify at the species level (Monadjem et al., 2015). It is therefore important to account for taxonomic updates before examining diachronic trends in paleoenvironments based on fossil lists published several decades ago. An extensive work of taxonomic description and revision of Pleistocene micromammals in South Africa is urgently needed, incorporating recent advances in systematics.

Another recent advancement in archeological and paleontological practices at the COH is the increased emphasis on rigorous excavation strategies and detailed stratigraphic analysis. It has now become standard practice to record the precise provenance of materials within the deposit using Cartesian coordinates (XYZ). This allows for the subsequent spatial repositioning of the fossil remains and facilitates analyses of spatial patterns in order to understand accumulation events within a fossil site. Unfortunately, the precise origin of the material within Member 1 from previous micromammal studies listed in Table 2 is undisclosed, posing challenges in assessing the extent to which these assemblages might represent some geomorphological palimpsests. Furthermore, the fossils studied by Avery are presently dispersed across various collections, impeding access to many of the specimens. Consequently, the material analyzed in this study offers a fresh complementary insight into the micromammalian biodiversity of Swartkrans, with a better stratigraphic control.

2. Materials and methods

2.1. Fossil samples

The micromammalian material studied in this paper derives from Member 1 Lower Bank (SWT1/LB) collected between 2006 and 2007 during the SPRP excavation of decalcified or loose sediments. The material is currently housed at the Evolutionary Studies Institute, University of the Witwatersrand, in Johannesburg. The microfauna was recovered among other small residues by dry sieving using a 5-mm mesh over a 2-mm mesh screen. The sieved residues from the 5-mm mesh were then wet sieved. Unfortunately, this mesh size does not allow for the complete recovery of the smallest skeletal elements (e.g., isolated teeth, phalanges, and caudal vertebrae) (Lyman, 2012). This has inevitably impacted the representation of the smallest taxa to some extent.

The whole micromammal assemblage initially consisted of multiple spatially referenced samples, each containing unsorted bulk fossil material retrieved through excavation and sediment sieving. Sorting, taxonomic identifications, and taphonomic analysis were made under a binocular microscope. Micromammals were selected, and other taxa (including birds, reptiles, amphibians, or larger mammals) were set aside for future studies. All micromammalian bones, including unidentifiable fragments, were counted and taphonomically analyzed. Mandibles, maxillae, and isolated teeth were then extracted for taxonomic identification. As a first step, 11,039 remains were counted for SWT1/LB, of which 7579 remains of micromammals identifiable at least anatomically were analyzed. This sample size was considered sufficient to accurately represent the proportional distribution of the different skeletal elements. Given that taxonomic and ecological analyses do not require postcranial remains, we subsequently extracted around 1200 additional craniodental remains from the remaining bulk of the micromammalian assemblage.

Craniodental fossil specimens were labeled from 001 with an SWT1/LB-MF- prefix. 'SWT' refers to the Swartkrans material collected during SPRP excavation ('T' refers to the Transvaal Museum, where the fossils were originally curated), '1/LB' designates the Lower Bank of Member 1, and 'MF' refers to microfauna.

The SPRP team adopted this system of designation to facilitate the distinction of newly excavated material from fossils discovered during earlier excavations at Swartkrans, which have been designated by the prefixes SK, SKW, or SKX.

2.2. Modern spotted eagle-owl coprocoenosis

In addition to the fossil material, a contemporary assemblage of small mammal remains, retrieved from intact and decayed pellets of the spotted eagle-owl (*B. africanus*) (Fig. 2C), was collected from a cavity in the twilight zone of the bottom of the Swartkrans Cave (Fig. 2D, E).

The spotted eagle-owl is a medium- to large-sized owl species that has a wide distribution through sub-Saharan Africa and the Arabian Peninsula. It is the most common owl found in southern Africa, and it thrives in a variety of biomes, favoring open habitats and avoiding dense forests (König et al., 2009). It often lives in close proximity to human habitation.

The spotted eagle-owl is usually not considered a significant accumulator in the Quaternary sites of South Africa. Still, its presence today at Swartkrans suggests that it cannot be overlooked. We directly observed a spotted eagle-owl near the collection site, and local workers frequently see them in the area. The bone material was found mixed with sediment and feces of the rock hyrax (*Procavia capensis*) that inhabits the cave. Given the predominantly disaggregated nature of the material, the count of pellets was not possible. The maximum number of bones visible on the ground surface was collected by hand (as the access to the cavity is rather narrow).

Analyses of modern pellet assemblages provide useful comparative material and analogues with which to compare and contrast fossil microvertebrate data (Denys et al., 2023). This assemblage holds significant interest as it represents a contemporary, in situ replication of the micromammal fossil accumulation at Swartkrans. Therefore, comparing the fossil fauna with its modern counterpart allows for an assessment of changes in species composition over time. Similarly, comparing the taphonomic profiles of both the fossil and modern assemblages enable the identification of whether the bone accumulations were built up by the same predator.

2.3. Comparison with micromammal assemblage from Cooper's D

The results of taphonomic and (palaeo)ecological analyses conducted on both the fossil and modern assemblages of Swartkrans were compared to the data recorded for the fossil microfaunal assemblage of Cooper's D, which was the subject of a recent publication (Linchamps et al., 2023a). This fossil deposit has been dated to approximately 1.4 Ma (Pickering et al., 2019) and has yielded rich microfaunal (e.g., Pavia et al., 2022; Matthews and Steininger, 2023), mesofaunal (e.g., Cohen et al., 2019), and macrofaunal assemblages (e.g., Hanon et al., 2022a, 2022b), including remains attributed to *P. robustus* (Steininger et al., 2008). The localities of Swartkrans and Cooper's Cave are separated by a distance of approximately 2400 m, which implies that the hunting range of the birds of prey that nested in the caves overlapped at least partially (Fig. 3). For instance, the territory size of the barn owl *T. alba* can cover anywhere from 0.5 to 9 km^2, sometimes more, depending on food and nest site availability (Andrews, 1990; König et al., 2009). Therefore, one may expect that differences in the reconstructed climate and landscapes reflect variations in environmental conditions over time rather than mere landscape features due to local microclimatic and hydrological conditions. The diachronic comparison is all the more relevant, given that the three assemblages (Swartkrans fossil ~ 2.2 Ma, Cooper's D ~ 1.4 Ma, Swartkrans modern) were analyzed by the same authors, using the same analytical methodology, thereby minimizing potential interobserver influence.

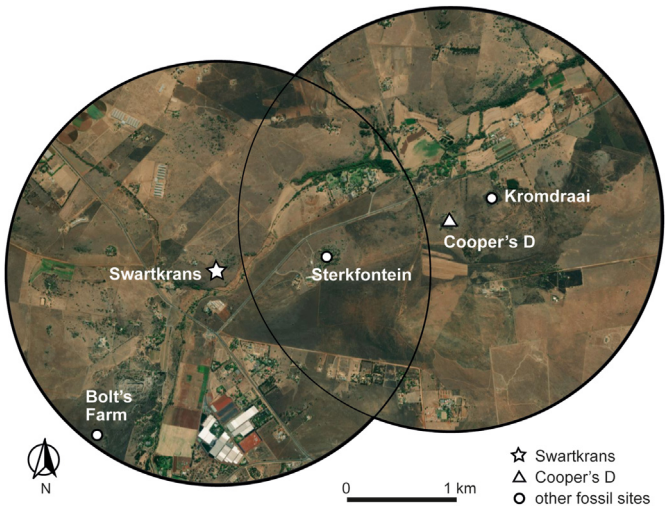

Figure 3. Circles with a radius of 2 km drawn around Swartkrans and Cooper's D fossil sites, in relation to other fossil sites of the Cradle of Humankind in South Africa. The area of each circle represents an average hunting range of a barn owl.

2.4. Quantification of remains

We used four quantification units based on Andrews (1990) and Lyman's (1994) methodologies: the number of remains, number of identified specimens, minimum number of elements (MNE), and MNI.

The MNE was obtained by recording the most abundant bone portion for each skeletal element (distal part, distal part + shaft, shaft, shaft + proximal part, proximal part, complete bone). The MNI was calculated on the craniodental remains only, based on the most preserved lateralized elements (the hemimandible, hemimaxilla, or isolated premolar/molar).

2.5. Taxonomic identifications

Taxonomic identifications of both modern and fossil material were undertaken by comparing Swartkrans specimens with modern and fossil osteological collections stored in the Ditsong National Museum of Natural History (Pretoria, South Africa), Museum National d'Histoire Naturelle (Paris, France), and Evolutionary Studies Institute (Johannesburg, South Africa). To assist in identification, we used the identification key provided in Linchamps et al. (2023b), as well as pictures and information from other sources (e.g., De Graaff, 1981; Happold, 2013; Monadjem et al., 2015). Fossils have been identified to the species level when diagnostic criteria were available; otherwise, we opted for a more cautious identification at the genus level. Identification of modern specimens has been made to the species level when feasible. Measurements of maximum length and width of teeth were taken using digital calipers to the nearest 0.01 mm. Pictures of the specimens were taken using the LC30 digital color camera for microscopy (3.1 megapixels) and NIKON D3300 digital camera (24.2 megapixels) with a macro lens and extension rings.

2.6. Taphonomic analyses

Taphonomic investigation of both the fossil and modern Swartkrans assemblages followed standard methodology for micromammal studies described in Andrews (1990), Fernández-

Jalvo and Andrews (1992), and Stoetzel et al. (2011) and updated for digestion in Fernández-Jalvo et al. (2016).

The fragmentation rate was calculated for the femora, the tibiae, and the humeri. The same set of breakage used for calculation of MNE was used here (distal part, distal part + shaft, shaft, shaft + proximal part, proximal part, complete bone). Quantification of breakage was then summarized into complete vs. incomplete bones. Measure of breakage can bring information on the origin of accumulation, yet apart from predators, many other agencies can damage fossil pellet-derived assemblages, e.g., calcification/decalcification cycles, trampling, rock slides and falls, water transportation, sediment compaction, etc. It is still relevant for comparing the preservation state of the material.

Skeletal representation describes the proportions by which each of the prey skeletal elements is represented in the assemblage. It was originally created for distinguishing between different predator types responsible for coprocoenoses (scats and pellets; for example, Dodson and Wexlar, 1979; Andrews, 1990; Matthews, 2002; Matthews et al., 2005). In the case of fossil accumulations, other postdepositional events not related to predation may alter further the skeletal representation, including water transportation, bioturbation, brecciation, etc. The skeletal representation is expressed in percentages of representation (PRs) that are calculated as follows: PR = OF/(TF * MNI) * 100, where OF is the frequency of every skeletal element observed in the pellet assemblage and TF is the theoretical frequency of each skeletal element from a fully preserved skeleton (for a typical mouselike murid, TF = one cranium, two hemimandibles, two hemimaxillae, two scapulae, two humeri, two radii, two ulnae, two hemipelves, two femora, two tibiae, 36 vertebrae, four incisors, 12 molars, 56 phalanges, 20 metapodials, and 24 ribs).

The impact of enzymatic processes within the digestive tract leaves characteristic marks on bones from coprocoenoses that can hardly be confused with other postdepositional alterations. We analyzed and quantified digestion traces on both isolated and in situ incisors, as well as on femoral heads. While molars are also a key element for analyzing digestive marks, they need to be further re-evaluated for South African small mammals to provide more accurate patterns that may lead to better taphonomic results. Given this limitation, and considering that the digestive patterns of incisors and femoral heads remain consistent regardless of the region, we focused on those elements for our study. For the fossil material, we carefully rinsed the incisors and femora with water to document evidence of acid etching, taking care not to damage the bones. We considered four grades of digestion for both fossil and modern material: light, moderate, heavy, and extreme (Andrews, 1990; Fernández-Jalvo and Andrews, 2016).

To assess the predation origin of the fossil assemblage, we used Andrews' (1990) classification of predators into five categories based on the frequency and intensity of digested elements. Species in Category 1, such as nocturnal owls such as *T. alba*, produce minimal modifications to their prey assemblages, whereas those in Category 5, such as terrestrial mammalian carnivores, cause the most significant alterations.

We also completed the taphonomic study of the Cooper's D micromammalian assemblage by incorporating the previously missing digestion rates for the femoral heads and in situ incisors. For this latter assemblage, the number of bone elements included in the new study is comparatively low due to the high rate of manganese infiltration and the encrustation of calcareous sediments on the bones, which obscures their surfaces (Fig. 4).

The covering of bones with brown to black manganese coating is common in fossil assemblages from the COH, particularly on fossils derived from decalcified sediments (Cukrowska et al., 2005). This coating originates from the dissolution of surrounding dolomite, which releases manganese and iron that combine to form a variable thickness layer of manganese dioxide that accumulates on the bone surface. This phenomenon can complicate taphonomic analysis by hindering the examination of bone surfaces and may also hinder taxonomic identifications when the encrustation is excessively thick. We quantified the percentage of bone elements infiltrated by manganese for the Swartkrans assemblages (Fig. 4A–C) and Cooper's D (Fig. 4D). Bones were recorded as being covered by manganese when more than 75% of the surface exhibited a brown coloration. At Swartkrans, one can also encounter pockets of material confined to specific narrow areas that are less affected by manganese than the surrounding material (Fig. 4C); a more detailed spatial taphonomic study would be needed to analyze and better understand these patterns.

2.7. Paleoecological analyses

Prior to paleoecological analyses, we undertook rarefaction/extrapolation analysis in order to visually quantify and assess species richness from the results of sampling (Krebs, 1999). This approach uses Chao estimators (Chao et al., 2014) to draw a single accumulation curve that combines rarefaction (standardization of the diversity measures to a reduced set of samples) and extrapolation (prediction of the diversity measures for the increased number of samples), enabling the comparison among the three micromammal samples with an uneven number of pellets.

We then applied the Taxonomic Habitat Index (THI), a method commonly used in micromammal studies for paleoenvironmental reconstruction. The THI was initially developed by Andrews and Nesbit-Evans and published for the first time in Nesbit-Evans et al. (1981) for determining habitat of Miocene sites in Western Kenya based on the whole mammalian fauna. It was subsequently applied to several fossil assemblages of small mammals from Africa (Fernández-Jalvo et al., 1998; Stoetzel et al., 2011, 2018; Nel and Henshilwood, 2016) and other parts of the world. This approach, based on presence/absence data, considers the diversity of preferred habitats across the micromammal species of the studied community without taking into account their relative proportions. For each genus, a total score of one is distributed among the different habitats frequented by each taxon. Here, we consider five habitats, which have been described by Andrews (2006) as follows:

- Forest: closed multiple canopy, tall tree, evergreen to semi-deciduous, herbaceous ground vegetation;
- Woodland: open to closed single canopy, tall tree, deciduous, herbaceous and grass ground vegetation;
- Bushland: open to closed single canopy, low to tall shrubs, deciduous, mainly grass ground vegetation;
- Grassland: trees and shrubs less than 20% canopy cover or absent;
- Semidesert: widely spaced shrub canopy, low, deciduous, mainly annual grass and herb ground vegetation.

The cumulative score obtained for each habitat is then weighted by the total number of taxa. Habitat scores for each extant genera were obtained from Leichliter (2018); they are based on ecological data available from the literature (for instance, in De Graaff, 1981; Happold, 2013; Monadjem et al., 2015; Wilson et al., 2016, 2017). Scores for each genus are available in the Supplementary Online Material (SOM) S1.

In southern Africa, several rodent genera are ubiquitous, inhabiting various types of habitats and distributed extensively across the country. Conversely, taxa with highly specific ecological requirements tend to be less abundant. This can have implications

Figure 4. Photograph of the general aspect of micromammal fossils from Swartkrans Member 1 Lower Bank (SWT1/LB) (A–C) and Cooper's D (D): A) bulk fossil material from Swartkrans, showing the brown coating on the bones; B) zoom on some skeletal elements; C) details of the bones from a pocket minimally affected by manganese; D) zoom on some micromammalian fossils from Cooper's D—note the preponderant encrustation of the bones. White scale bar: 5 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

for the outcomes of the THI as the scores of the habitats positioned at the extremes of the vegetation structure spectrum, such as forests or semidesertic areas, may be damped after weighting by the number of taxa within the community. Concurrently, as the species richness of an assemblage increases, THI scores are more likely to exhibit similarities across different rodent communities. To investigate this, we studied the representation of each habitat type through the THI method for rodent communities with a theoretical maximal species richness estimate across South Africa. We partitioned South Africa into 50 × 50 km grid cells and compiled the list of genera present within each of these cells using distributional data sourced from the Map of Life website (https://mol.org/datasets/?dt=range&sg=Mammals; Marsh et al., 2022), which aggregates expert range maps from various sources such as Wilson et al. (2016, 2017) or the *International Union for Conservation of Nature* Red List database (https://www.iucnredlist.org/). We then computed the THI scores for each of the rodent communities corresponding to a grid cell.

Many micromammal studies today apply the THI or related methodologies by weighting the results by taxonomic abundance (e.g., Bañuls-Cardona et al., 2017; Stoetzel et al., 2018; García-Morato et al., 2021; López-García et al., 2021). Such approaches can provide valuable complementary paleoenvironmental information, particularly when variations in abundance occur across different stratigraphic levels within an archeological sequence, and allow for the integration of these results with taphonomic analysis. However, multiple factors can influence these abundances, and in the COH, we hypothesize that the sieving techniques and strategies used for micromammal fossil recovery significantly impact the observed patterns. This factor should be quantitatively accounted for in future interpretations of abundance data.

3. Results

3.1. Taphonomy

Spotted eagle-owl pellets On average, 6.9% of the postcranial bones from the modern *B. africanus* coprocoenosis are fragmented (Table 3). Tibiae exhibit the lowest breakage rate, with 93.1% of the bones being intact, whereas humeri have the highest rate of

Table 3
Numbers of complete and fragmented long bones (expressed as NISP) and percentages of fragmentation, with mean fragmentation percentages from SWT1/LB and Cooper's D fossil assemblages and modern *Bubo africanus* coprocoenosis.

	Tibia			Humerus			Femur			Mean
	Complete	Fragmented	%Fragmented	Complete	Fragmented	%Fragmented	Complete	Fragmented	%Fragmented	**%**Fragmented
Swartkrans Member 1 LB	3	679	99.6	65	349	84.3	49	483	90.8	**91.5**
Cooper's D	28	297	91.4	66	153	69.9	47	278	85.5	**82.4**
B. africanus pellets	305	24	6.9	172	27	13.4	226	25	10	**6.9**

fragmentation, with 86.5% being intact. However, the fragmentation may be underestimated as we have collected only the bones visible on the ground surface, and smaller, more fragmented elements are likely to have remained buried in the sediment. A comparison of the anatomical representation profile of the spotted eagle-owl with that of the barn owl *T. alba* published in Linchamps et al. (2021) indicates that certain bones are proportionally less represented in the former, such as ribs, maxillae, radii, and scapulae (Fig. 5). Nevertheless, in both owl species, mandibles and femora exhibit good representation rates, exceeding 75%. The quantification and characterization of digestion traces show that 47.3% of isolated incisors and 37.5% of in situ incisors display signs of digestion, while 23.9% of femoral heads are digested (Table 4).

Fossil material A thin manganese dioxide coating is present on the surface of 84.5% of the fossils from Swartkrans ($n = 2340$) (Fig. 4A, B). This phenomenon is not uniformly distributed across the Lower Bank of Member 1, with the proportion of affected bones ranging from 52% (Fig. 4C) to 96.9%, depending on the sampling subarea. These values are lower than those recorded for the material from Cooper's D, where 97% of the examined bones are coated with manganese ($n = 2037$), with the layer reaching up to 1 mm in thickness (Fig. 4D). Bone breakage is significant in the SWT1/LB fossil assemblage, affecting 91.5% of limb bones, which is slightly higher than the 82.4% rate recorded for Cooper's D (Table 3). Tibiae exhibit the highest fragmentation rates, with fewer than 1% of complete bones recovered. Humeri are less fragmented, with approximately 15% of complete bones intact. A similar pattern is observed at Cooper's D. Mandibles and tibiae are the most well represented bones at SWT1/LB, and the anatomical representation profile resembles that of the *B. africanus* pellet-derived assemblage. The over-representation of mandibles at Cooper's D remains poorly understood but may be partly due to selective sorting during sieving or

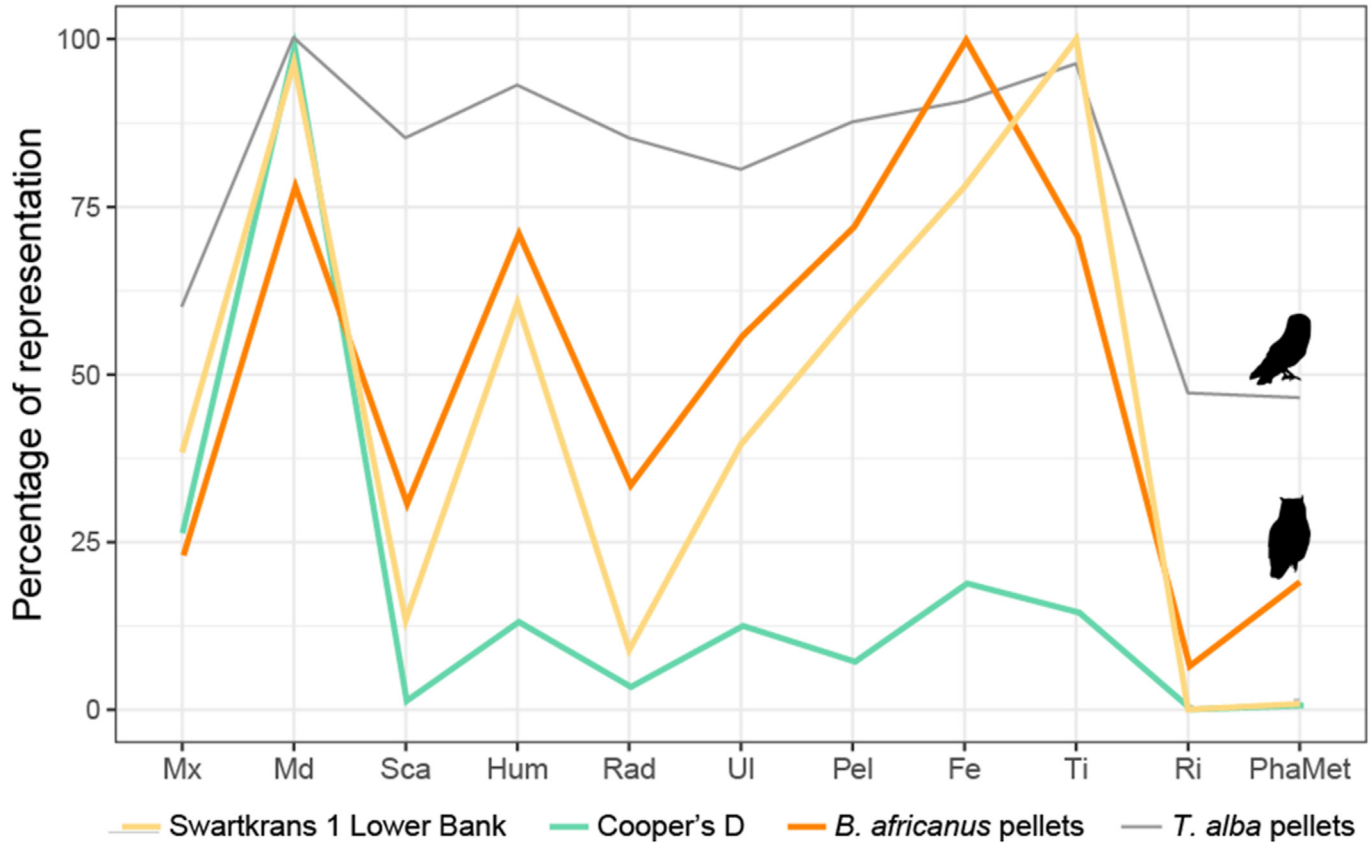

Figure 5. Profiles of skeletal representation (relative abundance) for the Swartkrans and Cooper's D fossil assemblages, and for the modern *Bubo africanus* pellet assemblage. Profiles are compared to values for *Tyto alba* (barn owl) from Linchamps et al. (2021). Mx = maxilla; Md = mandible, Sca = scapula; Hum = humerus; Rad = radius; Ul = ulna; Pel = hemipelvis; Fe = femur; Ti = tibia; Ri = rib; Pha = phalanx; Pha + Met = phalange + metapod. (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article.)

Table 4
Grades and percentages of digestion of rodent incisors and femora from Swartkrans and Cooper's D fossil assemblages and from modern *Bubo africanus* pellet assemblage.

	Swartkrans 1/LB		Cooper's D		*B. africanus*	
	NR	%	NR	%	NR	%
Isolated incisors	202		250		55	
None	187	92.6	219	87.6	29	52.7
Light	11	5.4	27	10.8	21	38.2
Moderate	4	2.0	4	1.6	4	7.3
Heavy	0	0	0	0	1	1.8
Extreme	0	0	0	0	0	0
Percentage of digestion		7.4		12.4		47.3
In situ incisors	54		45		320	
None	52	96.3	44	97.8	200	62.5
Light	2	3.7	1	2.2	113	35.3
Moderate	0	0	0	0	5	1.6
Heavy	0	0	0	0	2	0.6
Extreme	0	0	0	0	0	0
Percentage of digestion		3.9		2.2		37.5
Femoral heads	91		44		71	
None	83	91.2	1	95.5	54	76.1
Light	8	8.8	1	4.5	17	19.7
Moderate	0	0	0	0	2	2.8
Heavy	0	0	0	0	1	1.4
Extreme	0	0	0	0	0	0
Percentage of digestion		8.8		4.5		23.9

NR = number of remains; Swartkrans Member 1 LB = Swartkrans Member 1 Lower Bank.

storage. The fossil assemblage from Swartkrans displays low percentages of digestion: 7.4% of isolated incisors, 3.9% of in situ incisors, and 7.9% of femoral heads show signs of digestion (Table 4). Overall, the patterns of digestion are relatively similar between the two fossil assemblages, with values more closely resembling the coprocoenoses produced by Category 1 predators (such as *T. alba*) than the *B. africanus* assemblage examined in this study. It is likely that the same accumulation agent was responsible at both Swartkrans and Cooper's D and that *B. africanus* can be excluded as the primary accumulator of these two fossil assemblages.

3.2. Assemblage composition

Modern fauna The composition of the modern eagle-owl pellet collection from Swartkrans is given in Table 5. At least 16 micromammal taxa have been identified, which correspond to a minimum number of 227 preys. For rodents, 11 taxa were determined. The Muridae family is represented by at least eight species belonging to eight genera within the Gerbillinae (*Gerbilliscus*) and the Murinae (cf. *Lemniscomys*, *Mastomys*, *Micaelamys*, *Mus*, *Otomys*, *Rattus*, and *Rhabdomys*) subfamilies. Nesomyidae includes two Dendromurinae genera (*Dendromus* and *Steatomys*), and Bathyergidae are represented by the genus *Cryptomys*. Remains of shrews (genera *Crocidura*, *Suncus*, and *Myosorex*), macroscelid (*Elephantulus*), and one unidentified bat (only represented by postcranial skeletal elements) have also been identified. Nonmammalian microvertebrates include birds (indeterminate passerines), one frog, and one snake. Insects also contribute to the taxonomic diversity of the pellet assemblage: dor beetles (Geotrupidae), true weevils (Curculionidae), ground beetles (Carabidae), indeterminate beetles (Coleoptera), indeterminate cicadas (Cicadidae), lanternflies (Fulgoridae), and indeterminate grasshoppers (Orthoptera) have been identified.

Fossil fauna The fossil micromammal assemblage of the Lower Bank of Member 1 at Swartkrans comprises a total of 721 individuals (MNI) based on the 2117 craniodental remains analyzed (the number of identified specimens). It is composed of at least 20 different taxa (Table 6, Figs. 6 and 7) belonging to five orders: Rodentia (rodents), Afrosoricida (golden moles), Macroscelidea (elephant shrews), Eulipotyphla (shrews), and Chiroptera (bats). Rodents represent the most abundant micromammalian order (60.1% of the MNI of identified micromammals), while the second and third most abundant orders are, respectively, Eulipotyphla (31.4%) and Macroscelidea (7.9%). Afrosoricida and Chiroptera are much less represented (<1%).

Among rodents, the family Muridae is the most species-rich one, represented at Swartkrans by nine genera that include one Deomyinae (*Acomys*), one Gerbillinae (*Gerbilliscus*), and seven Murinae (*Aethomys, Dasymys,* cf. *Lemniscomys, Mastomys, Mus, Otomys,* and *Rhabdomys*). Nesomyidae are represented by five genera from the subfamilies Dendromurinae (*Dendromus/Poemys, Malacothrix,* and *Steatomys*) and Mystromyinae (*Mystromys* and *Proodontomys*), Bathyergidae by one genus (*Cryptomys* or/and *Fukomys*), and Gliridae by another single genus (*Graphiurus*).

The rich Swartkrans micromammal paleocommunity is numerically dominated by *Mystromys* sp. (31.7% of the MNI), indicative of grassland habitat. The shrews from the family Soricidae are almost as much abundant, representing 31.4% of the MNI. Of these, *Myosorex* seems to be very common with two other subordinate forms that probably belong to the genera *Crocidura* and *Suncus*. As these specimens are almost exclusively represented by fragments of mandible, identification to the genus is very risky, and we have therefore chosen not to go further in the taxonomic identification than at the conservative level of the family. Elephant shrews of the family Macroscelididae, which are represented by the genus *Elephantulus*, have also been recovered in abundance, representing 7.9% of the MNI. The genus *Otomys* accounts for 7.8% of the MNI; as such it is the second most abundant rodent genus in the SWT1/LB micromammal assemblage.

Other microvertebrates, including birds, reptiles, and amphibians, have been identified (but not counted) and set aside for further, more in-depth investigation.

3.3. Preliminary paleoecological interpretations

Under the principle of actualism, the presence of taxa associated with specific habitat types provides preliminary paleoenvironmental indications. The paleoenvironment reconstructed from the microfauna of Cooper's D by Linchamps et al. (2023a) represents an open landscape with a predominance of grassland

Table 5
Taxonomic representation, expressed as the number of identified specimens (NISP) and the minimum number of individuals (MNI), of the micromammal assemblage derived from modern pellets of the spotted eagle-owl (*Bubo africanus*).

Order	Family	Subfamily	Genus species	Modern			
				NISP		MNI	
				n	%	*n*	%
Rodentia	Bathyergidae	Bathyerginae	*Cryptomys hottentotus*	30	3.6	7	3.1
	Muridae	Gerbillinae	*Gerbilliscus brantsii/leucogaster*	80	9.5	26	11.5
		Murinae	cf. *Lemniscomys rosalia*	1	0.1	1	0.4
			Mastomys coucha/natalensis	154	18.2	45	19.8
			Micaelamys namaquensis	5	0.6	2	0.9
			Mus minutoides	16	1.9	5	2.2
			Otomys auratus/angoniensis	411	48.6	79	34.8
			Rattus rattus	70	8.3	24	10.6
			Rhabdomys bechaunae/dilectus	17	2.0	10	4.4
	Nesomyidae	Dendromurinae	*Dendromus melanotis/mystacalis*	13	1.5	7	3.1
			Steatomys krebsii/pratensis	22	2.6	7	3.1
Chiroptera			Chiroptera indet.	1	0.1	1	0.4
Eulipotyphla	Soricidae	Crocidurinae	*Crocidura* sp.	5	0.6	2	0.9
			Suncus infinitesimus/varilla	16	1.9	7	3.1
		Myosoricinae	*Myosorex cafer/varius*	3	0.4	3	1.3
Macroscelidea	Macroscelididae		*Elephantulus* indet.	1	0.1	1	0.4
Total identified micromammals				**845**	**100**	**227**	**100**
Indeterminate rodents				1		1	
Total micromammals				**846**		**228**	
Passeriformes			Passeriformes indet.	11		5	
Anura			Anura indet.	1		1	
Squamata			Serpentes indet.	1		1	
Total microvertebrates				**859**		**235**	
Coleoptera	Carabidae		Carabidae indet.			1	
	Curculionidae		Curculionidae indet.			1	
	Geotrupidae		Geotrupidae indet.			4	
			Coleoptera indet.			2	
Hemiptera	Cicadidae/Fulgoridae		Cicadidae/Fulgoridae indet.			1	
	Fulgoridae		Fulgoridae indet.			1	
Orthoptera			Orthoptera indet.			5	
Total preys						**250**	

NISP = number of identified specimens; MNI = minimum number of individuals.

Table 6
Taxonomic representation, expressed as the number of identified specimens (NISP) and the minimum number of individuals (MNI), of the fossil micromammal assemblage of Swartkrans Member 1 Lower Bank (SWT1/LB).

Order	Family	Subfamily	Genus species	SWT1/LB			
				NISP		MNI	
				n	%	*n*	%
Rodentia	Bathyergidae	Bathyerginae	*Cryptomys/Fukomys*	43	2.3	17	2.8
	Gliridae	Graphiurinae	*Graphiurus* sp.	2	0.1	1	0.2
	Muridae	Deomyinae	*Acomys* cf. *selousi*	7	0.4	4	0.6
		Gerbillinae	*Gerbilliscus* sp.	10	0.5	4	0.6
		Murinae	*Aethomys* spp.	26	1.4	8	1.3
			Dasymys bolti	11	0.6	5	0.8
			cf. *Lemniscomys*	2	0.1	2	0.3
			Mastomys sp.	26	1.4	13	2.1
			Mus sp.	67	3.6	29	4.7
			Otomys spp.	338	18.2	48	7.8
			Rhabdomys sp.	21	1.1	9	1.5
	Nesomyidae	Dendromurinae	*Dendromus/Poemys* spp.	29	1.6	15	2.4
			Malacothrix cf. *makapani*	11	0.6	5	0.8
			Steatomys sp.	24	1.3	9	1.5
		Mystromyinae	*Mystromys* sp.	698	37.3	196	31.7
			Proodontomys cookei	14	0.8	6	1.0
Afrosoricida	Chrysochloridae	Amblysomyinae	*Neamblysomus* cf. *julianae*	4	0.2	2	0.3
Chiroptera	Rhinolophidae		*Rhinolophus* cf. *clivosus*	2	0.1	2	0.3
Eulipotyphla	Soricidae		Soricidae spp.	375	20.2	194	31.4
Macroscelidea	Macroscelididae		*Elephantulus* spp.	143	7.7	49	7.9
Total identified micromammals				**1853**	**100**	**618**	**100**
Indeterminate rodents				264		103	
Total micromammals				**2117**		**721**	

NISP = number of identified specimens; MNI = minimum number of individuals; SWT1/LB = Swartkrans Member 1 Lower Bank.

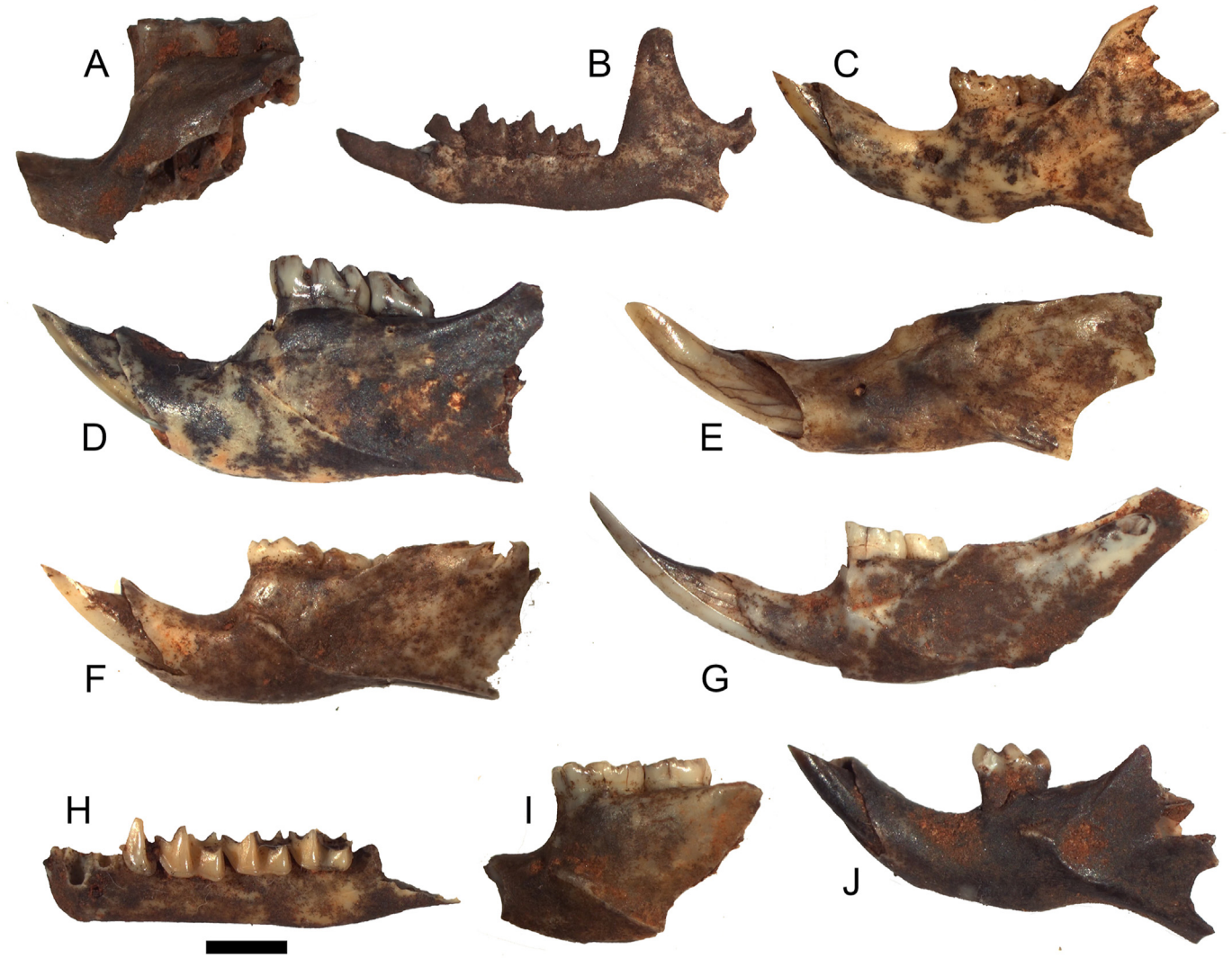

Figure 6. A sample of left mandibles of fossil micromammals from Swartkrans Member 1 Lower Bank (SWT1/LB): A) *Dasymys bolti*; B) *Myosorex* sp.; C) *Malacothrix* cf. *makapani*; D) *Gerbilliscus* sp.; E) *Graphiurus* sp.; F) *Mastomys* sp.; G) *Proodontomys cookei;* H) *Rhinolophus* sp.; I) *Aethomys* sp.; J) *Steatomys* sp. Scale bar: 2 mm.

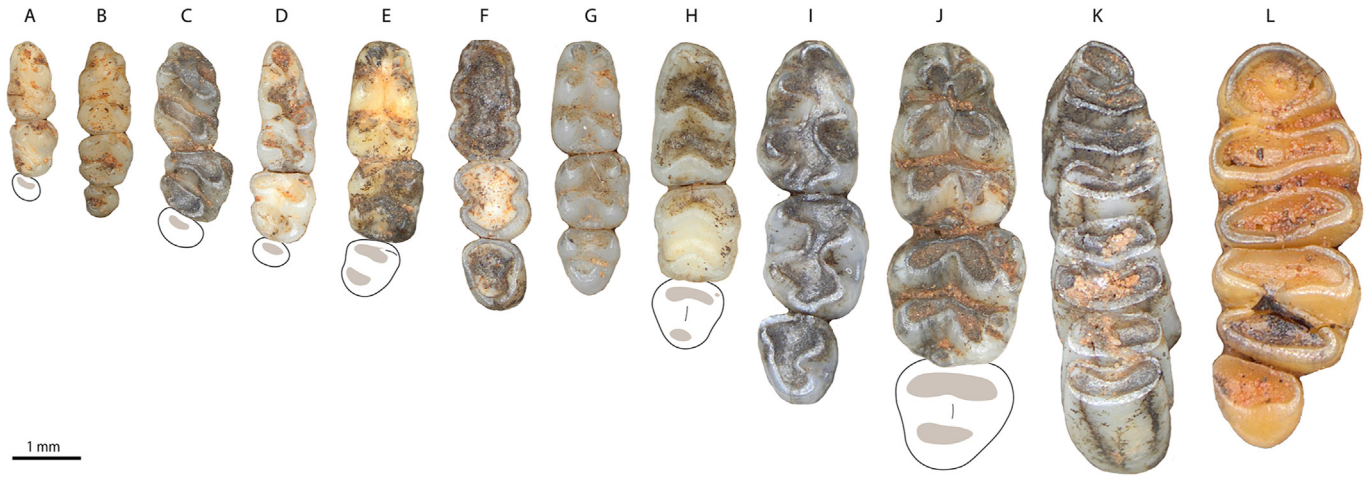

Figure 7. Occlusal views of the right lower cheek dentition of several fossil rodents from Swartkrans Member 1 Lower Bank (SWT1/LB): A) *Dendromus/Poemys* sp.; B) *Mus* sp.; C) *Steatomys* sp.; D) *Malacothrix* cf. *typica* sp.; E) *Acomys* cf. *selousi*; F) *Proodontomys cookei*; G) *Rhabdomys* sp.; H) *Mastomys* sp.; I) *Mystromys* sp.; J) *Aethomys* sp.; K) *Otomys* sp.; L) *Gerbilliscus* sp. The schematic contour of missing teeth was completed based on the anatomy of isolated teeth. Scale bar: 1 mm.

and savannah vegetation, along with the proximity of rocky outcrops and a perennial river. At Swartkrans, the microfauna indicates a relatively similar environment with a mosaic of habitats: a predominant grassland environment (indicated by the presence of grassland-adapted taxa such as *Otomys* and *Mystromys*), with patches of savanna (*Aethomys*, *Gerbilliscus*, cf. *Lemniscomys*), semiarid vegetation (*Malacothrix*), proximity to rocky outcrops (*Acomys*, *Graphiurus*), and a stream or a permanent waterhole (*Dasymys*). The presence of *Graphiurus*, exclusive to the fossil assemblage of Swartkrans, could indicate the presence of arboreal cover or at least some form of structure, such as hollow trees or rocky crevices.

The application of paleoenvironmental reconstruction methods based on the whole community requires that micromammal assemblages be sufficiently representative of the diversity of the past or present faunal community. To investigate the effects of sample size upon further community analyses and subsequent paleoecological interpretations, rarefaction/extrapolation curves were computed for the three micromammal assemblages (Fig. 8A). Rarefaction curves suggest that the samples differ in terms of the number of individuals, as reflected by the lengths of the curves, but show relatively similar estimated species richness. Figure 8A shows that both fossil assemblage curves approach a horizontal plateau (a theoretical asymptote means that the inventory effort is optimal), while the curve for the *B. africanus* pellet assemblage still increases after extrapolation. Factors influencing species richness in this latter assemblage could result from insufficient sampling or environmental degradation associated with human activities. Further ecological analyses on micromammal communities from the COH may shed light on this question.

The THI shows in all three assemblages an environment predominantly dominated by grassland and, to a lesser extent, bushland habitats (Fig. 8B). The reconstruction of the Swartkrans environment suggests a more closed landscape than Cooper's, with wooded habitats (forest and woodland) better represented. This trend is primarily due to the presence of the African dormouse *Graphiurus* (Gliridae, Graphiurinae), which is absent from the Cooper's D faunal spectrum. These arboreal rodents are excellent climbers and occur in forest, woodlands, or kopjes, where they can hide in rocky crevices. The reconstructed landscape of Cooper's D is characterized by a greater semiarid component than elsewhere, which can be explained by the presence of several rodent genera absent from Swartkrans that occur in arid and semiarid environments with limited precipitation, such as the short-tailed gerbil of the genus *Desmodillus* (Muridae, Gerbillinae) and the long-eared mouse *Malacothrix* (Nesomyidae, Dendromurinae). The modern landscape reconstructed from the *B. africanus* assemblage shows intermediate trends between Swartkrans and Cooper's D. However, the low species diversity of this assemblage, likely affected by important representation biases, undermines the validity of this reconstruction.

Given the ubiquitous nature of many rodents in South Africa and the relative stability of the COH microfaunas during the Pleistocene, the application of the THI method to fossil rodent faunas of this area may have certain limitations, particularly in its ability to represent certain habitats and detect consistent patterns of environmental change through time. Thus, we aimed to test the behavior of this method at the scale of South Africa by calculating the taxonomic habitat spectra based on rodent communities with theoretical maximum diversity, as illustrated in Fig. 9.

Certain patterns emerge, which can be described qualitatively as follows. First, there is a relatively good concordance between the distribution of natural environments and the ranges of scores for each of the five habitats. Hence, the highest forest scores are found along the eastern coast bordering the Indian Ocean and in the northeastern part of the country, which encompasses inland forests; the highest woodland scores are concentrated in the northeastern part of the country, coinciding with the savannah environments; the bushland habitat exhibits a less contrasting score distribution, with its highest values being observed in the northern part of the Northern Cape Province; the highest grassland scores are observed in the southwestern part of the Western Cape Province and in the inland region encompassing the Free State, Gauteng, and Mpumalanga Provinces, the latter region being predominantly characterized by grassland environments; the highest scores for the semiarid habitat are concentrated in the northwestern part of the country, particularly in the vicinity of the Kalahari Desert. The THI method thus succeeds in returning environmental predictions consistent with the surrounding environment. However, the results also show a tendency toward the over-

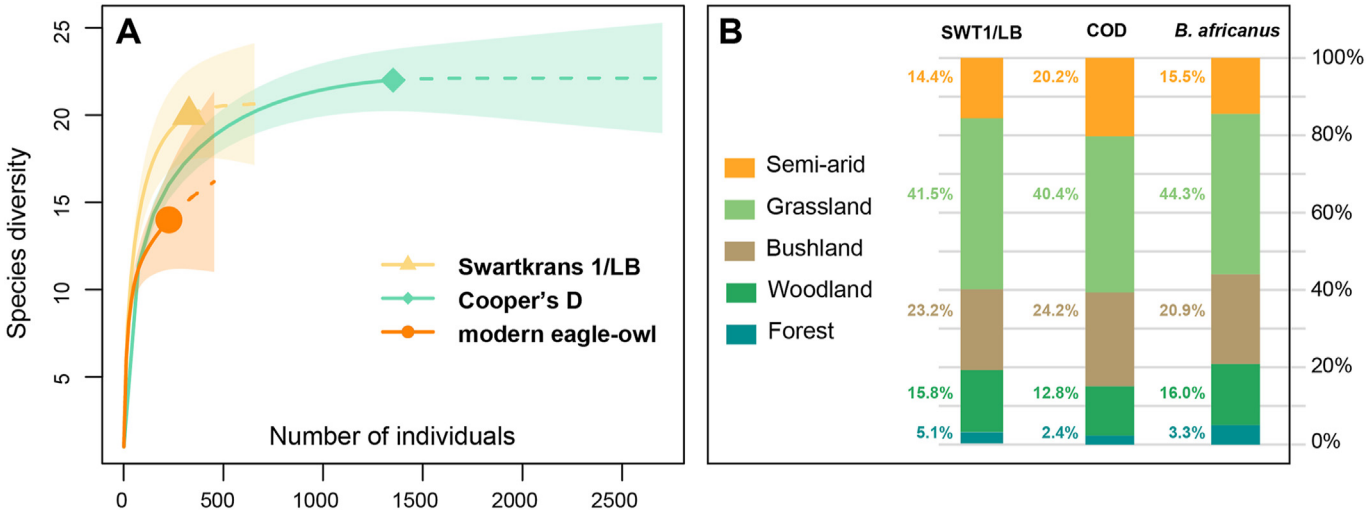

Figure 8. A) Point-by-point individual rarefaction–extrapolation curves for the seven micromammal assemblages (Hill number = 0: species richness); the solid line is the rarefaction curve; the dotted line is the extrapolation curve for twice the MNI. B) Taxonomic Habitat Index (THI) based on the presence/absence and habitat preferences of the rodent genera within each assemblage. SWT1/LB: fossil assemblage of Swartkrans Member 1 Lower Bank, COD: fossil assemblage of Cooper's D, *Bubo africanus*: modern pellet assemblage from *B. africanus*. MNI = number of individuals. (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article.)

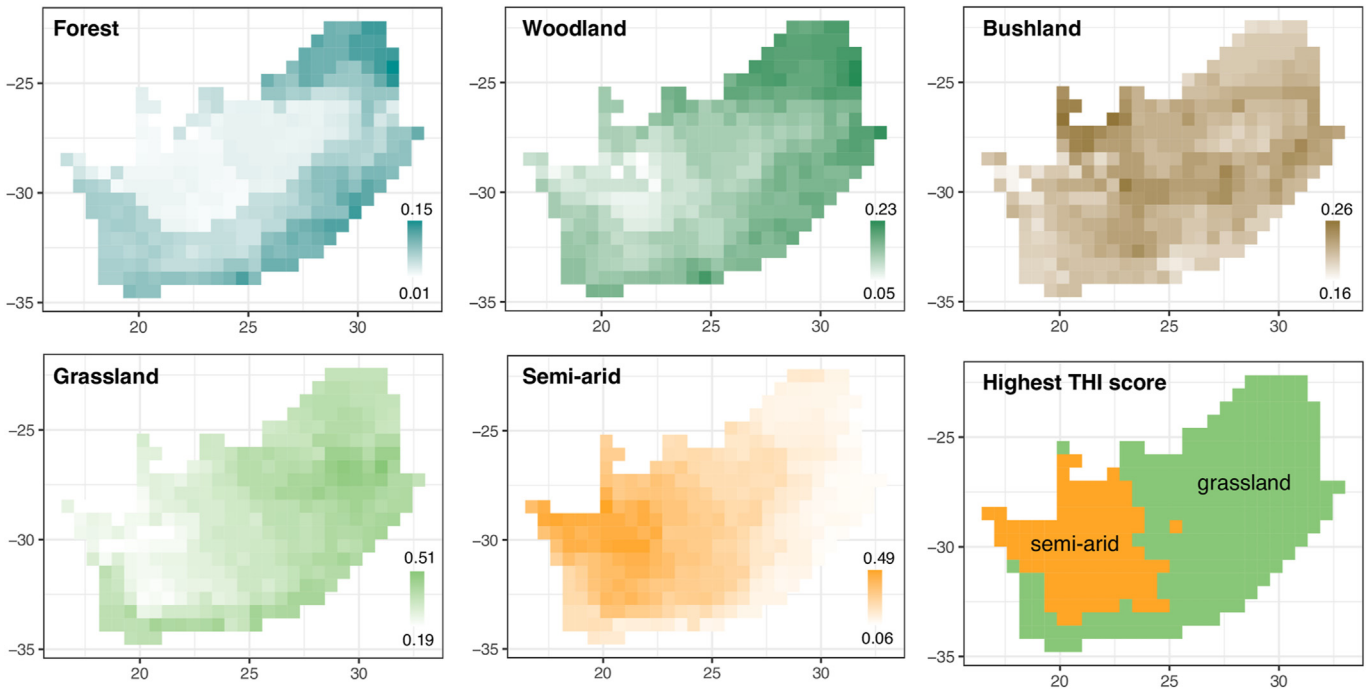

Figure 9. Values of each habitat score from the taxonomic habitat spectra based on multiple rodent communities across South Africa. Community composition was calculated using distribution data of rodent species sourced from the Map of Life website (https://mol.org/species/). (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article.)

representation of grassland habitats at the expense of forest (and to a lesser extent woodland) habitat. Indeed, regardless of the grid cell under consideration, the minimum score for grassland (0.19) will always surpass the maximum score for forest (0.15). This disparity can be attributed to the limited number of genera with strong forested habitat affinities (such as *Cricetomys, Graphiurus, Grammomys,* or *Thallomys*). Similarly, the bushland habitat is better represented than the forest in all the studied grid cells, yet its scores are more moderate than those of grassland, ranging between 0.16 and 0.26. This reflects to some extent the ubiquitous and transitional nature of the bushland habitat. Interestingly, the semiarid habitat can exhibit both very high scores (0.49) and very low scores (0.06), making it a suitably discriminative habitat category for paleoenvironmental reconstructions. Regardless of the rodent community under consideration, the habitat with the highest score on the THI spectrum will consistently be either grassland or semidesert environment (Fig. 9).

4. Discussion

4.1. Formation of the micromammal fossil assemblage of Swartkrans Member 1 (Lower Bank)

In the microfaunal assemblage of Swartkrans Member 1 Lower Bank, only a small proportion of skeletal elements bears traces of digestive corrosion. However, the large quantity of fossils and the diversity of micromammalian taxa that typically do not inhabit cave environments leave no doubt that this assemblage is the result of predator accumulation. This is a crucial point for the paleoenvironmental interpretation of the faunal assemblage, for the reason that its taxonomic composition may not only be related to the local ecological conditions, including vegetation and climate, but also to the dietary preferences and hunting strategies of the predator. The low incidence and degree of digestion observed on incisors and femora indicate a Category 1 predator, i.e., producing 'very little modification' (Andrews, 1990), responsible for the various small mammal assemblages. The taphonomic results also showed that it is possible to distinguish between barn owl and spotted eagle-owl accumulations based on patterns of digestion only. Therefore, it is likely that *B. africanus*, which currently occupies the cave, was not the main predator for the accumulation of the various fossil assemblages in Swartkrans. Only a few candidates among South African birds of prey fall in this Category 1: the marsh owl *Asio capensis*, the barn owl *T. alba,* and the African grass owl *Tyto capensis*. While both *A. capensis* and *T. capensis* nest on the ground (typically in a hollow within a patch of tall grass), *T. alba* favors hollow trees, attics of large buildings, and rock cavities between cliffs or in caves (König et al., 2009). Of these three owls, the most probable agent is thus *T. alba*, whose fossil remains have been identified at Swartkrans Member 3 (Brain, 1981; Watson, 1991) and in various other Plio-Pleistocene fossil deposits in the region (Pavia, 2020; Pavia et al., 2022). This conclusion aligns with that of Avery (2001), who identified *T. alba* as the predator responsible for accumulating the samples from Swartkrans based on the range of identified prey species and evidence of digestion on in situ lower molars of *M. albicaudatus*. Barn owls usually swallow their prey whole, sometimes decapitating the largest prey first but still swallowing both parts (Andrews, 1990). As a result, and because the degree of digestion is low, the bones in pellets usually show minimum fragmentation and digestive corrosion (Dodson and Wexlar, 1979; Denys, 1985; Andrews, 1990; Linchamps et al., 2021).

Unlike digestive corrosion, fragmented bones and altered skeletal representation are not necessarily related to predation activities since many depositional and postdepositional processes may cause fragmentation (trampling, rock fall, sedimentary compaction, sieving, etc.) or loss of remains that will affect skeletal representation (hydraulic sorting of bones, mesh size used for sieving, etc.). The taphonomic analysis of these two signatures remains valuable nonetheless for elucidating site formation processes and assessing the integrity of the deposit. Either before or after burial of the

bones, particular environmental and deposition conditions may influence an assemblage and its constituent skeletal elements; only through comprehensive taphonomic analysis can such elusive past events be identified.

The significantly high fragmentation rates of long bones recorded at SWT1/LB are likely attributed to postdepositional factors. Various abiotic agents may have played a significant influence in the taphonomic alteration of the assemblage, including sediment reworking, sediment pressure, and calcification/decalcification cycles. In cave sites, trampling can also contribute significantly to fragmentation. This phenomenon may be caused by various agents, such as owls introducing prey into the cave, as well as from the presence of other cave visitors (including hominins and other animals) that trample over pellets littering the cave floor. Fernández-Jalvo et al. (2022) have conducted experiments to test the impact of trampling on rodent bones and showed that some patterns in breakage and skeletal element representation can help to identify and distinguish trampling damage from other alterations. It is possible, however, that the configuration of the paleocave system of Swartkrans, consisting, like several other sites within the Cradle, of underground cave deposits featuring steep vertical or angled shafts, may have posed significant challenge for fauna to access the cave chamber (Dirks and Berger, 2013; Dirks et al., 2015; Val et al., 2015). Flowing water and falling rocks may also have increased breakage of the bones. Based on the presence of numerous water-worn pebbles and various water-worn bone fragments, Brain (1993) provided evidence that water flowed through cave spaces during the formation of the Member 1 Lower Bank, occasionally with strong flows, entering from the surface through shaft openings. Profiles of skeletal representation (Fig. 5) indicate a loss of skeletal elements, and the good representation of Korth's dispersal groups II/III and III (Korth, 1979) supports the transportation of some skeletal elements by water. Loss of smallest skeletal elements could also have resulted from the recovery process (which consisted of sieving using a 5-mm mesh over a 2-mm mesh screen) as it has been shown to occur even using a 0.5-mm mesh during excavations (Avery, 2007; Marín-Monfort et al., 2022). As it stands, it is challenging to determine which postdepositional process had the most significant impact on the microfaunal assemblage, and each likely played a role to some extent.

The identification of the same predator at Swartkrans and Cooper's D offers an ideal framework to compare the faunal spectra and study changes in paleoenvironmental conditions over time based on the micromammalian community.

4.2. Comparison of the faunal spectra

The microvertebrate assemblage of Swartkrans Member 1 Lower Bank comprises a diverse fauna, including at least 16 genera of rodents, along with some representatives of soricids, macroscelids, bats, and chrysochlorids. It is possible that a greater diversity of rodents will be recorded as more bone remains are unearthed, and future excavations may perhaps provide further insights into this community. A similar taxonomic diversity is found at Cooper's D, yet the comparison of faunal spectra in Figure 10 highlights specificities for each assemblage. A first salient observation is that the Swartkrans assemblage stands out due to the significant abundance of soricids, which accounts for 31.4% of the MNI. Regrettably, in light of current knowledge on the ecology of this highly speciose group, it is still challenging to interpret this abundance in terms of environmental characteristics. Based on the examination of an extensive dataset of modern micromammal assemblages accumulated by barn owls from southern Africa (Faith et al., 2019), Linchamps (2024) found a significant positive

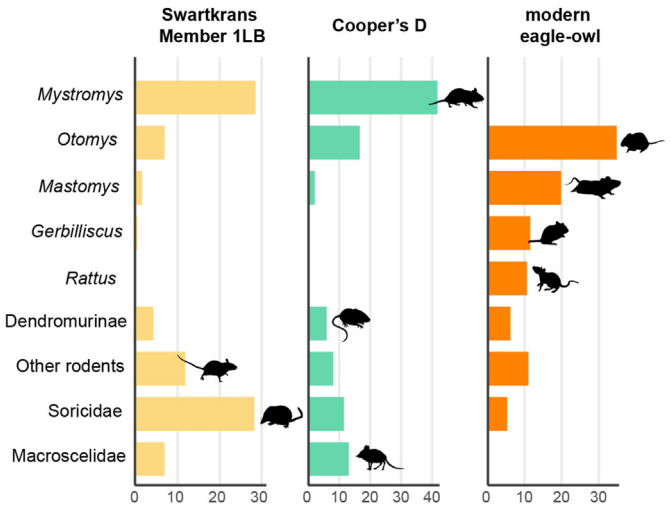

Figure 10. Histograms showing the relative abundance of micromammalian taxa among the three studied assemblages. Several animal silhouettes have been downloaded from *phylopic*.org. (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article.)

correlation between the presence of soricids and that of *Otomys* ($r = 0.72$), *Rhabdomys* ($r = 0.71$), and *Mus* ($r = 0.63$) but failed to find a relevant ecological explanation. In South Africa, shrews are represented by the three genera *Myosorex*, *Crocidura*, and *Suncus*. Further molecular studies on extant species coupled with morphometric analyses of both fossil and modern taxa would elucidate the paleoecological implications of their presence in the fossil record, but this task is complicated by the important morphological similarity and size overlap between species and even genera.

The microfauna of Cooper's D is characterized by the high abundance of *Mystromys* and *Otomys*, which together account for 58.3% of the MNI. These two rodent genera are associated with grassland habitats and exhibit various morphological and physiological adaptations related to grass consumption.

The current micromammalian community of the COH, represented by the *B. africanus* pellet assemblage, exhibits a composition markedly different from the two fossil assemblages, both in terms of predominant taxa and their abundance. Comparing the content of spotted eagle-owl pellets with that of the barn owl from two adjacent localities, Brain (1981) found virtually no difference in terms of prey selection between the two owl species. Therefore, it is anticipated that the species composition of the micromammalian bone assemblage would vary little, if at all, whether one or the other owl is responsible for its accumulation. Here, the *B. africanus* pellet-derived fauna is numerically dominated by *Otomys auratus/angoniensis* and by three other taxa that can thrive in anthropogenic environments: *Mastomys coucha/natalensis*, *Gerbilliscus brantsii/leucogaster*, and *Rattus rattus*. The latter is an invasive rodent that has spread across the vast majority of South Africa (except for the drier areas) and is now common in most human-associated habitats. Species of the *Gerbilliscus* and *Mastomys* genera can be abundant in agricultural areas, where they may cause important damage to crops (Singleton et al., 2010). The rodent fauna identified in the pellet assemblage is therefore heavily impacted by human activities. It appears to only partially reflect the surrounding rodents' natural environment. This is regrettable as it hinders comparative analyses that aim to better understand the dynamics of composition and structure of rodent communities from the Plio-Pleistocene to the present day. Prospectively, it will be valuable to

conduct further surveys in undisturbed areas using pellet analyses and/or trapping sessions, for instance, among the various private game reserves that surround the Sterkfontein Valley.

The comparison of the faunas from the two fossil assemblages also provides some chronological indications supporting the antiquity of Swartkrans Member 1 Lower Bank relative to Cooper's D. Given the similarity of the Pleistocene microfaunas of the Cradle, methods based on the first-appearance datum and last-appearance datum of species are difficult to exploit for establishing a precise chronology of the deposits (Denys, 1990; Sénégas, 2000; Linchamps et al., 2023a). However, the identification of extinct species and ancestral forms within rodent lineages appears more promising, and the genus *Dasymys* may be one good candidate for this endeavor. At SWT1/LB, all specimens of *Dasymys* have been taxonomically assigned to the fossil species *Dasymys bolti*. This species was named by Broom for describing specimens from Bolt's Farm but never published. It was later described and diagnosed by Denys (1990) then Sénégas (2000). They argue that some of the morphological features are too derived for considering *D. bolti* as ancestral to modern species *Dasymys capensis, Dasymys robertsii*, and *Dasymys incomtus* and attribute the fossils from the COH to *D. bolti*. In 'modern' *Dasymys*, rows of cusps are arranged in transverse rows that often isolate as parallel enamel islands (Avery, 1998; Linchamps et al., 2023b); the first lower molar has a well-pronounced anteromedian cusp that is somehow isolated from labial and lingual anteroconids, whereas the cusps t1, t2, and t3 of the first upper molars are much more aligned than in *D. bolti* (Fig. 11). In this latter species, molars are more stephanodont and the anterocentral cusp of the lower first molar is reduced than that in modern *Dasymys*. In contrast to Swartkrans, both forms are present within the micromammal assemblage of Cooper's D, which probably indicates a more recent age for Cooper's D and the possibility of a palimpsest resulting from significant time-averaging. Further detailed analyses of the material may aid in refining the chronological delineation of this indication.

4.3. A new fossil micromammal assemblage: implications for the Cradle of Humankind paleoenvironments

The micromammal assemblage of Swartkrans Member 1 Lower Bank is interpreted as the signature of an open environment, with predominant grassland habitat and patches of savanna, and indications of semiarid vegetation, nearby woodland and rocky habitats, and permanent water. This variety of habitats and vegetation types allowed for the coexistence within the same territory of a diverse range of small mammals. Such indications align well with most paleoenvironmental reconstructions already made for the Member 1 of Swartkrans based on the small (Avery, 1998, 2001) and large mammal faunas (Brain, 1993; Watson, 1993; de Ruiter, 2003; Lehmann, 2004; de Ruiter et al., 2008; de Ruiter, 2022).

By comparing the paleoenvironments of Swartkrans (ca. 2.2–1.8 Ma) and Cooper's D (ca. 1.4 Ma), we can propose a simplistic scenario of the evolution of the landscape in the COH during the Early Pleistocene. The environment at Swartkrans appears to be slightly more closed and less arid than at Cooper's D, suggesting a trend toward increased aridity during this time interval. This is consistent with some paleoclimatological and paleoenvironmental studies that have indicated an increasing aridification, leading to a transition from a C3 to C4 ecosystem in southern Africa (Vrba, 1985; Hopley et al., 2006; Schubert et al., 2006; Herries et al., 2010). In this region, wetter climatic conditions likely prevailed before 2 Ma and until 1.7 Ma (Caley et al., 2018). After approximately 1 Ma, southern Africa underwent a progressive and sustained increase in aridity (Steininger, 2011; Caley et al., 2018).

In the COH, the limited availability of local paleoenvironmental markers such as pollens or sediment cores due to the geomorphological and taphonomic characteristics of the karst systems emphasizes the significance of fossil faunal assemblages as the primary source of evidence for reconstructing the habitats of Plio-Pleistocene hominin-bearing sites. However, environmental interpretations based on fauna are inherently susceptible to systematic biases stemming from a combination of factors, including predepositional, peridepositional, and postdepositional processes, sampling and recovery practices, and analytic choices. We also showed in this study that the application of the THI to South African rodent genera tends to systematically over-represent semiarid and grassland habitats. Such biases may explain that paleoenvironmental reconstructions based on faunal lists in the COH have produced diverse, sometimes conflicting paleoclimatic inferences (see, for instance, the synthesis of faunal-based paleoenvironmental reconstructions in de Ruiter, 2022). Furthermore, the lack of tight chronological and stratigraphic control for these assemblages poses a significant challenge in interpreting faunal responses to climate change (Pickering et al., 2019). Many of these

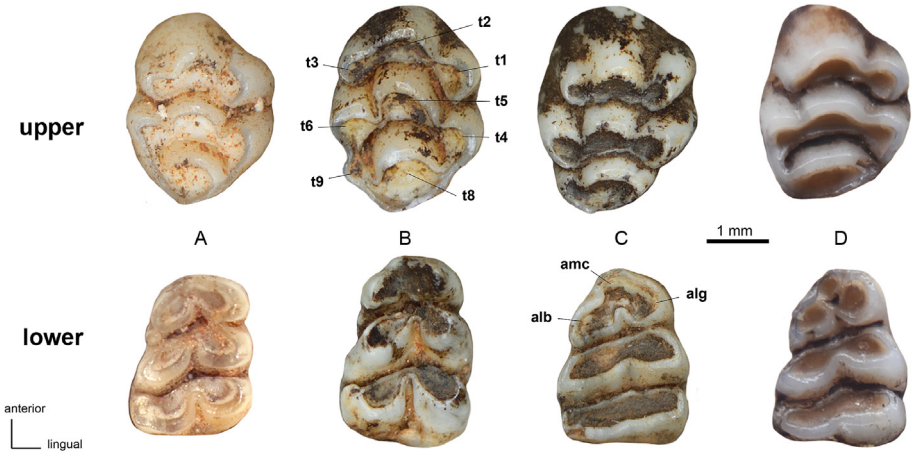

Figure 11. First upper right and lower left molars from extant and fossil *Dasymys*. A) *Dasymys bolti* from Swartkrans; B) *Dasymys bolti* from Cooper's D; C) *Dasymys* cf. *robertsii* from Cooper's D; D) modern *Dasymys robertsii* from Ditsong National Museum of Natural History collections. Upper molar: t1 = anterostyle; t2 = lingual anterocone; t3 = labial anterocone; t4 = enterostyle; t5 = protocone; t6 = paracone; t8 = pseudohypocone; t9 = metacone. Lower molar: alb = labial anteroconid; amc = anteromedian cusp; alg = lingual anteroconid.

assemblages have been described as time-averaged, representing a mixture over time of remains from organisms that were not contemporaneous (Behrensmeyer, 1982; Bobe et al., 2007; O'Regan and Reynolds, 2009; Hopley and Maslin, 2010).

Nonetheless, the publication of new fossil faunal lists, or the revision of existing ones in light of recent advancements in systematics and paleontological research, remains a crucial preliminary step before delving into the study of past environments and comprehending the interactions between fossil hominins and their ecosystems. By adhering to standardized criteria and methodologies for taxonomic, taphonomic, and paleoenvironmental analysis, the examination and comparison of new micromammal assemblages can mitigate the sources of variability mentioned earlier. The investigation of new material from ongoing excavations in the COH should progressively facilitate more cohesive interpretations from both taphonomic and paleoecological perspectives.

5. Conclusions

This study provides the taxonomic analysis of the micromammalian fossil assemblage from the Lower Bank of Member 1 at the Swartkrans cave site, dating to ca. 2.2 Ma, collected during the SPRP excavation. This assemblage exhibits a high taxonomic diversity, with a small mammal community numerically dominated by *Mystromys* sp., a rodent genus closely associated with highveld and middle- to high-altitude grassland environments. The comparison of the faunal spectrum of Swartkrans with that of Cooper's D (dated to ca. 1.4 Ma) has shown differences in the representation and abundance of various micromammal taxa, which can be interpreted preliminarily from a paleoenvironmental perspective. The reconstructed environment at Swartkrans suggests a habitat predominantly composed of grassland with patches of savannah, slightly more closed and less arid than at Cooper's D. Taphonomic analysis of the Swartkrans fossil assemblage indicates an accumulation of bone remains by *T. alba* or a related species. This inference finds support in the neotaphonomic analysis conducted on modern *B. africanus* pellets collected from the Swartkrans cave as part of this study. The bone remains contained within these pellets exhibit substantially higher percentages and grades of digestive corrosion than Swartkrans micromammal fossils and modern or fossil assemblages accumulated by *T. alba*. Over recent decades, advancements in natural sciences for the study of fossil communities (e.g., in taphonomy, stratigraphy, and palaeoecology) and extant organisms (ecology, systematics, and taxonomy), coupled with a concerted effort toward improved repeatability of study protocols, have laid the groundwork for the current paradigm in micromammal studies. In the future, the publication of additional faunal lists from new excavations in the COH is expected to enable a comprehensive and well-supported synthesis of climate and environmental evolution during the Pleistocene.

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Author contributions

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Supplementary Online Material

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