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Medium and large-sized Glires (Rodents and Lagomorphs) from the early Pleistocene Cooper's D locality in the Cradle of Humankind, Gauteng, South Africa

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ABSTRACT

Remains of mesomammals, i.e. intermediate-sized mammals, are ubiquitous in southern African fossil sites. Even though they do not constitute a taxonomically cohesive group, medium-sized mammals share common ecological traits and are subject to similar taphonomic processes, making them essential for understanding past ecosystems. This study focuses on craniodental remains of medium- and large-sized rodents and lagomorphs from the Early Pleistocene hominin-bearing site of Cooper's Cave in the Cradle of Humankind. The Cooper's D deposit, dated to approximately <1.4 Ma, has provided a wealth of faunal material, including many mesomammal remains. This contribution presents an updated taxonomic analysis of fossil material, including morphological descriptions with new diagnostic criteria, ecological information about the different taxa, and preliminary taphonomic observations. Notably, this assemblage documents the oldest known occurrence of the genus *Geosciurus* in South Africa, pushing its attested presence back by over one million years.

1. Introduction

Glires constitute a monophyletic clade that includes the orders Rodentia (rodents) and Lagomorpha (rabbits, hares, and pikas). Among the most distinctive anatomical features, they are characterized by continuously growing incisors—one pair of upper incisors in rodents and two pairs in lagomorphs—which are separated from the cheek teeth by a diastema, as well as the absence of canines. Ecologically, they are mostly small herbivorous animals with reduced dispersal ability. Both rodents and lagomorphs exhibit a wide range of body sizes, with the term mesomammals commonly used to refer to medium to large species thereof. In this category are grouped mammals of intermediate size between micromammals (below 200–500 g, depending on the authors) and larger mammals weighing more than 20 kg: in southern Africa, they include large rodents (such as porcupines, springhares, and cane rats), hares and rabbits, hedgehogs, hyraxes, small primates, or small carnivores, for instance. Although mesomammals encompass a taxonomically, morphologically and ecologically diverse group of animals, they share several common traits that justify their joint study in fossil assemblages: they are preyed upon by several predators, including small to large-sized carnivores, hominins, and large birds of prey; they are likely to be affected by similar taphonomic processes, including predator and (post)-depositional damage; due to their intermediate size, their remains, particularly the cranio-dental elements useful for identification, necessitate the use of small to medium-sized mesh sieves to ensure the recovery of smaller elements. Despite their ubiquitous presence in Pleistocene fossil assemblages from Southern Africa (Avery, 2019), these taxa have received relatively less attention compared to their micro and macro counterparts.

The Pleistocene hominin-bearing locality of Cooper's Cave is located in the Cradle of Humankind World Heritage site, approximately 1.5 km northeast of Sterkfontein. This karst system corresponds to an area of 303 × 198 m in which three spatially distinct infills have been identified: Cooper's A, B, and D (Berger et al., 2003; de Ruiter et al., 2009).

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The deposit of Cooper's D (COD) has produced a rich and extensively studied fauna (an extensive bibliography is provided below), as well as seven remains attributed to the species *Paranthropus robustus* (de Ruiter et al., 2009). It was originally dated by U-Pb to 1.526 ± 0.088 Ma for the basal speleothem and *ca*. 1.4 Ma for a flowstone hanging in the middle of the deposit sequence (de Ruiter et al., 2009). More recently, new U-Pb dating of the basal speleothem indicated an age of 1.375 ± 0.113 Ma (Pickering et al., 2019), which implies that COD is equal to or younger than this age. In an analysis of the large mammalian palaeoguild, Hanon et al. (2022a) stated that the accumulation period could have lasted until 1 Ma. Cooper's D is probably the most thoroughly studied site in the Cradle of Humankind in terms of its faunal composition, with numerous studies having provided the taxonomic description of microvertebrates (Pavia et al., 2022; Linchamps et al., 2023a; Matthews and Steininger, 2023) and large-bodied mammals (Hartstone-Rose et al., 2007; Steininger et al., 2008; de Ruiter et al., 2009; DeSilva et al., 2013; Folinsbee and Reisz, 2013; Val et al., 2014; O'Regan and Steininger, 2017; Badenhorst and Steininger, 2019; Hanon et al., 2022a, 2022b). Within the mesomammals, studies have been published on mustelids and viverrids (O'Regan et al., 2013), and herpestids (Cohen et al., 2019). In this contribution, we provide new and updated taxonomic analysis of medium- and large-sized rodent and lagomorph craniodental remains, accompanied by morphological descriptions and palaeoecological information. Some of these remains had been published previously by Berger et al. (2003) and de Ruiter et al. (2009) but are here taxonomically reassigned, along with additional material discovered since. A preliminary taphonomic analysis of long bones was also conducted to obtain information on the agents and processes that could have produced or altered their accumulation.

2. Materials and methods

The fossil material examined here was recovered during excavations of decalcified sediments at Cooper's D, which took place between 2001 and 2018. It comprises 53 cranial elements and 109 postcranial elements. This material is currently housed at the Evolutionary Studies Institute (ESI), University of the Witwatersrand, Johannesburg. Each specimen reported has been attributed an identification number following the format: locality – specimen (e.g., CD1542).

Fossil identifications were carried out using modern and fossil comparative collections of the ESI, the Ditsong National Museum of Natural History (DNMNH), Pretoria, and the Muséum national d'Histoire naturelle (MNHN), Paris. Identifications have also relied on descriptions, measurements, and photographs of fossil and modern specimens published in taxonomic studies, including Azzarà et al. (2022) for the genus *Hystrix*, Pickford & Mein (2011) for the pedetids, Denys et al. (2003) and Pelaez-Campomames et al. (2020) for the sciurids, and Sen and Pickford (2022) for the leporids.

The rodent and lagomorph taxonomic classification follows Wilson et al. (2017, 2016). Pictures of the material were taken using Nikon digital camera D 5500 coupled with AF-S Micro Nikkor 60 mm and macro extension tubes. Measurements of the craniodental elements were taken using a digital calliper to the nearest 0.1 mm. Bivariate plots and principal component analysis (PCA) are used to visualise size and morphological variation. They were performed with the software R 4.1.2 using *FactoMineR* package.

For the taxonomic survey, we used the number of identified specimens (NISP) and the minimum number of individuals (MNI) described in Lyman (1994, 2008). Teeth are referred to as a combination of letters and numbers that indicate the type and the position of the teeth: the abbreviations used for designating the type of tooth are I = incisor, P = premolar, M = molar; the letter "d" before a type of tooth indicates that it is a deciduous tooth; the number after the letter indicates the position, with superscript for upper jaw and subscript for lower jaw. Thus, P_4 is a lower fourth premolar and dM^3 is a decidual upper third molar.

Regarding taphonomic analysis, a total of 109 postcranial specimens have been observed for bone surface modifications under a binocular microscope Olympus SZ2-ILST (10 μm–40μm). Pictures were taken using a mounted camera and LCmicro software (v.2.1). We identified bone surface modifications based on previously published descriptions, in particular the action of carnivores (Maguire et al., 1980; Binford, 1981; Brain, 1981; Cruz-Uribe, 1991; Pickering, 2002; Kuhn et al., 2010; Fourvel, 2012), diurnal and nocturnal raptors (Hockett, 1991; Serra, 2000; Lloveras et al., 2008, 2009a; Armstrong and Avery, 2014; Armstrong, 2016a), hominins (Binford, 1981; Brain, 1981; Potts and Shipman, 1981; Shipman and Rose, 1983; Behrensmeyer et al., 1986; Patou, 1987; Blumenschine, 1988, 1995; Blumenschine and Selvaggio, 1988; Fiorillo, 1988, 1989; Olsen and Shipman, 1988; Lyman, 1994b; Blumenschine et al., 1996; Patou-Mathis, 1997; Domínguez-Rodrigo et al., 2009, 2010; Lloveras et al., 2009b; Armstrong, 2016b; Fernández-Jalvo and Andrews, 2016), and rodents (Brain, 1980, 1981; Maguire et al., 1980).

3. Results

3.1. Systematic palaeontology

Superorder EUARCHONTOGLIRES Murphy et al., 2001

Order RODENTIA Bowdich, 1821

Family HYSTRICIDAE G. Fischer, 1817

Genus HYSTRIX Linnaeus, 1758

Porcupines of the genus *Hystrix* are the largest of all African rodents, weighing up to 20 kg. They are readily distinguishable from other rodents by the presence of long, sharp quills along the length of the back. Two species of porcupines are recognized in Africa today: *Hystrix cristata*, which occurs in savannas from western, central, and eastern Africa, and *Hystrix africaeaustralis,* which has a wide sub-equatorial distribution. The two species are morphologically very close but have distinct distribution, except for a small overlap in East Africa. Fossil remains of *H. africaeaustralis* have been found in many sites in the Cradle of Humankind, including Swartkrans (Brain, 1993; de Ruiter, 2003), Sterkfontein (Reynolds et al., 2003; Reynolds and Kibii, 2011; Val and Stratford, 2015), Gladysvale (Lacruz et al., 2002, 2003), and Gondolin (Adams and Conroy, 2005; Adams, 2010, 2018; Engelbrecht et al., 2023). Two extinct species have been described in South Africa: *Xenohystrix crassidens* Greenwood (1955) and *H. makapanensis* Greenwood (1958). *Xenohystrix crassidens* is only listed at Makapansgat (Pliocene) by Greenwood (1955, 1958). Azzarà et al. (2022) list *H. makapanensis* at Makapansgat (Members 3 and 4) and Gondolin (Members GD2, GDA), and *H.* cf. *makapanensis* at Kromdraai (Member A), Swartkrans (Member 1 and/or 2), and Sterkfontein (Dump 8, Dump 10, Member 5).

Hystrix sp.

Referred specimens. CD203 left broken incisor fragment; CD861 right M_2; CD862 left M^3; CD864 fragment of maxilla with left P^4; CD865 left hemimandible with M_1, M_2 and erupting M_3; CD3437 right P_4; CD3460 left upper incisor fragment; CD6805 right hemimandible with M_1, M_2; CD6806 right erupting M_3; CD8482 right M^2 or M^3; CD10380 enamel fragment; CD16672 left worn indeterminate upper tooth (P_4, M_1 or M_2); CD16696 right M^3; CD17300 left M^2 or M^3; CD17432 enamel fragment; CD17436 left erupting M_3; CD20217 left emerging P^4; CD24356 right M_1.

Description. The two hemimandibles CD865 (left) and CD6805 (right) belong to the same juvenile individual whose permanent P_4 has not erupted yet (Fig. 1). The incisor CD203 and the erupting M_3 CD6806 are also associated with this individual. The mandibular corpus is massive, much more robust than the ESI collection specimens of the same age class, with a strong masseteric ridge as in *H. makapanensis* (Azzarà et al., 2022). The posterior portion of the mandible is missing. The occlusal pattern of the teeth is similar to modern and fossil

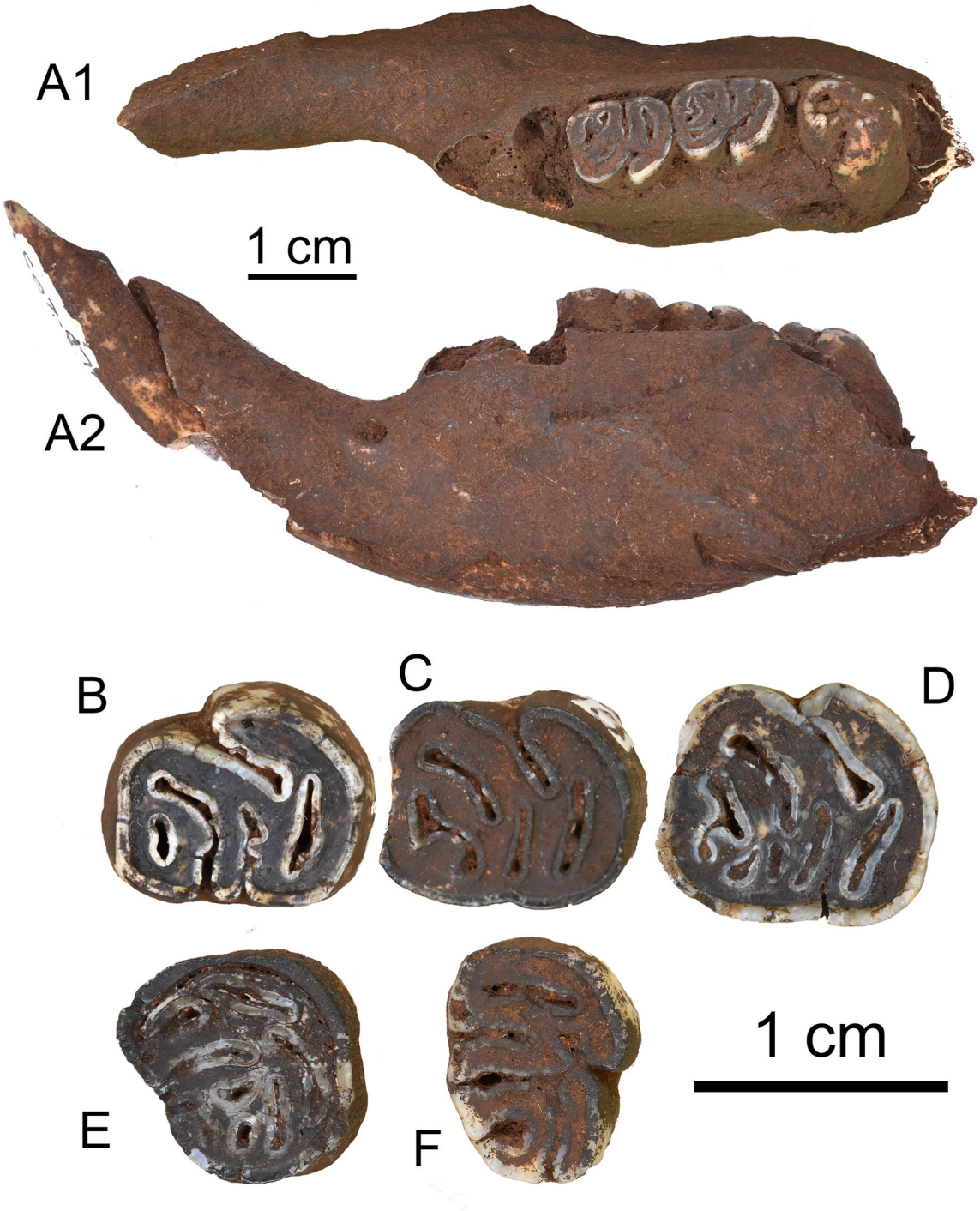


Fig. 1. Mandible and teeth of *Hystrix* sp. From Cooper's D: A, left hemimandible with M_1, M_2, and erupting M_3 (A1 labial view, A2 occlusal view - CD865) and incisor fragment (CD203); B, right P_4 (CD3437); C, right M_1 (CD24356) D, right M_2 (CD861); E, right M^2 or M^3 (CD8482); F, right M^3 (CD16696). The upper 1 cm scale bar applies to the mandible, the lower 1 cm scale bar applies for the five teeth.

H. africaeaustralis, but the dentition is larger than specimens at a similar stage of wear. Additionally, the M_1 is not significantly smaller than the other lower teeth as in modern African porcupines (see Fig. 2).

Other *Hystrix* remains from Cooper's D include several lower and upper cheekteeth. The three cheekteeth CD3437 (right P_4), CD24356 (right M_1), and CD861 (right M_2) are believed to belong to the same individual due to similar size and wear. The premolar P_4 is the longest tooth (CD3437: length 10.85 mm, width 8.91 mm), the molar M_1 is slightly smaller (CD24356: length 9.99 mm, width 8.25 mm) and the molar M_2 is larger than all ESI specimens (CD861: length 10.8 mm, width 9.61 mm). The P_4 is high crowned, while both the M_1 and the M_2 have shorter crowns. The roots are small, not well-formed, as in *H. makapanensis* from Gondolin (Azzarà et al., 2022). The teeth retain a deep hypostriid and a hypostriid that is well-developed but not joined to posterior mesoflexid as in *H. makapanensis*. The upper teeth are high and have marked apical curvature. The molar CD8482 (M^2 or M^3) is sub-circular in occlusal view (length 9.30 mm; width 8.68 mm). The two molars M^3 CD862 (left) and CD16696 (right) belong to the same individual and are wider mesially than distally Except for the dimensions of the teeth and the size of the M_1 in proportion to the toothrow, the dental



Fig. 2. Upper and lower left cheekteeth of modern *P. capensis* in labial view, compared with dental material from Cooper's D: A, right P^4 (CD9260); B, indeterminate upper molar (CD3458); C, indeterminate upper molar (CD1165); D, indeterminate upper molar (CD3442); E, left M_1 (CD3445); F, fragmented lower incisor (CD867).

characters distinguish the COD specimens from *H. makapanensis*. The remains look closer to modern *H. africaeaustralis*, but the proportions of the mandible and the teeth of the specimens are significantly larger. The material has been conservatively attributed to *Hystrix* sp.

Family PEDETIDAE Gray, 1825

Genus PEDETES Illiger, 1811

Members of the family Pedetidae Gray, 1825 are medium to large-sized African rodents, characterized in their craniodental anatomy by a hystricomorph skull associated with sciurognathous mandibular characters and bilophodont cheekteeth (Linchamps et al., 2023b; Da Cunha et al., 2024). They are represented by one extant genus, *Pedetes* Fitzinger, 1867, and five extinct genera: †*Parapedetes* Stromer, 1922 and †*Rusingapedetes* Pickford and Mein, 2011 from the Early Miocene, †*Megapedetes* Macinnes, 1957 from the Early to the Middle Miocene, †*Propedetes* Mein and Pickford, 2008 and †*Oldrichpedetes* Pickford and Mein, 2011 from the Miocene to the Pliocene (Pickford and Mein, 2011).

The genus *Pedetes* today contains two large species distributed in East and South African grasslands and arid savannas: *P. capensis* (Foster, 1778) occurs in southern Africa, and *P. surdaster* Thomas, 1902 in Tanzania and Kenya (Monadjem et al., 2015). The body form of *Pedetes* is modified for saltatorial locomotion, with long hindlimbs and long hindfeet, short forelimbs, and long tail. Fossils of various species attributed to *Pedetes* have been found in numerous sites in southern Africa throughout the Plio-Pleistocene (Avery, 2021): †*P. gracilis* Broom (1934) is described in Taung (Broom, 1934), †*P. hagenstadti* Dreyer and Lyle (1931) in Florisbad (Dreyer and Lyle, 1931) and *P. capensis*Foster, 1778 in several sites including Florisbad, Sterkfontein, Wonderwerk, and Swartkrans (Brain, 1993; Brink, 1987; Kuman and Clarke, 1986; Val and Stratford, 2015; Brink et al., 2016).

Pedetes capensis (Forster, 1778)

Referred specimens. CD867 fragmented lower incisor; CD1165 indeterminate upper molar; CD3442 indeterminate upper molar; CD3458 indeterminate upper molar; CD3445 left M_1; CD9260 right P^4.

Description. The teeth from Cooper's D are relatively well preserved, although CD1165, CD3442, and CD3458 lack one extremity. The hypsodont, open-rooted cheekteeth are bilophodont. They consist of two lophs separated by a median transverse valley encompassing the entire height of the tooth, which unite on the lingual side for the upper teeth and the labial side for the lower teeth. The distinction between isolated upper and lower cheekteeth is based on the upper teeth being curved in the anteroposterior axis only, while the lower teeth are curved in both the anteroposterior and the linguolabial axes. P^4 is high (H = 19.06 mm) and well curved with a deep mesostria. The teeth are larger than those of †*P. gracilis* (Broom, 1934). They are very similar in shape and size (see Appendix A1 for table with teeth dimensions) to the modern *Pedetes capensis* specimens examined in MNHN and DNMNH and are therefore attributed to this latter species.

Family SCIURIDAE Fischer de Waldheim, 1817

Subfamily XERINAE Osborn, 1910

Tribe XERINI Murray, 1866

In Africa, the modern sciurids originally included a single subfamily Xerinae Osborn, 1910 that contains two tribes: Xerini Osborn, 1910 (African and some Eurasian ground squirrels) and Protoxerini Moore, 1959 (African tree squirrels). The Eastern gray squirrel *Sciurus carolinensis* (Subfamily Sciurinae) was also introduced to South Africa in the early 20th century, but its presence is restricted to the most south-western part of the Western Cape. Until recently, the tribe Xerini was composed of one Asian genus *Spermophilopsis* Blasius, 1884 and two African genera: the monotypic *Atlantoxerus* Forsyth Major, 1893 and the genus *Xerus* Hemprich and Ehrenberg, 1833 consisting of four species divided into three subgenera: *X. inauris* (Zimmermann, 1780) and *X. princeps* (Thomas, 1929) (included in the subgenus *Geosciurus*), *X. erythropus* (E. Geoffroy, 1803) (subgenus *Euxerus*) and *X. rutilus* (Cretzschmar, 1828) (subgenus *Xerus*). The fossil and modern representatives of this tribe share various characteristic dental features, such as the metaloph disconnected from the protocone in the upper cheek-teeth, and the presence of ectolophid and hypoconulid in the lower molars (Kryštufek et al., 2016). Recently, molecular and morphological phylogenies have led to the generic revision of *Xerus* (which now includes only *X. rutilus*) and the recognition of *Geosciurus* (which now includes *G. inauris* and *G. princeps*) and *Euxerus* (which includes *E. erythropus*) as two distinct genera (Kryštufek et al., 2016). This clarification makes the generic division of Xerini more concordant with biogeography, fossil history, and dental morphology of taxa.

Geosciurus is now considered as the only genus present in southern Africa, with two species partially overlapping in their distribution: *G. inauris* occurs widely in open savannas and arid zones from Namibia, Angola and Botswana, while *G. princeps* has a narrower distribution restricted to western escarpment in Namibia with extralimital

occurrence in the south of Angola and the north of South Africa (Herron et al., 2005; Monadjem et al., 2015). Members of this genus are large terrestrial squirrels that live in simple burrow systems (Happold, 2013). The preferred habitat of *G. inauris* is open semi-arid country with hard ground (Smithers, 1971); it also occurs in *Acacia* scrubs on flood plains, pans, river beds and sandy veld (De Graaff, 1981), in calcrete soils along riverbeds (Amtmann, 1975), and in areas with short annual grass (Happold, 2013). *G. princeps* seems to have a preference for rocky habitats (Roberts, 1951; Herzig-Straschil and Herzig, 1989). The two species are morphologically similar, but De Graaff (1981) and Denys et al. (2003) note various subtle differences in skull and dentition; unfortunately, they do not differ in the occlusal patterns of the upper molars.

When looking at the fossil history of the genus, the scarcity of fossil material that has been discovered in South Africa is particularly striking. The first occurrence of *G. inauris* (described as *Xerus*) is to be found at Florisbad in Middle Pleistocene deposits (Cooke, 1955; Kuman and Clarke, 1986); for the Holocene, remains are identified in fewer than ten fossiliferous sites (Avery, 2019). The scarcity of the fossil record raised questions about the biogeographic history of the genus and possible taphonomic or palaeoecological biases that prevented the recovery of remains.

Genus GEOSCIURUS Smith, 1834

Geosciurus cf. *inauris*

Referred specimens. Two isolated maxillary fragments that were found to belong to the same individual. The right maxilla (CD5465) preserves the premolar P^4 and the molars M^1 and M^2, and the left maxilla (CD920) holds the alveoli of the same teeth. In the summer of 2024, the fossils were inadvertently damaged during handling by a visitor. The description provided below was completed prior to this fragmentation. While the diagnostic features of the fossil remain intact, the photographs included in this study reflect its original condition and do not represent its current state (see Fig. 3).

Description. The CD5465 specimen displays several skull features that are characteristic of *Geosciurus*, and that distinguish it from other members of the Xerini tribe: the absence of a minute P^3 (present in *Atlantoxerus* and *Euxerus*), a longer toothrow (smaller in *Atlantoxerus* and *Xerus*), and a metaloph connected with the posteroloph (unattached in *Atlantoxerus, Euxerus,* and *Xerus*). The specimen is similar in size to modern *G. inauris* and *G. princeps,* these two species being morphometrically indistinguishable based on the craniodental measurements available for the specimen CD5465 (Fig. 4).



Fig. 3. Occlusal view of the upper jaw of *Geosciurus* cf. *inauris* (CD5465 right maxilla, CD920 left maxilla).

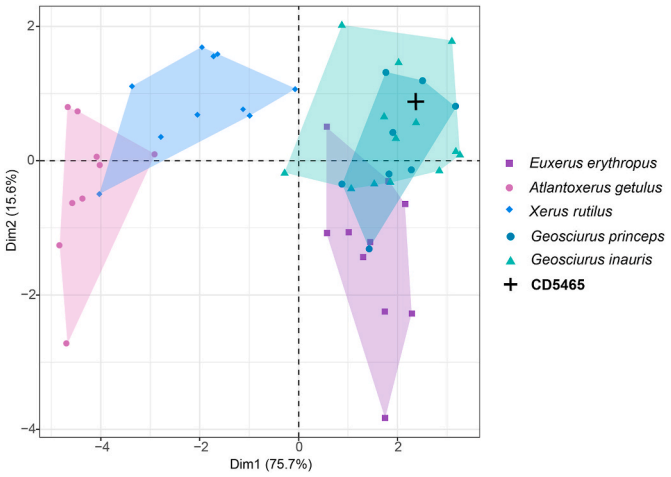


Fig. 4. Morphological principal component analysis (PCA) for species delimitation of sciurids from the tribe Xerini using nine craniodental measurements. These measurements are available in Appendix A2.

The maxillae show well-developed masseter knobs. The upper teeth display intermediate wear, which complicates the comparison with modern specimens as various dental characters of the Xerini vary at different wear stages. Denys et al. (2003) claimed that a mesostyle is present in the first and second upper molars of *G. princeps* and absent in *G. inauris*, but the sample of observed specimens was limited in her study, and we observed that this character was variable in DMNH specimens of both species. The mesostyle is present in CD5465. Additionally, Denys et al. (2003) found that the position of the anterior cingulum in the P^4 could be used to distinguish the two species: the anterior cingulum is connected to the protocone in *G. princeps*, while it ends very low to the cusp and is separated from it by a transverse valley in *G. inauris*. This feature appeared to be more reliable for distinguishing the two species, although it is not completely invariable and can be affected by wear (valid for 40 out of the 51 specimens of *G. inauris* and 19 out of the 20 specimens of *G. princeps* observed in DNMN zoological collections). In CD5465, the anterior cingulum is low and fairly isolated from the protocone despite an intermediate stage of wear (Fig. 5), which coincides most closely with *G. inauris*. We found an additional character that appears to work well on extant DNMH specimens to differentiate the two species using the maxillary bone: the bone margin that connects the masseter knob to the labial wall of the infraorbital foramen is convex and well individualized in *G. inauris*, while it is concave and merges with the anterior part of the maxilla in *G. princeps* (valid for 40 out of the 51 specimens of *G. inauris* and 19 out of the 20 specimens of *G. princeps* observed in DNMN zoological collections). The first condition is observed in CD5465, which aligns with *G. inauris* (see the black arrows in Fig. 5). The protocone of the premolar P^4 is approximately the same size as the hypocone and is linked to it by a loph, and the metacone is only slightly larger than the paracone. The hypocone and protocone are well differentiated. The molars M^1 and M^2 have very similar occlusal morphology. In both M^1 and M^2, the metaloph is straight, rather long and connected to the hypocone, whereas in modern *G. princeps* and *G. inauris* it is shorter and connected to the posteroloph. The anteroloph joins the protocone. The central valley occurring between the protoloph and the metaloph is wide, and it closes lingually less obliquely than most modern observed specimens. Overall, CD5465 shows high resemblance with modern specimens of *G. inauris*, but also displays a few distinguishing features that do not match with other specimens at a same stage of wear. Pending the discovery of a larger sample, we attributed the Cooper's D specimen to *Geosciurus* cf. *inauris*.

Order LAGOMORPHA Brandt, 1855

Family LEPORIDAE Fischer de Waldheim, 1817

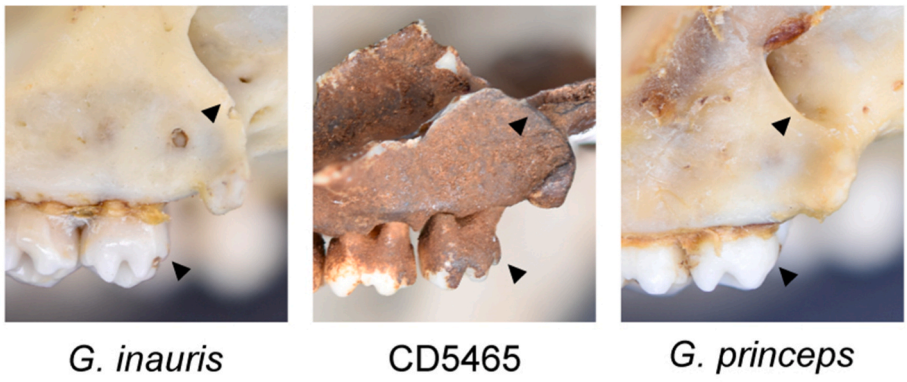


Fig. 5. Labial view of the maxilla of *G. inauris* (left), CD5465 (middle), and *G. princeps* (right), showing differences in two qualitative characters of the maxilla (shape of the labial edge of the infraorbital foramen that connects to the masseteric knob) and the P^4 (position of the anterior cingulum), as indicated by the two black rows.

Genus PRONOLAGUS Lyon, 1904

Fossil leporids are scarce in the Plio-Pleistocene fossil record of southern Africa. The genera *Lepus* Linnaeus, 1758 and *Pronolagus* Lyon, 1904 have been documented from the Pliocene (Avery, 2019), while the earliest appearance of *Bunolagus* Thomas (1929), is recorded at Boomplaas Cave, dating to the Late Pleistocene (Faith, 2013). The remains of *Pronolagus* and *Lepus* became more prevalent in faunal assemblages from the Middle Stone Age and the Later Stone Age, as seen in sites such as Diepkloof Rock Shelter (Steele and Klein, 2009), Die Kelders Cave 1, and Pinnacle Point Site 5–6 (Armstrong, 2016b). This reflects changes in human subsistence strategies, including an expanded dietary diversity, notably the inclusion of small, fast game such as hares and birds (Stiner et al., 2000; Steele and Klein, 2009; Clark and Kandel, 2013; Armstrong, 2016b).

Rock-hares from the genus *Pronolagus* are medium to large-size hares with medium-sized ears that are closely associated with rocky habitats (Happold, 2013). The genus contains four extant species with a distribution mainly restricted to southern Africa: *P. crassicaudatus* (I. Geoffroy, 1832), *P. randensis* Jameson, 1907, *P. rupestris* (A. Smith, 1834) and *P. saundersiae* Hewitt, 1927. Despite being identified in a dozen fossil localities from southern Africa, material attributed to *Pronolagus* had not been comprehensively described until the recent work of Sen and Pickford (2022) who reviewed the dental and skeletal morphology of the four extant species and described a new species †*P. humpatensis* from the Early Pleistocene of Angola.

Anatomically, the genus *Pronolagus* can be distinguished from *Bunolagus* and *Lepus* by a combination of craniodental characters that were summarized in von Koenigswald et al., 2010 and Sen and Pickford (2022). For the upper jaw, the genus *Pronolagus* is characterized by a width of the mesopterygoid space (choanae) lesser than the length of the hard palate (greater than the length of the hard palate in both *Lepus* and *Bunolagus*), the presence of antero-external shoulders on zygoma (also present in *Lepus*, absent in *Bunolagus*), a grove on the principal incisor located close to the inner margin (as in *Bunolagus*, while the position of the grove is variable in *Lepus*) and not filled with cement (not filled in *Bunolagus*, filled in *Lepus*), a deep re-entrant fold (hypoflexus) in P^3-M^2 tilted at its midway, bordered with thick enamel on its anteroexternal and posterointernal walls (in *Bunolagus*, the hypoflexus is short, with a dentine crest in its buccal elongation; in *Lepus*, it is deep, straight, and has crenulated enamel all along its walls). For the lower jaw, *Pronolagus* can be identified based on the V-shape of the anterolophid that forms the primary shearing blade in P_4-M_2 (V-shaped in *Bunolagus*, smoothly curved or V-shaped in *Lepus*) and the presence of a thick band of enamel at the posterior enamel of the posterolophid which forms a secondary shearing blade in P_4-M_2 (this enamel band is thin and worn down in both *Bunolagus* and *Lepus*).

Pronolagus cf. *rupestris*

Referred specimens. CD383 left maxilla with no teeth; CD1163 right hemimandible with no teeth; CD2439 isolated right lower molariform; CD3443 right hemimandible with no teeth left; CD3450 left hemimandible with complete toothrow; CD5458 left hemimandible with M_1, M_2, M_3; CD6801 right hemimandible with P_4, M_1, M_2, M_3; CD6802 left hemimandible with M_1, M_2; CD6803 right hemimandible with P^3, P^4, M^1, M^2; CD6802a left maxilla with P^4, M^1; CD7800 left hemimandible with P_3, P_4, M_1, M_2; CD7842 right hemimandible with P_4, M_1, M_2; CD7865 left maxilla with P^2, P^3, P^4, M^1, M^2; CD7964a right maxilla with P^3, P^4, M^1; CD7964b left and right maxillae with P^3 and P^4 still attached to the right maxilla; CD7964c isolated lower molariform; CD7965 left + right maxillae with no teeth left; CD8480a broken right hemimandible holding P_3, P_4, M_1; CD8480b left hemimandible with P_3, P_4, M_1; CD8481 left mandible with P_3, P_4, M_1, M_2; CD8488 left digested hemimandible with no teeth; CD17233 right hemimandible with P_3, P_4; CD18345 isolated right lower molariform; CD19254 left and right maxillae with complete toothrow; CD20427 right hemimandible with complete toothrow; CD20510 left hemimandible with P_4, M_1, M_2, M_3; CD21852 right hemimandible with M_1; CD21915 left hemimandible with M_1, M_2, M_3.

Description. The material is relatively fragmented, with most specimens consisting of either maxillae with or without the cheek teeth, or anterior parts of the mandible bearing the cheek teeth and occasionally the lower incisor. Despite a few specimens being covered by thick manganese encrustations, the surfaces of bones and teeth are relatively well-preserved. The distal ends of incisive foramina on the maxillae are wide, as in *P. rupestris, P. saundersiae* and *P. randensis* (narrower in *P. crassicaudatus*). The choanae (mesoptyergoid space) are moderately large and their width is approximately 60% of the length of the hard palate, which is greater than the proportions found in *P. randensis*. On the specimen CD19254 (Fig. 6), the maxillae preserve the complete tooth row, displaying dental features that share similar traits with *P. rupestris* and *P. saundersiae*.

There are only two flexa on the anterior edge of P^2, such as in *P. randensis, P. rupestris* and *P. saundersiae* (there are three in *P. crassicaudatus*). The enamel along anterior walls of the hypoflexus in upper molariform teeth is much less wrinkled than in *P. crassicaudatus* and *P. randensis*.

During our stays at the DNMNH, we faced difficulties finding definitive qualitative dental criteria to differentiate between *P. rupestris* and *P. saundersiae*. This morphological similitude can likely be attributed by the close genetic distance between the two species, with a posterior molecular divergence date estimated at 1.65 ± 0.69 Ma (Matthee et al., 2004). They are partially morphologically distinguishable using craniodental measurements, with *P. rupestris* being slightly smaller than *P. saundersiae*. The most relevant measurements for separating the two species are the maximal width of the P^4 alveolus (*P. rupestris*: mean = 5.3 mm, min = 4.6 mm, max = 5.6 mm, n = 10;

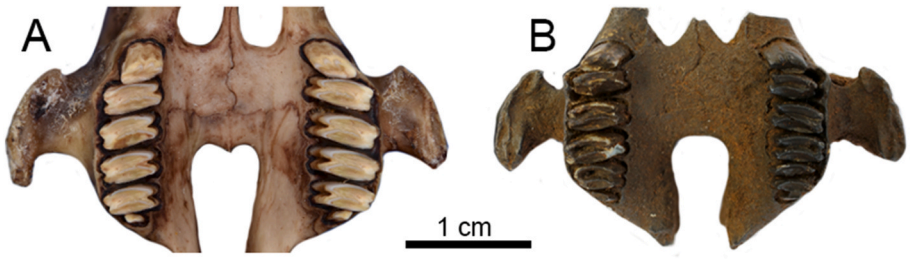


Fig. 6. Maxillae in ventral view of (A) modern *Pronolagus rupestris* (DNMNH-44547) and (B) fossil *Pronolagus* cf. *rupestris* (CD19254) from Cooper's D.

P. saundersiae: mean = 5.8 mm, min = 5.3 mm, max = 6.2 mm, n = 7) and the distance between the tip of the zygomatic shoulder and the lingual anterior edge of the P^3 alveolus (*P. rupestris*: mean = 8.2 mm, min = 7.2 mm, max = 8.5 mm, n = 10; *P. saundersiae*: mean = 9.4 mm, min = 8.3 mm, max = 10.1 mm, n = 7), although we acknowledge that the number of specimens observed is small. By taking multiple measurements from both the upper and lower jaws (available in Appendix A3), it was possible to partially distinguish between modern *P. rupestris* and *P. saundersiae* species using a Principal Component Analysis, although substantial overlap existed (Fig. 7).

However, many of these measurements were not consistently available in the COD fossils. Additionally, specimens from Cooper's D exhibit smaller size compared to modern adult *P. rupestris* and *P. saundersiae*, distinguishing them from most measured specimens of the two modern species. Fig. 7 provides a visual representation of the size disparity between COD specimens and measured modern species in terms of the length of P^2-M^3 at the alveolar level and the maximum width of M_1. Two hypotheses can potentially explain this size difference: (1) the specimens from COD could represent a distinct form, possibly corresponding to an as yet undescribed species or an ancestral form of the modern species *P. rupestris*; (2) these specimens might be juveniles of the species *P. rupestris* or *P. saundersiae*. In fact, the overrepresentation of juvenile individuals has been observed in numerous archaeological and actualistic assemblages accumulated by raptors or carnivores (e.g., Cochard, 2004a, 2004b; Schmitt, 1995).

To test these hypotheses, we examined the long bones (e.g., humerus, radius, and ulna for the forelimb bones, femur and tibia for the hindlimb bones) attributed to *Pronolagus* from the COD assemblage. By examining the sequence of bone epiphyseal fusion, one may be able to determine the age of each individual. For instance, the distinction can be made between juveniles and adults of the European hare *Lepus europaeus* (Stroh, 1931; Bujalska et al., 1965; Broekhuizen and Maaskamp, 1979; Driver, 1985) and the black-tailed jackrabbit *Lepus californicus* (Lechleitner, 1959) based on the ossification of epiphyseal cartilage of various long bones. Unfortunately, comparative materials are still lacking for establishing with confidence the age of *Pronolagus* specimens, and the hypothesis that the criteria used for *Lepus* are also applicable to *Pronolagus* could not be verified (see last section of the discussion). Additionally, this task is somewhat challenging at Cooper's D, where some of the material is covered in manganese, complicating the examination of bone surfaces. Nevertheless, the specimens could be categorized into three groups based on the stages of epiphyseal fusion in their long bones (Pelletier et al., 2020), which could be interpreted as age classes: 14 specimens with unfused epiphyses, probably indicative of juveniles; 3 specimens with partially fused epiphyses, probably indicative of subadult; 24 specimens with all epiphyses fused, indicative of adults. It appears that different age categories are represented in the postcranial material. However, it is currently not possible to directly associate the cranial remains described in this publication with the examined postcranial bones. Therefore, we have opted for a conservative and parsimonious identification of the fossil material as *Pronolagus* cf. *rupestris*. Future comparisons of *Pronolagus* remains from additional Plio-Pleistocene sites within the Cradle will help resolve this issue.

3.2. Taphonomy

The glire bones from Cooper's D, just as the large mammal fauna (Hanon et al., 2022a, 2022b), are generally covered by a manganese coating, which impacts the visibility of the bone surfaces. We observe taphonomic evidence of predation (i.e. pits, punctures, scores and digestion) on at least 18 postcranial bone elements (Fig. 8). The pits and punctures are generally of a small size, located either on or close to the

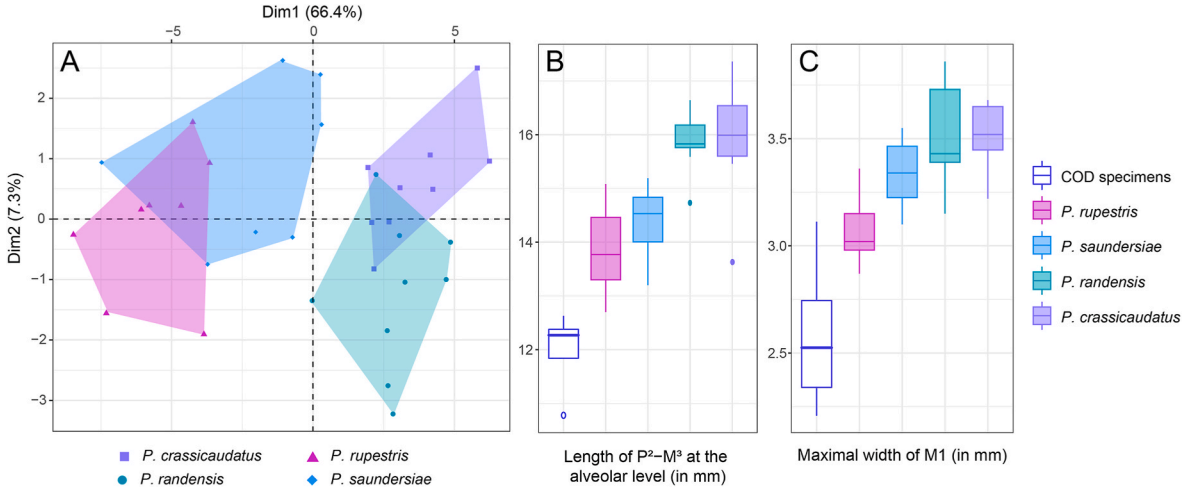


Fig. 7. A, morphological principal component analysis (PCA) for species delimitation of modern *Pronolagus*, based on 26 craniodental measurements. B & C, boxplots showing the distribution of measurements (in mm) for the length of P^2-M^3 at the alveolar level and of maximum width of M_1. All measurements are available in Appendix A3.

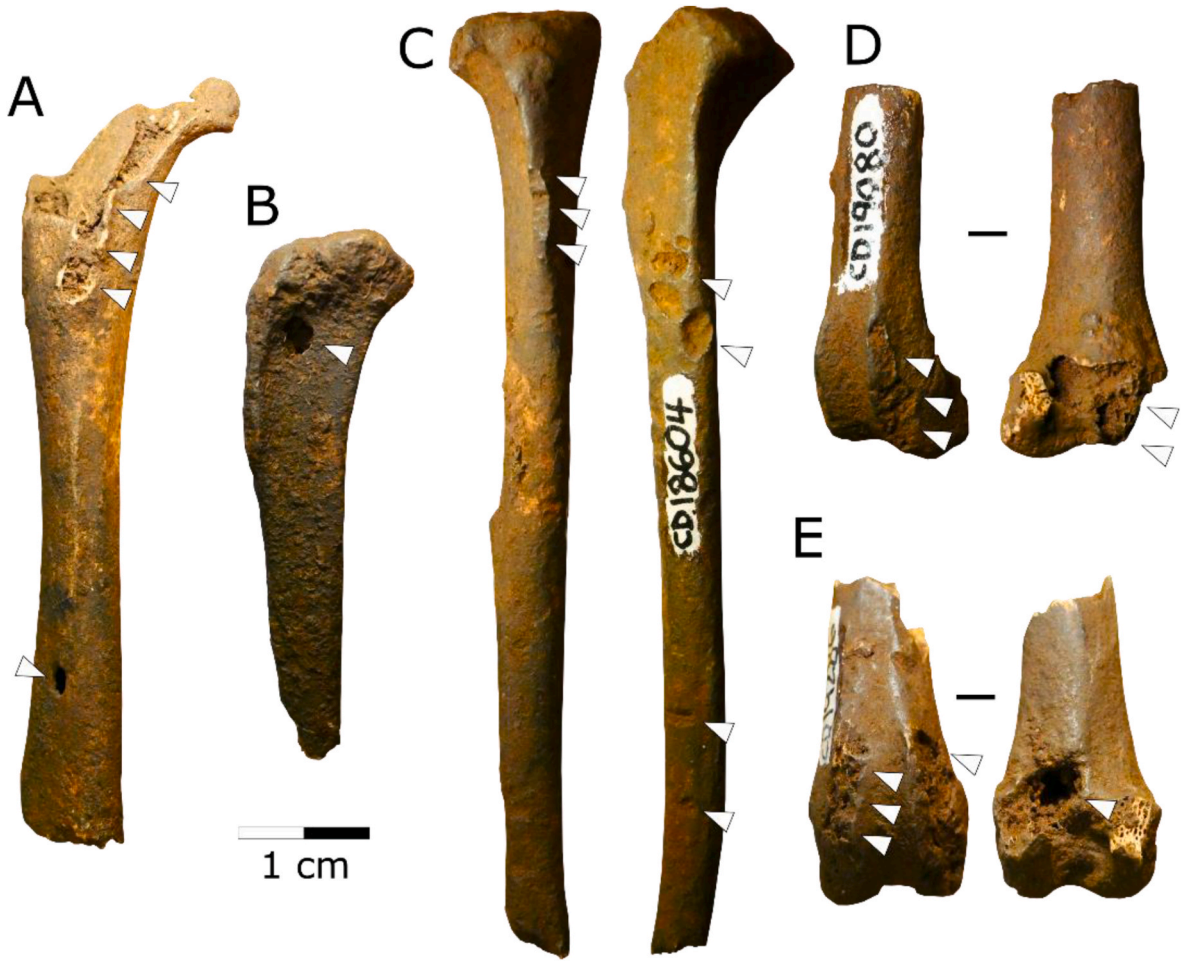


Fig. 8. Glire long bones with identified bone surface modifications. A, a left femur with a small carnivore puncture and gnawing (CD9362). B, a tibia with a puncture mark (CD890). C, a right tibia with multiple tooth pits (CD18604). D, a distal femur with gnawing marks (CD19080). E, a distal femur with puncture marks and gnawing marks (CD19286).

epiphysis (CD1169, CD9349, CD9548, CD9592, CD10834, CD19269, CD19286, CD22526) or on the shaft of long bones (CD890, CD9362, CD9515, CD10588, CD10636, CD18604, CD20225). A mandible (CD8488) shows evidence of digestion. Tooth or claw scores are visible on a femur shaft (CD10636). Damage related to gnawing activity is also observed on a distal femur (CD19080). So far, there is no evidence of anthropogenic modification (i.e. butchery marks or burning damage) on the bones.

4. Discussion and conclusions

4.1. Origin of the accumulation

Some glire remains display evidence of digestion and tooth marks by predators. To investigate this, a preliminary taphonomic survey has been performed, which encompasses cranio-dental and postcranial remains. The studied assemblage is numerically dominated by *Pronolagus* cf. *rupestris*, which is favored prey for large nocturnal or diurnal birds of prey and small to medium-sized carnivores. Taphonomic analysis of the larger mammals from Cooper's D indicates that leopards, hyenids (likely the brown hyena, *Parahyaena brunnea*), and canids contributed to the accumulation of bones (Hanon, 2019; Hanon et al., 2022a). Pavia et al. (2022) suggested that canids, possibly black-backed jackals, were primarily responsible for accumulating the francolin bones in the assemblage. Additionally, it has also been suggested that hominins may have played a role as accumulation agents for the large mammal fauna (Hanon et al., 2022c). Predation damage observed on the glire postcranial bones is more consistent with a small carnivore signal (i.e. gnawing damage); however, it is not possible to exclude the role of birds of prey (i.e. punctures and digestion) at this stage. So far, no damage related to anthropogenic activities has been identified on Glire specimens. A more detailed taphonomic study of the material, including for instance anatomical representation and analysis of breakage, and its comparison with published actualistic studies for African predators, should provide further information on the origin and history of the accumulation, but this is beyond the scope of this study.

4.2. Palaeobiodiversity, Palaeogeography, palaeoenvironments

The remains and new taxa identified in this study (Table 1) contribute to the expansion of the mammalian list for the Cooper's D

Table 1
Medium and large-sized Glire craniodental material from Cooper's D, with the number of identified specimens (NISP) and estimates of the minimum number of individuals (MNI).

Order	Family	Taxon	NISP	MNI
Lagomorpha	Leporidae	*Pronolagus* cf. *rupestris*	28	9
Rodentia	Hystricidae	*Hystrix* sp.	17	3
	Pedetidae	*Pedetes capensis*	6	1
	Sciuridae	*Geosciurus* cf. *inauris*	2	1
Total			53	14

assemblage. A new genus, *Geosciurus*, has been identified, and the specimens previously classified under the genus *Lepus* (as per De Ruiter et al., 2009) have now been reclassified as *Pronolagus*.

The identification of *Geosciurus* cf. *inauris* at Cooper's D represents the earliest known occurrence of this genus in South Africa. While remains attributed to *Xerus* sp. were previously identified in breccia blocks from Berg Aukas in Namibia, dated to the Plio-Pleistocene period (Pelaez-Campomames et al., 2020), the chronological precision of these findings remains broad. Thereafter, the first documented mention of *Geosciurus* is from Florisbad, as *Xerus capensis*, where fauna has been chronologically associated with the Middle or Late Pleistocene period (Kuman and Clarke, 1986). This discovery pushes back the presence of this genus in South Africa by over a million years, offering insights into the chronology, biogeography and phylogeny of the Xerini. Thanks to combined morphological and molecular phylogenies (Herron et al., 2005; Kryštufek et al., 2016) and the discovery of new fossils (Denys et al., 2003; Pelaez-Campomames et al., 2020), the evolution of Xerini in Africa is becoming clearer; yet some gaps remain in our understanding of the phylogeographic history of the genus *Geosciurus* and its divergence with members from the sister clade *Xerus* + *Atlantoxerus*. It is likely that future studies of mesomammal fossils in the Cradle of Humankind will yield additional remains of this genus, which will help to characterize morphological evolution over the last million years.

The taxa identified in this study also provide new palaeoenvironmental insights comparable to those derived from the micro- (Linchamps et al., 2023a) and macro- (Hanon et al., 2022b) mammalian faunas in that they are mostly indicative of grassland or open savannah environments. The micromammal fossil fauna from Cooper's D is numerically dominated by *Mystromys* and *Otomys*, two rodent genera adapted to grassland habitats. Regarding the large fauna, the Antilopini and Alcelaphini dominate the assemblage. Members of those two tribes are considered good markers of open and arid environments. The avian fauna described by Pavia et al. (2022), dominated by *Francolinus* sp., points to a similar open environment. This palaeoenvironmental signal is further supported by evidence from the mesomammals. Porcupines from the genus *Hystrix* are tolerant of a wide range of habitats, especially if caves or rocky outcrops are nearby, but they avoid environments that are too wet or too arid. These nocturnal rodents rest during the day in burrows, caves and rock crevices and are primary herbivores, feeding on roots, bulbs, tubers, and fruits (De Graaff, 1981). Porcupines play a significant role as taphonomic agents in many African archaeological and palaeontological sites by transporting, accumulating, and gnawing bones (Brain, 1981). However, at Cooper's D, marks of rodent gnawing activity on bone surfaces are scarce (less than 1% of NISP) so it is unlikely that the cave was used as a den by porcupines (Hanon et al., 2022a). Squirrels of the genus *Geosciurus* frequent semi-arid open environments, preferably where grass cover is low. The presence of *Pedetes* suggests an open landscape with sparse grasses and minimal woody vegetation near a water source, while *Pronolagus* is notably associated with open, rocky habitats (Happold, 2013). Today, *P. rupestris* has a disjunct distribution, with a range in South Africa separated by approximately 1200 km from a second range, forming a vertical band between southwest Kenya, Tanzania, Malawi, and eastern Zambia. Matthee and Robinson (1996) have shown that those two populations have been isolated from each other for a long period based on the absence of shared mtDNA lineage. The Cradle of Humankind is situated between these two areas, and the presence of this species at Cooper's D may represent a relic of a wider, continuous distribution during the Early Pleistocene. This supports previous hypotheses of Matthee and Robinson (1996) based on geographical genetic population structure. Furthermore, in South Africa, this species is generally found at lower altitudes compared to the other three species of the genus (Matthee and Robinson, 1996) and has the most geographically distant range from the Cradle of Humankind. Its presence, coupled with the absence of the other three species (*P. saundersiae, P. randensis,* and *P. crassicaudatus*) that could thrive in the favorable conditions at Cooper's D, is surprising. This pattern may reflect temporal changes in the life history traits of these species, including aspects of ecological structuration and dispersal abilities.

4.3. Mesomammals: an overlooked group in archaeological and palaeontological sites

Fossil mesomammals are often overlooked in taxonomic studies primarily due to methodological reasons. Due to their intermediate size, their remains are scattered between microfauna and macrofauna collections and are rarely considered by specialists in either group. However, large lagomorphs and rodents, such as red rock hares and springhares, are key agents in the food web and constitute prey for several avian and carnivore predators; they can also impact plant communities through their seed dispersal abilities and grazing or seed removal behaviour (e.g., Duthie and Robinson, 1990; Wilson et al., 2017, 2016), making them important for understanding and characterizing past environments. As a corollary, the limited attention given to these taxa results in a relatively small number of comparative specimens available in museum collections, as well as limited data about their anatomy, evolution, biology, and ecology. For this study, we encountered the challenge of accessing a complete osteological series to track the growth and anatomical development of *Pronolagus*. Unfortunately, the DNMNH zoological collection, which is the most comprehensive collection we have been able to examine, consists almost exclusively of adult individuals. Two questions remained that could only be clarified by studying a series of ontogenetic stages.

(1) It is known that the age of prey influences the characteristics of lagomorph accumulations produced by predators (Cochard, 2004a), particularly regarding the taphonomic modifications affecting the assemblage. The variability expressed in the frequency and degree of bone alterations according to the prey age complicates the identification of the potential predator(s) responsible for the accumulation. Only mesofaunal reference collections that include different stages of development can help tackle this issue.
(2) The consistently small size of the specimens found at Cooper's has two possible explanations: either all the individuals (MNI = 9) are juveniles, or the specimens perhaps belong to an extinct species or chrono-species smaller than the modern representatives. Only one young specimen of *P. rupestris* (DNMNH 42183) among the ten specimens examined in the DNMNH collections has craniometric measurements relatively close to those of the Cooper's D fossils. However, the postcranial skeletal elements of this specimen, which are used to determine the age of leporids, were not accessible. By looking at the epiphyseal sequence of the long bones from Cooper's D material, it appears that all age classes are represented; yet, even the bones with complete fusion of the epiphyses (i.e., supposedly adults) have smaller proportions than those of modern adult individuals. Therefore, the question of the identity of the *Pronolagus* from Cooper's D, identified in this study conservatively as *Pronolagus.* cf. *rupestris*, remains not fully resolved. Only a well-documented mesofaunal reference collection, comprising individuals of varied ages and sexes, will address those two issues in the future.

The present contribution demonstrates the significant potential of these taxa, whose study offers numerous insights from palaeontological, palaeoenvironmental, and biogeographical perspectives, among others. It also serves as an advocacy for better consideration of mesofauna in palaeontological studies. Completing the faunal inventory of a fossil site through the identification of medium-sized taxa significantly enhances our understanding of palaeobiodiversity. This can also have a significant impact on palaeoenvironmental reconstructions, especially when using methods based on the presence/absence of taxa (e.g. Linchamps et al.,

2023c) or taxon-free approaches that use body size distributions, such as the method of cenograms (e.g., Giberneau and Montuire, 1996).

CRediT authorship contribution statement

Pierre Linchamps: Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Raphaël Hanon:** Writing – review & editing, Methodology, Investigation. **Emmanuelle Stoetzel:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition. **Brigette Cohen:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Christine Steininger:** Writing – review & editing, Validation, Resources, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization.

Data availability

All data used in the analysis for this study are included in the manuscript and supplementary files.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quaint.2024.11.008.

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