

Mongoose Manor: Herpestidae remains from the Early Pleistocene Cooper's D locality in the Cradle of Humankind, Gauteng, South Africa

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Received 22 January 2018. Accepted 20 December 2018

Mongoose (Herpestidae) are an important component of African ecosystems, and a common constituent of southern African fossil assemblages. Despite this, mongoose fossils from the Cradle of Humankind, Gauteng, South Africa, have received relatively little interest. This paper presents the diverse mongoose craniodental assemblage from the early Pleistocene fossil locality Cooper's D. A total of 29 mongoose specimens from five genera were identified at Cooper's, including numerous first appearances in the Cradle or in South Africa. The exceptional mongoose assemblage at Cooper's likely reflects the effects of an unknown taphonomic process, although mongooses follow other carnivore groups in the Cradle in displaying an apparent preference for the southern part of the Cradle. This investigation shows the value of mongooses as palaeoecological indicators and supports previous interpretations of the environment at Cooper's as grassland with a strong woody component near a permanent water source.

Keywords: *Paranthropus* locality, palaeoecology, *Herpestes*, *Ichneumia*, *Atilax*, *Mungos*, *Galerella*.

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INTRODUCTION

Small carnivores have been recovered from many Quaternary fossil deposits; however, this group is in general poorly studied. Small carnivores in this context refers to members of the families Herpestidae (mongooses), Viverridae (civets) and Mustelidae (badgers, otters, weasels) with body mass less than 25 kg. In this publication, we present an assemblage of Herpestidae craniodental remains from the Cooper's D fossil locality in the Cradle of Humankind, Gauteng, South Africa (Fig. 1). The viverrids and mustelids from this site are published in O'Regan *et al.* (2013). Cooper's D has an unusually diverse mongoose assemblage, which sheds new light on their biochronology, as well as environmental conditions in the Cradle during the Early Pleistocene.

Mongooses are an important component of southern African ecosystems with at least 12 different species known from modern sub-Saharan Africa (Table 1; Skinner & Chimimba 2005). These species occur in a wide range of habitats including dry grassy plains, forests and marshy environments (Hinton & Dunn 1967). Mongooses are essentially omnivorous carnivores who typically feed on arthropods, small vertebrates and plant foods. They generally rest in cavities among tree roots or rocks, or in burrows (Hinton & Dunn 1967). Larger carnivores and birds of prey have been implicated as predators of

mongooses (Hinton & Dunn 1967), and these predators may be responsible for the inclusion of small mammal remains in fossiliferous cave settings. In recent years there has been new impetus in the study of these intriguing animals (e.g. Clutton-Brock *et al.* 2001; le Roux *et al.* 2008; Madden *et al.* 2009), as the ecology and habits of many of these species is not well understood. This lack of understanding is also seen in the past, as many taxa have sparse fossil records (Werdelin & Peigné 2010). Investigation into the mongoose assemblage from Cooper's thus has much potential for elucidating the biochronogeography and ecology of this family in southern Africa during the early Pleistocene.

Cooper's Cave is a fossil locality consisting of a series of karstic fossiliferous localities (designated A, B and D) in the dolomites of the Monte Christo Formation (Malmani Subgroup, Transvaal Supergroup). It is located approximately 1.5 km northeast of the Sterkfontein Caves and 1 km southwest of Kromdraai in the Cradle of Humankind World Heritage Site (Berger *et al.* 2003; de Ruiter *et al.* 2009) (Fig. 1). Work at Cooper's Cave has been concentrated on Cooper's D, where the richest fossiliferous deposits are located. Cooper's D consists of a long and narrow fissure with an east–west trend. The fissure is walled on either side by dolomite, the roof has eroded and the fissure is filled with calcified and decalcified sediments (de Ruiter *et al.* 2009; Val *et al.* 2014). There are two

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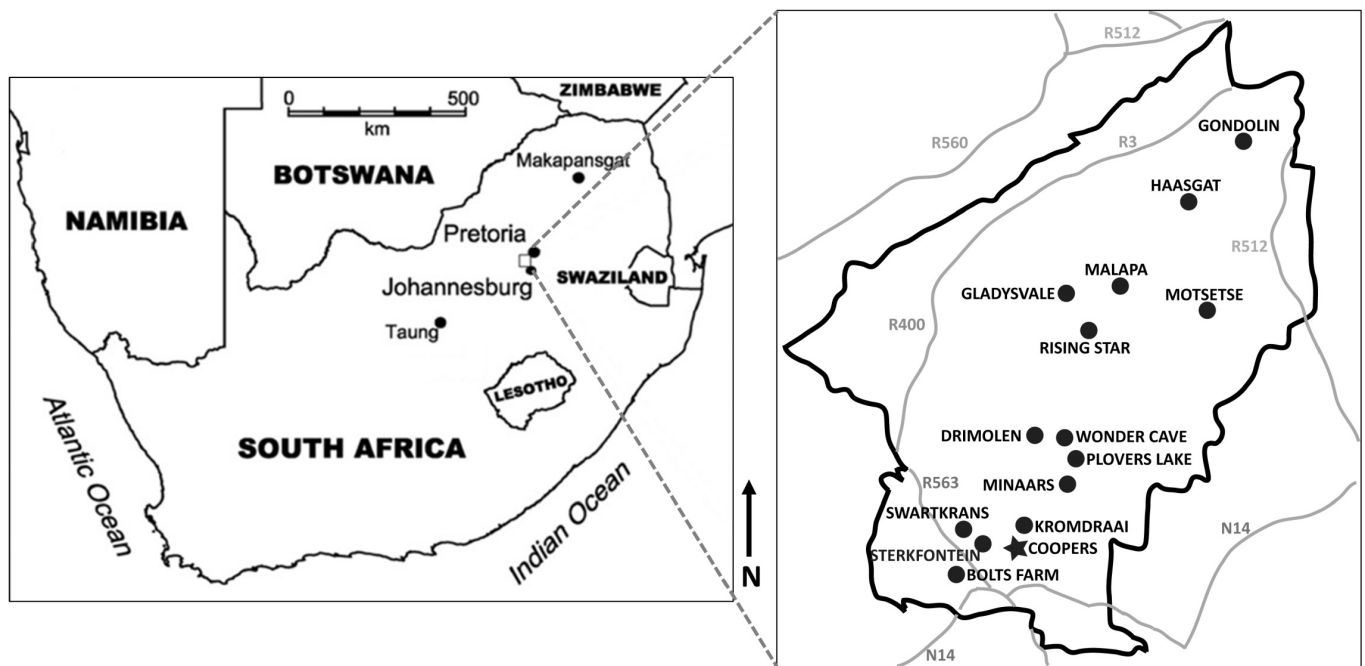


Figure 1. Location of Plio-Pleistocene fossil localities within the Cradle of Humankind and South Africa.

distinct but contemporaneous areas of fill (east and west fill respectively) within Cooper's D based on abundance of fossils, degree of sorting and type of clasts (de Ruiter *et al.* 2009). Remains from the east and west fills are here considered together as a single unit, following de Ruiter *et al.* (2009). Uranium-lead dating of flowstones in Cooper's D have identified that the majority of the fossils were deposited between 1.37 and 1.53 Ma (de Ruiter *et al.* 2009; Pickering *et al.* 2009). Excavations in Cooper's D were opened in 2001 and the site has produced hominin remains of the species *Paranthropus robustus* Broom, 1938 (Steininger *et al.* 2008). Cooper's D preserves large numbers of faunal remains including many bovids (Steininger 2011), a rich and diverse carnivore assemblage (Hartstone-Rose *et al.* 2007, 2010; O'Regan *et al.* 2013; O'Regan & Steininger 2017), suids (de Ruiter *et al.* 2009), microfauna (Vilakazi, 2014) and primates (Folinsbee & Reisz 2013; De Silva *et al.* 2013). Fossils from Cooper's D are well preserved, and this study provides the first description of the mongoose craniodental material from this site.

MATERIALS AND METHODS

The Cooper's D fossil material described here was collected during field seasons from 2001 through 2016 and are housed in the Bernard Price Collections of the Evolutionary Studies Institute (ESI), University of the Witwatersrand, Johannesburg. Sediments from the excavations were sieved with a 5, 3 and 1 mm mesh to optimize recovery. All specimens were identified using the modern and fossil comparative collections of the ESI and the Ditsong National Museum of Natural History, Pretoria. Comparisons with fossil taxa that were not available in these collections were undertaken with the aid of published literature (e.g. *Mungos dietrichi* in Petter (1987)). Craniodental measurements follow von den Driesch (1976) and all measurements were taken with digital callipers and are reported to 0.1 mm. A description of the measurements and abbreviations utilized here can be found in Table 2. Members of the family Herpestidae vary in size from species with a body mass of 0.2 kg to those with a mass of 5 kg (Table 1). For convenience, when

Table 1. Body size, habitat and size classes for extant Herpestidae species in southern Africa. Data collated from Skinner & Chimimba (2005).

Species name	Common name	Mean body mass (kg)	Size class	Habitat
<i>Helogale parvula</i>	Dwarf mongoose	0.2	Small	Savanna to open country
<i>Cynictis penicillata</i>	Yellow mongoose	0.6	Small	Semiarid, open country
<i>Suricata suricatta</i>	Suricate / meerkat	0.7	Small	Open, arid
<i>Galerella sanguinea</i>	Slender mongoose	0.5	Small	Catholic requirements
<i>Galerella pulverulenta</i>	Cape grey mongoose	0.6–0.9	Small-medium	Wide tolerance, associated with rocky areas
<i>Mungos mungo</i>	Banded mongoose	1.3	Medium	Wide tolerance, associated with riverine woodland
<i>Paracynictis selousi</i>	Selous' mongoose	1.7	Medium	Savanna to open
<i>Bdeogale crassicauda</i>	Bushy-tailed mongoose	1.5–1.9	Medium	Broken habitat and rocky areas
<i>Atilax paludinosus</i>	Marsh mongoose	3.0	Large	Associated with water with adjacent reed beds or semi-aquatic grass
<i>Herpestes ichneumon</i>	Large grey mongoose	3.1	Large	Riparian conditions, in savanna
<i>Rhyncogale melleri</i>	Meller's mongoose	2.3–3.0	Large	Savanna
<i>Ichneumia albicauda</i>	White-tailed mongoose	4.0–4.9	Large	Savanna woodland (well-watered)

Table 2. Abbreviations and measurements utilized in the text.

BFM	Breadth of foramen magnum
BL	Buccolingual
BOC	Breadth across occipital condyles
CD	Cooper's D
HFM	Height of foramen magnum
HM	Height of mandible behind m1
HP	Height of mandible between P ₂ and P ₃
HR	Height of mandibular ramus
Indet.	Indeterminate
JC	Sterkfontein Jacovec Cavern
KB	Kromdraai B
LC	Sterkfontein Lincoln Cave system
LPM	Length of premolar row
LMR	Length of molar row
LTR	Length of cheek tooth row
L/63	Sterkfontein post-Member 6 infill
Mb	Stratigraphic Member
Mb5E	Sterkfontein Member 5 East Oldowan infill
Mb5W	Sterkfontein Member 5 West Early Acheulean infill
MD	Mesiodistal

discussing mongoose species in this investigation we have separated the family into three arbitrary size classes, namely: small mongooses with a mass of less than 1 kg; medium species with mass between 1 kg and 2 kg; and large mongooses with a mass greater than 2 kg (Table 1). The mean body masses for mongooses given in Table 1 were estimated from Skinner & Chimimba (2005) and are used here only as a means to describe and differentiate within a large and diverse taxonomic group.

There has long been debate on the correct use of the genus *Galerella*, whether as a separate genus or as a subgenus within *Herpestes* (see Wozencraft 1993; Skinner & Chimimba 2005). We here follow Werdelin & Peigné (2010) who retain *Galerella* as a separate genus, despite evidence that suggests it does not constitute a monophyletic group (Veron *et al.* 2004). The fossil species *Atilax mesotes* Ewer, 1956a, *Crossarchus transvaalensis* Broom, 1937 and *Herpestes palaeoserengensis* Dietrich, 1942 are somewhat contentious in their attributions and we here define our usage of these taxa. *Atilax mesotes* was originally attributed to the genus *Herpestes* (Ewer 1956a); however, we follow subsequent researchers (Werdelin & Peigné 2010; Kuhn *et al.* 2011) who have transferred the species to *Atilax*, based on Ewer's (1956a) description of the species as being on the lineage to the modern marsh mongoose. *Crossarchus transvaalensis* is a rare species in the Cradle of Humankind. The original fossil was attributed to this genus as 'the teeth came nearer to that genus than any other Herpestine' (Broom 1937, 1939). Werdelin & Peigné (2010) note the absence of cusimanses mongooses (like *Crossarchus* spp.) in southern Africa today and suggest that the relationship of *C. transvaalensis* to this group is obscure; however, the lack of material makes improved attribution difficult. We thus continue to utilize *Crossarchus transvaalensis*. Dietrich (1942) first described the species *Mungos palaeoserengensis* from Laetoli. Petter (1963) later reassigned the species to genus *Herpestes* and later still to *Galerella palaeoserengensis* (Petter 1987). Attribution to *Galerella* was based primarily on cranial length and morphology of the tympanic bullae and Werdelin &

Peigné (2010) continued to follow this classification. However, most recently, Werdelin & Dehghani (2011) cite a number of features, especially of the dentition, in their attribution of the species back to *Herpestes palaeoserengensis*. We utilize this latter classification in this analysis.

RESULTS

Systematic Palaeontology

Order Carnivora Bowdich, 1821

Family Herpestidae Bonaparte, 1845

Genus *Herpestes* Illiger, 1811

Herpestes ichneumon (Linnaeus, 1758)

Material

CD5737, right maxillary fragment with canine, P¹ and P²; CD5725, right maxillary fragment with P² alveolus, and P³ and P⁴ (Fig. 2e,f); CD19130, isolated right P⁴; CD5933, isolated right M¹; CD5714, isolated occipital (Fig. 2i) with associated mandibular fossa.

Description

The maxillary fragments are relatively robust and were derived from a medium- to large-sized mongoose. In the fragment CD5725, the inferior point of the infraorbital foramen is situated above the middle of the P³ roots and the foramen then extends anteriorly in an oblique manner to a position anterior of the P³. The upper canine associated with specimen CD5737 is relatively long (Table 3 and Fig. 3A) and slightly curved and the lingual and labial faces are convex. The distal border is slightly carinate and there is an anterolingual crest that continues into a weak basal cingulum that is most strongly developed posteriorly. There is a small postcanine diastema in specimen CD5737. The P¹ is small, conical and single-rooted. The P², in specimens CD5737 and CD5725, both have three roots resulting in a triangular basal contour. The main cusp of specimen CD5737 is tall and situated centrally between the two buccal roots. The P² displays small basal cingula anteriorly, posteriorly and lingually and the latter cingulum is somewhat ridge-like. The P³ (CD5725) is larger than the P² and likewise displays three roots. The main cusp is high and centrally situated. The P³ displays small basal cingula anteriorly, posteriorly and lingually; however, the cingula in the P³ differs from those of the P², in being more prominent. The lingual root additionally bears a small cusp. The P⁴ preserved in specimens CD5725 and CD19130 has three roots (Fig. 3D). The protocone is conical and separated from the paracone by a deep carnassial notch. The protocone extends anteriorly of the parastyle. The paracone, which is the largest cusp, is transversely compressed. A mesiobuccal cingulum supports a small parastyle. The metastyle is trenchant and long, nearly the same length as the paracone. CD5933 preserves a slightly worn M¹. It has three roots and a triangular basal contour which is transversely elongated with a highly oblique buccal border. The protocone is the largest and tallest cusp. It is crescent-shaped with a rounded lingual

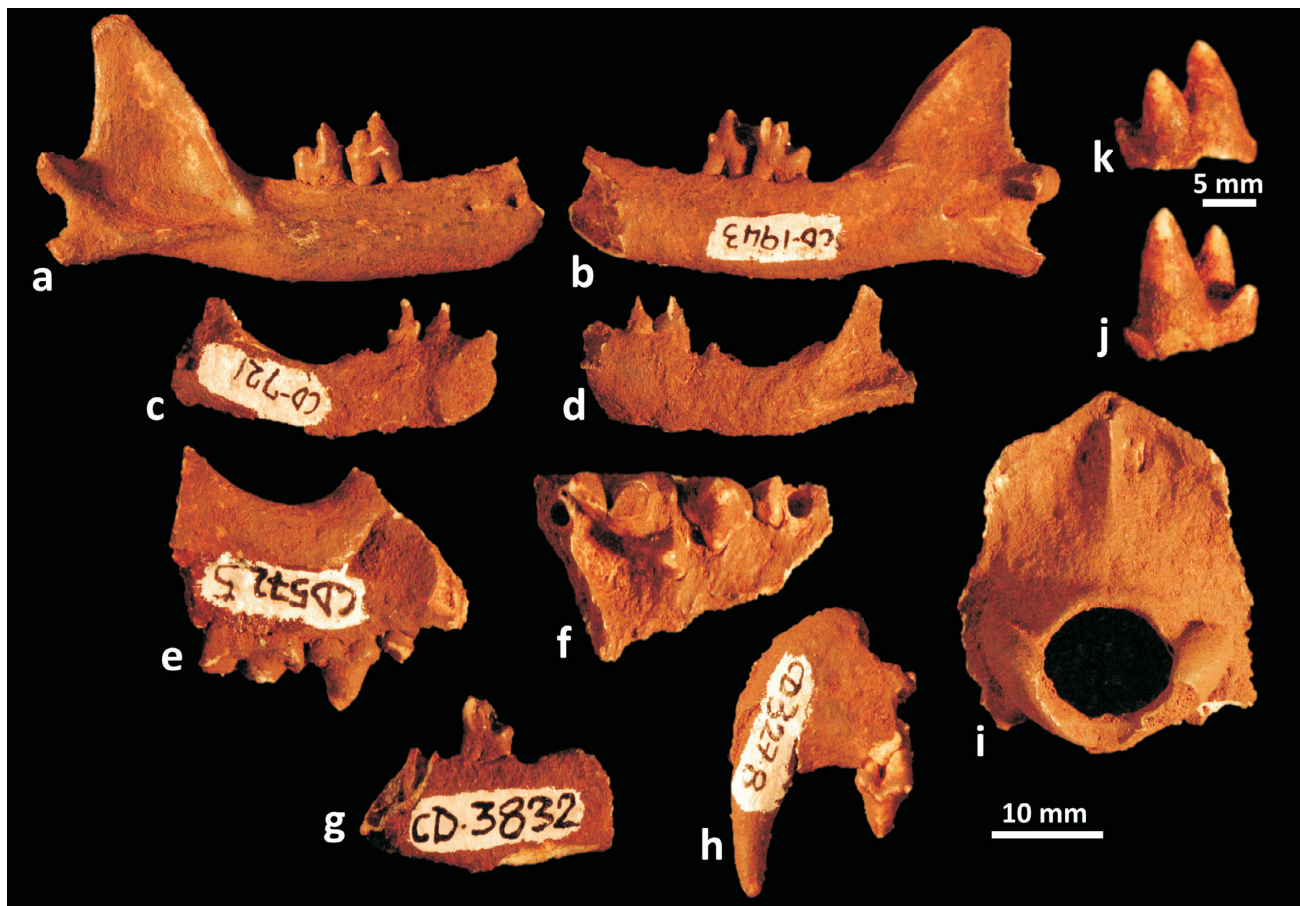


Figure 2. A selection of mongoosid fossils recovered from Cooper's D; (a) CD1943, right mandibular fragment in lingual view, *Mungos* sp.; (b) CD1943, right mandibular fragment in buccal view, *Mungos* sp.; (c) CD721, left mandibular fragment in buccal view, ?*Galerella* sp.; (d) CD721, left mandibular fragment in lingual view, ?*Galerella* sp.; (e) CD5725, right maxillary fragment in lingual view, *Herpestes ichneumon*; (f) CD5725, right maxillary fragment in occlusal view, *Herpestes ichneumon*; (g) CD3832, right mandibular fragment in buccal view, *Mungos* sp.; (h) CD3278, left maxillary fragment in lingual view, cf. *Ichneumia* sp.; (i) CD5714, isolated occipital in caudal view, *Herpestes ichneumon*; (j) CD21892, isolated right P4 crown in buccal view, *Mungos* aff. *dietrichi*; (k) CD21892, isolated right P4 crown in lingual view, *Mungos* aff. *dietrichi*.

base and is well separated from the remainder of the tooth. The paracone and metacone are smaller, similar in size and well separated from each other, and there is a parastyle anteriorly and a distinct metastylar lobe distobuccally.

The occipital fragment (CD5714) is consistent in size with a large-bodied mongoosid (as defined in Table 1) (Table 4 and Fig. 4); the foramen magnum and occipital condyles are preserved but the auditory bullae, normally highly diagnostic for species identification, were not preserved. The supraoccipital crest is well developed and highly pointed at the midline. The nuchal line is well developed superiorly but disappears before reaching the foramen magnum (Fig. 2i). The occipital condyles are bulbous and the lateral borders of the occipital display distinct pinching above the level of the foramen magnum.

Discussion

The material described above is consistent with *Herpestes ichneumon*, and can be separated from modern specimens of *Atilax paludinosus* Cuvier, 1829 by its smaller size, gracile canine structure and the presence of a P¹. The size of the dental remains of the Cooper's *Herpestes ichneumon* compares favourably with the two, similarly sized, modern species *H. ichneumon* and *Ichneumia albicauda* Cuvier, 1829 (Fig. 3). However, the material described can

be separated from *I. albicauda* in the structure of the P² and M¹. The lingual root and cusp of the P² of *I. albicauda* are situated much more posteriorly, almost in line with the distal cingulum. In addition, the M¹ of *I. albicauda* is robust, with high cusps and lacks the strong metastylar lobe observed in CD5933 (Fig. 3E). Metrics of the occipital portion of specimen CD5714 are within the lower range of variation for modern *H. ichneumon* (Table 4, Fig. 4). The Cooper's *H. ichneumon* can also be differentiated from extinct mongoosid species. For example, *H. palaeoserengensis* differs from the Cooper's material in the structure of the P² and P³, and its smaller size (Fig. 3B,C). The P² and P³ of *H. palaeoserengensis* are only double rooted and the P³ lacks a lingual cingulum. The Cooper's material is larger than dental remains of *C. transvaalensis* and is less robust in all characteristics than dental remains of *A. mesotes*. In summary, the Cooper's material is morphologically indistinguishable from modern *H. ichneumon* specimens

Genus *Ichneumia* G. Cuvier, 1829

cf. *Ichneumia* sp.

Material

CD3278, left maxillary fragment with canine, P¹ alveolus, and P² (Fig. 2h).

Table 3 (continued)

	C ¹		P ²		P ³		P ⁴		M ¹		C ₁		P ₂		P ₃		P ₄		M ₁		
	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	
Indet. Herpestidae	3.2	2.4																			
Indet. Herpestidae	3.9	2.9																			
Indet. Herpestidae	4.0	3.0																			
Indet. Herpestidae	3.3	2.4										2.7	2.0								
Indet. Herpestidae												4.5	3.7								
Indet. Herpestidae																					
<i>Suricata major</i> (Hendey 1974a)					5.9	4.5	7.0	7.5	8.1	4.5	4.5	4.9	3.1	5.1	3.3	6.5	4.3	6.2	4.5		
<i>Cynictis penicillata brachyodon</i> (Ewer 1956b)							4.7	4.6	6.8	3.7	3.4	3.9	2.8	1.9	4.5	2.3	5.0	3.1			
<i>Hologale palaeogractilis</i> (Petter 1987)	2.6	1.9	2.9	1.5	3.5	2.2	5.0	3.7	4.6	2.5	2.7	2.0	1.8	1.6	3.1	1.6	3.6	-	4.5	2.4	

Description

This specimen is similar in size (Table 3, Fig. 3A,B) to the maxillary fragment of *H. ichneumon* described above (CD5737) but differs in a number of important characteristics. The canine is long, relatively slender and tapers to a point. The lingual face is flattened, the buccal face convex. The distal border is slightly carinate and there is an anterolingual crest that continues into a minor basal cingulum that is most strongly developed posteriorly. There is a short postcanine diastema. A P¹ alveolus is present, and there is a slightly larger gap between the P¹ and P² in this specimen, than in CD5737. The P² is double rooted and narrow. Inspection of the posterior root showed this root to be much larger than the anterior root and it appeared that this may be the result of the lingual and posterior roots merging. The apex of the main cusp is centrally placed. There are small basal cingula positioned anteriorly and posteriorly and the distal border is carinate. There is no lingual cusp or cingulum but the P² widens distally.

Discussion

The P² of modern *I. albicauda* specimens displayed the same tooth root structure as the P² of CD3278. In addition, the metrics of CD3278 fall within the lower range of variation in modern *I. albicauda* (Table 3, Fig. 3A,B). The double-rooted nature of the P² in specimen CD3278 also separates it from modern and fossil *H. ichneumon*. The fossil species *H. palaeoserengensis* and *A. mesotes* have similar P² root structure as CD3278; however, both extinct taxa can be differentiated from CD3278, as the P² of *H. palaeoserengensis* lacks accessory cusps and the apex of the main cusp was situated slightly posteriorly of the midline. In addition, the dentition of *H. palaeoserengensis* was smaller than the dentition of CD3278, while the teeth of *A. mesotes* are larger and more robust than the Cooper's specimen.

Genus *Atilax* F. Cuvier, 1826

Atilax paludinosus G. Cuvier, 1829

Material

CD8840, isolated right lower canine; CD9119, isolated partial left P³; CD7329, right edentulous maxillary fragment from alveoli of canine to the anterior root of P³.

Description

The lower canine (CD8840) is robust and strongly recurved (Table 3, Fig. 5A). The distal border is carinate and there is a lingual crest that continues into a weak basal cingulum extending to the distal border. There is also a very weak crest that extends from the tip of the canine along the distobuccal face. The partial P³ from specimen CD9119 is large and highly robust (Fig. 3F). It includes the mesial half of the main cusp and the anterior root. There is a distinct cingulum arising from the buccal side of the tooth and enclosing the entire anterior half of the main cusp. The anterior border of the main cusp is carinate and there is a minute cusp at the point where the anterior

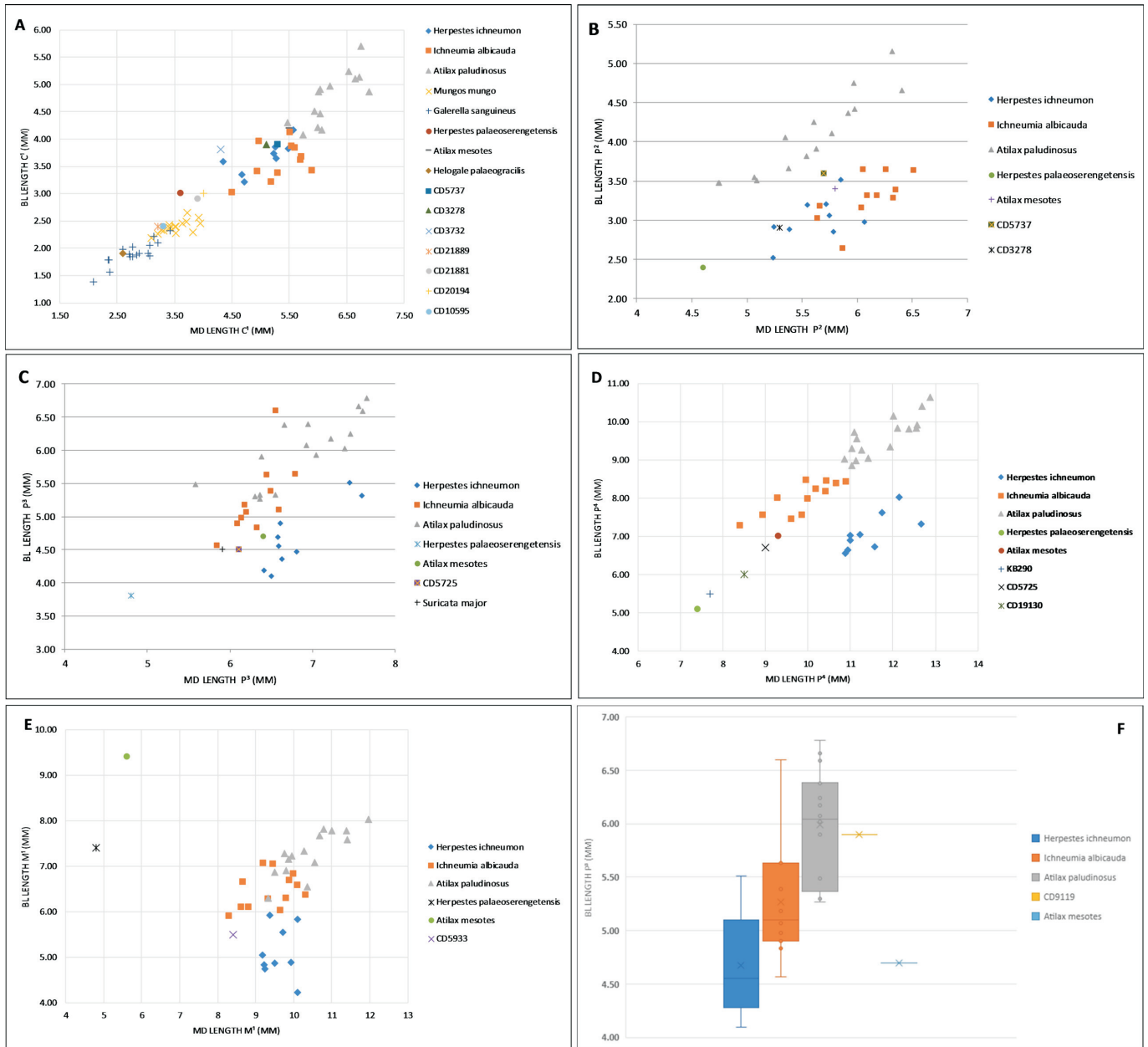


Figure 3. Biplots of dental measurements (mm) on modern and fossil mongooses; (A) MD and BL length of C¹; (B) MD and BL length of P²; (c) MD and BL length of P³, (D) MD and BL length of P⁴; (E) MD and BL length of M¹; (F) BL Length of P³.

border joins the cingulum. Due to the incomplete nature of specimen CD9119 only the BL length could be accurately measured (Fig. 3F). The maxillary fragment (CD7329) is large and robust, greater in size than specimens CD5737 and CD5725 (both *H. ichneumon*) and specimen CD3278 (*I. albicauda*) already described (Table 3, Fig. 3A,B). The canine alveolus is substantial, suggesting a large canine tooth had been present. There is no postcanine diastema and the P¹ is absent. The P² and P³ are crowded closely together. The palatal foramen occurs midway between the two roots of the P².

Discussion

The robusticity of the dentition and maxilla of specimens CD 8840, CD9119, and CD7329 is characteristic of the species *A. paludinosus* or *A. mesotes*. However, the dental metrics of the Cooper’s material are closer to the mean for *A. paludinosus* than *A. mesotes* (Table 3, Fig. 3F and

Fig. 5A), and the latter species differs from the Cooper’s material in the structure of the lower canine and the P³. *Atilax mesotes* is known from a small number of specimens and the range of variation for this species is not yet well understood; however, we feel confident attributing this material to the modern species based on the structural differences observed between *A. mesotes* and the Cooper’s material. The lower canine of *A. mesotes* has a better developed distal cingulum and lacks the lingual cingulum observed in CD8840, while the P³ of *A. mesotes* lacks the strongly carinate anterior border and slight cusp on the cingulum present in CD9119. The absence of the P¹ in specimen CD7329 may indicate affinity with *A. paludinosus*, but there is variability in this feature. For example, Rosevear (1974: 295), found in a study in West Africa, that 11 out of 26 *A. paludinosus* specimens retained the P¹, but that they were absent in ‘nearly all southern and eastern African specimens’. Ewer (1956a) also found that southern

Table 4. Measurements (in mm) of crania and mandibles for modern and fossil mongoose species including the Cooper's D mongooses. All measurements by B.C. unless stated otherwise stated, see Table 2 for explanation of abbreviations.

		Cranial			Mandible					
		BFM	HFM	BOC	LPM	LMR	LTR	HP	HM	HR
<i>Herpestes ichneumon</i>	CD5714	Mean	11.0	20.5						
<i>Herpestes ichneumon</i>	(n = 8)	Range	11.6–14.7	20.7–25.0						
<i>Ichneumia albicauda</i>		Mean	13.7	9.5						
<i>Ichneumia albicauda</i>	(n = 11)	Range	12.8–14.5	8.4–10.7						
<i>Atilax paludinosus</i>		Mean	14.0	10.0						
<i>Atilax paludinosus</i>	(n = 14)	Range	12.4–14.8	9.3–10.7						
Mandible										
<i>Mungos mungo</i>		Mean	13.3	9.0	22.4	7.3	8.1	19.9		
<i>Mungos mungo</i>	(n = 15)	Range	12.9–13.9	8.1–9.5	21.2–23.3	6.7–8.8	7.1–9.2	18.5–21.7		
<i>Mungos</i> sp.	CD1943		12.0	8.7	20.6	7.4	7.7	19.8		
<i>Mungos</i> sp.	CD3832			7.2			7.4			
<i>Mungo dietrichi</i>					24.9		8.1			
<i>Mungo dietrichi</i>	(Petter 1963, 1987)									
<i>Galerella sanguinea</i>		Mean	11.4	7.6	19.0		6.5	18.1		
<i>Galerella sanguinea</i>	(n = 17)	Range	9.8–12.5	6.9–8.3	17.7–20.6		5.2–7.9	14.9–21.0		
? <i>Galerella</i> sp.	CD721		10.5	8.7	19.1	7.2	5.9			
? <i>Galerella</i> sp.	CD8315					5.2				
? <i>Galerella</i> sp.	CD3290					5.6				
<i>Herpestes palaeoserengensis</i>			16.0		21.5					
<i>Herpestes palaeoserengensis</i>	(Petter 1987)									
<i>Helogale palaeogracilis</i>			10.2		15.6					
<i>Helogale palaeogracilis</i>	(Petter 1987)									

African *A. paludinosus* specimens lack the P¹; however, our examination of the material in the Ditsong Museum found one specimen from a sample of 17 that retained a P¹. Therefore, the presence or absence of a P¹ cannot be con-

sidered a reliably diagnostic feature; however, given that the majority of *A. paludinosus* specimens lack a P¹ and the other morphological similarities, the Cooper's material is here attributed to *A. paludinosus*.

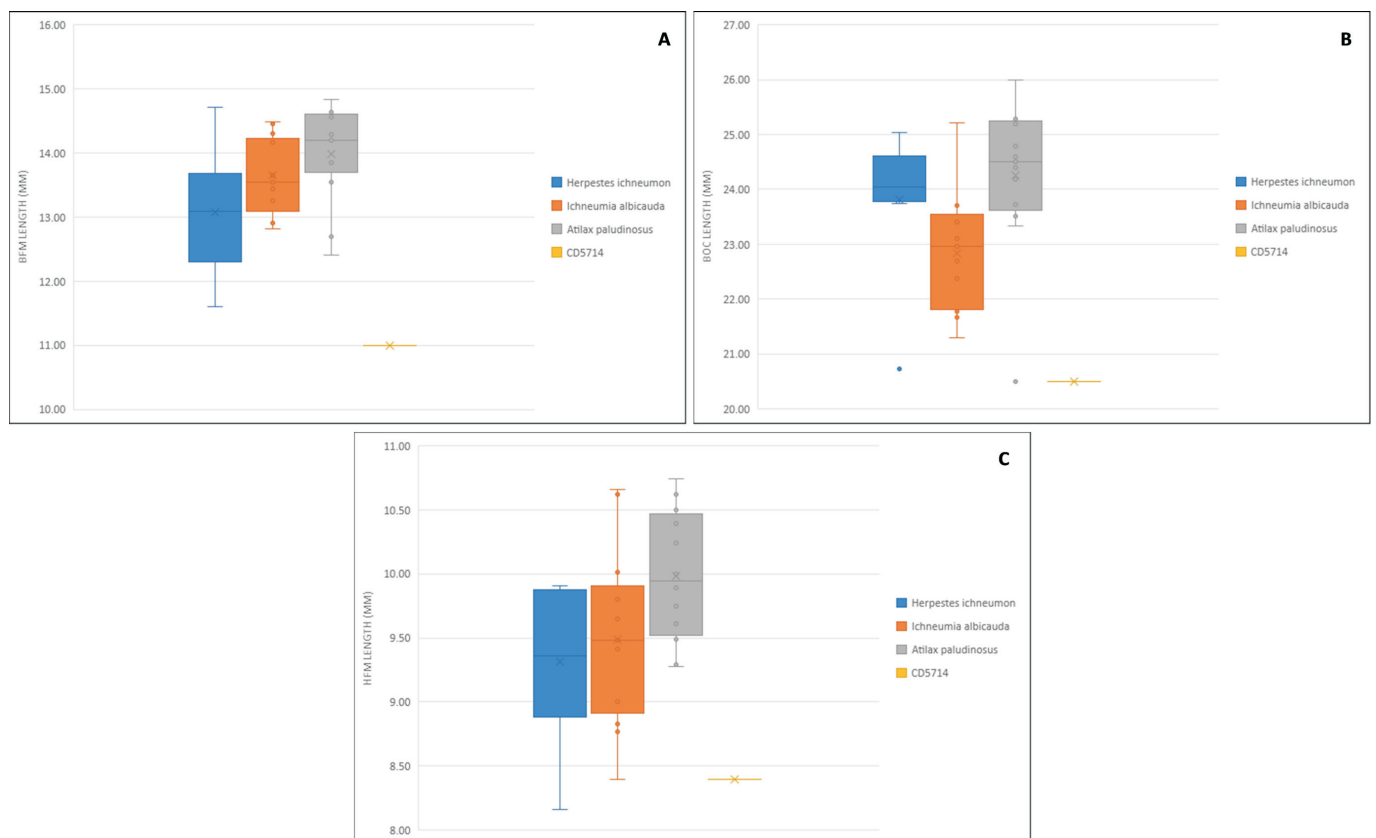


Figure 4. Plots of cranial measurements (mm) on modern and fossil mongooses; (A) breadth across the foramen magnum; (B) breadth across of occipital condyles; (C) height of the foramen magnum.

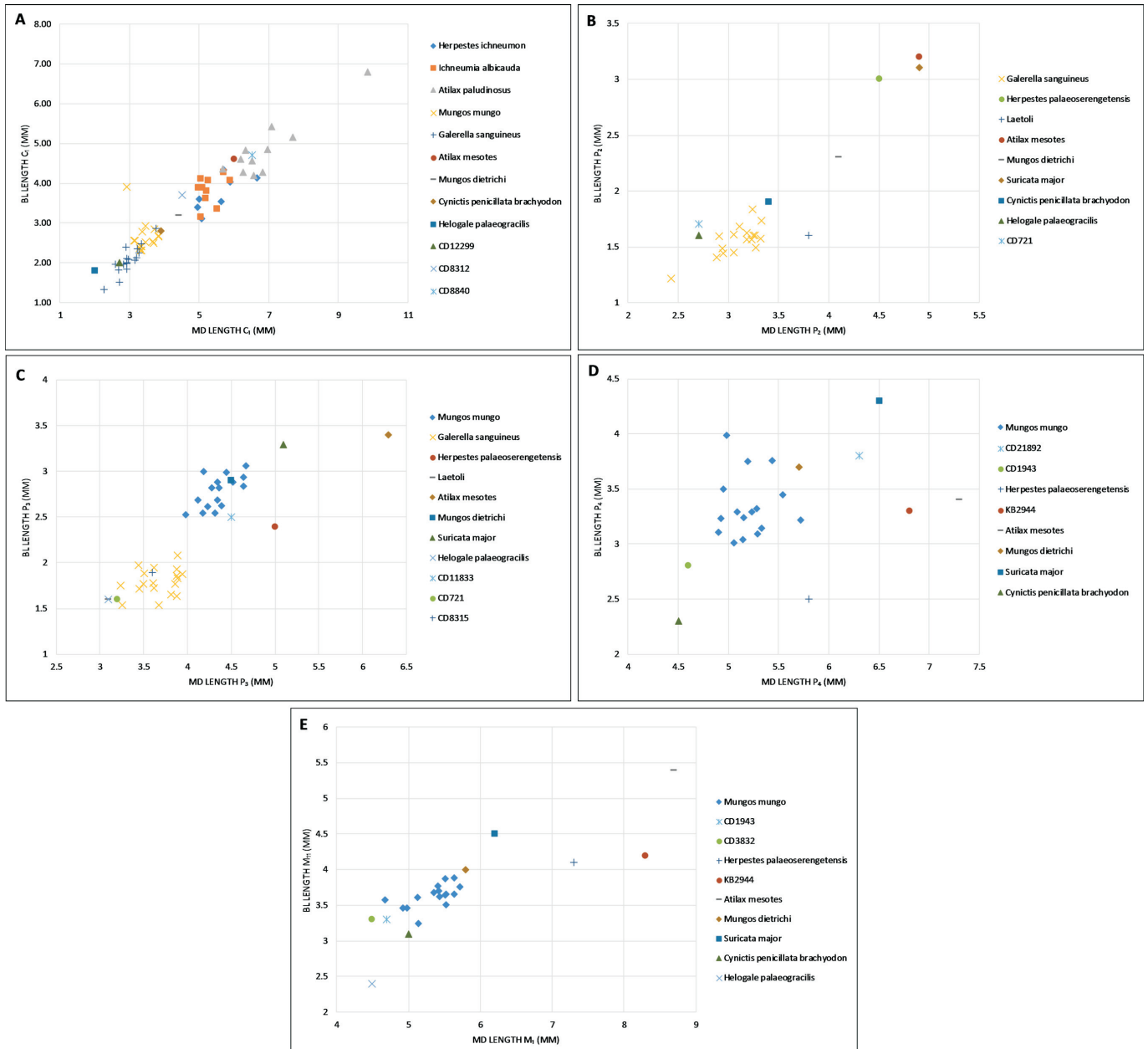


Figure 5. Biplots of dental measurements (mm) on modern and fossil mongooses; (A) MD and BL length of C₁; (B) MD and BL length of P₂; (C) MD and BL length of P₃; (D) MD and BL length of P₄; (E) MD and BL length of M₁.

Genus *Mungos* E. Geoffroy Saint-Hilaire & F. Cuvier, 1795

Mungos* aff. *dietrichi Petter, 1963

Material

CD21892, isolated right P₄ crown (Fig. 2k,j).

Description

The P₄ has a quadrangular, almost trapezoidal, basal contour. The main cusp is tall, conical and anteriorly situated and there is a well separated and large posterior accessory cusp placed buccally on the distal border of the main cusp. The distolingual cingulum is bordered by a distinct hypoconid. There is a minute anterior cusp, and the apex of the main cusp of the P₄ is positioned over the anterior root. The posterior accessory cusp is high, well separated from the main cusp, and positioned buccally along the posterior margin of the main cusp.

Discussion

This specimen is substantially larger than CD1943 (*Mungos* sp. described below) (Fig. 5D). The P₄ morphology of specimen CD21892 differs from CD1943 and modern *Cynictis penicillata* Cuvier, 1829, *Suricata suricatta* von Schreber, 1776 and *Mungos mungo* Gmelin, 1788 in the highly reduced anterior accessory cusp. A minute anterior cusp, such as observed in specimen CD21892, is a characteristic observed in *M. dietrichi* Petter, 1963. The accessory cusp was not observed in any of the modern *M. mungo* ($n = 16$) specimens observed in this analysis, which were collected from several populations across southern Africa. CD21892 has a similar buccolingual length to *M. dietrichi* but the mesiodistal length is much greater and *M. dietrichi* has a more rectangular basal contour. On the other hand, the mesiodistal length of this specimen is most similar to *Suricata major* Hendey, 1974, yet this species lacks an anterior accessory cusp. Although this

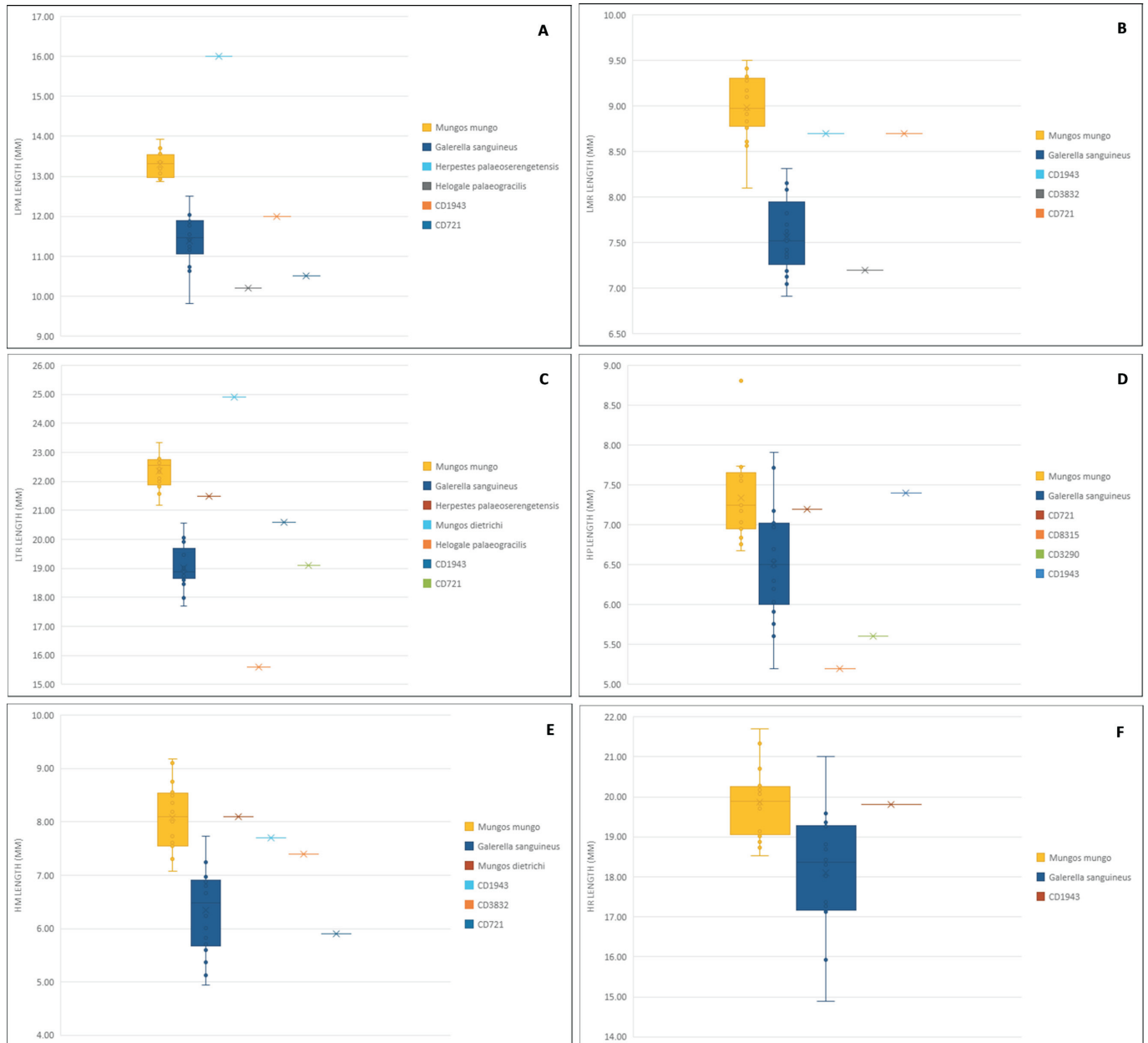


Figure 6. Plots of mandibular measurements (mm) on modern and fossil mongooses; (A) length of the premolar row; (B) length of the molar row; (C) length of the cheek tooth row; (D) height of the mandible between P_2 and P_3 ; (E) height of the mandible behind M_1 ; (F) height of the ramus.

material is insufficient for a definitive identification, the P_4 morphology has greatest affinity with the fossil species *M. dietrichi*.

Mungos sp.

Material

CD1943, right mandibular fragment from P_2 alveolus to ramus, with P_4 and M_1 present (Fig. 2a,b); CD3832, right mandibular fragment from P_4 alveolus – M_2 with M_1 present (Fig. 2g); CD11833, isolated right P_3 .

Description

The mandible (specimen CD1943) is relatively gracile and shallow with a flattened ventral border. The anterior mental foramen is located mesial of the P_2 , while the posterior mental foramen is situated below the posterior root of the P_2 . The coronoid is tall relative to the tooth row, and

there is a small retromolar space. The masseteric fossa, located posteriorly to the M_2 alveolus, is deep and anteriorly wide. The angular process is robust and displays a slight eversion. The tip of the angular process is absent; however, the size of the remaining portion indicates that it extended beyond the articular condyle. The P_1 is absent and there is a small postcanine diastema. The apex of the main cusp of the P_4 is positioned over the anterior root. The posterior accessory cusp is high, well separated from the main cusp, and positioned buccally along the posterior margin of the main cusp. The P_4 displays a small but distinct anterior accessory cusp and a substantial distolingual cingulum. The P_3 specimen (CD11833) has an oval basal contour. The main cusp is situated over the anterior root and has a concave distal border. There is a minute anterior accessory cusp and a posterior cingulum on the P_3 . The M_1 (seen in specimens CD1943 and CD3832) has a sub-rectangular basal contour, and the large protoconid

is distally orientated. The paraconid and metaconid are lingual and the latter is small and not well separated, occurring on the distal border of the paraconid. The trigonid cusps are clustered together and the quadrangular talonid is roughly equal in length to the trigonid. The distal border of the talonid displays two distinct cusps, well separated from the paraconid and metaconid.

Discussion

The morphology of the Cooper's material compares most favourably with modern *M. mungo*. It differs from the genera *Galerella* Grey, 1865, *Herpestes* and *Genetta* Cuvier, 1816 by the low degree of shear in the dentition. The M_1 of specimens CD1943 and CD3832 differ from the M_1 of *C. penicillata* and *S. suricatta* in the degree of separation of the metaconid and paraconid. Additionally, the rami in these species are short, compared to the ramus of specimen CD1943 (Fig. 6F). Specimen CD11833 is indistinguishable from the P_3 of modern *M. mungo*. Specimens CD1943 and CD3832, despite their strong resemblance to *M. mungo*, fall within the lower size range for this species (Table 3, Fig. 5E). Compared to extinct mongoose fossils, the P_3 of specimen CD11833 is similar in size and morphology to the fossil species *M. dietrichi* (Fig. 5C). However, the mandible in *M. dietrichi* differs in a number of characteristics from specimen CD1943. *Mungos dietrichi* lacks a retromolar space and the ventral border is slightly convex. The P_4 of specimen CD1943 is similar in structure to *M. dietrichi*, but the posterior cingulum is more pronounced in CD1943. The arrangement and relative size of the trigonid cusps of the M_1 in specimen CD1943 differs subtly from *M. dietrichi*, and the distal border of the M_1 talonid in *M. dietrichi* lacks the accessory cusps observed in CD1943. Finally, the P_4 and M_1 in the Cooper's material is smaller than specimens from *M. dietrichi*. Morphologically the Cooper's material most closely resembles the modern genus *Mungos*; however, numerous morphological differences separate it from the modern species and from extinct members of the genus. It is unclear at this stage whether this material represents a new species, and we have thus left the diagnosis as *Mungos* sp., pending further discoveries. While the material from the genus *Mungos* described in this paper precludes definitive diagnosis, the morphological variation (particularly between specimens CD21892 and CD1943) is substantial and they are considered here different enough to warrant attribution to different taxa.

Genus ?*Galerella* sp. Gray, 1865

Material

CD721, left mandible fragment extending from distal portion of canine alveolus to posterior of M_2 alveolus with P_2 and P_3 still *in situ* (Fig. 2c,d); CD8315, right mandible fragment with P_3 and the P_4 alveolus; CD3290, right edentulous mandible fragment extending from M_1 alveolus to angular process, missing the ramus.

Description

Both mandible fragments are gracile and shallow

(Fig. 6). The mandibular symphysis of specimen CD721 extends to below the P_2 . There is no P_1 and a small postcanine diastema is visible. The posterior mental foramen is situated below the anterior root of the P_3 , and the ventral border of the mandible appears flat. The masseteric fossa is anteriorly wide and opens below the M_2 , and there is no retromolar space. The angular process in specimen CD3290 is robust, rounded and shorter than the articular condyle. The P_2 and P_3 (specimens CD721 and CD8315) display high cusps, resulting in a sharp appearance to the dentition. In both the P_2 and P_3 the main cusp is situated over the anterior root and a posterior cingulum is present. On the P_3 (CD721) there is an anterior cingulum and a substantial distobuccal accessory cusp. The P_2 , on the other hand, lacks the anterior cingulum and displays a minute posterior cusp on the buccal side. The distal face of the P_2 is concave, while the distal face of P_3 is convex. The depth of the mandible in CD8315 and CD3290 is smaller than CD721, but otherwise these specimens are very similar in their morphology.

Discussion

The small size and degree of shear in the dentition indicate an affinity with genus *Galerella*; additionally, the Cooper's specimens are similar in size to the modern species *Galerella sanguinea* Rüppel, 1836 (Fig. 5B,C, Fig. 6). *Galerella* species may be differentiated from other small mongooses (*C. penicillata*, *S. suricatta* and *M. mungo*) by the extension of the mandibular symphysis below the P_2 and the presence of a retromolar space; characteristics also observable in the Cooper's specimens. The presence of a posterior accessory cusp in the P_3 of the Cooper's material separates it from modern specimens of *C. penicillata* and *M. mungo* and aligns the material with genus *Galerella*. Similarly, *S. suricatta* can be ruled out, as the P_2 of this species displays an anterior cingulum not observed in the Cooper's material.

The Cooper's material is smaller than fossil remains of *Herpestes* sp. from Swartkrans, *Galerella pulverulenta* Wagner, 1839 from Sea Harvest and *Galerella* sp. from Laetoli (Werdelin & Dehghani 2011). The Cooper's D remains described above are, however, similar in size to *Helogale palaeogracilis* Dietrich, 1942 from Laetoli (Petter 1987). The *Galerella* sp. from Laetoli differs from the Cooper's material in the structure of the P_3 , which displays additional posterior cusps. Similarly, *H. palaeogracilis* can be separated from the Cooper's material by the appearance of an anterior cingulum on the P_2 . Overall, the Cooper's material shows many characteristics of genus *Galerella*, but the state of preservation precludes a more definite identification.

Herpestidae gen. et sp. indet. (large)

Material

CD5989, fragmented neurocranial remains and isolated complete upper incisor tooth row with right I^1 – I^3 present; CD7328, isolated upper incisor; CD7307, right premaxilla with I^3 – I^2 and the mesial portion of the canine alveolus.

Description and discussion

Specimens CD 5989 and CD 7307 (premaxillae) are consistent in size with a large mongoose species such as *Atilax paludinosus* or *Herpestes ichneumon* (Table 1) and compare favourably with each other. The approximate size of CD5989 from right I³ to left I³ is 9.7 mm. The incisor tooth row is slightly curved and the I³ is slightly larger than the neighbouring incisors. However, there is no gap between I³ and I². The isolated incisor (CD7328) is of a comparable size to the I³ from specimens CD5989 and CD7307. The Cooper's material is likely to originate from one of the larger mongoose species, like *G. sanguineas*, or *I. albicauda* already described, but not enough material is preserved to make a more accurate diagnosis.

Herpestidae gen. et sp. indet. (small)

Material

CD3282, right mandible with alveoli P₂–M₁, and associated isolated right P₄.

Description

The mandible is small with a straight ventral border and a stepped profile immediately posterior to the symphysis, which extended below the P₂. The anterior mental foramen is situated below the distal root of P₂, while the posterior mental foramen is situated below the distal root of the P₃. The apex of the main cusp of the P₄ is situated over the mesial root. There is a distal accessory cusp, somewhat buccally situated on the posterior face of the main cusp and a small basal 'cusplet' located mesially. The substantial distal cingulum extends slightly onto the lingual and buccal faces of the tooth.

Discussion

This material shares characteristics with, but cannot be definitively linked to, a number of species. The P₄ is similar in size to modern *C. penicillata* and to the Cooper's *Mungos* sp. (CD1943) described above. However, CD3282 has a shallower and less robust mandible than CD1943 (Table 4, Fig. 6) and the distal cingulum of the P₄ was more extensive. Modern *C. penicillata* display a stepped mandible similar to specimen CD3282; however, the P₄ is more robust in the modern species. The P₄ structure is most similar, especially in respect of the extensive distal cingulum to *S. suricatta*. Thus, on the basis of the present data it is not possible to identify the material to the generic level.

Indeterminate Herpestidae

Material

CD7335, left edentulous mandible with alveoli of P₂–M₁; CD 3280, anterior left and right hemi-mandibles with left and right P₁ and left P₂; CD3732, CD21889, CD20194, CD10595 isolated upper left canines; CD21881, upper right canine; CD12299, CD8312 isolated lower right canines.

Description and Discussion

CD7335 is a small and gracile mandible with a flat

ventral border. The symphysis extends below the P₂, but there are no other diagnostic characteristics. CD3280 is a small and highly gracile mandible showing partially erupted dentition. The P₃ is slender, with the main cusp situated over the anterior root. There is a small, buccally situated posterior accessory cusp, a minute anterior accessory cusp and a distal cingulum which is bordered posteriorly by a small accessory cusp. Without doubt this material originates from a juvenile mongoose; however, due to its fragmentary nature it is not possible to identify the genus.

Upper canines in the mongooses have very similar morphology among species. All the specimens described here (CD3732, CD21889, CD20194, CD10595, CD21881) are slightly curved and tapered to a point, with a flattened lingual face and a convex buccal face. The distal border is weakly carinate and there is a minute mesiolingual crest, which in some cases extends into a weak basal cingulum. The size of these specimens is given in Table 3. Specimen CD12299 is a minute, strongly recurved, lower canine. The lingual face is flattened and the buccal face convex. The posterior border is carinate and there is a well developed lingual cingulum. Specimen CD12299 is smaller than the canines observed in the smallest modern mongoose species, *Helogale parvula* Sundevall, 1847 (Fig. 5A). Specimen CD8312 is a large lower canine broken just above the alveolus. Due to the lack of diagnostic characteristics in canines of modern mongooses and the extensive overlap in the size range of canines, it is not possible to identify this material below the family level.

DISCUSSION

The Cooper's D fossil deposit has produced a diverse herpestid assemblage, with at least five genera identified from 29 craniodental specimens. The cave deposits of the Cradle of Humankind in the Witwatersrand valley have provided extensive fossil collections for Plio-Pleistocene South Africa; however, the Herpestidae assemblages from many of these localities are small or poorly studied. As yet, no mongooses have been recovered from the fossil sites Gondolin, Haasgat, Gladysvale, Bolt's Farm, Rising Star or Motsetse (Lacruz *et al.* 2003; Berger & Lacruz 2003; Adams *et al.* 2007; Adams 2010, 2012; Gommery *et al.* 2012; Dirks *et al.* 2015). Malapa and Drimolen preserve only a small number of herpestids, both in terms of genera identified (two) and total number of specimens (NISP 5 and 4, respectively; Table 5) (O'Regan & Menter 2009; Kuhn *et al.* 2011; Adams *et al.* 2016). Cooper's D resembles Sterkfontein, Swartkrans and Kromdraai in preserving a high diversity of mongooses (four to five genera each). The abundance of mongoose material at Cooper's D (NISP 29) likewise resembles Swartkrans (NISP 45) and Kromdraai (NISP 12); unfortunately equivalent data from Sterkfontein are not available (Watson 2004; Reynolds & Kibii 2011; Fourvel *et al.* 2016; Fourvel *et al.* 2018). It can be very difficult to separate out small or fragmentary mongoose remains from those of other small carnivores (Mustelidae and Viverridae), and in earlier papers Herpestidae was previously thought to be part of Viverridae and the groups were analysed together. Thus, the indeterminate

Table 5. Mongoose fossils from the Cradle of Humankind, Gauteng, South Africa, including Cooper's D.

Fossil locality	Stratigraphic Member	Species	NISP	MNI	References
Malapa		<i>Atilax cf. mesotes</i>	1	1	Kuhn <i>et al.</i> 2011
		<i>cf. Herpestidae</i>	4		
Drimolen		<i>aff. Suricata suricatta</i>	1	1	O'Regan & Menter (2009) Adams <i>et al.</i> (2016)
		<i>cf. Cynictis penicillata</i>	3	1	
Swartkrans	Mb 2, 3	<i>Atilax sp.</i>	4	2	Watson (2004)
	Mb 2, 3	<i>Cynictis penicillata</i>	5	2	de Ruiter <i>et al.</i> 2003
	Mb 1	<i>Herpestes ichneumon</i>	2	1	de Ruiter <i>et al.</i> 2003
	Mb 2	<i>Galerella sanguinea</i>			
	Mb 2, 3, 5	<i>Suricata suricatta</i>	10	8	
	Mb 1	<i>Suricata sp.</i>	1	1	de Ruiter <i>et al.</i> 2003
	Mb 1, 3, 5	<i>Herpestidae</i> indet.	24		
Sterkfontein	Mb5E, Mb5W	<i>cf. Mungos sp.</i>			Reynolds & Kibii (2011)
	Stw53, Mb5E, Mb5W, L/63, LC	<i>Suricata sp.</i>			
	L/63	<i>Herpestes ichneumon</i>			
	Mb5E	<i>Herpestes</i> indet.			
	JC	<i>Cynictis penicillata</i>			
Kromdraai	KA	? <i>Crossarchus transvaalensis</i>	1	1	Brain 1981; Broom 1937, 1939
	KA	<i>Atilax mesotes</i>	1	1	Ewer (1956a); Brain(1981)
	KB	<i>Galerella cf. sanguinea</i>			Hendey (1973); Fourvel <i>et al.</i> (2016)
	KB	<i>Herpestes sp.</i>	1	1	Braga & Thackeray (2016)
	KB	<i>Viverridae/Herpestidae</i> indet.	9		Fourvel <i>et al.</i> (2016)
Cooper's		<i>Herpestes ichneumon</i>	5	5	This publication
		<i>cf. Ichneumia sp.</i>	1	1	
		<i>Atilax paludinosus</i>	3	1	
		<i>Mungos aff. dietrichi</i>	1	1	
		<i>Mungos sp.</i>	3	1	
		? <i>Galerella sp.</i>	3	2	
		<i>Herpestidae</i> indet. (large)	3		
		<i>Herpestidae</i> indet. (small)	1		
	Indeterminate <i>Herpestidae</i>	9			

specimens from sites like Kromdraai are often characterized as *Viverridae/Herpestidae* indet. and may contain remains from both families. Reynolds (2010) observed a similar pattern in the large carnivores, where Cooper's D, Kromdraai, Swartkrans and Sterkfontein preserved more diverse large carnivore assemblages than other Cradle sites. There is a close geographical association between these fossil sites, as all are located in the southern part of the Cradle (Fig. 1), and Reynolds (2010) concluded that large carnivores appeared to exploit the southern end of the Cradle more intensively than the northern regions. Given the large mongoose assemblages in sites from the southern part of the Cradle, it is possible that mongooses also utilized the southern part of the Cradle more intensively than the north, perhaps reflecting some local environmental conditions favourable to carnivores. There are, however, some issues with this hypothesis. The small carnivore assemblage of Kromdraai currently does not support this pattern, although Braga *et al.* (2016) have indicated that a large amount of new carnivore material has been recovered from the site in recent excavations and is being prepared for publication. Additionally, the fossil fauna at Swartkrans and Sterkfontein accumulated over a long time period (in excess of a million years) and are generally considered palimpsests (Reynolds 2010). The Cooper's D material, on the other hand, is bracketed between 1.37 Ma and 1.53 Ma; this serves to emphasize the exceptional nature of the small carnivore assemblage of

Cooper's which has accumulated over a shorter time span. Additionally, the 29 specimens described here consist of only the craniodental portion of the assemblage and the abundance and diversity of Cooper's mongooses may increase substantially once the postcranial material is analysed. This pattern may, in addition, represent a sampling error as the sites in the southern part of the Cradle have been more extensively researched than those in the northern part.

The wider African fossil record of *Herpestidae* is patchy, and many species are poorly represented until the Pleistocene (Werdelin & Peigné 2010). Cooper's D preserves fossils of mongoose species or genera which add to our understanding of the evolution or dispersal of those species, particularly in southern Africa, during a period of intense faunal changeover. The genus *Herpestes* is known from as far back as 15.8 Ma (Werdelin & Peigné 2010) and first appears in southern Africa in the Early Pliocene (Langebaanweg; Hendey 1974). The modern species (*H. ichneumon*) first appears around 3.5 Ma at Laetoli (Werdelin & Dehghani 2011) and is known in the Cradle from Kromdraai (1.95 Ma; Braga *et al.* 2017) and Swartkrans (1.6 Ma; Watson 2004). The Laetoli and Cooper's *H. ichneumon* material show little difference from the modern taxon, which indicates that this species has undergone little alteration over the last 3 million years. *Galerella sanguinea* is known from as far back as 7.5 Ma (Toros-Menalla; Peigné *et al.* 2005); although some authors

doubt the specific validity of this specimen, especially given it is otherwise absent from the fossil record until the Middle Stone Age (MSA) (Werdelin & Peigné 2010). Extinct members of the genus are known from eastern Africa from 3.5 Ma (Petter 1973, 1987). The only southern African localities to produce *Galerella* material is Makapansgat Member 3, dated to around 3 Ma (Reed 1996), Swartkrans Member 2 (1.1 Ma; Vrba 1985; de Ruiter *et al.* 2003) and Kromdraai B whose date is currently uncertain but rests around 2 Ma (Braga *et al.* 2017). To the best of our knowledge no *Ichneumia* specimens have been recorded in southern Africa prior to the Middle Pleistocene; and thus, Cooper's represents the first tentative appearance of *Ichneumia* in South Africa. In other parts of Africa, the modern species (*I. albicauda*) has been recorded at the Terminal Miocene (Lemudung'o; Howell & García 2007), although Werdelin & Peigné (2010) cast doubt on this diagnosis and, more securely, from the Early Pliocene Lukeino Formation (Werdelin & Peigné 2010). The genus *Atilax* is not known on the continent until the Early Pleistocene, appearing as the modern species (*A. paludinosus*) at Olduvai II (1.7 Ma; Petter 1973; Werdelin & Peigné 2010), which appears to be the only record for the genus outside of South Africa. The genus appears to be a relatively common component of the South African MSA and Cradle small carnivore fauna assemblages. It is known at Swartkrans Members 2 and 3 (1.1 Ma and 0.7 Ma, respectively; Vrba 1985); and the extinct species *A. mesotes* has been observed in Kromdraai A (<1.95; Ewer 1956a) and a tentative example is known from Malapa (1.97 Ma Kuhn *et al.* 2011). Cooper's thus represents the earliest example of the modern species in South Africa. Fossil African occurrences of the genus *Mungos* are exclusively of extinct species (Werdelin & Peigné 2010). *Mungos dietrichi* is the most common member of the genus in the fossil record and is known from at least four Plio-Pleistocene localities in Eastern Africa, the oldest of which is Laetoli (Petter 1987; Werdelin & Peigné 2010). The genus is known from only one other locality in the Cradle, Sterkfontein Member 5 (approximately 1.4–1.7; Reynolds & Kibii 2011). Cooper's is thus the first southern African locality to produce even a tentative specimen of *Mungos dietrichi*. This late appearance of the species suggests that *M. dietrichi* had a rapid dispersal during the late Pliocene and was a common component of fossil faunas around the Plio-Pleistocene turnover, especially in eastern Africa. The modern species (*M. mungo*) is first observed in the Cradle at the MSA locality of Plovers Lake (de Ruiter *et al.* 2008).

There may prove to be an underlying environmental or ecological cause for the diverse mongoose accumulation at Cooper's; however, there are many possible biases which can negatively affect mongoose preservation and recovery. It should be emphasized before discussing taphonomic biases that this investigation analysed only the Herpestidae *craniodental* remains from Cooper's D and the extent and preservation condition of postcranial remains for these animals from the site is not yet known. Preservation biases for small carnivores can include sampling bias, sieving and decalcification. Sieve mesh size

can strongly affect recovery of small bones and species in excavations (Buss & Borges 2008), and the deployment of small mesh sieves at Cooper's will have ensured the recovery of small specimens which might have been overlooked in other deposits. Additionally, Cooper's, unlike many fossil localities in the Cradle, contained decalcified sediments, which would have allowed the recovery of many more fossil specimens than brecciated sites. However, it is not known to what extent the process of decalcification may have resulted in post-depositional fracturing of bones. The large mongoose assemblages observed at Cooper's, Swartkrans, Sterkfontein and Kromdraai could also be a result of sample size bias. Southwood & Henderson (2000) indicate that smaller and rarer animals are more likely to be identified in larger samples. Cooper's, Swartkrans, Sterkfontein and Kromdraai have long histories of exploration and large numbers of fossils have been excavated and analysed from these sites, increasing the likelihood of recovery of small or rare taxa. An additional explanation for this pattern is accumulation processes. De Ruiter *et al.* (2009), in a preliminary analysis of taphonomic modifications at Cooper's, identified the activity of hyaena in the accumulation of remains. Val *et al.* (2014) identify several lines of evidence which indicate occupation of Cooper's D by brown hyaenas but find that both hyaenas and leopards appear to have contributed to the primate assemblage from the site. Hyaenas and leopards have, similarly, been implicated as accumulators in Sterkfontein (Pickering 1999; Pickering *et al.* 2004a,b; Kibii 2004; Reynolds & Kibii 2011) and Swartkrans (Brain 2004; Carlson & Pickering 2004; Pickering *et al.* 2004a), along with porcupine and abiotic processes (slope wash and natural death traps; Brain 1981; Kibii 2004, 2007). Kibii (2000, 2004) identified larger carnivores, based on carnivore behaviour described by Brain (1981), as the likely accumulators of smaller carnivores at Sterkfontein. Micromammals in Sterkfontein and Swartkrans were likely accumulated by predatory birds, and Avery (2001) has identified the barn owl (*Tyto alba*) as the probable agent. Brown hyaenas are often implicated as the likely accumulators of small carnivores like mongooses based on observations made by Brain (1981), who recorded brown hyaenas feeding on small carnivores, especially when denning with cubs. Pokines & Peterhans (2007) have recorded remains of the Egyptian mongoose (*H. ichneumon*) in spotted hyaena dens. However, predatory birds can feed on prey as large as rabbits and accumulate substantial bone assemblages (Lloveras *et al.* 2008, 2009, 2014). They are also known to take mongoose or small carnivore prey opportunistically (Hinton & Dunn 1967). Future taphonomic research into small carnivores at these sites will help to elucidate accumulating agents for small carnivores and the likely distance over which their remains may have been accumulated, and therefore reflect local environmental conditions.

Modern mongooses are known from a wide variety of habitats. Some species are catholic in their habitat preferences, while others are more habitat specific. The potential for small carnivores, particularly mongooses, as palaeoecological indicators has received little attention to

date. The mongooses of Cooper's D provide a strong indication for riparian conditions and/or a proximity to water in a savanna environment. Modern *H. ichneumon* is widely distributed across African savannas (Kingdon 1977) and throughout its distributional range is associated with riparian conditions. The marsh mongoose (*A. paludinosus*) prefers areas with reasonable cover (such as reed beds and thick stands of semi-aquatic grasses) close to streams and marshy ground (Kingdon 1977; Skinner & Chimimba 2005). Despite these close habitat associations, both species can wander widely (up to 1–2 km from water source) while foraging in adjacent dry terrain. In the case of Cooper's, the Blaaubank River would provide the necessary habitat for these species. *Atilax paludinosus*, unlike most mongooses, feeds primarily on amphibians and crustacea (Skinner & Chimimba 2005), which were probably derived from the river and associated vegetation. Cooper's D has remains from two (tentative) taxa of *Mungos*. It is unknown to what extent these taxa may reflect the habits of the modern banded mongoose (*M. mungo*) but it is reasonable to tentatively draw comparisons with the modern species, acknowledging that there may be some differences. The banded mongoose has a wide habitat tolerance but commonly occurs in riverine conditions (Skinner & Chimimba 2005). The structure of the vegetation appears to affect the location of this species, more than the proximity to water (Skinner & Chimimba 2005). The banded mongoose requires woodland, thick underbrush, fallen logs and other substrate detritus along with termitaria. *Mungos* is the only example of a possibly gregarious mongoose from Cooper's D, although other gregarious species (*Suricata*) are known within the Cradle. Both *H. ichneumon* and *I. albicauda* are known to occur in savanna or savanna woodland environments and *Galerella* species have catholic habitat tolerances. de Ruiter *et al.* (2009) describe the Cooper's environment as predominantly grassland, with nearby woodlands and a permanent water source, while Steininger (2011) suggests a more woody environment. The strong riverine signal presented by the Cooper's mongoose fossils and dense vegetation indicated by *Mungos* suggest a strong woody signal consistent with Steininger's (2011) findings.

CONCLUSION

In summary, Cooper's D preserves a diverse mongoose assemblage that includes a number of first appearances in both the Cradle and the South African fossil record. Brown hyaena is generally inferred as the accumulating agent for these animals, but further taphonomic studies would be beneficial. Additionally, the potential of mongooses to act as accumulating agents of micromammals themselves has not been effectively investigated, although Cohen & Kibii (2018) have shown that some other small to medium-sized carnivores such as the honey badger (*Mellivora capensis*) have high potential as bone accumulators. Mongooses have proven to be useful palaeoecological indicators and they provide evidence for proximity to a stream with riparian vegetation within a savanna or savanna woodland environment in the

Cradle. We therefore stress the potential importance of this poorly studied group in terms of species diversity and as palaeoecological indicators.

The authors would like to express their appreciation to the Ditsong National Museum of Natural History and the Evolutionary Studies Institute at the University of the Witwatersrand for access to their comparative and fossil collections. In particular we thank Teresa Kearney, Curator of the Modern Small Mammal collection, and Stephany Potze and Lazarus Kgasi, Collection Managers of the Palaeontological Collections at the Ditsong National Museum of Natural History, and Bernard Zipfel, Senior Collections Curator at the Evolutionary Studies Institute for their assistance. We are grateful for comments on this manuscript provided by an anonymous reviewer. This study was financially supported by awards to B.F.C. from the Palaeontological Scientific Trust (PAST), the South African National Research Foundation, the University of the Witwatersrand Postgraduate Merit Award and the DST-NRF Centre of Excellence in Palaeosciences. C.M.S. would like to thank PAST and the DST-NRF Centre of Excellence in Palaeosciences for their support.

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