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

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ABSTRACT

Mongooses (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 of 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. 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*

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.

<<Insert Figure 1 here>>

Mongooses are an important component of Southern African ecosystems with at least 12 different species known from modern Sub-saharan Africa (Table 1; Skinner and 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 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 1.4 and 1.5 Ma (de Ruiter *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 and Steininger 2017), suids (de Ruiter et al. 2009), microfauna (Vilakazi, 2014) and primates (Folinsbee and 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.

<<Insert Table 1 here>>

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 optimise 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 utilised 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 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 and 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 and 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 palaeoserengetensis* 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 utilise *Crossarchus transvaalensis*. Dietrich (1942) first described the species *Mungos palaeoserengetensis* from Laetoli. Petter (1963) later reassigned the species to genus *Herpestes* and later still to *Galerella palaeoserengetensis* (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 palaeoserengetensis*. We utilise this latter classification in this analysis.

<<Insert Table 2 here>>

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, P^1 and P^2; CD5725, right maxillary fragment with P^2 alveolus, and P^3 and P^4 (Fig. 2 e, f); CD19130, isolated right P^4; CD5933, isolated right M^1; CD5714, isolated occipital (Fig. 2 i) 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 P^3 roots and the foramen then extends anteriorly in an oblique manner to a position anterior of the P^3. 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 P^1 is small, conical and single-rooted. The P^2, 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 P^2 displays small basal cingula anteriorly, posteriorly and lingually and the latter cingulum is somewhat ridge-like. The P^3 (CD5725) is larger than the P^2 and likewise displays three roots. The main cusp is high and centrally situated. The P^3 displays small basal cingula anteriorly, posteriorly and lingually, however the cingula in the P^3 differs from those of the P^2, in being more prominent. The lingual root additionally bears a small cusp. The P^4 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 mesio-buccal cingulum supports a small parastyle. The metastyle is trenchant and long, nearly the same length as the paracone. CD5933 preserves a slightly worn M^1. 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 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 mongoose (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 supra-occipital 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.

<< Insert Figure 2 here >>

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 P^1. 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 P^2 and M^1. The lingual root and cusp of the P^2 of *I. albicauda* are situated much more posteriorly, almost in line with the distal cingulum. In addition, the M^1 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 mongoose species. For example, *H. palaeoserengetensis* differs from the Cooper's material in the structure of the P^2 and P^3, and its smaller size (Fig. 3B, C). The P^2 and P^3 of *H. palaeoserengetensis* are only double rooted and the P^3 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 Coopers material is morphologically indistinguishable from modern *H. ichneumon* specimens

<<Insert Table 3 here>>

<<Insert Figure 3 here>>

<<Insert Table 4 here>>

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Genus *Ichneumia* G. Cuvier, 1829

cf. *Ichneumia* sp.

Material

CD3278, left maxillary fragment with canine, P^1 alveolus, and P^2 (Fig. 2h).

Description

This specimen is similar in size (Table 3, Fig. 3) 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 P^1 alveolus is present, and there is a slightly larger gap between the P^1 and P^2 in this specimen, than in CD5737. The P^2 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 P^2 widens distally.

Discussion

The P^2 of modern *I. albicauda* specimens displayed the same tooth root structure as the P^2 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 P^2 in specimen CD3278 also separates it from modern and fossil *H. ichneumon*. The fossil species *H. palaeoserengetensis* and *A. mesotes* have similar P^2 root structure as CD3278, however both extinct taxa can be differentiated from CD3278, as the P^2 of *H. palaeoserengetensis* lacks accessory cusps and the apex of the main cusp was situated slightly posteriorly of the midline. In addition, the dentition of *H. palaeoserengetensis* was smaller than the dentition of CD3278, while the teeth of *A. mesotes* are larger and more robust than the Coopers specimen.

Genus *Atilax* F. Cuvier, 1826

***Atilax paludinosus* G. Cuvier, 1829**

Material

CD8840, isolated right lower canine; CD9119, isolated partial left P^3; CD7329, right edentulous maxillary fragment from alveoli of canine to the anterior root of P^3.

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 P^3 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 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. 3). The canine alveolus is substantial, suggesting a large canine tooth had been present. There is no postcanine diastema and the P^1 is absent. The P^2 and P^3 are crowded closely together. The palatal foramen occurs midway between the two roots of the P^2.

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. 3 and Fig. 5A), and the latter species differs from the Cooper's material in the structure of the lower canine and the P^3. *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 P^3 of *A. mesotes* lacks the strongly carinate anterior border and slight cusp on the cingulum present in CD9119. The absence of the P^1 in specimen CD7329 could indicate an 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 P^1, but that they were absent in 'nearly all southern and eastern African specimens'. Ewer (1956a) also found that southern African *A. paludinosus* specimens lack the P^1, however our examination of the material in the Ditsong Museum found one specimen from a sample of 17 that retained a P^1. Therefore, the presence or absence of a P^1 cannot be considered a reliably diagnostic feature, however given that the majority of *A. paludinosus* specimens lack a P^1 and the other morphologically similarities, the Cooper's material is here attributed to *A. paludinosus*.

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

***Mungos* aff. *dietrichi* Petter, 1963**

Material

CD21892, isolated right P_4 crown (Fig. 2 k, j).

Description

The P_4 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 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.

Discussion

This specimen is substantially larger than CD1943 (*Mungos* sp. described below) (Fig. 5D and Fig. 6). The P_4 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 material is insufficient for a definitive identification, the P_4 morphology has greatest affinity with the fossil species *M. dietrichi*.

Genus *Mungos* Geoffroy Saint-Hilaire & Cuvier, 1795

***Mungos* sp.**

Materials

CD1943, right mandibular fragment from P_2 alveolus to ramus, with P_4 and M_1 present (Fig. 2 a, b); CD3832, right mandibular fragment from P_4 alveolus - M_2 with M_1 present (Fig. 2 g); 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 Coopers 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 Coopers material is smaller than specimens from *M. dietrichi*. Morphologically the Coopers 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.

<<Insert Figure 5 here>>

<<Insert Figure 6 here>>

?*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. 2 c, 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 Coopers specimens are similar in size to the modern species *Galerella sanguinea* Rüppel, 1836 (Fig. 5, 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 Coopers specimens. The presence of a posterior accessory cusp in the P_3 of the Coopers 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 Coopers 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 Coopers material in the structure of the P_3, which displays additional posterior cusps. Similarly, *H. palaeogracilis* can be separated from the Coopers material by the appearance of an anterior cingulum on the P_2. Overall, the Coopers 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 I^3 to left I^3 is 9.7 mm. The incisor tooth row is slightly curved and the I^3 is slightly larger the neighbouring incisors. However, there is no gap between I^3 and I^2. The isolated incisor (CD7328) is of a comparable size to the I^3 from specimens CD5989 and CD7307. The

Coopers 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 P_2 - M_1, and associated isolated right P_4.

Description

The mandible is small with a straight ventral border and a stepped profile immediately posterior to the symphysis, which extended below the P_2. The anterior mental foramen is situated below the distal root of P_2, while the posterior mental foramen is situated below the distal root of the P_3. The apex of the main cusp of the P_4 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 P_4 is similar in size to modern *C. penicillata* and to the Coopers *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 P_4 was more extensive. Modern *C. penicillata* display a stepped mandible similar to specimen CD3282, however the P_4 is more robust in the modern species. The P_4 structure is most similar, especially in respect to 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 P_2 – M_1; CD 3280, anterior left and right hemi-mandibles with left and right P_1 and left P_2; 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 P_2, but there are no other diagnostic characteristics. CD3280 is a small and highly gracile mandible showing partially erupted dentition. The P_3 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. 5). 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 is 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 specimens from sites like Kromdraai are often characterised 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 utilised 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 1.4 Ma and 1.5 Ma; this serves to emphasise 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.

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 absence 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, first 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). Coopers 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 emphasised 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 Coopers 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 Coopers, Swartkrans, Sterkfontein and Kromdraai could also be a result of sample size bias. Southwood and Henderson (2000) show that smaller and rarer animals are more likely to be identified in larger samples. Coopers, 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 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 hyena in the accumulation of remains. Val *et al.* (2014) identify several lines of evidence which indicate occupation of Cooper's D by brown hyenas but find that both hyenas and leopards appear to have contributed to the primate assemblage from the site. Hyenas 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 hyenas are often implicated as the likely accumulators of small carnivores like mongooses based on observations made by Brain (1981), who recorded brown hyenas feeding on small carnivores, especially when denning with cubs. Pokines & Peterhans (2007) have recorded remains of the Egyptian mongoose (*H. ichneumon*) in spotted hyena 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 hyena 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-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.

<<Insert Table 5 here>>

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FIGURE LEGENDS

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

Figure 2. A selection of mongoose 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. *Ichenumia* 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*.

Figure 3. Biplots of dental measurements (mm) on modern and fossil mongooses; a) MD and BL length of C^1: b) MD and BL length of P^2; c) MD and BL length of P^3, d) MD and BL length of P^4; e) MD and BL length of M^1; f) BL Length of P^3.

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 C_1; b) MD and BL length of P_2; c) MD and BL length of P_3; d) MD and BL length of P_4; e) MD and BL length of M_1.

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; height of the ramus.

TABLES

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

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

Table 2. Abbreviations and measurements utilised in this 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

Table 3. Measurements (in mm) of maxillary and mandibular dentition for modern and fossil mongoose species including the Cooper's D mongooses, all measurements by BC unless stated otherwise. See Table 2 for explanation of abbreviations.

		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**
Herpestes Ichneumon (n=8)	Mean	5.1	3.7	5.6	3.0	6.8	4.7	9.6	7.1	9.6	5.1	5.6	3.7								
	Range	4.3-5.6	3.2-4.2	5.2-6.1	2.5-3.5	6.4-7.6	4.1-5.5	8.3-10.5	6.6-8.0	9.2-10.1	4.2-6.0	5.0-6.6	3.1-4.3								
Herpestes ichneumon	CD5737	5.3	3.9	5.7	3.6																
Herpestes ichneumon	CD5725					6.1	4.5	9.0	6.7												
Herpestes ichneumon	CD19130							8.5	6.0												
Herpestes ichneumon	CD5933									8.4	5.5										
Herpestes palaeoserengetensis (Petter 1987)		3.6	3.0	4.6	2.4	4.8	3.8	7.4	5.1	4.8	7.4	3.5	-	4.5	3.0	5.0	2.4	5.8	2.5	7.3	4.1
Herpestes sp. (Hendey 1973)	KB290							7.7	5.5												
Herpestes sp. (Hendey 1973)	KB2944																	6.8	3.3	8.3	4.2
Ichenumia albicauda (n-11)	Mean	5.4	3.6	6.1	3.3	6.3	5.3	9.9	8.0	9.4	6.5	5.3	3.8								
	Range	4.5-5.9	3.0-4.1	5.6-6.5	2.7-3.7	5.8-6.8	4.6-6.6	8.4-10.9	7.3-8.5	8.3-10.3	5.9-7.1	5.0-5.9	3.2-4.3								
cf. *Ichneumia* sp.	CD3278	5.1	3.9	5.3	2.9																
Atliax paludinosus (n=14)	Mean	6.2	4.8	5.6	4.1	6.9	6.0	11.8	9.6	9.9	7.3	6.9	4.9								
	Range	5.5-6.9	4.1-5.7	4.7-6.4	3.5-5.2	5.6-7.7	5.3-6.8	10.9-12.9	8.9-10.6	10.9-12.0	6.3-8.0	5.7-9.8	4.2-6.8								
Atilax paludinosus	CD8840											6.5	4.7								
Atilax paludinosus	CD9119					-	5.9														
Atilax mesotes (Ewer 1956a)		5.5	4.2	5.8	3.4	6.4	4.7	9.3	7.0	5.6	9.4	6.0	4.6	4.9	3.2	6.3	3.4	7.3	3.4	8.7	5.4

Mungos mungo (n=15)	Mean															4.4	2.8	5.2	3.3	5.4	3.6
	Range															4.0-4.7	2.5-3.1	4.9-5.7	3.0-4.0	4.7-5.7	3.3-3.9
Mungos aff. *dietrichi*	CD21892																	6.3	3.8		
Mungos sp.	CD1943																	4.6	2.8	4.7	3.3
Mungos sp.	CD3832																			4.5	3.3
Mungos sp.	CD11833															4.5	2.5				
Mungos dietrichi (Petter 1963, 1987)								5.8	7.1	4.7	7.2	4.4	3.2	4.1	2.3	4.5	2.9	5.7	3.7	5.8	4.0
Galerella sanguinea (n=17)	Mean											3.0	2.1	3.1	1.6	3.7	1.8	4.5	2.2	5.1	2.9
	Range											2.3-3.8	1.3-2.9	2.4-3.3	1.2-1.8	3.2-3.9	1.5-2.1	4.2-4.9	2.0-2.6	4.5-5.5	2.7-3.4
?*Galerella* sp.	CD721													2.7	1.7	3.2	1.6				
?*Galerella* sp.	CD8315															3.6	1.9				
Galerella sp. Laetoli (Werdelin & Dehghani 2011)														3.8	1.6	3.1	1.6				
Herpestidae gen. et sp. indet. (small)	CD3282																	4.9	2.7		
Indet. Herpestidae	CD3732	4.3	3.8																		
Indet. Herpestidae	CD21889	3.2	2.4																		
Indet. Herpestidae	CD21881	3.9	2.9																		
Indet. Herpestidae	CD20194	4.0	3.0																		
Indet. Herpestidae	CD10595	3.3	2.4																		
Indet. Herpestidae	CD12299											2.7	2.0								
Indet. Herpestidae	CD8312											4.5	3.7								
Suricata major (Hendey 1974a)						5.9	4.5	7.0	7.5	4.5	8.1			4.9	3.1	5.1	3.3	6.5	4.3	6.2	4.5

Cynictis penicillata brachyodon (Ewer 1956b)							4.7	4.6	3.7	6.8	3.9	2.8	3.4	1.9			4.5	2.3	5.0	3.1
Helogale palaeogracilis (Petter 1987)	2.6	1.9	2.9	1.5	3.5	2.2	5.0	3.7	2.5	4.6	2.0	1.8	2.7	1.6	3.1	1.6	3.6	-	4.5	2.4

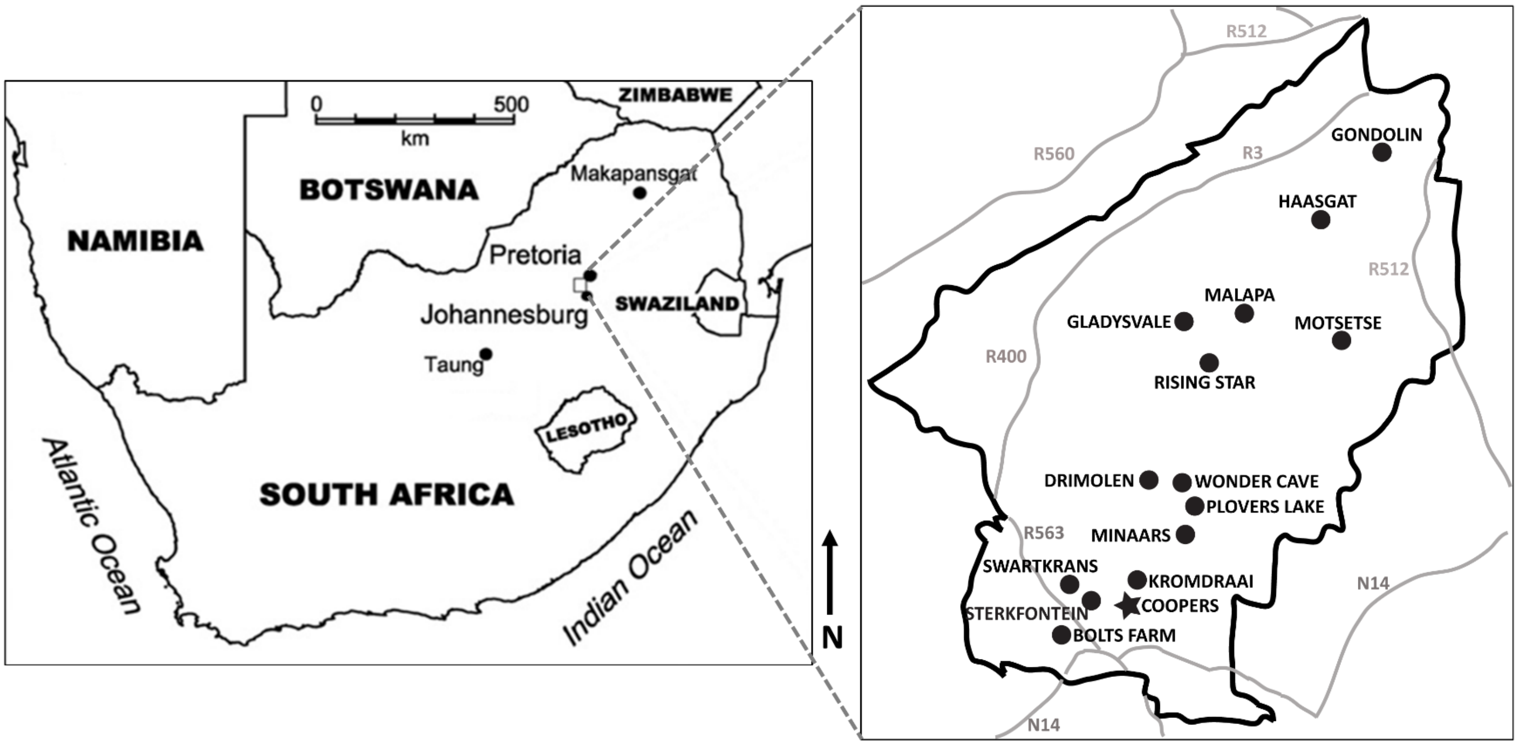
Table 4. Measurements (in mm) of crania and mandibles for modern and fossil mongoose species including the Cooper's D mongooses. All measurements by BC unless stated otherwise stated, see Table 2 for explanation of abbreviations.

			Cranial					
			BFM	**HFM**	**BOC**			
Herpestes ichneumon	CD5714		11.0	20.5	10.8			
Herpestes ichneumon		Mean	13.1	23.9	11.1			
(n=8)		Range	11.6-14.7	20.7-25.0	10.3-12.2			
Ichneumia albicauda		Mean	13.7	9.5	22.8			
(n=11)		Range	12.8-14.5	8.4-10.7	21.3-25.2			
Atilax paludinosus		Mean	14.0	10.0	24.3			
(n=14)		Range	12.4-14.8	9.3-10.7	20.5-26.0			
			Mandible					
			LPM	**LMR**	**LTR**	**HP**	**HM**	**HR**
Mungos mungo		Mean	13.3	9.0	22.4	7.3	8.1	19.9
(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
Mungos sp.	CD1943		12.0	8.7	20.6	7.4	7.7	19.8
Mungos sp.	CD3832			7.2			7.4	
Mungo dietrichi (Petter 1963, 1987)					24.9		8.1	
Galerella sanguinea		Mean	11.4	7.6	19.0		6.5	18.1
(n=17)		Range	9.8-12.5	6.9-8.3	17.7-20.6		5.2-7.9	14.9-21.0
?*Galerella* sp.	CD721		10.5	8.7	19.1	7.2	5.9	
?*Galerella* sp.	CD8315					5.2		
?*Galerella* sp.	CD3290					5.6		
Herpestes palaeoserengetensis (Petter 1987)			16.0		21.5			
Helogale palaeogracilis (Petter 1987)			10.2		15.6			

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

Fossil Locality	**Stratigraphic Member**	**Species**	**NISP**	**MNI**	**References**
Malapa		Atilax cf. mesotes	1	1	Kuhn et al. 2011
		cf. Herpestidae	4		
Drimolen		aff. Suricata suricatta	1	1	O'Regan & Menter (2009)
		cf. Cynictis penicillata	3	1	Adams et al (2016)
Swartkrans	Mb 2, 3	Atilax sp.	4	2	Watson (2004)
	Mb 2, 3	Cynictis penicillata	5	2	de Ruiter et al 2003
	Mb 1	Herpestes ichneumon	2	1	
	Mb 2	Galerella sanguinea			de Ruiter et al 2003
	Mb 2, 3, 5	Suricata suricatta	10	8	
	Mb 1	Suricata sp.	1	1	de Ruiter et al 2003
	Mb 1, 3, 5	Herpestidae indet.	24		
Sterkfontein	Mb5E, Mb5W	cf. Mungos sp.			Reynolds & Kibii (2011)
	Stw53, Mb5E, Mb5W, L/63, LC	Suricata sp.			
	L/63	Herpestes ichneumon			
	Mb5E	Herpestes indet.			
	JC	Cynictis penicillata			
Kromdraai	KA	?Crossarchus transvaalensis	1	1	Brain 1981: Broom 1937, 1939
	KA	Atilax mesotes	1	1	Ewer (1956a); Brain(1981)

	KB	Galerella cf. sanguinea			Hendey (1973); Fourvel et al. (2016)
	KB	Herpestes sp.	1	1	Braga & Thackeray (2016)
	KB	Viverridae/Herpestidae Indet.	9		Fourvel et al. (2016)
Coopers		Herpestes ichneumon	5	5	This publication
		cf. Ichneumia sp.	1	1	
		Atilax paludinosus	3	1	
		Mungos aff. dietrichi	1	1	
		Mungos sp.	3	1	
		?Galerella sp.	3	2	
		Herpestidae indet. (large)	3		
		Herpestidae indet. (small)	1		
		Indeterminate Herpestidae	9		



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R560
R3
GONDOLIN
HAASGAT
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MALAPA
GLADYSVALE
MOTSETSE
R400
RISING STAR
DRIMOLEN
WONDER CAVE
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Figure 1.

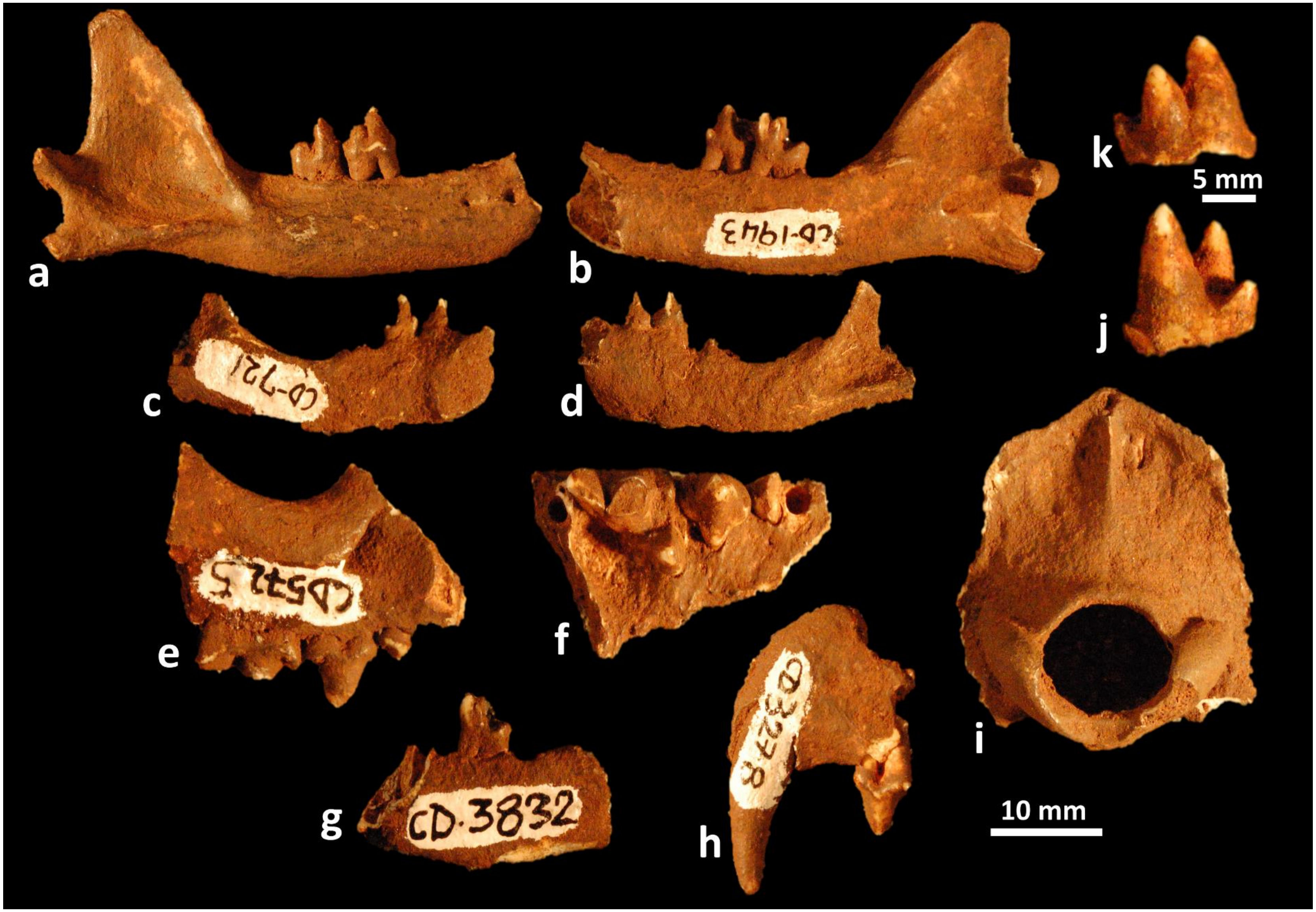
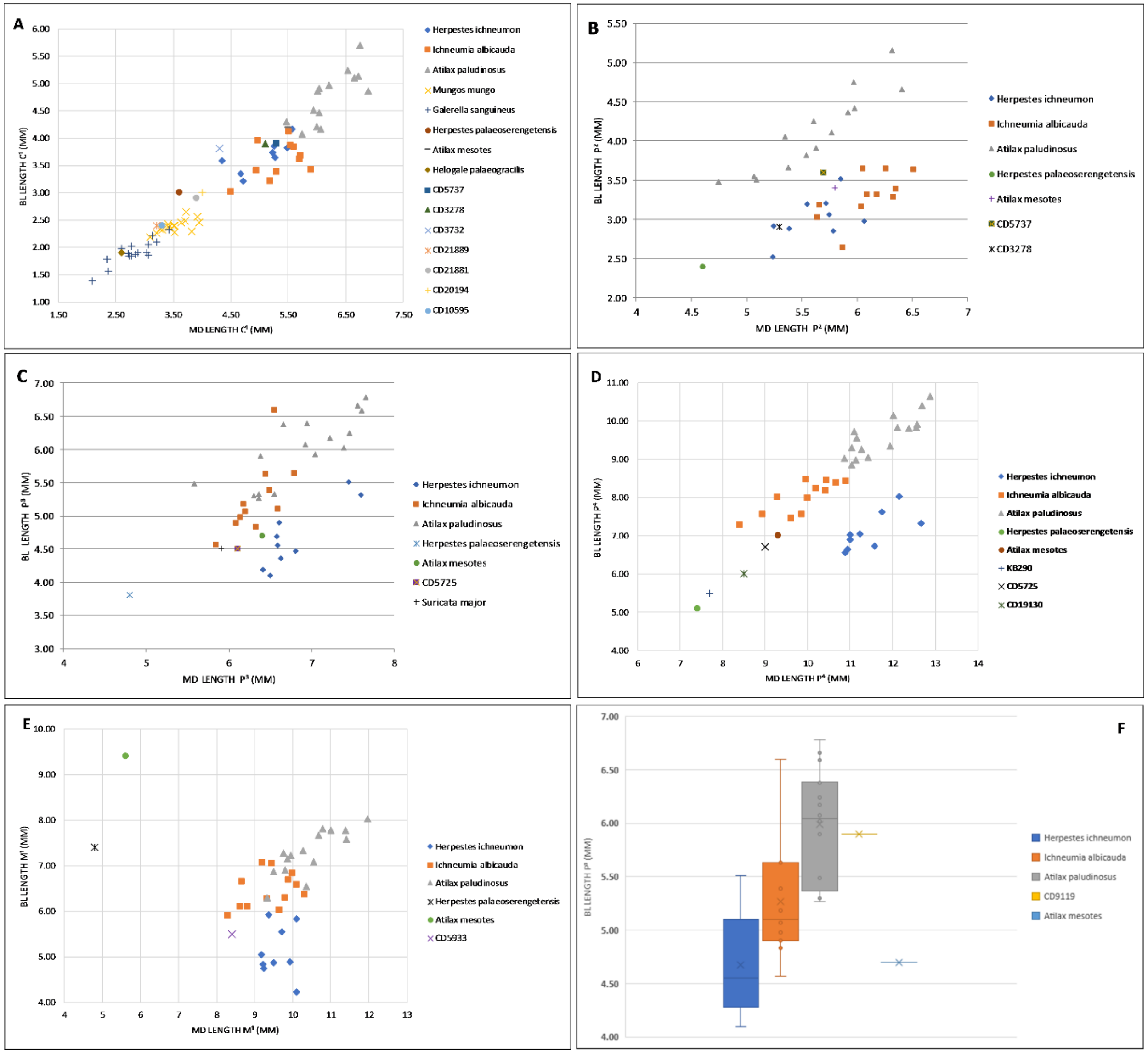


Figure 2.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BL LENGTH C^1 (MM)
MD LENGTH C^1 (MM)
Herpestes ichneumon
Ichneumia albicauda
Atilax paludinosus
Mungos mungo
Galerella sanguineus
Herpestes palaeoserengetensis
Atilax mesotes
Helogale palaeogracilis
CD5737
CD3278
CD3732
CD21889
CD21881
CD20194
CD10595
B
BL LENGTH P^2 (MM)
MD LENGTH P^2 (MM)
Herpestes ichneumon
Ichneumia albicauda
Atilax paludinosus
Herpestes palaeoserengetensis
Atilax mesotes
CD5737
CD3278
C
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MD LENGTH P^3 (MM)
Herpestes ichneumon
Ichneumia albicauda
Atilax paludinosus
Herpestes palaeoserengetensis
Atilax mesotes
CD5725
Suricata major
D
BL LENGTH P^4 (MM)
MD LENGTH P^4 (MM)
Herpestes ichneumon
Ichneumia albicauda
Atilax paludinosus
Herpestes palaeoserengetensis
Atilax mesotes
KB290
CD5725
CD19130
E
BL LENGTH M^1 (MM)
MD LENGTH M^1 (MM)
Herpestes ichneumon
Ichneumia albicauda
Atilax paludinosus
Herpestes palaeoserengetensis
Atilax mesotes
CD5933
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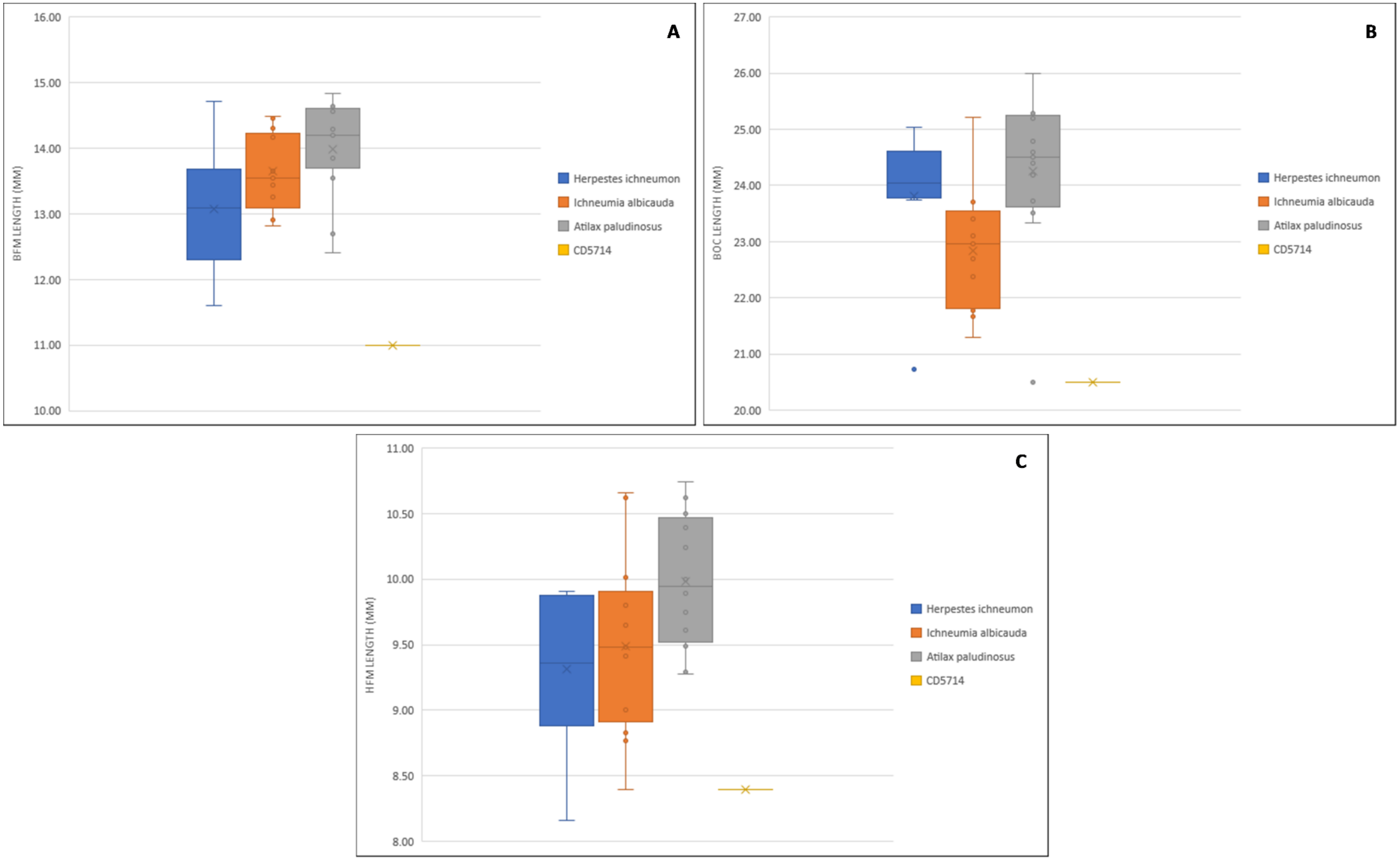
Ichneumia albicauda
Atilax paludinosus
CD9119
Atilax mesotes

Figure 3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BFM LENGTH (MM)
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Atilax paludinosus
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BOC LENGTH (MM)
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Ichneumia albicauda
Atilax paludinosus
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HFM LENGTH (MM)
Herpestes ichneumon
Ichneumia albicauda
Atilax paludinosus
CD5714

Figure 4.

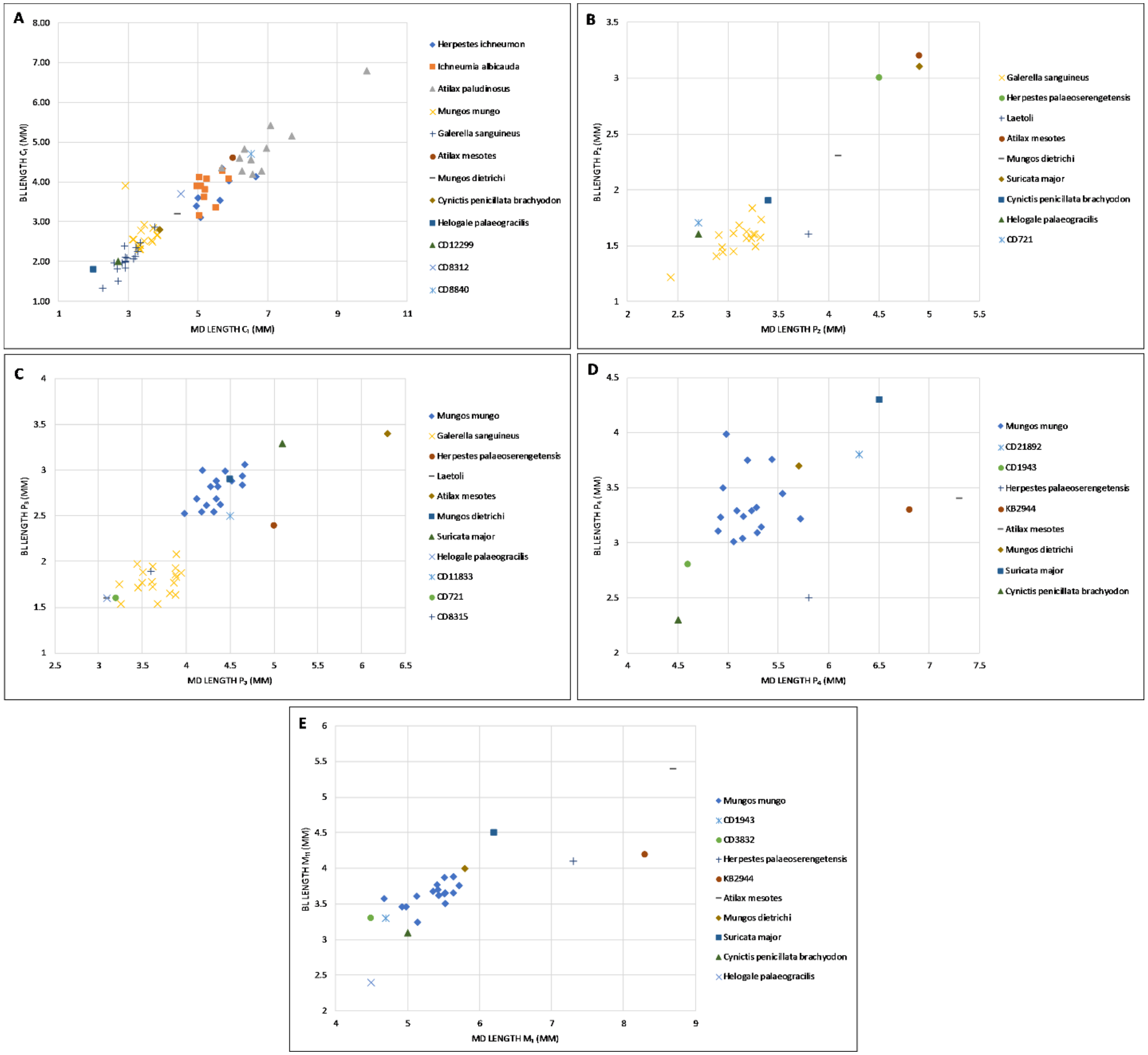
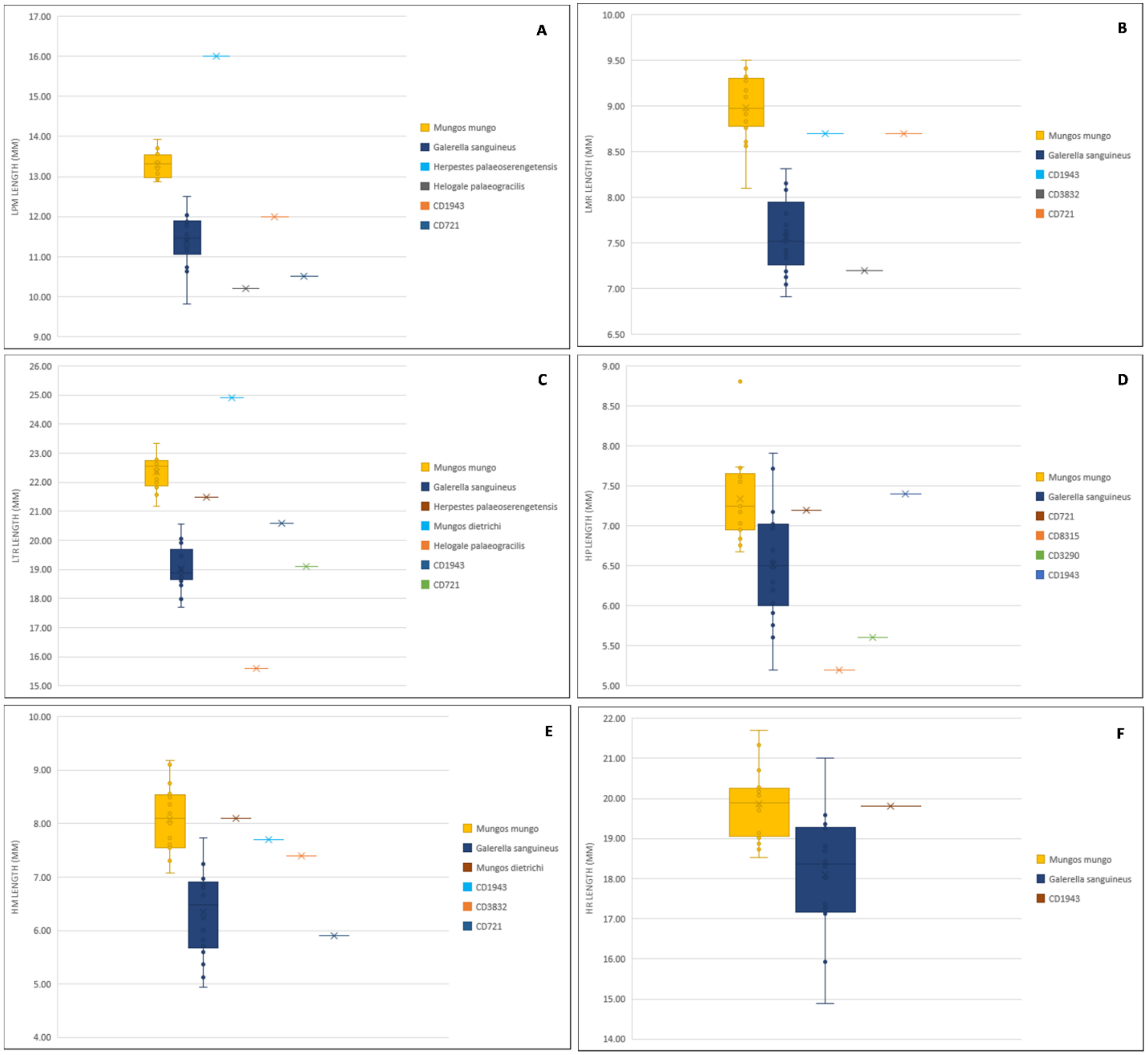

A
8.00
7.00
6.00
5.00
4.00
3.00
2.00
1.00
BL LENGTH C_1 (MM)
1
3
5
7
9
11
MD LENGTH C_1 (MM)
Herpestes ichneumon
Ichneumia albicauda
Atilax paludinosus
Mungos mungo
Galerella sanguineus
Atilax mesotes
Mungos dietrichi
Cynictis penicillata brachyodon
Helogale palaeogracilis
CD12299
CD8312
CD8840
B
3.5
3
2.5
2
1.5
1
BL LENGTH P_2 (MM)
2
2.5
3
3.5
4
4.5
5
5.5
MD LENGTH P_2 (MM)
Galerella sanguineus
Herpestes palaeoserengetensis
Laetoli
Atilax mesotes
Mungos dietrichi
Suricata major
Cynictis penicillata brachyodon
Helogale palaeogracilis
CD721
C
4
3.5
3
2.5
2
1.5
1
BL LENGTH P_3 (MM)
2.5
3
3.5
4
4.5
5
5.5
6
6.5
MD LENGTH P_3 (MM)
Mungos mungo
Galerella sanguineus
Herpestes palaeoserengetensis
Laetoli
Atilax mesotes
Mungos dietrichi
Suricata major
Helogale palaeogracilis
CD11833
CD721
CD8315
D
4.5
4
3.5
3
2.5
2
BL LENGTH P_4 (MM)
4
4.5
5
5.5
6
6.5
7
7.5
MD LENGTH P_4 (MM)
Mungos mungo
CD21892
CD1943
Herpestes palaeoserengetensis
KB2944
Atilax mesotes
Mungos dietrichi
Suricata major
Cynictis penicillata brachyodon
E
6
5.5
5
4.5
4
3.5
3
2.5
2
BL LENGTH M_1 (MM)
4
5
6
7
8
9
MD LENGTH M_1 (MM)
Mungos mungo
CD1943
CD3832
Herpestes palaeoserengetensis
KB2944
Atilax mesotes
Mungos dietrichi
Suricata major
Cynictis penicillata brachyodon
Helogale palaeogracilis

Figure 5.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LPM LENGTH (MM)
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15.00
14.00
13.00
12.00
11.00
10.00
9.00
Mungos mungo
Galerella sanguineus
Herpestes palaeoserengetensis
Helogale palaeogracilis
CD1943
CD721
B
LMR LENGTH (MM)
10.00
9.50
9.00
8.50
8.00
7.50
7.00
6.50
Mungos mungo
Galerella sanguineus
CD1943
CD3832
CD721
C
LTR LENGTH (MM)
26.00
25.00
24.00
23.00
22.00
21.00
20.00
19.00
18.00
17.00
16.00
15.00
Mungos mungo
Galerella sanguineus
Herpestes palaeoserengetensis
Mungos dietrichi
Helogale palaeogracilis
CD1943
CD721
D
HP LENGTH (MM)
9.00
8.50
8.00
7.50
7.00
6.50
6.00
5.50
5.00
Mungos mungo
Galerella sanguineus
CD721
CD8315
CD3290
CD1943
E
HM LENGTH (MM)
10.00
9.00
8.00
7.00
6.00
5.00
4.00
Mungos mungo
Galerella sanguineus
Mungos dietrichi
CD1943
CD3832
CD721
F
HR LENGTH (MM)
22.00
21.00
20.00
19.00
18.00
17.00
16.00
15.00
14.00
Mungos mungo
Galerella sanguineus
CD1943

Figure 6.