

Felidae from Cooper's Cave, South Africa (Mammalia: Carnivora)

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ABSTRACT

The Cooper's Cave System has produced a diverse fossil assemblage including the remains of *Paranthropus robustus* Broom, 1938, and early *Homo* Linnaeus, 1758. The majority of the faunal remains come from Cooper's D, which dates to c. 1.5–1.4 Ma. Here we describe 158 craniodental and postcranial felid fossils from Cooper's D, including *Dinofelis* cf. *aronoki*. These fossils indicate the presence of four large felid genera at Cooper's D: *Dinofelis* Zdansky, 1924, *Megantereon* Croizet & Jobert, 1828, *Panthera* Oken, 1816 (two species) and *Acinonyx* Brookes, 1828, plus two smaller taxa: *Caracal* Gray, 1843 and *Felis* Linnaeus, 1758. This assemblage may mark the first appearance of the modern cheetah *Acinonyx jubatus* (Schreber, 1775) in Africa, as well the first occurrence of the East African species *Dinofelis* cf. *aronoki* in southern Africa. This taxon appears intermediate in features between *Dinofelis barlowi* (Broom, 1937) and *Dinofelis piveteaui* (Ewer, 1955). We compare the Cooper's D felid assemblage with those from other sites in the Cradle of Humankind, Gauteng, and discuss several scenarios for the evolution of the genus *Dinofelis* in eastern and southern Africa.

RÉSUMÉ

Les félidés de la Grotte Cooper, Afrique du Sud (Mammalia: Carnivora).

La grotte de Cooper a livré un assemblage diversifié de fossiles incluant des restes de *Paranthropus robustus* Broom, 1938 associés à ceux des premiers *Homo* Linnaeus, 1758. La majorité des restes provient du site de Cooper D, daté d'environ 1,5 à 1,4 Ma. Dans ce travail, nous décrivons 158 dentaires et os post-craniaux appartenant à des Felidae fossiles de Cooper D, dont *Dinofelis* cf. *aronoki*. Ces fossiles attestent de la présence de quatre genres de grands Felidae: *Dinofelis* Zdansky, 1924, *Megantereon* Croizet & Jobert, 1828, *Panthera* Oken, 1816 (deux espèces) et *Acinonyx* Brookes, 1828, ainsi que de deux genres de plus petite taille: *Caracal* Gray, 1843 et *Felis* Linnaeus, 1758. Cet assemblage semble marquer la première occurrence du guépard moderne *Acinonyx jubatus* (Schreber, 1775) en Afrique, ainsi que la première occurrence de l'espèce d'Afrique orientale *Dinofelis* cf. *aronoki* en Afrique du sud. Cette espèce présente des caractéristiques intermédiaires entre *Dinofelis barlowi* (Broom, 1937) et *Dinofelis piveteaui* (Ewer, 1955). L'assemblage de Felidae de Cooper D est comparé à ceux d'autres sites dans le « Berceau de l'Humanité », Gauteng, et plusieurs scénarios de l'évolution du genre *Dinofelis* sont discutés.

KEY WORDS

Cooper's Cave,
Felinae,
Machairodontinae,
Megantereon,
Panthera,
Acinonyx,
Caracal,
Felis.

MOTS CLÉS

Grotte de Cooper,
Felinae,
Machairodontinae,
Megantereon,
Panthera,
Acinonyx,
Caracal,
Felis.

INTRODUCTION

Cooper's Cave is one of many hominin-bearing sites located in the UNESCO Sterkfontein, Swartkrans, Kromdraai and Environs World Heritage Site, South Africa. Known as a fossil-bearing site since 1939 (Shaw 1939; 1940) this site is made up of three distinct localities, Cooper's A, B and D each with a unique geomorphology (de Ruiter *et al.* 2009). The majority of fossils come from the Cooper's D deposit, which has so far produced 183 identifiable individuals. These include carnivores (Kuhn *et al.* 2016; O'Regan *et al.* 2013; Hartstone-Rose *et al.* 2007, 2009; Lacruz *et al.* 2006), primates, including *Theropithecus oswaldi* (Andrews, 1916) (Folinsbee & Reisz 2013; DeSilva *et al.* 2013), hominins (de Ruiter *et al.* 2009), and unusually for the southern African sites, a number of suids (de Ruiter *et al.* 2008). Seventeen larger carnivore taxa have been identified (de Ruiter *et al.* 2009; O'Regan *et al.* 2013; Kuhn *et al.* 2016), including seven felids representing both extinct and extant taxa. Here we describe the fossil felid material from the Cooper's D deposit (dated to c. 1.5–1.4 Ma, de Ruiter *et al.* [2009]), including *Dinofelis* cf. *aronoki*, and additional specimens of *Megantereon whitei* (Broom, 1937). Some of the *Dinofelis* Zdansky, 1924 specimens have previously been discussed in Lacruz *et al.* (2006) and O'Regan & Menter (2009), but the identification of further *Dinofelis* material in the Cooper's D collection, in particular a complete P4, has allowed us to reconsider the designation of the material. In addition to the *Dinofelis* remains included in Lacruz *et al.* (2006), a particularly small specimen of *Megantereon whitei* has also been published from the site (Hartstone-Rose *et al.* 2007). This specimen is not re-described here, but is included in the discussions and analyses for completeness.

MATERIALS AND METHODS

All specimens were identified using the modern and fossil carnivore comparative collections in the Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, and Ditsong (formerly Transvaal) National Museum of Natural History, Pretoria. *Homootherium* spp. postcrania were not represented in these collections, so illustrations in Ballesio (1963) were used for comparison. Comparisons with *D. aronoki* Werdelin & Lewis, 2001 were through comparison with Werdelin & Lewis (2001) with additional photographs kindly provided by L. Werdelin. All measurements were taken by HOR, unless otherwise stated. If a specimen has been previously described, the reference is given in parentheses.

ABBREVIATIONS

Specimen and collection prefixes

CD	Cooper's D;
DN	Drimolen;
KA	Kromdraai A;
KB	Kromdraai B;
M	Makapansgat;
AZ	Archaeozoology collection at the Ditsong Museum;
BPI	Evolutionary Studies Institute (formerly the Bernard Price Institute).

Cranial measurement

L	Mesial-distal length of tooth;
B	greatest Buccal-lingual breadth of tooth;
Bant	breadth across anterior accessory cusp;
Ba	anterior breadth including protocone;
Bbl	breadth across the carnassial blade;
Lm	length of metastyle;
CB	breadth across the occipital condyles;
Lproto	length of protoconid;
Lpara	length of paraconid;
Depth A	anterior depth of mandible before to the P ₃ ;
Depth P	posterior depth of mandible after the M ₁ ;
BP4	breadth of the mandibular corpus below the P ₄ ;
Diastema	length of canine-P ₃ diastema.

Postcranial measurement

TL	total length;
PWM-L	Proximal mediolateral width;
PWA-P	Proximal antero-posterior width;
DWMax	maximum distal mediolateral width;
DBMax	maximum distal antero-posterior breadth;
PWMax	maximum proximal mediolateral width from femoral head to greater trochanter;
ND	superior-inferior femoral neck diameter;
HD	superior-inferior femoral head diameter;
HeadW	mediolateral width of the head of the astragalus;
NeckW	mediolateral width of the neck of the astragalus;
DW	distal mediolateral width across the epicondyle.

SYSTEMATICS

Order CARNIVORA Bowdich, 1821

Family FELIDAE Fischer, 1817

Subfamily MACHAIRODONTINAE Gill, 1872

Genus *Dinofelis* Zdansky, 1924

TYPE SPECIES. — *Dinofelis abeli* Zdansky, 1924 (junior synonym of *D. cristata*) by original designation.

Dinofelis cf. *aronoki*

(Figs 1, 2; Tables 1, 2, 3)

Dinofelis sp. – Lacruz *et al.* 2006: 94–96.

Dinofelis aff. *piveteaui* – O'Regan & Menter 2009: 331–340.

MATERIAL EXAMINED. — **Craniodental from Coopers D** (all described in Lacruz *et al.* (2006), with the exception of CD 15696 and CD 19265): CD 16765a+b, right premaxilla fragment with I¹–I³ (Fig. 1G); CD 16769a+b, left C^s (Fig. 1H; Table 1); CD 15696, left P³ (Fig. 1I, J; Table 1); CD 7323a–d, right premaxilla with P³ (Fig. 1D, E) and partial P⁴ (Fig. 1F; Table 1); CD 19961, complete P⁴ (Fig. 1A–C; Table 1); CD 18836, rear portion of right mandible with P₄ and partial M₁ (Fig. 1K, L; Table 2); CD 19265, left M₁ in mandible fragment (Fig. 1M, N; Table 2). **Craniodental from Drimolen**, all described and figured in O'Regan & Menter (2009): DN 1012, a right maxillary fragment with complete P⁴ and M₁, plus partial C^s and complete P³ alveoli; DN 780, right P³; DN 986, right P₄; DN 1020, posterior portion of premolar, probably right P³. **Postcranial material.** CD 19953, a right MT 3 (Fig. 2A, B; Table 3); CD 3233, a left proximal tibia (Fig. 2C–E; Table 3); CD 7359, a right proximal ulna (Fig. 2F, G); CD 038, a left ulna notch fragment. **Postcrania from Drimolen** described in O'Regan & Menter (2009):



FIG. 1. — Craniodental specimens of *Dinofelis* cf. *aronoki*: **A–C**, CD 19961 in buccal (**A**), lingual (**B**) and occlusal (**C**) views; **D**, maxillary fragment CD 7323b, c, d in buccal view; **E**, CD 7323b, c, d in occlusal view; **F**, buccal view of P4 fragment CD 7323a, associated with 7323b, c, d; **G**, CD 16765a+b, right premaxilla fragment with roots of I1–I3; **H**, upper canine fragment CD 16769a+b; **I**, **J**, CD 15696, an isolated P3, in lingual (**I**) and buccal (**J**) views; **K**, **L**, CD 18836, right mandible with P4 and M1 in buccal (**K**) and occlusal (**L**) views; **M**, **N**, CD 19265, left M1 in mandible fragment in buccal (**M**) and occlusal (**N**) views. Scale bars: 1 cm.

TABLE 1. — Measurements (in mm) of crania and maxillary dentition of all felid specimens from Cooper's D. Abbreviation: a, approximately.

Specimen number	Side	Taxon	C		P3			P4				—	
			L	B	L	B	Bant	L	Ba	Bbl	Lp	Lm	CB
CD 16769A+B	left	<i>D. cf. aronoki</i>	23.2	13.0	—	—	—	—	—	—	—	—	—
CD 19961	right	<i>D. cf. aronoki</i>	—	—	—	—	—	34.8	11.7	—	12.8	14.2	—
CD 7323	right	<i>D. cf. aronoki</i>	—	—	17.2	8.2	6.9	—	—	—	—	>14.4	—
CD 15696	right	<i>D. cf. aronoki</i>	—	—	a17.4	a8.4	a6.2	—	—	—	—	—	—
CD 3835	right	Machairodontinae indet.	—	—	a17.2	a8.2	—	—	—	—	—	—	—
CD 3691	both	<i>cf. P. pardus</i> (Linnaeus, 1758)	—	—	—	—	—	—	—	—	—	—	41.5
CD 3871	left	<i>A. jubatus</i> (Schreber, 1775)	—	—	—	—	—	a27.7	—	8.5	10.7	12.3	—
CD 691	left	<i>Felis s. lybica</i> Forster, 1780	5.78	4.4	—	—	—	—	—	—	—	—	—
CD 3258	right	Felidae indet.	—	—	11.0	5.3	3.8	—	—	—	—	—	—

TABLE 2. — Measurements (in mm) of mandibles and mandibular dentition of all felid specimens from Cooper's D. Abbreviation: a, approximately.

Specimen number	Side	taxon	P/3			P/4			M/1 cat				DEPTH		B	Dias-tema
			L	B	Bant	L	B	Bant	L	B	Lproto	Lpara	A	P	P/4	
CD 19265	left	<i>D. cf. aronoki</i>	–	–	–	–	–	–	26.9	11.9	16.4	13.8	–	–	–	–
CD 18836	right	<i>D. cf. aronoki</i>	–	–	–	21.8	9.4	7.6	a26.7	11.7	16.3	–	–	–	15.7	–
CD 1555	right	<i>cf. D. cf. aronoki</i>	–	–	–	–	–	–	–	–	–	–	29.5	–	–	>11.5
CD 10452	right	<i>M. whitei</i> (Broom, 1937)	–	–	–	–	–	–	–	–	–	a8.8	–	–	–	–
CD 1514	left	Machairodontinae indet.	–	–	–	–	–	–	a28.2	a9	–	–	–	32.1	–	–
CD 675	right	<i>Felis</i> sp.	5.2	2.8	1.7	–	–	2.3	–	–	–	–	7.9	–	4.8	>5.1

DN 15, left distal ulna; DN 720, left distal radius; DN 86, left distal radius; DN 772, left proximal second metacarpal; DN 2149a-c, associated right tibia, astragalus and calcaneum; DN 2092, left calcaneum; DN 2571, right navicular; DN 12, left second metatarsal; DN 17, left third metatarsal; DN 14, left fourth metatarsal; DN 18, left fifth metatarsal, lacking proximal articulation.

DESCRIPTION

Craniodental material

CD 19961 (Fig. 1A-C). Complete P⁴ that has been glued across the paracone-metastyle border. It is a good fix, with no misalignment, making measurements possible (Table 1). CD 19961 has a much reduced protocone, and a small ectoparastyle that is in line with the parastyle. The metastyle is not elongated, and has a small rounded area of enamel on its tip. The enamel is rugose.

CD 7323a, b, c, d (Fig. 1D-F). Series of associated right maxillary specimens. The dental specimens of a complete P³ and two fragments of a P⁴ were published by Lacruz *et al.* (2006), but their association with the maxillary fragment (CD 7323d) was not noticed at this time (Fig. 1D, E). Starting with CD 7323a+b (the P⁴) the central portion of the tooth is missing, leaving only the parastyle and metastyle. There is a large ectoparastyle with the cusp tip in line with the parastyle (Fig. 1D), and the metastyle is not elongated (Fig. 1F). In comparison with CD 19961, the ectoparastyle is larger in CD 7323 and although the end of the metastyle is curved, it is not as pronounced as CD 19961. CD 7323c is an isolated right P³ shown refitted into the maxilla in Fig. 1D, E. It is shown in Fig. 3 in Lacruz *et al.* (2006), but note that their caption is incorrect, as it says that it shows CD 3835, another isolated P³ from the site. The anterior accessory

cusps of CD 7323c are unusual, as it has two, both in line with the protocone and curving slightly linguallly. They are both smaller than the posterior accessory cusp. A tiny cusplet is also present on the anterior buccal surface, and there is a small cusp present on the tip of the posterior cingulum. The maxillary fragment (CD 7323d) comprises the anterior portion of the P⁴ alveolus, the full P³ alveolus (into which CD 7323c refits) and the edge of the canine alveolus. The edges of the diastema are worn, but it must have been very small (Fig. 1E). It is not possible to see if a P² was present. The pinch point of the maxilla is at the posterior root of the P³.

CD 16765a+b, CD 16769a+b, CD 15696, CD 18836, CD 19265 (Fig. 1G, H). These five craniodental specimens may be associated, based on their proximity to one another when recovered. CD 16765a+b is a right premaxilla with the roots of the I¹, I² and I³ (Fig. 1G). All incisors would have been large; the I³ is in two pieces, but was almost the size of a small leopard canine. The I¹ has a small accessory cusp on the medial lingual surface, but the rest of the crown is broken. CD 16769a+b is the central portion, including the enamel margin, of a large mediolaterally flattened canine with very strong keels on its labial and lingual surfaces (Fig. 1H). The keels clearly show that it is *Dinofelis*, and it is from a young animal, as the root was still open.

CD 15696 (Fig. 1I-L). Left P³, which, like CD 7323c, has an extra anterior accessory cusp, and a buccal cusplet. The anterior cusps are very low, and the cusps are slightly linguallly set (Fig. 1I, J). There is a strong posterior cingulum. The similarity of features between CD 7323c and CD 15696 suggest that they may be antimeres.



FIG. 2. — Postcranial specimens of *Dinofelis* cf. *aronoki*: **A, B**, right third metatarsal (CD 19953) in medial (**A**) and lateral (**B**) views; **C–E**, CD 3233, left tibia in lateral (**C**), medial (**D**) and superior views (**E**); **F, G**, CD 7359 right ulna fragment in lateral (**F**) and medial (**G**) views. Scale bars: 1 cm.

CD 18836 (Fig. 1K, L; Table 2). Lower left mandible broken vertically immediately prior to the P_4 , and just after the posterior portion of the M_1 . The P_4 is complete, with large accessory cusps, plus a small cusp on same orientation on the tip of the posterior cingulum. The protocone has two pinched grooves on the buccal surface effectively making the edges of the cusp more blade-like (Fig. 1K). The paraconid of the M_1 is damaged, but it can be seen that the tooth is deeply scooped out on the lingual surface (Fig. 1L). There is no talonid on the protoconid. The masseteric fossa is deep and ends just below the posterior of the M_1 , only the edge of the mental foramen can be seen, and it would have been under the posterior root of P_3 . The inferior lingual surface of the mandible is ridged.

CD 19265 (Fig. 1M, N; Table 2). Very slightly worn left M_1 fitting into a buccal fragment of ramus (Fig. 1M). There is a small bladelet on the anterior surface of the paraconid, and a slight curve on the posterior edge of the protoconid, but no evidence of a talonid. The lingual surface of the tooth is deeply scooped (Fig. 1N), in the classic *Dinofelis* pattern. The very shallow edge of the masseteric fossa is just visible, ending just below the back of the protoconid. If this series of specimens are associated, then CD 19265 is the antimere of the broken M_1 of CD 18836, however it is slightly larger than this specimen.

Postcranial material

CD 19953 (Fig. 2A; Table 3). Complete right 3rd metatarsal that closely matches DN 17, an MT3 identified as *Dinofelis* from Drimolen (O'Regan & Menter 2009). The only differences between the two specimens are that in CD 19953 the proximal facet curves a little more onto the anterior surface (Fig. 2A) and the epicondyles are larger. It also appears similar to KNM-ER 722T (identified as *D. piveteaui* (Ewer, 1955) in Werdelin & Lewis 2001: fig. 20) except that the anterior is curved in CD 19953, while it appears straight in the Kenyan specimen.

CD 3233 (Fig. 2C–E; Table 3). Left proximal tibia with $\frac{1}{3}$ of the shaft. There is a large protuberance on the lateral surface of the proximal articulation (Fig. 2E), and a deep fossa below the facets on the posterior surface. The fibular facet is large (Fig. 2C). Overall it looks very like DN 2149a (*Dinofelis*), except that this is from a smaller individual, and the muscle markings on the rear of the shaft are even more pronounced in CD 3233.

CD 7359 (Fig. 2G). Right proximal ulna fragment that is broken across the notch. It is broadened posteriorly and there is a deep fossa proximal to the notch on the medial surface (Fig. 2G), noted by Werdelin & Lewis (2001) as a characteristic *Dinofelis* trait. CD 038 is a left ulna notch fragment, which

is also posteriorly broad with a fossa on the medial surface. It is from a slightly larger individual than CD 7359, but is otherwise a good match and has been assigned to *Dinofelis* cf. *aronoki*.

COMPARISONS

Craniodental comparisons are undertaken on a tooth-by-tooth basis, starting with the upper dentition.

Incisors

There is little morphology left on the premaxilla with damaged incisors (CD 16765a+b), however, it can be seen that there was a small medial accessory cusp on the I¹, and that the I³ was very large. Overall, it is slightly smaller than the holotype of *D. piveteaui* (KA 61).

Canines

The upper canine is very mediolaterally flattened, and very slightly (1 mm) larger than that of KA 61.

Upper P³

CD 7323c and CD 15696 are both shorter with more reduced and slightly more lingually placed anterior accessory cusps than P³s of *Dinofelis piveteaui* (KA 61 and MT 06/07). In this way they are more similar to DN 780 from Drimolen. It is possible that the two Cooper's specimens are antimeres, but they were found 10 metres apart in the deposit. The lingual bulge finishes at the junction between the protocone and anterior accessory cusp in CD 7323c and CD 15696, while in KA 61 and MT 06/07 it finishes about halfway along the protocone. In both CD 7323c and CD 15696 there is an extra, very low, anterior accessory cusp, so there are two before the protocone in both specimens. There is also an extra anterior accessory cusp visible in Motsetse specimen MT 06/07, but in this case it is a small and very sharp cusp in line with the others. Both CD 7323c and CD 15696 have tiny extra cusplets on the buccal surface, a feature that is also seen in *Dinofelis piveteaui* from Kromdraai (KA61) and Motsetse (MT 06/07), but not in *D. barlowi* (Broom, 1937) (BF 55-23). The anterior accessory cusps of KNM ER 2612 (*D. petteri* Werdelin & Lewis, 2001) and KNM ER 3880 (*D. aronoki*) are also small and lingually placed, but they do not have any additional cusps or cusplets (J. Kibii pers. comm.). The posterior cingulum is present but small with a cusp on the tip in CD 7323c and CD 15696. The posterior cingulum with small cusp is also present in *D. petteri* specimens (KNM-ER 2612 and KNM-ZP 444) and the *D. aronoki* type specimen (KNM-ER 3880) but is almost absent in MT 06/07 (*D. piveteaui*).

Upper P⁴

The two Cooper's D upper P⁴s differ slightly. CD 19961 has a tiny protocone and all the cusps are aligned in a row like *D. piveteaui*, yet the metastyle is not elongated. The ectoparastyle is present and distinct, but not as clear as that of CD 7323a+b which is much larger. The type specimen of *D. aronoki* (ER-3880) lacks an ectoparastyle, while in *D. petteri* it appears variable (ER 2612 lacks an ectoparastyle, and

KNM-ZP 444 has a small, centrally placed cusp in line with the parastyle [J. Kibii pers. comm.]). The lack of an ectoparastyle in *D. aronoki* marks a difference between this species and the southern African specimens and *D. piveteaui*, but it is a variable trait. O'Regan (2002) found that in a sample of 30 modern jaguars (*Panthera onca*), 25 had an ectoparastyle but it was only present in one out of 20 leopards. The metastyle is not elongated in CD 7323a+b, DN 1012 nor in *D. aronoki* (ER 3880) or *D. petteri* (ZP 444). The protocone is missing from CD 7323a+b, is small in CD 19961, and slightly larger in DN 1012. Unfortunately the protocone is broken in *D. aronoki* (KNM-ER 3880), and both *D. petteri* specimens (ER 2612, ZP 444) have a larger protocone than CD 19961. Turner (1987a) highlights the double ogival curve of the anterior edge of the paracone in *Dinofelis barlowi* and its absence in *D. piveteaui*. This feature is not present in CD 19961, DN 1012 or *D. aronoki*. The comparative metrics of African *Dinofelis* P⁴s are shown in Figures 3 and 4. Fig. 3 demonstrates that metrically the Cooper's D tooth is narrower across the protocone than all other recorded specimens, while Fig. 4 shows that the metastyle is not elongated like that of *D. piveteaui*, falling instead with *D. barlowi* and *D. aronoki*.

Maxilla

The postcanine diastema is short in both CD 7323d and DN 1012, making them most similar to *D. piveteaui* and *D. petteri*. Both Cooper's D and Drimolen specimens are slightly damaged, but their diastemas would have been no more than c. 5 mm, while that of *Dinofelis aronoki* (KNM-ER 3880) appears to have been at least 1 cm (based on photographs although the specimen is distorted) and *D. barlowi* (BF 55-22) approximately 11 mm (O'Regan & Menter 2009). The maxilla of CD 7323d is pinched at the posterior root of the P³, while in *D. aronoki* (KNM-ER 3880) it appears to be pinched prior to the P³ (although it is heavily reconstructed), and in DN 1012 and KA 61 it is pinched at the anterior root of the P³ (O'Regan & Menter 2009).

Lower P⁴

There is one P⁴ from Cooper's D, in the partial mandible CD 18836. In comparison with KA 62 and MT 03 (both *Dinofelis piveteaui*), the Cooper's D specimen is intermediate in size between the two. KA 62 is more robust and the cusps are clearer and larger, while in MT 03 they are lower and more rounded. They also lean slightly lingually, while those of CD 18836 are more upright, but the protocone and anterior accessory cusp are slightly backwards sloping. In KA 62 the anterior cusp is almost directly at the edge of the tooth, while in CD 18836 it is set very slightly back. The anterior portion of CD 18836 is much narrower than the posterior portion, this is also seen in MT 03 (*D. piveteaui*), KNM-ER 3880 and ER 1549 (both *D. aronoki*), but not in the other specimens available for study (*Dinofelis barlowi* [BF 55-23], *D. piveteaui* (KA 62) and *D. darti* (Toerien, 1955) [M 607]). The P⁴ of CD 18836 has a very strong posterior cingulum, which is also seen in KA 62 and MT 03, and ER 1549 (a mandible identified as *D. aronoki* [Werdelin & Lewis 2001]), but not in the other specimens.

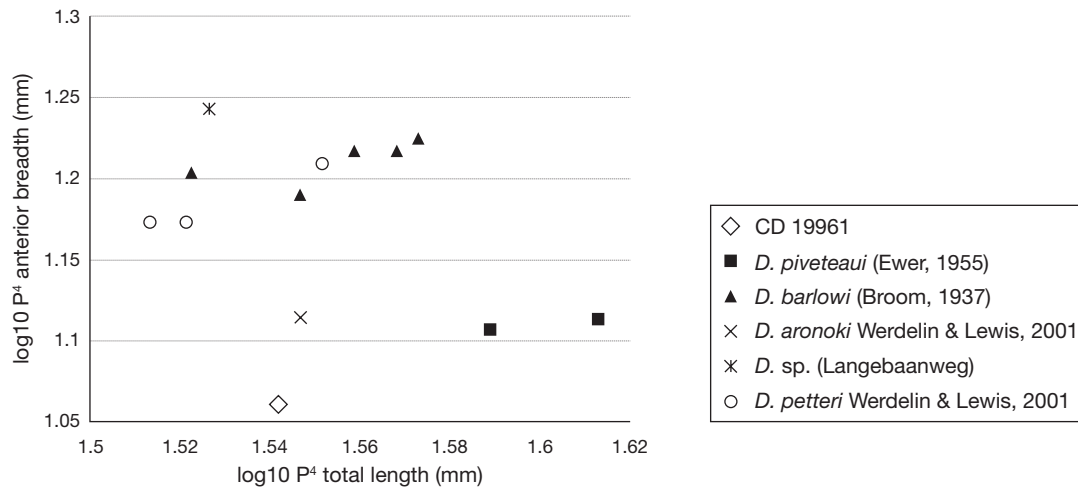


FIG. 3. — Log10 total length of P⁴ plotted against anterior breadth at the protocone of the P⁴ for six African *Dinofelis* Zdansky, 1924 species. Data from Werdelin & Lewis (2001), Lacruz *et al.* (2006) and this study.

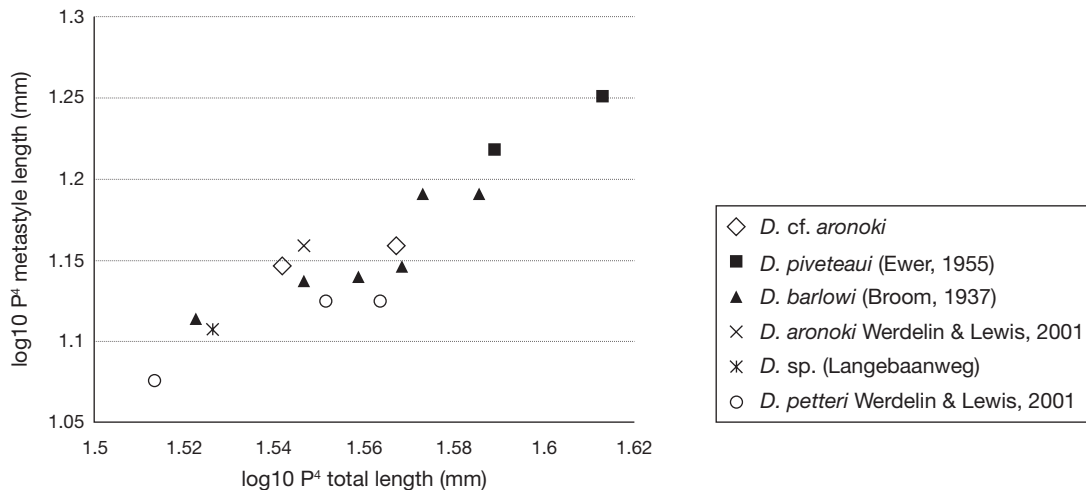


FIG. 4. — Log10 total length of P⁴ plotted against metastyle length of the P⁴ for six African *Dinofelis* Zdansky, 1924 species. Data from Werdelin & Lewis (2001), Lacruz *et al.* (2006) and this study.

Lower M₁

Two lower M₁s have been recovered from Cooper's D, both contained in ramus fragments – CD 19265 and CD 18836. These M₁s are deeply scooped out, making the cusps appear concave on the lingual surface. They closely match the *D. piveteaui* lower M₁ in mandible KA 63 in size and morphology, the only slight difference is that the talonid bulge is slightly more obvious in KA 63 than in CD 19265, and no talonid is visible in CD 18836. We have observed that the protoconid is considerably longer than the paraconid in the Cooper's D specimens, but there are few comparable specimens complete enough to metrically test this feature against other taxa. This elongation of the protoconid is also seen in ER 1549 (*D. aronoki*), but not in *D. petteri* (KNM-KP 30397) or ER 3880 (*D. aronoki*).

Ramus morphology

In CD 18836 the masseteric fossa is deep and ends just below the posterior of the M₁. The broken edge of a men-

tal foramen can be seen, and would have been under the posterior root of P₃. The lingual inferior surface is ridged, a feature that is not seen in SK 335 (identified as *Dinofelis* sp.), or KNM-KP 30397 (*D. petteri*), but is present in ER 3880, and may have been present in ER 1549, but this area is damaged.

DISCUSSION OF *DINOFELIS* REMAINS

Overall, the material from Cooper's D is similar to both *Dinofelis piveteaui* and *Dinofelis aronoki*. The specimens from Cooper's D and Drimolen have a clear ectoparastyle on the P⁴, and an elongated protoconid on the M₁. Both these features differentiate this material from the type of *D. aronoki* (ER 3880). On the other hand the material differs from *D. piveteaui* as the metastyle of the P⁴ is not elongated, although the protocone is greatly reduced. Overall, the similarities of the Cooper's D and Drimolen specimens are to *D. aronoki* rather than *D. piveteaui* and have here been referred to that species. However,

we note that the mandible ER 1549 from the Upper Burgi member, Koobi Fora, referred to *D. aronoki* by Werdelin & Lewis (2001), appears to be more similar to the Cooper's material than it does to the type specimen of *D. aronoki* (ER 3880). The possibility that the variability seen in the Upper Burgi material might represent two species was noted by Werdelin & Lewis (2001: 234), but the material was not sufficient to make a distinction at the time. While we cannot be certain of intra-specific variability within *Dinofelis* species, owing to an overall paucity of material at any one site, these differences in the carnassials between the type material of *D. aronoki* and the material referred here to *D. cf. aronoki*, may be significant, and it is possible that the new South African material represents a new species which cannot be diagnosed on the available material. We therefore refer it to *D. cf. aronoki*, pending the discovery of further material, when further work may shed light on the evolution of these late machairoidont species in Africa.

Genus *Dinofelis* Zdansky, 1924

cf. Dinofelis aronoki

MATERIAL EXAMINED. — **Cranial.** CD 1555, right anterior mandible fragment from symphysis to P₃ alveoli (Table 2). CD 15660, two refitting I² crown fragments.

Postcranial. CD 670, a damaged right MT4 (Table 3); CD 650, a right MT 4 shaft fragment; CD 3284, a 1st phalanx; CD 1195, a dew claw 1st phalanx; CD 979, a 3rd phalange; CD 3881, a left distal tibia (Table 3); CD 5674, a right unciform; CD 654, a right femoral head (Table 3); CD 3712 + CD 5972, two refitting pieces of a right distal radius (Table 3).

DESCRIPTION

CD 1555 is an edentulous right mandible fragment, with the lower portion of the symphysis present, retaining the alveoli of the I₃ and C_i, plus the complete diastema and both alveoli for the P₃. There is a small symphyseal bulge, but it is clearly not a flange with a near vertical ramus, as seen in *Megantereon whitei* from the same site (CD 5997; Fig. 5B). There is a single, very large, mental foramen below the anterior root of the P₃. The inferior border of the mandible is straight. There is a distinct dip on the lingual surface of the ramus that is also seen in CD 18836 (*Dinofelis cf. aronoki*) and M607 (*D. darti* from Makapansgat) and is much less pronounced in leopard. CD 15660 is a fragmentary I² in two pieces; it has a large central cusp and a pronounced accessory cusp, with a tiny worn extra cusplet between the two. It matches well with KA 61 (*Dinofelis piveteaui* from Kromdraai A), although a slight ridge leads from the accessory cusp to the lingual surface, which is not as pronounced as that of KA 61.

Postcrania

CD 3712 and CD 5972. Two refitting right distal radius fragments. The bone is intermediate in size between lion and

leopard, with a narrower articulation (anterior-posterior) than is seen in leopard. The ulnar facet is very large and placed slightly off-centre with strong ridges above it. It is similar to, but smaller, than DN 86 a *Dinofelis* specimen from Drimolen. However, the distal facet is more rectangular in the Coopers specimen and the ridge along the fusion line is not so distinct. It is therefore assigned to *cf. Dinofelis*.

CD 5674. Complete right unciform. It is not from a pantherine cat. It matches an unnumbered *Dinofelis* specimen from Makapansgat in size and in the length of the distal facet, although the anterior surface is a slightly different shape. It also matches KNM-ER 722I, *Dinofelis piveteaui*, illustrated in Werdelin & Lewis (2001: fig. 19). It is therefore assigned to *Dinofelis*.

CD 1195. Complete first dew claw phalanx, which appears to have been slightly gnawed. There are two clear and equally-sized lobes to the proximal articulation and has a distinct protuberance on the dorsal surface. In lion the proximal articulation is not so defined, and in *Homotherium* (as shown by Ballesio 1963) one facet is smaller than the other. It is most like an unnumbered *Dinofelis* sp. specimen from Makapansgat, and it has therefore been referred to that genus.

CD 654. Right proximal femoral head broken across the neck. The articulation continues onto the neck a little, a feature that is not seen in the extant cats, but is seen in Makapansgat *Dinofelis* specimen 16190M. The articulation also extends onto the neck in *Megantereon whitei*. However, the head is not as rounded in *Megantereon* Croizet & Jobert, 1828 KB 5333L as it is in CD 654, and it has therefore been assigned to *Dinofelis*. CD 3881 is a distal tibia, broken just above the articulation. The distal articulation is broader than that of the leopard, and the shaft of *Megantereon* is more triangular rather than squared as in this specimen. It is a good match for DN 2149a, *Dinofelis* from Drimolen, but it is from a smaller animal. CD 670 and CD 650 are *Dinofelis*-sized right 4th metatarsals. CD 670 is almost complete, but the proximal articulation is large missing. CD 650 is a shaft fragment with the beginnings of the proximal articulation. Both are much more robust than leopard, and have similarities to DN 14 from Drimolen, however there are some slight differences in the position of the remaining facets, so they have been assigned to *cf. Dinofelis aronoki*. CD 3284 is a complete first phalanx, which is a good match for KB 6037 (*Dinofelis* sp.). It is slightly shorter than this specimen, but has a slightly flattened shaft and the same dip on the dorsal surface between the condyles. CD 979 is a large felid third phalanx. It is too small for *Homotherium* (if the unnumbered Makapansgat specimen is *Homotherium*, as suggested by Werdelin & Lewis [2001: 190]), and is a good size match for an unnumbered *D. darti* paw that is also from Makapansgat.

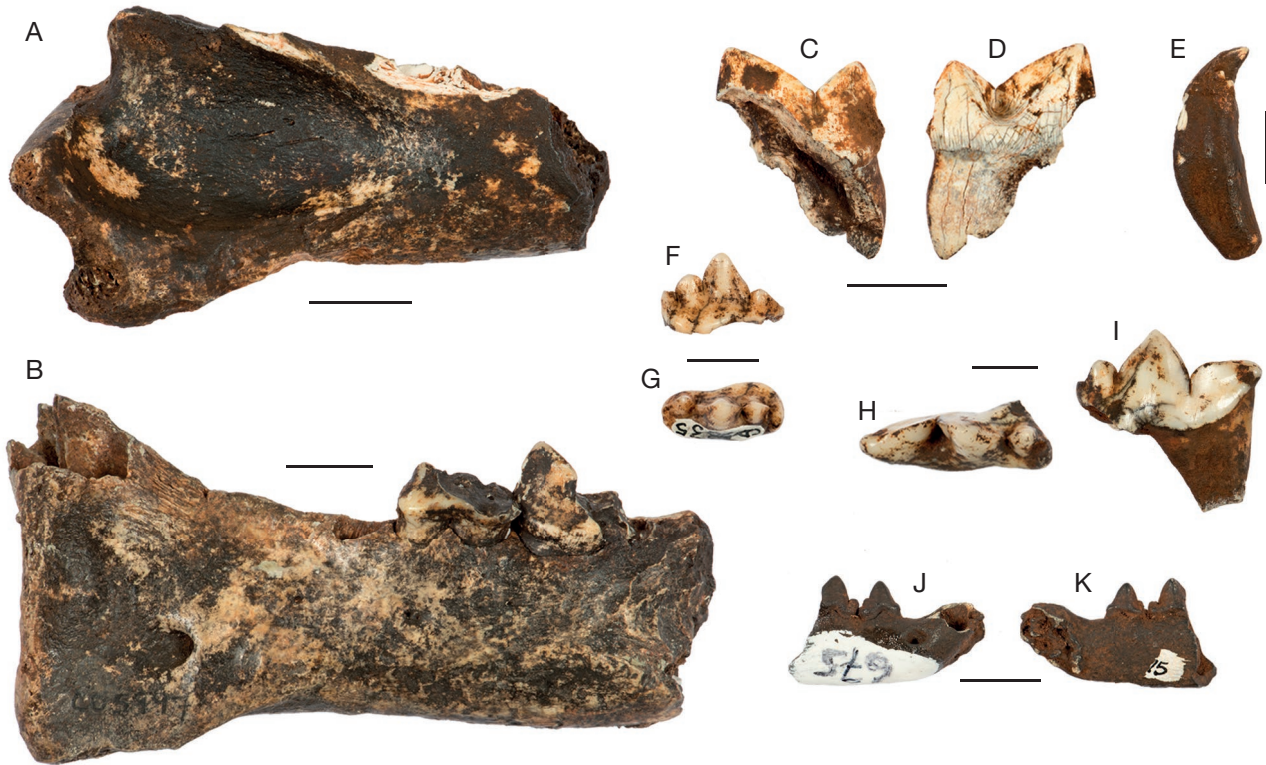


FIG. 5. — Craniodental felid specimens; **A–D**, *Megantereon whitei* (Broom, 1937); **A**, CD 5963, buccal view of right mandible; **B**, CD 5997, buccal view of left mandible; **C**, **D**, CD 10452 in buccal (**C**) and lingual (**D**) views of lower M_1 ; **E**, cf. *Megantereon whitei*, CD 10497, left upper I^3 with two cusplets on medial surface; **F**, **G**, Machairodontinae indet., CD 3835, right upper P^3 in lingual (**F**) and occlusal (**G**) views; *Acinonyx jubatus* (Schreber, 1775), CD 3871, left upper P^4 lacking protocone in occlusal (**H**) and lingual (**I**) views; **J**, **K**, *Felis* sp.: CD 675, right mandible with lower P_3 and partial P_4 in buccal (**J**) and lingual (**K**) views. Scale bars: 1 cm.

Genus *Megantereon* Croizet & Jobert, 1828

Megantereon whitei (Broom, 1937) (Fig. 5)

MATERIAL EXAMINED. — **Craniodental.** CD 5963, right posterior mandible fragment with M_1 roots (Fig. 5A); CD 5997, left mandible from symphysis to M_1 (Fig. 5B, and see Hartstone-Rose *et al.* 2007); CD 10452, damaged right M_1 (Fig. 5C, D; Table 2); **Postcranial:** CD 3221, left proximal tibial epiphysis; CD 7336, left navicular; CD 5978, right navicular.

DESCRIPTION AND TAXONOMIC ASSIGNMENT

The three craniodental specimens are clearly attributable to *Megantereon* (Fig. 5A–D). The most complete, CD 5997, is shown in Fig. 5B and fully described by Hartstone-Rose *et al.* (2007). The other two specimens are also from the lower jaws.

CD 5963 is a posterior fragment of mandible, broken horizontally above the condyle and also anterior to the M_1 alveolus (Fig. 5A). The masseteric fossa is shallow and extends to the posterior root of the M_1 , but the most notable feature is the very small distance (22 mm) between the angle of the ramus and the condylar process. The coronoid process must have been correspondingly small, and this indicates that the specimen can only have belonged to a very small machiariodont. CD 5963 is of similar size to CD 5997, although the carnassial in CD 5963 may have been

slightly larger. CD 10452 is an unworn M_1 that is broken across the protoconid (Fig. 5C, D). The paraconid is small (length: 8.7 mm) with a relatively larger protoconid. It is much smaller than KA64, and is most similar to the heavily damaged type specimen of *Megantereon whitei* (TM 856) from Schurveberg (Broom 1937; Turner 1987b). In contrast, both the P_4 and M_1 of CD 5997 are smaller than those of TM 856. As discussed by Hartstone-Rose *et al.* (2007) the previously known *Megantereon whitei* material from Cooper's D is very small, and these specimens fit within that hypodigm. They most closely fit with the morphology of the type specimen of *M. whitei*, and there is growing consensus that *M. whitei* is the only Pleistocene species of the genus *Megantereon* in Africa (Palmqvist *et al.* 2007; Werdelin & Peigné 2010). Therefore the Cooper's D specimens are assigned to this species.

Three postcranial specimens have also been assigned to *M. whitei*. An isolated proximal epiphysis from a left tibia with some damage to the ventral edge (CD 3221) is an excellent match for KB 5333M, a partial skeleton of *Megantereon whitei* published by Vrba (1981). The two navicularae (CD 7336 and CD 5978) may be antimeres and are very similar to the illustrations of *M. cultridens* (Cuvier, 1824) from Senéze (Christiansen & Adolfsen 2007) and KB 6018 (*Megantereon whitei*). In comparison with DN 2571 (here referred to *D. cf. aronoki*) the two Cooper's D navicularae are smaller, not so thick and have less clearly defined facets.

cf. *Megantereon whitei*

MATERIAL EXAMINED. — **Craniodental.** CD 10497, left I³ (Fig. 5E). **Postcranial.** CD 1415, right tibia (Table 3); CD 1156, right 2nd Metatarsal, CD 3268, left 2nd Metatarsal (Table 3).

DESCRIPTION AND TAXONOMIC ASSIGNMENT

CD 10497 is a complete I³ that closely matches KA 64, a crushed *Megantereon* cranium from Kromdraai A. However, CD 10497 has two cusps on the medial surface (Fig. 5E) rather than the one seen in KA 64. It is most likely that this is simply an aberrant individual, but for this reason the specimen is assigned cf. *Megantereon whitei*. CD 1415 is the damaged distal portion of a tibia, with the epiphyseal fusion line still visible. The shaft is rounded in cross-section, like that of KB 5333T (*Megantereon whitei*), while those of *Dinofelis* (DN 2149a and 16201M) are much more triangular. The distal articulation is broad and there are two sections to the fibula facet, like that of KB 5333T. Overall it is most like KB 5333T and is therefore assigned to cf. *Megantereon*. CD 1156 is a right 2nd metatarsal, lacking the distal condyle and with some damage to the proximal articulation. The shaft is less rounded than that of a modern leopard (AZ 1063), but is similar to that of KB 5339A, and the position and shape of the MT3 facets match those of the *Megantereon* specimen. However, it is substantially smaller than KB 5339A, hence its referral as cf. *Megantereon*. CD 3268 is a proximal left 2nd metatarsal and half of the shaft. The proximal articulation is extended dorsally, behind the main facet. This extension is also seen in *Megantereon* (KB 5339A) but not in leopard or puma. It is therefore assigned to cf. *Megantereon*.

MACHAIRODONTINAE indet.

MATERIAL EXAMINED. — **Cranial.** CD 3835, right P³ (Fig. 5F-G; Table 1); CD 1514, left posterior mandible fragment with M₁ roots in alveoli (Figured in Lacruz *et al.* 2006: fig 5; Table 2).

Postcranial. CD 1368, right unciform; CD 7708, left unciform; CD 717, left proximal 2nd Metacarpal (Table 3); CD 1500, right proximal 2nd Metacarpal (Table 3); CD 1524 right proximal 3rd Metacarpal (Table 3); CD 5703, left proximal 3rd Metacarpal (Table 3); CD 7354, right proximal 4th Metacarpal (Table 3); CD 3271, complete right 5th Metacarpal (Table 3); CD 682, left proximal 5th metacarpal (Table 3); CD 1501, 1st phalanx fragment.

DESCRIPTION AND TAXONOMIC ASSIGNMENT

CD 3835 (Fig. 5F, G) is a P³, published by Lacruz *et al.* (2006) as *Dinofelis* sp., but note that this is not the tooth shown in their figure 3 (the specimen numbers were transposed and their figure 3 shows CD 7323c, a clear *Dinofelis* tooth). CD 3835 is highly likely to be from a machairodont, but the morphology differs from the other *D.* cf. *aronoki* specimens and the possibility that it is *Megantereon* cannot be excluded. CD 1514 is an edentulous mandible fragment, broken at the P₄ and lacking the mandibular angle and top portion of the ascending ramus. The M₁ alveolus is very large, longer than CD 18836 (a complete M₁), yet the ramus itself is very shallow. The edges of the alveolus are very sharp, perhaps

suggesting some sort of infection, which may have increased the alveolar margins slightly. Alternatively, it may just be remodelling following the eruption of the tooth. The inferior margin of the ramus is curved, and there is no sign of the lingual ridge that is present in CD 18836 and M 607 (*D. darti* from Makapansgat). It is apparent that the M₁ roots were not complete, indicating that this was a young animal at death. This specimen was published as *Dinofelis* sp. by Lacruz *et al.* (2006), but the shallow mandible in combination with the size of the carnassial makes this assignment doubtful. It is not *Megantereon*, as it is too large, and the inferior margin of the ramus is curved rather than straight. The alveolus would fit the Motsetse *D. piveteaui* carnassial, but is much longer than any other *D. piveteaui* or *D. barlowi* specimen. However, in KA 63, the inferior border of the ramus is straighter than CD 1514, and the shape of the masseteric fossa is very different. It is clearly from a young animal, which makes assignment to species difficult and the possibility that it is a young *Homotherium* cannot be excluded. It has therefore been referred to Machairodontinae indet.

Ten postcranial specimens are also assigned to Machairodontinae indet. Unciforms CD 1368 and CD 7708 appear to be antimeres and are smaller than a modern leopard, but are larger and different to caracal. An unnumbered *Dinofelis* unciform from Makapansgat is much squarer and slightly more twisted than the Cooper's specimens. They are very similar to the inner view of the Senéze *M. cultridens* specimen figured in Christiansen & Adolfssen (2007: fig. 19M), but differ from the outer view of the same bone (2007: fig. 19N), for this reason they are assigned as Machairodontinae indet. Four right metacarpals CD 1500, CD 1524, CD 7354 and CD 3271 refit to form the proximal portion of a front foot, referred to here as 'the paw'. All four specimens in the paw are slightly smaller and have proximal articulations that are narrower medio-laterally than is seen in the modern leopard, puma and cheetah. They are much more gracile than specimens assigned to *Dinofelis* and appear similar to the Senéze *Megantereon cultridens* material illustrated in Christiansen & Adolfssen (2007). They are also slightly more gracile than KB 5333U, the only metacarpal assigned to *Megantereon* that is available for comparison. As the craniodental *Megantereon* material from Coopers shows that it is a small cat, perhaps gracility in the postcrania is also to be expected, but in the absence of better comparative material they are here assigned to Machairodontinae indet., with the recognition that they may be *Megantereon*. CD 717 is a leopard-sized 2nd metacarpal that is slightly more robust than the 'paw' (Table 3), but less robust than KB 5333U (*Megantereon*). There are minor differences in morphology between it and CD 1500, but they are much more similar to each other than to any other specimens. CD 5703 is a proximal 3rd metacarpal that is very similar to CD 1524 and is clearly not leopard or cheetah. CD 682 is a proximal left 5th metacarpal that is very similar to CD 3271, but also similar to Makapansgat specimen '14' identified as *Dinofelis*. CD 1501 is the proximal part of a dew claw first phalanx. It has two clear proximal facets, while lion and leopard have

only one. It is larger than the cheetah and is therefore most likely to be machairodont.

Subfamily PANTHERINAE Pocock, 1917
Genus *Panthera* Oken, 1816

Panthera leo (Linnaeus, 1758) (Lion)

MATERIAL EXAMINED. — Postcranial: CD 10783 a right 1st Metacarpal; CD 3879 and CD 10814 both 1st phalanges.

DIAGNOSIS AND DISCUSSION

CD 10783 is a very large 1st metacarpal. Illustrations of *Dinofelis piveteaui* (Werdelin & Lewis 2001: fig. 19G) and *Homotherium* (Ballesio 1963) show that the facet for the 2nd metacarpal is medially placed in these machairodonts while in CD 10783 and the pantherines it covers much of the proximal surface. In the three lion MC1s available for comparison, it closely matches AZ 771, except that the fossil is from a larger animal (total length = 44.3 mm, distal breadth 18.3 mm), although it differs from BPlc186 and AZ 421 (also lions). CD 3879 is slightly damaged proximally and CD 10814 is complete. They are both from large, lion-sized felids, although the depressions on the medial and lateral sides of the distal articulation are much deeper than those seen in the modern lion. They are considerably larger than the phalanges identified as *Dinofelis* from Kromdraai B (KB 6036, KB 6037, KB 6038) and do not appear to be *Homotherium* (Ballesio 1963). These specimens are all referred to *Panthera leo*, but note comments below regarding large pantherines in Africa.

Panthera cf. P. leo

MATERIAL EXAMINED. — CD 8282, left 5th metatarsal (Table 3).

DIAGNOSIS AND DISCUSSION

CD 8282 is a very large pantherine metatarsal. There are minor morphological differences between CD 8282 and the modern lions – the proximal articulation is more ventrally placed in the fossil, and the MT4 facet is round in CD 8282 and more oval in the lion. However, it is clearly not *Homotherium* spp., as it lacks the distinctive rectangular proximal articulation that are seen in that genus, and it is almost twice the size of the Drimolen *Dinofelis* specimens. Broom (1948) designated a large pantherine canine of uncertain provenance (either from Bolts Farm or Sterkfontein) as *Felis shawi* Broom, 1948, and Ewer (1956) referred some large lion-like specimens from Kromdraai A to *Panthera ?shawi*. Turner (1986) examined fossil lion material from Sterkfontein and Swartkrans and indicated that the South African fossil lions were larger than their modern conspecifics and similar in size to the Middle and Late Pleistocene lions from Europe. However, Geraads (2008; 2016) discusses the possibility of a large, non-lion pantherine in

North Africa, and it is also possible that the large Cooper's specimen represents this taxon.

Panthera pardus (Linnaeus, 1758)
(Leopard)

MATERIAL EXAMINED. — **Postcranial.** CD 3277, left proximal radius (Table 3); CD 7369, left radius – distal epiphysis only (Table 3); CD 1526, right ulna – distal epiphysis only; CD 1956, patella; CD 5957, 3rd Metatarsal (Table 3); CD 3836, 4th Metatarsal (Table 3); CD 8288, and CD 1537, both 1st phalanges.

DESCRIPTION AND TAXONOMIC ASSIGNMENT

Forelimb

CD 3277 is a proximal radius. It is smaller than the East African *Dinofelis* specimens illustrated in Werdelin & Lewis (2001) although the angle between the shaft and head is similar. The Kromdraai *Megantereon* radii (KB 5333O and KB 5336) are both larger and have a more robust radial tuberosity than is seen in CD 3277. A distal radial epiphysis (CD 7369) has a large ulnar facet, indicating that it is not a cheetah, and overall shape of the carpal facets is squarish, whereas it is more rectangular in *Dinofelis* and *Megantereon*. Morphology of the radius, both proximally and distally appears to be quite variable in modern leopards, particularly the outline and depth of the proximal articulation, but CD 3277 and CD 7369 are both most similar to modern leopards. An isolated distal epiphysis from a right ulna (CD 1526) is also assigned to *P. pardus*, as the styloid process in *Dinofelis* is much more bulbous and *Dinofelis* is larger overall.

Hindlimb

CD 1956 is a tear-drop shaped patella with some damage to the dorsal surface. It is substantially smaller than KB 5377, a patella described as cf. *Megantereon* from Kromdraai B. No *Dinofelis* patellae were available for study, but CD 1956 is very similar to a modern leopard (AZ 420) and is therefore been referred to that species. Two metatarsals have also been referred to *P. pardus*. CD 5957 is a complete right 3rd metatarsal, broken into three pieces. It is very gracile in comparison with *Dinofelis*, of a similar length but slenderer. The posterior facet of the MT4 articulation is curved, in DN17 it is not curved, while in KB 5334B (*Megantereon whitei*) it is flat and angled medially. Again the morphology of the leopards appears to be highly variable, but for a medium-sized felid this specimen is much more like *P. pardus* than any of the other similar sized species. CD 3836 is the proximal articulation plus 1/3rd of the shaft of a left 4th metatarsal. It has some slight pathological bone growth on the dorsal surface and the articulation for the 5th metacarpal. Despite this it is clear that it is neither *Dinofelis* nor *Megantereon* – *Dinofelis* (DN 14) has a much more rounded articulation for the 3rd metatarsal, while this articulation is flatter and the proximal articulation is a little larger in *Megantereon* (KB 5339C). CD 1537 is a complete 1st phalanx with a small chip from the dorsal surface, while CD 8288 has a small amount of damage on the distal condyle. Both are very good matches for modern leopard.

cf. *Panthera pardus* (Linnaeus, 1758)
(Leopard)

MATERIAL EXAMINED. — **Craniodental.** CD 701, left C₁; CD 16744, I₂; CD 9602, I₃; CD 6210, I₃; CD 3691, posterior portion of cranium (Table 1). Postcranial: CD 6672 + CD 6673, refitting fragments of a right distal femoral epiphysis; CD 2053, left distal femoral epiphysis; CD 5996, humerus, proximal diaphysis only.

DIAGNOSIS AND DISCUSSION

These specimens are all leopard-sized. CD 701 is the enamel cap of a lower canine, there is no dentine infill and the crown is completely unworn, indicating it was unerupted. The crown is unkeeled (so it is not *Dinofelis*) and has one lingual groove near the tip, but it is small in comparison with modern leopards. CD 16744 is a small and heavily worn left I₂ with pyrolusite encrustation. CD 6210 is a broken and worn right I₃ with pyrolusite encrustation. The crown is strongly curved with a clear internal cingulum. CD 9602 is a large left I₃ with a possible accessory cusp. It is slightly narrower medio-laterally than a modern leopard (AZ 420) and also lacks the internal cingulum. CD 3691 is the posterior portion of a cranium, with both auditory bullae, both occipital condyles, and a small portion of the sagittal crest. CD 6672 and CD 6673 are refitting fragments of a right distal femoral epiphysis. They are the same size and morphology as CD 2053, a left distal femoral epiphysis, suggesting that they may be antimeres. They are good, but not exact, matches for *Panthera pardus*, however there were no distal *Megantereon* femora available to compare them with. CD 5996 is a humeral diaphysis in three pieces, it is entirely unfused and is a good match for a male leopard of similar age (AZ 420), however the medial ridge appears much more pronounced in the modern specimen.

Subfamily FELINAE Fischer, 1817
Genus *Acinonyx* Brookes, 1828

Acinonyx jubatus (Schreber, 1775)

MATERIAL EXAMINED. — **Craniodental.** CD 3871, left P₄ (Fig. 5H, I; Table 1); CD 9614 left I₃.

DIAGNOSIS AND DISCUSSION

CD 3871 is an almost complete P₄, just lacking the mesial border of the protocone. Despite this it can be seen that the protocone was much reduced in comparison with the pantherines. The ectoparastyle is very large, in contrast to *Megantereon* where there is no ectoparastyle (Christiansen & Adolfssen 2007; KA 64 pers. obs.). Other than the protocone being slightly more anteriorly placed in CD 3871 it is a very good match for the modern cheetah. The isolated lower incisor CD 9614 has a clear accessory cusp on the buccal surface and is a robust tooth with a relatively short crown. Other than the slight difference in the protocone position on the P₄, the Cooper's D specimens match those of the modern cheetah, and are referred to this species.

Genus *Caracal* Gray, 1843

Caracal caracal (Schreber, 1776)
(Caracal)

MATERIAL EXAMINED. — CD 9172, a left 1st metacarpal.

DESCRIPTION AND TAXONOMIC ASSIGNMENT

This specimen is complete, but heavily encrusted with pyrolusite. From the size (total length = 18.5 mm) and visible morphology it is a good match for caracal. Note that the specimen (CD 324) tentatively identified as a lower carnassial of a caracal in Berger *et al.* (2003) is the posterior portion of a very heavily damaged P₄ and is not identifiable.

Genus *Felis* Linnaeus, 1758

Felis silvestris lybica Forster, 1780
(African wild cat)

MATERIAL EXAMINED. — CD 691, left CS (Table 1).

DESCRIPTION AND TAXONOMIC ASSIGNMENT

This is a small upper canine with a broken tip. One lingual and two buccal grooves are visible in the enamel, it is clearly a small felid and based on its size, it is most likely to be *F. s. lybica* the African wildcat.

Felis sp.

MATERIAL EXAMINED. — CD 675, anterior fragment of right mandible with canine alveolus, P₃ and damaged P₄ (Fig. 5J, K; Table 2); CD 17790, proximal right femur and half shaft.

DESCRIPTION AND TAXONOMIC ASSIGNMENT

CD 675 is a right mandible fragment from a very small felid (Fig. 5J, K). The anterior portion of the mandible is present, including a damaged canine alveolus, complete P₃ and a damaged P₄. There are two mental foramina, one is large and halfway along the symphysis, while the other is much smaller and situated below the anterior root of the P₃. The P₄ is broken vertically after the protocone, and the corpus of the mandible is also broken here. The P₃ lacks an anterior accessory cusp and has almost no anterior cingulum, although the posterior accessory cusp and posterior cingulum are present. The P₄ has a well-defined anterior accessory cusp but also lacks the anterior cingulum. In *Felis s. lybica* the anterior accessory cusp is present on the P₃, the protocones are proportionally higher than that seen on CD 675, and the mandible is less gracile. However, the elongation of the protocone crown in *Felis nigripes* (Burchell, 1824) as shown in Salles (1992) and discussed in relation to the Malapa specimen in Kuhn *et al.* (2011) is not seen in this specimen. While there are minor morphological differences between CD 675 and the *F. s. lybica*

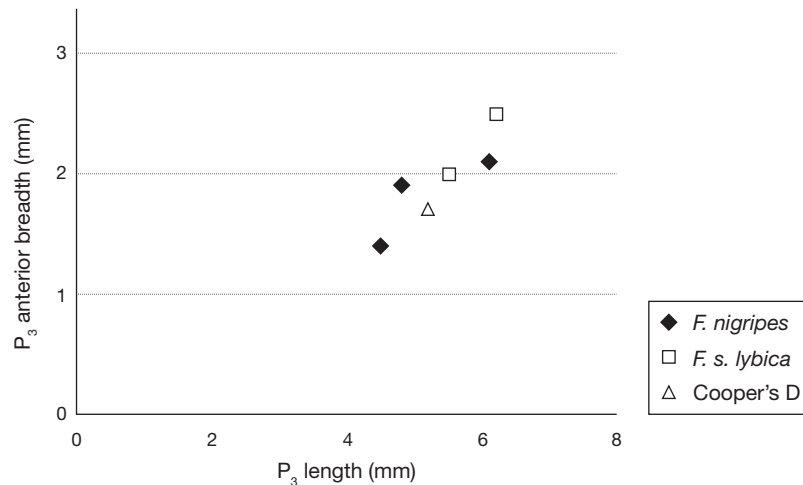


FIG. 6. — Length of P₃ plotted against anterior breadth of P₃ for *Felis nigripes* (Burchell, 1824), *Felis silvestris lybica* Forster, 1780 and CD 675, *Felis* sp.

specimens available to study, metrically the specimen falls into the area of overlap between the two species (Fig. 6). It is therefore referred to *Felis* sp. (*F. sylvestris lybica*/*F. nigripes* size). CD 17790 is a small proximal femur. The shape of the greater trochanter and the slight curve of the shaft suggest that it is felid, and it is a good match for both the *F. s. lybica* and *F. nigripes* specimens in the Ditsong museum collections.

FELIDAE indet.

Many of the specimens listed below as Felidae indet. may be machairodont, but a lack of comparative material means that they are currently only identified to the family level.

FELIDAE indet. large (Lion to *Dinofelis*-sized)

MATERIAL EXAMINED. — CD 1944, left 3rd metacarpal (Table 3); CD 1522, right 3rd metatarsal fragment (Table 3); CD 3847, distal metapodial; CD 5354, left calcaneum fragment; CD 3680, left cuboid; CD 1549, right 3rd metatarsal (Table 3); CD 1965, right pisiform; CD 3902 left scapholunar; CD 18837, right distal tibia fragment (Table 3); CD 3861, right astragalus (Table 3); CD 9860, sesamoid; First phalanges: CD 9729, CD 1532, CD 1547, CD 3867, CD 5955, CD 6760, CD 3223, CD 17479; CD 1550, CD 5974, CD 728, CD 5958, CD 3842; Second phalanges: CD 3869, CD 5439, CD 367, CD 3890, CD 3840, CD 16956, CD 9929.

DESCRIPTION

CD 1944 is the proximal portion of a large 2nd metacarpal. The proximal articulation is slightly damaged dorsally and is also greatly laterally expanded, more so than any *Dinofelis* specimens in Werdelin & Lewis (2001). CD 1522 is a large proximal 3rd metatarsal fragment. There are similarities to both *Dinofelis* and *Acinonyx*, however as only the

anterior portion of the articulation is present it is difficult to identify it more precisely. CD 3847 is a heavily gnawed distal metapodial from a large felid. CD 5354 is a short, robust left tuber calcis from a *Dinofelis*-sized calcaneum. CD 3861, an astragalus, is from a larger cat and does not seem to match any of the machairodonts. CD 3680, a left cuboid, is intermediate in size between the lion and leopard and appears very different to 16201M (*D. darti* from Makapansgat). CD 1549 is an almost complete metatarsal, just lacking the dorsal portion of the proximal articulation. It has similarities to both *Dinofelis* (DN 17) and *P. pardus*, however the shaft is much more angular in CD 1549 than is seen in these two taxa. CD 1965 is a right pisiform with a flattened head, much more so than the lion. It may represent *Dinofelis* but there is a lack of suitable comparative material. CD 3902 is a good size match for an un-numbered *Dinofelis* scapholunar from Makapansgat, but the orientation and depth of facets is very different. CD 18837 is a distal tibial articulation with a fragment of shaft. It is intermediate in size between leopard and *Dinofelis*, with very pronounced ridges on the shaft and broad distal processes. CD 9860 is a lion-sized sesamoid, it is very similar to a specimen from a lion forefoot (AZ 771), however there are no machairodont sesamoids to compare it with. Phalanges CD 9729, CD 3869 and CD 9929 are robust and lion-like, yet CD 9729 and CD 9929 are almost triangular in cross-section. First and second phalanges CD 1532, CD 1547, CD 3867, CD 5955, CD 6760, CD 3223, CD 17479, CD 1550, CD 5974, CD 3842, CD 3869, CD 5439, CD 367, CD 3890 CD 3840 and CD 16956, are all shorter than lion, but broader than leopard - they may represent *Dinofelis*. CD 728 is a robust 1st phalange that is broader and shorter than lion, but does not match the Kromdraai *Dinofelis* material, or published figures of *Homotherium* (Ballesio 1963). CD 5958 is a complete 1st phalange that looks more similar to the Senèze *Homotherium* material than any other taxon.

FELIDAE indet. medium-sized
(*Megantereon* to leopard-sized)

MATERIAL EXAMINED. — **Craniodental:** CD 1892, mandible fragment with condyle and angle of the ramus; CD 8305, left P₃; **Postcranial:** CD 1623, left 1st metacarpal; CD 6757, 1st phalanx; CD 1534, a right pisiform; CD 3996, right ulna fragment; CD 1530, left ulna fragment; CD 5712, left intermediate cuneiform; CD 3205, metapodial lacking proximal articulation (Table 3); **Distal metapodial fragments:** CD 7303, CD 3846, CD 3200, CD 7889, CD 7320, CD 13373; CD 640, CD 688 and CD 1626; **1st phalanges:** CD 17068, CD 1957, CD 3863, CD 1543, CD 2017 (distal only), CD 3864, CD 19951, CD 20004 (damaged), CD 7352, CD 3236, CD 3886 (dorsal surface only); **2nd phalanges,** CD 699, CD 5727, CD 5486, CD 7345, CD 11736, CD 1546, CD 1946, CD 1539, CD 17230, CD 3286, CD 1945, CD 7361; **3rd phalanges:** CD 7356, CD 6756, CD 7304, CD 5793, CD 11185, CD 3197; CD 5671, right intermediate cuneiform; CD 13342, left 2nd metacarpal (Table 3).

DESCRIPTION

CD 1892 is a posterior fragment of a mandible, lacking the coronoid process. The condyle is lozenge-shaped and there is only a short distance between the condyle and the angle of the ramus. It does not appear to be *Megantereon*, and is intermediate in size between caracal and leopard. CD 8305 is a small complete lower premolar, with a large upright protocone, small but distinct anterior and posterior accessory cusps and a posterior cingulum. All cusps are in a straight line from front to back. It is most similar to a cheetah tooth, except that the cheetah lacks a posterior cingulum, and the anterior accessory cusp is greatly reduced in comparison to the posterior accessory cusp, while in the cheetah they are usually of similar size. It refits into the P₃ alveolus of CD 18836 (here identified as *Dinofelis* cf. *aronoki*), although it is from the opposite side. It is much less robust than the equivalent tooth in *Dinofelis barlowi* (STS 131), and the anterior cusp is in line with the protocone rather than being lingually placed as seen in *D. aronoki*. The protocone is much higher than that seen in the Motsetse *D. piveteaui* specimens, and it is considerably shorter (L = approximately 11 mm) than any published *Dinofelis* P₃ from South Africa (see Lacruz *et al.* 2006 for comparative measurements). It has therefore been referred to Felidae indet., as it may represent either *Acinonyx* or *Dinofelis*. CD 3996 and CD 1530 are both olecranon processes from a right and left ulna respectively. They may be antimeres, as they are the same size and the proximal epiphyseal line is still visible on both. There are similarities with both leopard and the Senèze *Megantereon* specimen and thus they are referred to Felidae indet. CD 5712 is a left intermediate cuneiform with damage to the head. Both the cuboid facet and the cuneiform facets are larger and extended more proximally than those of the modern leopard, however the head is much more expanded in *Megantereon* (KB 6016 and KB 6017) than is seen in CD 5712. CD 1623 is a complete 1st metacarpal, the proportions of the proximal facet make it more similar to a machairodont than a pantherine. However, with no *P. pardus* specimens for comparison it is listed here as Felidae indet. CD 6757 is an asymmetric 1st phalanx that has been distally gnawed. First phalanges CD 17068 and CD 1957, and sec-

ond phalanges CD 699, CD 5727, CD 5486, CD 7345, CD 11736, CD 7352 and CD 3236 are all similar to modern *Acinonyx*, but *Megantereon* cannot be excluded. First phalanges CD 3863, CD 1543, CD 19951 and CD 20004 may represent leopard, while CD 2017 and CD 3864 are not leopard or cheetah and may be machairodont. Second phalanges CD 1546, CD 1946, CD 1539, CD 17230 and CD 3286 are all similar to modern leopard specimens, but *Megantereon* is also a possibility. CD 1945 and CD 7361 are both felid second phalanges that are smaller than leopard. Six 3rd phalanges (CD 7356, CD 6756, CD 7304, CD 5793, CD 11185, CD 3197) are leopard to cheetah size, but are not cheetah. There are two morphotypes, with CD 7356 and CD 6756 more similar to each other, and the remaining four also appearing alike. CD 1534, a pisiform, is strongly curved proximally. CD 3205 is a metapodial in two pieces, lacking the proximal end. The shaft is strongly curved and almost triangular in cross-section suggesting it may be a 5th metatarsal. Nine specimens (CD 7303, CD 3846, CD 3200, CD 7889, CD 7320, CD 13373, CD 640, CD 688 and CD 1626) are all probable felid distal metapodial condyles, some with fragments of shaft. It is worth noting that CD 7889 is unfused and therefore represented a younger individual, and that CD 640 and CD 688 are larger than the others and may plausibly be large leopard or small *Dinofelis*. CD 5671 is one half of an intermediate cuneiform, it is similar in morphology to leopard, but larger, and there are no *Dinofelis* cuneiforms to compare it with. CD 13342 is the proximal portion of a left 2nd metatarsal. It is slightly damaged and may have been gnawed. It is similar to CD 1500 (here assigned to Machairodontinae indet.), but the process is slightly sharper in CD 13342 (which is more like DN 772), and the facet for the 1st metacarpal is not quite as square as the other Cooper's D specimens. It is therefore assigned to Felidae indet.

FELIDAE indet. small
(*Felis sylvestris* to caracal-sized)

MATERIAL EXAMINED. — **Craniodental.** CD 3258, a right P₃ (Table 1); CD 13517, broken left C_i. **Postcranial.** CD 9431, right distal femur; CD 1592, left calcaneum (Table 3); CD 13516, 1st phalanx; CD 1492, 2nd phalanx; CD 19227, 2nd phalanx.

DESCRIPTION

CD 3258 is an isolated P₃, with small anterior and posterior accessory cusps, a cingulum and a relatively low protocone. There is a slight bulge of enamel on the lingual surface, just over the posterior root. It is similar to a leopard P₃ but much smaller. A similar tooth was found at Drimolen (DN 743) and also assigned to Felidae indet. CD 13517 is a caracal-sized C_i with two ridges visible at the base of the crown, one distal and one lingual; the rest of the crown is broken. CD 9431 is a heavily damaged distal femoral articulation. It has a slight groove on the medial condyle that only appears to be present in cats and is caracal-serval sized. CD 1592 is a left calcaneum with very long facets for the articulation

TABLE 3. — Postcranial measurements (in mm) of all felid specimens from Cooper's D. Abbreviations: see Material and methods; a, approximately.

Specimen	Element	Side	Taxon	TL	PWM-L	PWA-P	DW Max
CD 3712+CD5972	radius	right	cf. <i>D. aronoki</i>	–	–	–	37.7
CD 3277	radius	–	<i>P. pardus</i> (Linnaeus, 1758)	–	a22.8	17.2	–
CD 7369	radius	left	<i>P. pardus</i>	–	–	–	a29.6
Specimen	Element	Side	Taxon	TL	PW Max	ND	HD
CD 654	femur	right	cf. <i>D. aronoki</i>	–	–	a21	a28.1
Specimen	Element	Side	Taxon	TL	PW	DW max	DB max
CD 3233	tibia	left	<i>D. cf. aronoki</i>	–	52.9	–	–
CD 3881	tibia	left	cf. <i>D. aronoki</i>	–	–	38.2	23.7
CD 1415	tibia	right	cf. <i>Megantereon whitei</i> (Broom, 1937)	–	–	34.7	–
CD 18837	tibia	right	Felidae indet	–	–	38.6	24.5
Specimen	Element	Side	Taxon	TL	Neck W	Head W	–
CD 3861	astragalus	right	Felidae indet	–	17.5	22.5	–
Specimen	Element	Side	Taxon	TL	TB	Min Shaft W	
CD 1592	calcaneum	left	Felidae indet	43.7	15.9	7.5	–
Specimen	Element	Side	Taxon	TL	PWM-L	PWA-P	DW
CD 717	MC2	left	Machairdontinae indet.	–	12.2	–	–
CD 1500	MC2	right	Machairdontinae indet.	–	12	15.9	–
CD 13342	MC2	left	Felidae indet.	–	–	15.9	–
CD 5703	MC3	left	Machairdontinae indet.	–	14.4	13.2	–
CD 1524	MC3	right	Machairdontinae indet.	–	14.7	13.3	–
CD 1944	MC3	left	Felidae indet.	–	18.7	17.7	–
CD 7354	MC4	right	Machairdontinae indet.	–	11.4	13.6	–
CD 3271	MC5	right	Machairdontinae indet.	47.4	8.1	13.6	11.3
CD 682	MC5	left	Machairdontinae indet.	–	9.2	13.9	–
CD 3268	MT2	left	cf. <i>M. whitei</i> (Broom, 1937)	–	9.1	17.9	–
CD 19953	MT3	right	<i>D. cf. aronoki</i>	85.9	19.2	23.4	19
CD 5957	MT3	right	<i>P. pardus</i>	a74.1	15	18.9	14.4
CD 1549	MT3	right	Felidae indet.	a92	a18.6	–	17.12
CD 1522	MT3	right	Felidae indet.	–	20	–	–
CD 670	MT4	right	cf. <i>D. aronoki</i>	–	–	–	15.52
CD 3836	MT4	left	<i>P. pardus</i>	–	7.8	13.4	–
CD 8282	MT5	left	cf. <i>P. leo</i> (Linnaeus, 1758)	–	–	–	23.4
CD 3205	MT5	left	Felidae indet.	–	–	–	13.1

with the astragalus. It is most similar to caracal and serval, but it is difficult to choose between them. CD 13516 is a short, but very broad, first phalanx, it does not match any of the extant felid taxa. CD 1492 and CD 19227 are both similar to caracal second phalanges, but there are no serval specimens available for comparison.

DISCUSSION

In comparison with the original species lists published for Cooper's D in Berger *et al.* (2003) and de Ruiter *et al.* (2009), all taxa are still present, but with some modifications. The minimum numbers of individuals for the Cooper's D felids recorded in Table 4 are lower than those reported in de Ruiter *et al.* (2009), with the exception of *Megantereon whitei*, where the MNI has increased from one to two. The reduction in the other taxa (particularly leopard) is owing

to the uncertainty of attribution of fragmentary postcranial remains which may well represent leopard, but the possibility that they represent *Megantereon* cannot be excluded based on the available comparative material.

The small mandible referred to *Felis lybica* in Berger *et al.* (2003) is here described as *Felis* sp. It is intermediate in size between *Felis sylvestris lybica* and *Felis nigripes* and cannot be assigned to either with confidence. Until recently there was no fossil record of the black footed cat (*F. nigripes*) in South Africa, however it has now been reported from Malapa in the Cradle (Kuhn *et al.* 2011). As a species it is a southern African endemic and is the smallest of the African Felidae.

The postcranial lion remains are assigned to *P. leo* (in agreement with de Ruiter *et al.* 2009) rather than cf. *P. leo* as originally reported in Berger *et al.* (2003). Lions, despite being Africa's largest cat, are relatively rare in the fossil record. In the Cradle of Humankind (Gauteng), lion has also

TABLE 4. — Total number of identifiable felid specimens (NISP) by taxon, and minimum number of individuals for each species (MNI).

Taxon	NISP	MNI
<i>Dinofelis</i> cf. <i>aronoki</i> .	11	2
cf. <i>Dinofelis aronoki</i>	11	—
<i>Megantereon whitei</i>	6	2
cf. <i>Megantereon whitei</i>	5	—
Machairodontinae indet.	12	—
<i>Panthera leo</i>	3	1
<i>P. cf. leo</i>	1	—
<i>Panthera pardus</i>	8	1
cf. <i>P. pardus</i>	8	—
<i>Acinonyx jubatus</i>	2	1
<i>Caracal caracal</i>	1	1
<i>Felis sylvestris lybica</i>	1	1
<i>Felis</i> sp.	2	—
Felidae indet. (large)	31	—
Felidae indet. (medium)	49	—
Felidae indet. (small)	7	—
Total	158	9

been reported from Gladysvale (Lacruz, 2009), Swartkrans Member 1 Lower Bank (Turner 1993) and at Sterkfontein in the Silberberg Grotto, Member 4 (Turner 1986, 1987a), Member 5 East (Oldowan Infill) and Member 5 West (O'Regan 2007). Although the dating of deposits at Sterkfontein is not straightforward, the most recent estimates (as summarised in Reynolds & Kibii 2011) would place the Member 5 lions at a similar or slightly later date than those at Cooper's D.

Members of the genus *Acinonyx* are rarely found as fossils in Africa, yet it has a richer record in Europe (*Acinonyx pardensis* (Croizet & Jobert, 1828)). Two species of cheetah are known from the African fossil record – *Acinonyx aicha* Geraads, 1997, which is so far found only at Ahl al Oughlam in North Africa (Geraads 1997), and specimens from other sites in Gauteng, South Africa which have been referred to the modern species *A. jubatus* (Turner 1986, 1987a, 1993). These are from the Silberberg grotto, Sterkfontein (Turner 1987a), and Swartkrans members 2 (Turner 1986) and 3 (Turner 1993), while de Ruiter (2003) also lists *A. jubatus* in the Swartkrans Member 1 hanging remnant. The specimens identified here are very similar to the modern cheetah and given the doubts over the provenance of the cheetah from the hanging remnant (as discussed in de Ruiter 2003) and the difficulties dating the Swartkrans cave deposits, particularly Members 2 and 3 (de Ruiter 2003; Herries *et al.* 2009), the Cooper's D specimens may be the earliest well-dated material of the modern species in Africa.

The machairodonts are well represented in the Cooper's D deposits, with the recovery and identification of several more specimens of a particularly small *Megantereon whitei* as first discussed by Hartstone-Rose *et al.* (2007). However, the most significant felid finding from the site is the material described here as *Dinofelis* cf. *aronoki*. The sabre-toothed cat genus *Dinofelis* arose in the Late Miocene, and its biogeographic range extended from North America to Southern Africa, before it became extinct in the Pleistocene

(Werdelin & Lewis 2001). Africa appears to have been the evolutionary centre of the genus, with five species (plus another 3 suggested but unnamed by Werdelin & Lewis [2001]) recorded from the continent. There is some geographic variation in taxa, with *D. barlowi*, and *D. darti* only being present in South Africa, while *D. petteri* and *D. aronoki* have thus far only been recorded in East Africa, and the latest member of the genus *D. piveteaui*, known from both East and South African deposits. If the new material described here is conspecific with *Dinofelis aronoki* from East Africa, then it originated in East Africa and dispersed to South Africa, as has also been suggested for *D. piveteaui*. However, if further work identifies the South African material as a new species, then this has implications both for the evolution of *D. piveteaui* and for the evolution of the genus *Dinofelis* in Southern Africa. If the Koobi Fora and Cooper's D taxa are related, then it is plausible that *D. aronoki* is ancestral to *D. piveteaui*, which would be the most logical scenario as *D. piveteaui* is the most derived of all the *Dinofelis* species. If they are not related then the species at Cooper's D and Drimolen may represent a separate southern African lineage that parallels, but is not directly related to, *D. piveteaui*. Each scenario is dependent on the date of the sites and the morphological traits for each species. There is a small, but unlikely possibility that the differences between *D. piveteaui* and *D. cf. aronoki* could be sexual dimorphism and that they in fact represent males and females of the same species. However, for the dimorphism to be most pronounced in the carnassials would seem highly unlikely, as also discussed by Lacruz *et al.* (2006). The presence of an additional species of *Dinofelis* in southern Africa at 1.5–1.4 Ma is unexpected and is contrary to the patterns of decline seen in the other machairodont taxa, which were either extinct or almost so, by this point. The particularly small and late *Megantereon whitei* from the site, could be contrasted with the larger *Dinofelis* specimens, and may indicate some form of competition between the taxa. However, the exact dates of *D. piveteaui* in South Africa remain unclear, as both Kromdraai A and Motsetse are only dated by biostratigraphy, with no radiometric dates. This makes it difficult to elucidate the chronology and relationships between the taxa at the present time.

CONCLUSION

Felid fossils are often rare in palaeontological sites, but 155 have been identified from Cooper's D. They are notable for the wide variety of taxa represented including two sabre-toothed cats (*Megantereon* and *Dinofelis*), as well as most of the extant taxa found in southern Africa today (lion, leopard, cheetah, caracal). *Dinofelis* cf. *aronoki* is present at two sites within the Cradle – Cooper's D and Drimolen, and takes the known number of Plio-Pleistocene *Dinofelis* taxa in the cradle sites to three. There is clearly still much to learn, both about the size reduction and extinction of *Megantereon*, and about the radiation and subsequent extinction of the genus *Dinofelis*.

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