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A sabre-tooth felid from Coopers Cave (Gauteng, South Africa) and its implications for *Megantereon* (Felidae: Machairodontinae) taxonomy

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Metrical and morphological analysis of a new sabre-tooth felid mandible recovered from the Plio-Pleistocene hominid-bearing site of Coopers, South Africa, indicates that it can be assigned to the genus *Megantereon,* though it is by some measures the smallest individual of this taxon yet described. Comparison of morphological variability within this genus to that found within four extant, medium-sized felid species (*Acinonyx jubatus, Neofelis nebulosa, Panthera pardus* and *P. uncia*) and the extinct genus *Smilodon* (sister taxon of *Megantereon*) provides confirmation of the suggestion by Martínez-Navarro & Palmqvist (1995, 1996) that *Megantereon* is a geographically polymorphic genus comprised of at least two species: *M. cultridens* (Cuvier, 1824) of North America and Europe and *M. whitei* (Broom, 1937) of Africa and Europe.

Keywords: sabre-tooth, Plio-Pleistocene, palaeontology, carnivore.

INTRODUCTION

The early history of systematics research on the genus *Megantereon* led to a proliferation of specific names for morphologically similar specimens, many of which came from geographically and temporally proximate sites. Various sabre-tooth cats that fit the general description of the genus *Megantereon* have been assigned, over the last two centuries, to at least 11 species: *Megantereon cultridens* (Cuvier, 1824), *M. megantereon* (Croizet & Joubert, 1828), *M. falconeri* (Pomel, 1853), *M. sivalensis* (Falconer 1868), *M.* (*Machairodus*) *nihowanensis* (Teilhard de Chardin & Piveteau, 1930), *M. hesperus* (Gazin, 1933), *M.* (*Felis*) *whitei* (Broom, 1937), *M.* (*Machairodus*) *inexpectatus* (Teilhard de Chardin, 1939), *M.* (*Felis*) *gracile* (Broom & Schepers, 1946), *M. eurynodon* (Ewer, 1955) and *M. ekidoit* (Werdelin & Lewis, 2000). While the naming of new species still occasionally occurs, most recent works have seen this material as falling into three or fewer species (Ficcarelli 1978; Turner 1987, 1997; Martínez-Navarro & Palmqvist 1995, 1996; Sardella 1998; Palmqvist 2002).

Martínez-Navarro & Palmqvist (1995, 1996) suggest that the genus *Megantereon* contains up to three distinct species, including a predominantly African group for which the nomen *M. whitei* (Broom, 1937) is available. Four features distinguish the African clade: relatively small lower premolars; a diastema between the third and fourth lower premolars; relatively small carnassials (P^4 and M_1); and a relatively vertical mandibular symphysis (Martínez-Navarro & Palmqvist 1995). Specimens from several earlier Pleistocene localities of southern Europe (Spain and Greece) align themselves with the African taxon (Martínez-Navarro & Palmqvist 1995, 1996). Recently recovered specimens from Africa, as reported here and by Werdelin & Lewis (2000), support the existence of a distinct African species of *Megantereon,* and contribute to an African sample size large enough for statistical analysis.

We report here on a mesial fragment of a left mandible (CD 5997: Fig. 1), provisionally attributed to the Plio-Pleistocene sabre-tooth felid genus *Megantereon* (Berger *et al.,* 2003), from the site of Coopers Cave (26°00′46″S, 27°44′45″E), Gauteng Province, South Africa. This is the most complete mandibular specimen recovered from the Witwatersrand Basin, and the only one from this region that preserves the anterior chin and alveolar morphology.

Morphometric analysis of fossils attributed to *Megantereon,* along with four medium-sized extant felid species and one other extinct felid genus (*Smilodon*) allows an assessment of the number of morphologically distinct groups contained within the genus *Megantereon,* and of the claim for a distinct African species (*M. whitei*).

Diagnosis of Megantereon. *Megantereon,* a member of the family Felidae, subfamily Machairodontinae, is a genus of sabre-tooth felids found in Africa, Asia, Europe and North America. Unpublished body mass estimates based on the Orce and Dmanisi specimens suggest that *M. cultridens* weighed approximately 100 kg, about the size of a living Jaguar, *P. onca* (Palmqvist, pers. comm.). Based on its limb proportions, *Megantereon* is believed to have been a

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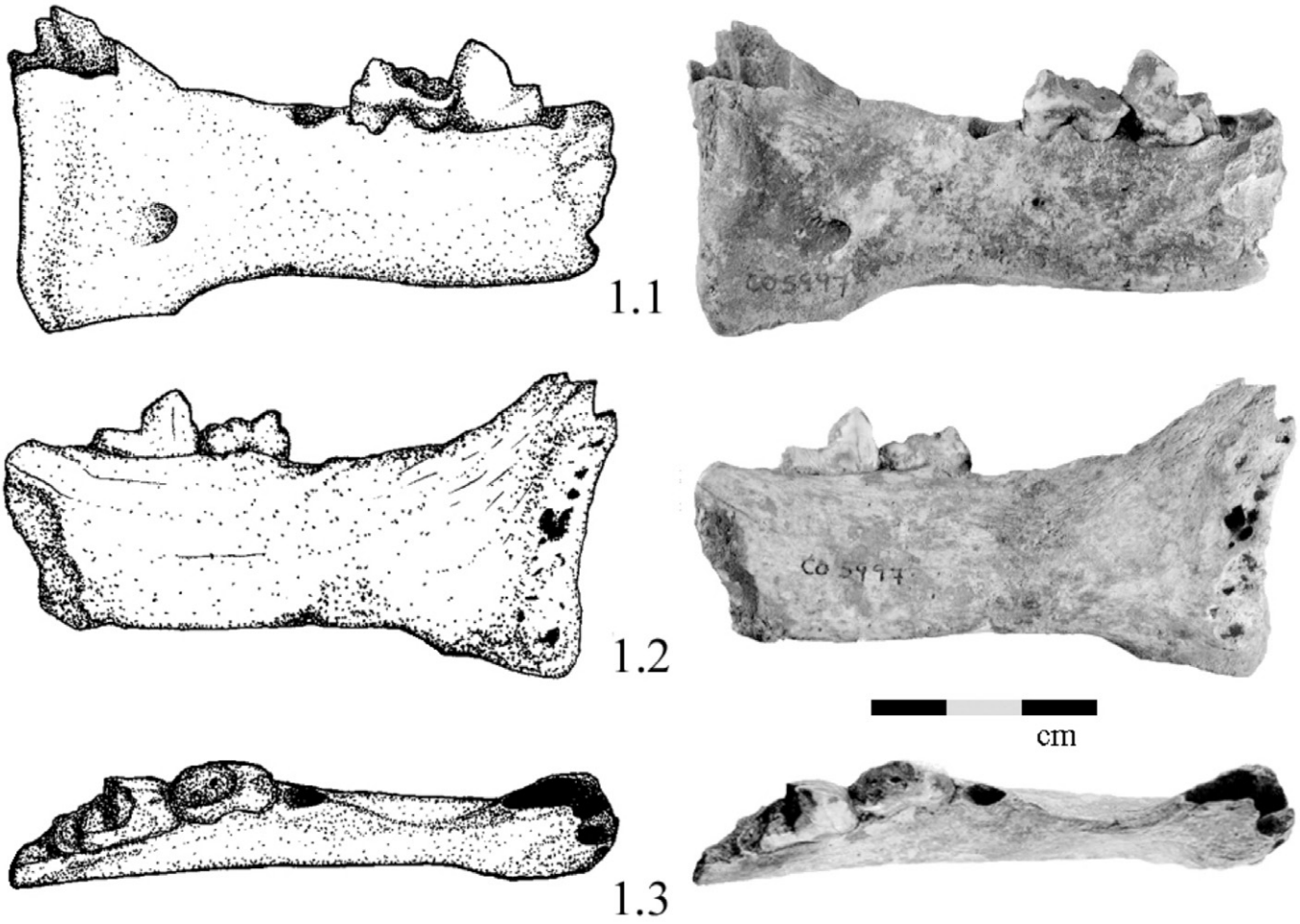


Figure 1. Lateral (**1.1**; mesial is left, superior is up), medial (**1.2**; mesial is right, superior is up) and occlusal views (**1.3** mesial is right, lateral is up) of CD 5997. Photographs and drawings by A.H-R.

partially arboreal carnivore occupying a closed forest niche (Marean 1989; Lewis 1997). Turner (1987: 1266) offered this diagnosis:

> A medium-sized, sexually dimorphic cat; short, high skull, triangular in profile with convex dorsal outline; extended glenoid apophysis; limbs and feet short and powerful, the forelimbs more so than the hindlimbs; tail reduced in length; upper canines elongated, compressed and curved; crenulations absent on all teeth; long post-canine diastema; upper and lower second premolars lost; upper and lower third premolar present and functional but very variable in size; P^4 protocone developed but variable in size; M^1 present but reduced; P^3–M^1 backward raking; main cusp of P^4 high crowned; M^1 lacking talonid or metaconid, paraconid shorter than protoconid and forming a relatively acute angle with it; mandible with short coronoid process, strong and vertical symphysis with enlarged flange extending well below the ventral margin of the horizontal ramus; single large mental foramen.

Berta & Galliano (1983) also note that *Megantereon* differs from *Smilodon* (namely *S. populator*) in its relatively smaller size, relatively larger mandibular flange and lack of canine serrations, among other less noticeable traits. It is generally accepted that *Megantereon* is more primitive than *Smilodon* as its upper and lower incisors are less enlarged and procumbent, and its upper canines are less enlarged than its larger sister genus (Berta & Galliano 1983; Turner 1997).

MATERIALS AND METHODS

Coopers Cave is situated approximately 45 km northwest of Johannesburg (Gauteng Province, South Africa), within the Cradle of Humankind World Heritage Area between the well-known fossil hominin-bearing sites of Sterkfontein and Kromdraai. The site presents a series of collapsed and deroofed breccia caves designated Coopers A, B and D. Renewed excavations in 2001 into *in situ*, decalcified sediments at Coopers D have produced a rich and varied faunal assemblage, including abundant carnivore material, dated on biostratigraphic grounds to between 1.6 and 1.9 million years ago (Mya) (Berger *et al.* 2003). It is from this deposit that CD 5997 is derived.

CD 5997 is compared with congeneric specimens, and the variation in *Megantereon* is compared to that found between the extinct genus *Smilodon* and four extant felid species: *Acinonyx jubatus* (cheetah), *Neofelis nebulosa* (clouded leopard), *Panthera pardus* (leopard) and *P. uncia* (snow leopard) (Tables 1, 2 & 3). The comparative extant felid species were chosen because they represent medium-sized cats – ranging from 20 kg (*N. nebulosa*) to 90 kg (*P. pardus*) – corresponding with the body size range

Table 1. Sample sizes of fossils and casts, by curatorial institution, of extinct felid study group examined in person.

Genus	Actual fossils	Casts	Total	Held at
Smilodon	5	6	11	AMNH
African *Megantereon* (excluding CD 5997)	3 (South African)		3	TM
		1 (East African)	1	AMNH
Non-African *Megantereon*	1	6	7	AMNH
	1 (type of *M. cultridens*)		1	NHM
CD 5997	1	0	1	WITS
Total	11	13	24	

AMNH: American Museum of Natural History, New York.
TM: Transvaal Museum, Pretoria.
NHM: Natural History Museum, London.
WITS: University of the Witwatersrand, Johannesburg.

Table 2. Sample sizes by sex of extant felid study group. All specimens held at AMNH.

Species	Males	Females	Unrecorded sex
Acinonyx jubatus	7	4	2
Neofelis nebulosa	2	1	3
Panthera pardus	8	5	0
P. uncia	3	3	2

Table 3. Country of origin of the *Panthera pardus* study group. All specimens held at AMNH.

Continent	Country	
Africa	Democratic Republic of Congo	5
	Tanzania	3
	Malawi	1
Asia	China	1
	India	3

of *Megantereon* (Turner 1997; Palmqvist, pers. comm.). *P. pardus* is particularly useful for comparison because, like *Megantereon*, it is found over a wide, multi-continental, geographic range (Table 3). The much larger fossil form *Smilodon* was chosen as the extinct comparison group because it is one of the closest related taxa to *Megantereon* and it is very well represented in the fossil record. All data – from both extinct and extant forms – were collected on adult individuals by AHR or incorporated from published literature (Ficcarelli 1978; Berta & Galliano 1983; Martínez-Navarro & Palmqvist 1995; Werdelin & Lewis 2000; Qiu *et al.* 2004). All comparative data on the extant felids were collected at the American Museum of Natural History. The data on the extinct genera were collected in various institutions on either actual fossils or museum quality casts (Table 1).

The taxonomic attribution, geological age (for fossil specimens) and sex (for extant specimens) were recorded for each specimen. Table 4 lists the morphometric variables that were collected wherever possible from each specimen. Where possible, measurements were taken on the left side of the mandible. All tooth measurements were taken at the alveolar margins (see Ficarelli 1978). This substantially increases the number of measurements available on many of the fossils (since many of the teeth are broken away or lost postmortem), including the CD 5997 mandible, which adds to the statistical robusticity of the analysis.

Published dental measures include crown dimensions (Werdelin & Lewis 2000; Martínez-Navarro & Palmqvist 1995; Berta & Galliano 1983; Ficcarelli 1978) and estimates or alveolar dimensions (Berta & Galliano 1983; Martínez-Navarro & Palmqvist 1995). To assess the validity of combining these different forms of data, we have evaluated each of the five specimens that overlap in our data sample and in the data sample used by Martínez-Navarro & Palmqvist (1995). For the 18 values that could be thus compared the average difference between our alveolar measurements and the reported crown measurements is 3.59% (S.D. 5.31%) (Table 5) which is similar to empirically derived intraobserver error taken on a single structure (see references in White 1991). While these forms of error may be additive (thus further reducing their accuracy), considering the relatively small size of the measurements and the accuracy of the measuring equipment, we regard this difference as negligible. One tooth (the M_1 of KA 64) gave particularly aberrant results in this comparison: our mesiodistal measurement is 7.3% lower than that of Turner (1987) and our buccolingual measurement is 21.34% higher. We believe that this outlier is due to a thick layer of Glyptal preservative which leaves the lingual border of the mandibular premolar-molar row difficult to measure. Though additional preparation has partially alleviated this problem, it is perhaps wise to view all measurements of these teeth with caution. If this single tooth (M_1 of KA 64) is excluded from our analysis of the difference between our measurements and those analysed by Martínez-Navarro & Palmqvist (1995), then the overall average percentage difference is reduced to 2.25% with a standard deviation of just 2.85% (Table 5).

RESULTS

Preservation of the specimen

CD 5997 consists of an apparently undistorted, 81.3 mm long mesial segment of an adult left mandibular corpus (Fig. 1). The dentary is not fused at the symphysis. Distally, the specimen is broken perpendicular to the occlusal plane approximately 9 mm distal to the distal margin of the M_1 alveolus. Also missing is the inferior-most margin of the mandibular flange, the missing portion measuring approximately 16 mm proximodistally

Table 4. Measurements taken (mm) to the nearest 0.1 mm.

Abbreviation	Definition	CD 5997	African and early European *Megantereon* group – including CD 5997 **Mean** (range*, *n*)	Late European, North American and Asian *Megantereon* group **Mean** (range*, *n*)
I1 BL	Buccolingual (BL) width and	**3.8**	**4.7** (3.8-5.7, 3)	**8.1** (1)
I1 MD	mesiodistal (MD) length, measured	**1.2**	**2.9** (1.2-5, 3)	**4.4** (1)
I2 BL	at the alveolar margins, of all lower	**5.9**	**5.7** (5.5-5.9, 3)	**7.9** (1)
I2 MD	teeth (I_1, I_2, I_3, C_1, P_3, P_4, M_1). The left	**2.6**	**3.5** (2.6-4.3, 3)	**6.2** (1)
I3 BL	side was used when available.	**5.9**	**6.4** (5.9-6.9, 3)	**9.3** (1)
I3 MD		**4.3**	**5.0** (4.3-5.8, 4)	**8.2** (1)
C BL		**9.5**	**9.2** (7.8-10.9, 4)	**11.5** (10-15, 9)
C MD		**8.7**	**7.0** (5.1-9.8, 5)	**8.0** (6.5-11.4, 7)
P3 BL		**2.8**	**3.7** (2.8-4.5, 6)†	**5.4** (4-6.6, 15)
P3 MD		**4.7**	**5.7** (4.7-6.9, 7)†	**9.9** (7-12.7, 16)
P4 BL		**6.2**	**6.9** (4.5-10.1, 9)	**8.4** (6.6-10.5, 19)
P4 MD		**13.9**	**13.9** (6.3-17.5, 9)	**18.9** (15.7-21.5, 21)
M1 BL		**8.7**	**8.9** (8.1-11.2, 9)	**9.8** (7.8-13, 19)
M1 MD		**16.8**	**17.9** (16.8-19.3, 9)	**21.5** (18.2-26, 20)
IC row	Incisor-canine row width measured from interdentale to the lateral most margin of the canine alveolus.	**13.3**	**17.7** (13.3-22.2, 2)	**28.3** (1)
PM row	Premolar-molar row length measured from the mesial margin of P_3 to the distal margin of M_1	**37.6**	**40.4** (37.1-44.7, 5)	**49.7** (47.3-50.9, 6)
CP diast	Canine-premolar (post-canine) diastema length measured from the mesial margin of P_3 to the distal margin of C_1	**24.4**	**32.6** (24.4-36.9, 3)	**24.9** (21.7-28.2, 2)
Symph height	Maximum symphyseal measurement. (Instrumentally determined.)	**36.9**	**43.4** (36.9-49.9, 2)	**35** (1)
Symph depth	Maximum symphyseal depth perpendicular to maximum symphyseal height.	**10.2**	**14.5** (10.2-18.9, 2)	**15.6** (1)
Ant P3 height	Maximum measurement of corpus in the coronal plane perpendicular to the long axis of the corpus mesial to the P_3 (instrumentally determined).	**23.2**	**24.3** (23.2-25.3, 2)	**27.1** (22.3-30.4, 3)
Ant P3 width	Maximum width of corpus in the coronal plane perpendicular to the 'Ant P3 height' measurement mesial to the P_3	**10.8**	**10.5** (10.2-10.8, 2)	**13.3** (9.1-16, 5)
Post M1 height	Maximum measurement of corpus in the coronal plane perpendicular to the long axis of the corpus distal to the M1 (instrumentally determined).	**24.6**	**27.3** (24.6-30, 2)	**30.9** (26.7-37, 4)
Post M1 width	Maximum width of corpus in the coronal plane perpendicular to the 'Post M1 height' measurement distal to the M1.	**11.0**	**12.1** (11.0-13.3, 2)	**13.3** (9.7-16.5, 5)

*Owing to the small sample sizes, ranges were used instead of standard deviations.
†Not including KNM-ST 23812, which reportedly exhibits agenesis of the P_3 (Werdelin & Lewis 2000). If this specimen were included here (as 0 in both measurements), the means would be reduced to 3.2 and 5.0 for the buccolingual and mesiodistal measurements, respectively.

by 6.8 mm mediolaterally and <2 mm superioinferiorly. Except for this small flake, the dentary is complete, from the distal break to the symphysis.

The incisors, canine and third premolar are missing post-mortem and their alveoli are encrusted with a thin (<0.1 mm) layer of sediment, indicating that the teeth were lost prior to fossilization. The fourth premolar is broken distal to the mesial accessory cusp and is sheared buccodistally. The carnassial (M_1) is similarly broken: the posterior half of the tooth is also sheared buccodistally, leaving intact only the paraconid. It does not appear that the shearing of these teeth is the result of natural occlusal wear, as none of the South African *Megantereon* specimens exhibit a wear pattern as extensive as this. However, it is possible that some or all of the breakage of these teeth occurred during the life of the animal and were modified by occlusal wear. Further analysis of the tooth damage and wear is warranted.

Taphonomy

The distal break displays gouge marks consistent with chewing by hyenas. In addition to the gnaw marks of a large carnivore at the proximal break, there are smaller tooth marks over much of the mandible, and dozens of

Table 5. Comparison of our alveolar measurements with the crown measurements used by Martínez-Navarro & Palmqvist (1995).

Specimen	Measurement	P3 MD	P3 BL	P4 MD	P4 BL	M1 MD	M1 BL
USNM 12614	Our measurement					19.75	8.03
	Berta &Galliano (1983)					19.80	8.50
	% Difference					**–0.25**	**–5.69**
KA 64	Our measurement			17.47		18.22	11.15
	Turner (1987)			17.00		19.60	9.00
	% Difference			**2.73**		**–7.30**	**21.34**
TM 856	Our measurement	6.85	3.89	14.78		17.65	8.62
	Turner (1987)	6.60	3.90	14.50		17.60	8.50
	% Difference	**3.72**	**–0.26**	**1.91**		**0.28**	**1.40**
STS 1588	Our measurement			13.49	7.10	19.29	8.45
	Turner (1987)			13.30	6.90	19.30	8.30
	% Difference			**1.42**	**2.86**	**–0.05**	**1.79**
ER 793	Our measurement			14.67	5.72	17.05	8.08
	Turner (1987)			14.40	6.40	17.10	8.10
	% Difference			**1.86**	**–11.22**	**–0.29**	**–0.25**
Average % difference	**3.59**						
S.D.	**5.31**						
Average % difference – KA64 M1	**2.25**						
S.D.	**2.85**						

round holes of differing sub-millimeter diameters perpendicular to the surface of entry (possibly representing insect activity).

Description

The morphology of CD 5997 is like that of other sabre-tooth cats, though it is relatively small in comparison with other members of *Megantereon,* an already relatively small sabre-tooth felid (Table 4). It has a long diastema between the highly reduced and laterally compressed mandibular canine and the reduced third premolar. It also has an exaggerated mandibular flange that extended below the ventral border of the symphysis with a marked antero-ventral ridge (Fig. 1). This mandibular flange, a feature for which the function is still unknown, is one of the most diagnostic characteristics of *Megantereon* in that it is larger than that found in most other Machairodonts (Emerson & Radinsky 1980). The mandibular flange of CD 5997 extends on the ventral border of the corpus inferior to and just posterior from the anterior-most projection of the anterior-most alveolar margin of the incisors (between I_1 and I_2) and continues posteriorly to approximately the midpoint between C_1 and P_3. It extends below the ventral border of the corpus about 7mm, but if its ventral-most aspect were intact, it probably would have extended 10 mm or so ventrally. The mandibular flange has a strong dorsoventral ridge marking its anterior margin, and lies predominantly lateral to the midline in the anterior view (not shown), extending below the level of the symphysis.

The symphysis itself is relatively long (Table 4), extending from the incisal alveoli superiorly, and extending inferiorly below a line representing the continuation of the ventral border of the corpus (Fig. 1). It is nearly vertically oriented and is highly pitted with symphyseal interdigitations. CD 5997 thus preserves a relatively complete, unbroken, hemimandibular symphysis (with only slight surface abrasion).

There is no indication that the masseteric fossa projects anteriorly to the distal margin of M_1. Nor is there any indication of notable grooves along the inferomedial surface of the corpus as has been described for specimens of '*M. hesperus*' (Berta & Galiano 1983).

As noted above, all of the teeth except for P_4 and M_1 have fallen out, and the remaining ones are so worn or damaged as to render their analysis difficult. Based on alveolar dimensions, the incisors appear to have been relatively small, mesiodistally compressed and slightly crowded. Based on the depth of the alveoli, they do not appear to have been very high-crowned. However, the canine alveolus is very deep which suggests that the canine was relatively substantial. It too was probably laterally compressed. The alveolus of the P_3 is sufficiently encrusted (see above) so as to render its analysis difficult. However, it appears to have contained a tooth with the largest root being distal, the second largest root being mesial.

The P_4 and M_1 are broken and worn (see above). The P_4 displays an elliptical occlusal outline and marked bulging of the enamel above the cervicoenamel junction. The occlusal outline of the M_1 is longer and more rectangular. The paraconid bears a sharp distal margin indicating the typical felid carnassial notch.

Taxonomic affinities of CD 5997

CD 5997 can be identified as *Megantereon* based on both quantitative and qualitative evidence. Though the specimen is overall the smallest in our sample other than that from South Turkwel, which was not viewed in person (Table 4), it falls within or very close to the *Megantereon* range in all measures of shape (Table 6). Qualitatively, the specimen clearly comes from a small-bodied sabre-tooth

Table 6. Shape derivatives of measurements taken. Shape = BL/MD

Abbreviation	CD 5997	African and early European *Megantereon* group **Mean** (Range*, *n*)	Late European, North American and Asian *Megantereon* group **Mean** (Range*, *n*)
I1	**3.3**	**2.1** (1.1–3.3, 3)	**1.8** (1)
I2	**2.3**	**1.7** (1.3–2.3, 3)	**1.3** (1)
I3	**1.4**	**1.3** (1.2–1.4, 3)	**1.1** (1)
C	**1.1**	**1.3** (1.1–1.7, 4)	**1.4** (1.1–1.6, 7)
P3	**0.6**	**0.6**† (0.6–0.8, 5)	**0.6** (0.4–0.8, 15)
P4	**0.4**	**0.5** (0.4–0.7, 9)	**0.4** (0.4–0.5, 19)
M1	**0.5**	**0.5** (0.4–0.6, 9)	**0.5** (0.4–0.5, 19)
Symph (height/depth)	**3.6**	**3.1** (2.6–3.6, 2)	**3** (1)
Ant P3 (height/width)	**2.1**	**2.4** (2.1–2.7, 2)	**2.4** (1.9–2.8, 3)
Post M1 (height/width)	**2.2**	**2.25** (2.24–2.25, 2)	**2.2** (1.9–2.3, 4)

*Owing to the small sample sizes, ranges were used instead of standard deviations.
†Not including KNM-ST 23812, which reportedly exhibits agenesis of the P_3 (Werdelin & Lewis 2000).

felid with reduced premolars, an increased post-canine diastema and the diagnostic ventral mandibular flange. Again, though it is relatively small in many, though not all, respects, CD 5997 appears to exhibit typical *Megantereon* morphology.

Metric comparisons

Only the premolar-molar row dimensions provided sample sizes large enough for multivariate analysis. All of the seven original variables (mesiodistal and buccolingual measurements from each of the three teeth, as well as the entire premolar-molar row length) and the four variables extrapolated from that data (tooth shape = mesiodistal/buccolingual index for each tooth, tooth row compression = sum of mesiodistal measurements of the three teeth/premolar-molar row length) show segregation to varying degrees, consistently separating the fossils into at least two *Megantereon* populations with the Plio-Pleistocene African and Dmanisi specimens and the early Pleistocene fossils from Greece and Spain grouping separately from all others (Tables 4 & 6). The two measurements of the third premolar (Figs 2 & 3) along with the premolar-molar row length (Fig. 4) are particularly useful in making this distinction, as there is almost no overlap between the two populations in these variables, as indicated by Martínez-Navarro & Palmqvist (1995, 1996). The degree of separation between the two *Megantereon* populations, in terms of these three variables, is not only highly significant ($P < 0.01$ in two-tailed *t*-tests) in each of the cases, but is more extreme than the degree of separation between all other felid taxa examined (with the exception of premolar-molar row length for *Neofelis* and *Smilodon,* these latter taxa being also the most disparate in overall body size).

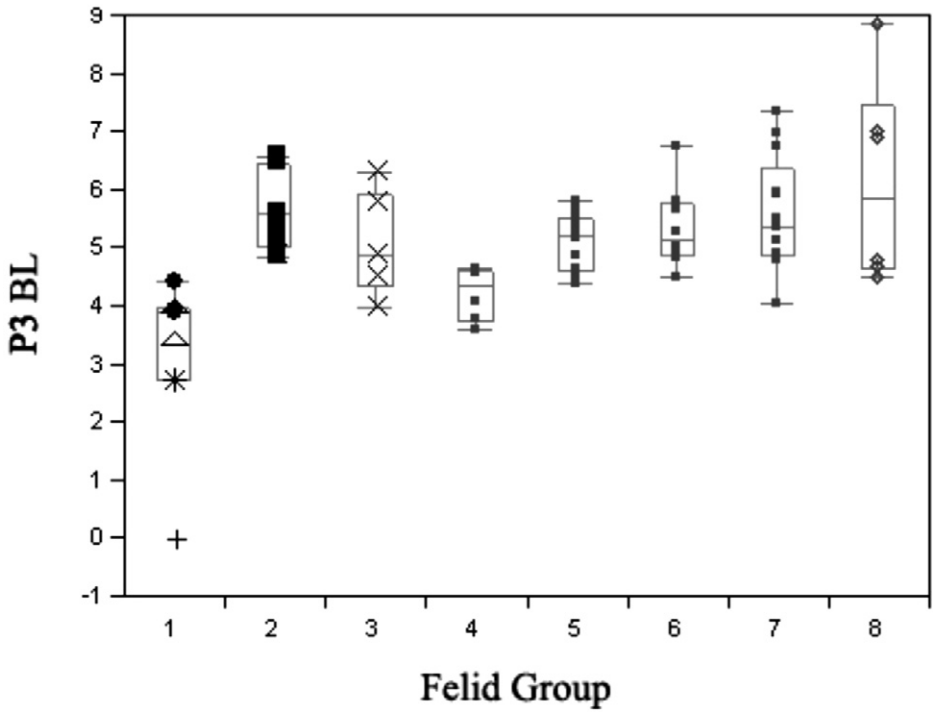


Figure 2. Box plots of third premolar buccolingual measurement by genus/species group. Legend: Group 1 = African and Early European *Megantereon*, 2 = North American and Late European *Megantereon*, 3 = Asian *Megantereon*, 4 = *Neofelis*, 5 = *Acinonyx*, 6 = *Panthera uncia*, 7 = *P. pardus*, 8 = *Smilodon*. Asterisk = CD 5997, triangles = Early European *Megantereon*, '+' = South Turkwel *Megantereon*, closed circles = other African *Megantereon*.

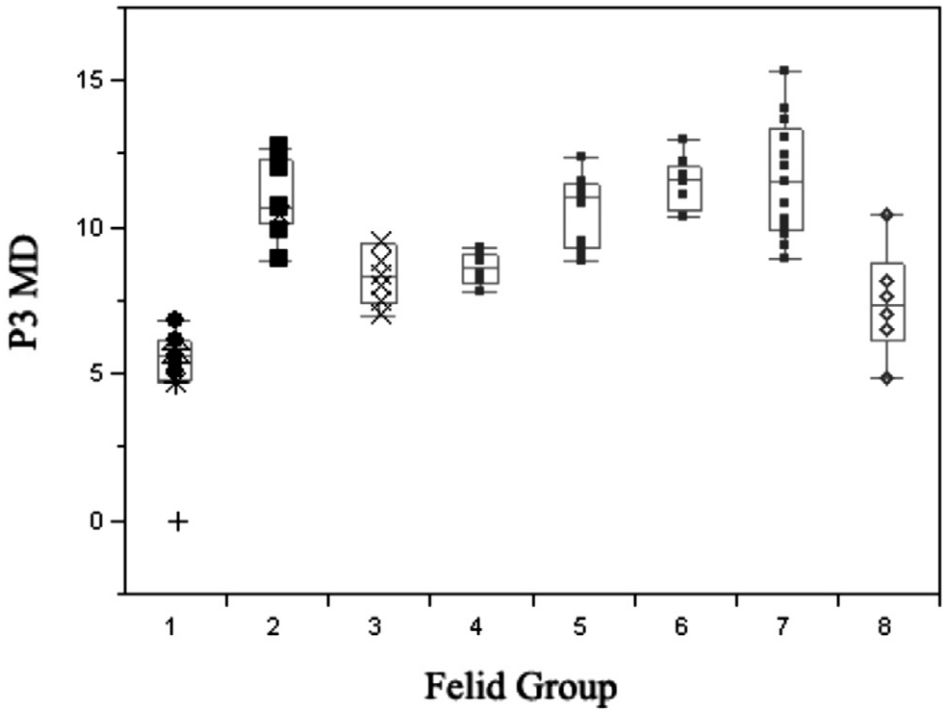


Figure 3. Box plots of third premolar mesiodistal measurement by genus/species group. Legend as in Fig. 2.

Likewise, a principal components analysis of the premolar-molar row variables (the six mesiodistal and buccolingual alveolar measurements of the premolars and molar) yields similar results (Figs 5 & 6). Given the positive factor loadings of the metric variables in the first principal component (Fig. 5, Table 7), which accounts for 62.58% of the variation within the total sample, this component may be interpreted as a size vector which is predominantly driven by the P_4 and M_1 dimensions. Generally the first principal component accounts for size variation, as is the case in our sample, and it often contains less information about systematic/phylogenetic relationships than do later components that examine more detailed shape relationships within the data. However, size should not be neglected, because differences in gross size are important in the identification of many felids (which can vary tremendously in size but conservatively in shape). As shown in Figure 5, the first principal component (PC1) separates the two groups of *Megantereon* (with the Asian specimens possibly as a third distinct grouping). The difference in the mean of PC1 scores between the African/Early European group and Late European and North American *Megantereon* is significant ($P < 0.01$) based on a two-tailed *t*-test. The Asian specimens group with the

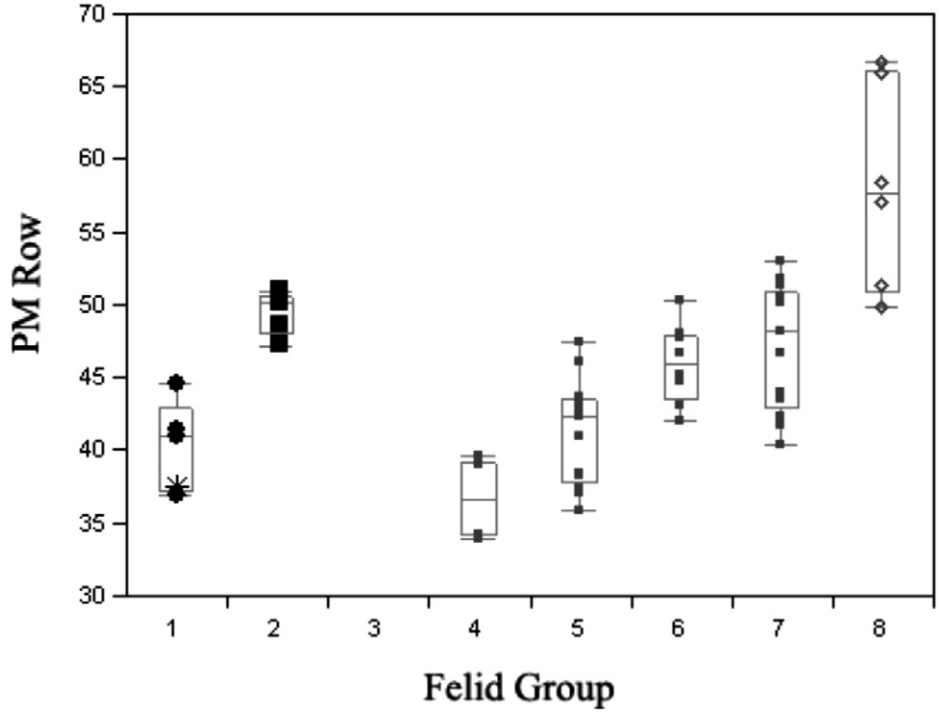


Figure 4. Box plots of premolar-molar row length by genus/species group. Legend as in Fig. 2.

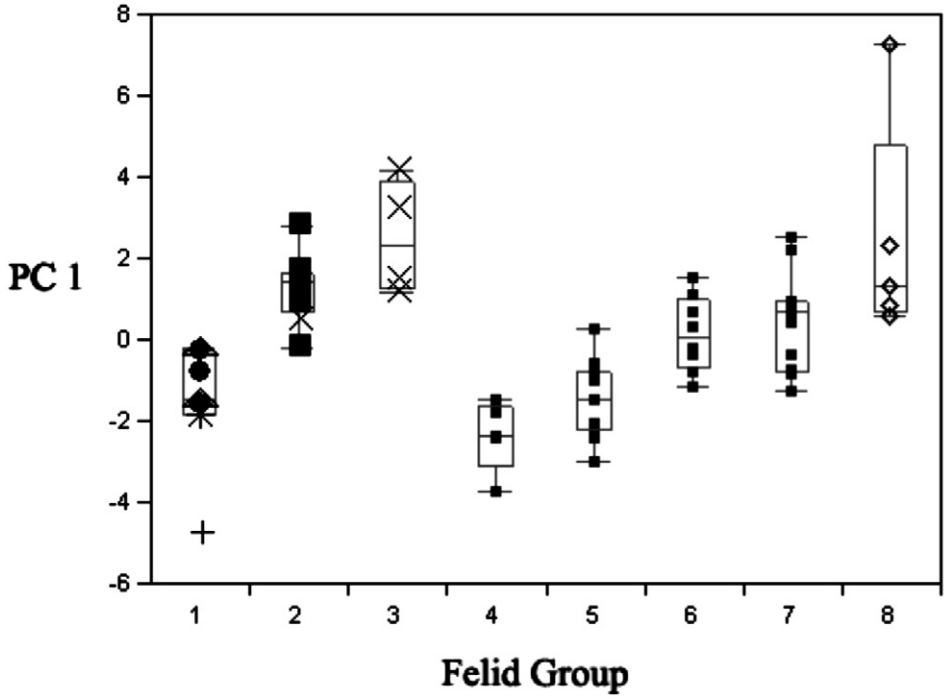


Figure 5. Box plots of the first principal component by genus/species group. Legend as in Fig. 2.

Later European group for this variable.

The same findings obtain with the second principal component (PC 2: Fig. 6) which accounts for 25.90% of the variation within the total sample and separates the two *Megantereon* groups ($P < 0.01$) as well. Based on variable loadings (Table 7), principal component two reflects an inverse relationship between the mesiodistal and buccolingual lengths of P_3 and M_1. Interestingly, in terms of PC2 (Fig. 6), the African/Early European group of *Megantereon* clearly clusters with the *Smilodon* specimens (see discussion). They also group statistically with the Asian specimens for this variable.

Table 7. Principal components on correlations of all felid groups sampled.

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
Eigenvalue	3.75	1.55	0.30	0.18	0.12	0.10
Percentage	62.58	25.90	4.93	2.97	1.99	1.63
Cum. percentage	62.58	88.48	93.41	96.38	98.37	100.00
Eigenvectors						
P_3 BL	0.36	0.47	-0.68	-0.38	0.17	0.07
P_3 MD	0.14	0.74	0.37	0.48	0.27	0.02
P_4 BL	0.47	0.06	0.55	-0.51	-0.28	0.37
P_4 MD	0.49	0.01	-0.09	0.27	-0.59	-0.57
M_1 BL	0.44	-0.34	0.18	-0.11	0.69	-0.41
M_1 MD	0.44	-0.34	-0.22	0.53	0.05	0.60

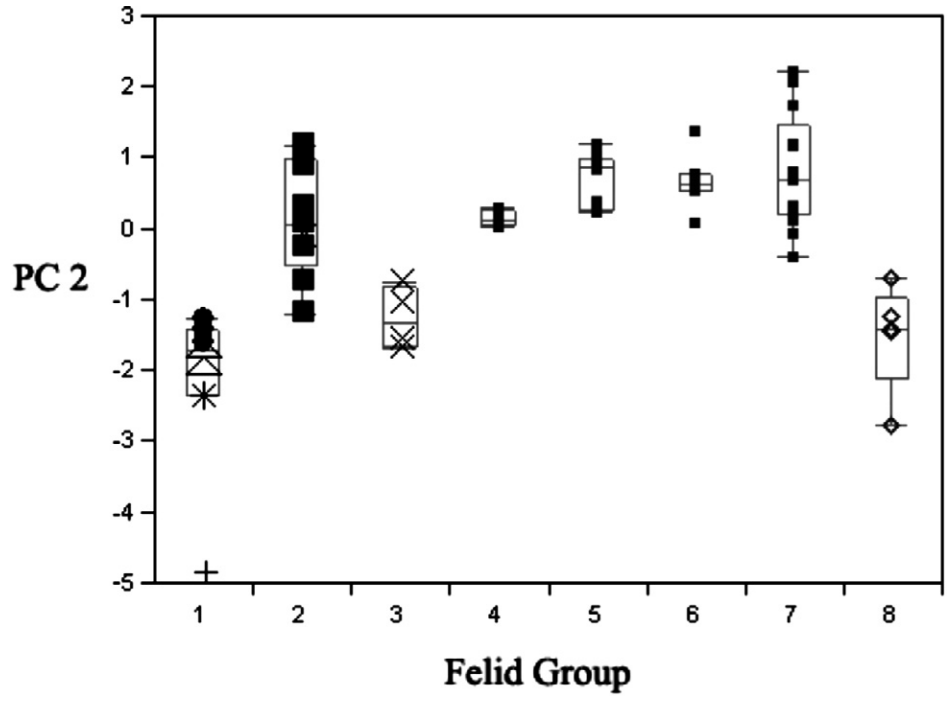


Figure 6. Box plots of the second principal component by genus/species group. Legend as in Fig. 2.

The other principal components, accounting for the remaining 11.52% of the variation within the premolar-molar data, do not show any consistent patterns of separation between any of the study groups. These components have eigenvalues of less than one (Table 7) and thus can be interpreted in terms of random variation. The first two principal components clearly separate the specimens of *Megantereon* into at least two distinct groups, as do the univariate analyses. In fact, the divergence displayed by these combined analyses is greater than most of the differences evident between the means of the extant felid groups. Based on the clear separation of the *Megantereon* groups (African/Early European vs Late European/North American) as seen in the significant *t*-tests for the raw variables and principal component scores, we reject the null hypothesis that *Megantereon* is monomorphic (and by inference, monospecific). The Asian specimens may represent a third species given that they are statistically distinct from the African/Early European group in the first principal component, and the Late European/North American for the second principal component (see discussion). While the specimen from South Turkwel is the most metrically unique among the genus, until further specimens are described that are morphologically and metrically similar, it cannot be statistically determined to represent a new species.

DISCUSSION

The nomen *Megantereon whitei* (Broom, 1937) has taxonomic precedence, and we therefore agree with Martínez-Navarro & Palmqvist (1995) that the evidence warrants a resurrection of this taxon to accommodate an African/Early European group. The Late European/North American group should maintain its designation as *Megantereon cultridens* (Cuvier, 1824). This Late European/North American group probably contains multiple species as Martínez-Navarro & Palmqvist (1996) suggest (with the Asian specimens making a likely bid for separation); however, the present analysis cannot resolve this issue.

Might the size differences between the groups represent sexual dimorphism? The variation between the two *Megantereon* groups is similar to that between the two sexes of leopard (*P. pardus*) – the most sexually dimorphic extant taxon examined – for most premolar-molar row bivariate comparisons, although principal components analysis reveals a substantial degree of metric variability in terms of size and shape for *Megantereon*, greater than for any living felid species. However, we feel it is improbable that only males would have been recovered in one geographic sample and only females in the other. In fact, assuming random sampling of the *Megantereon* populations in each region, there is an exceptionally remote chance of getting a distribution as or more extreme than that observed (eight of eight African specimens being of the small sex and 10 of the thirteen non-African specimens being of the larger sex) assuming an even sex ratio. Though it could be argued that there is some agent in Africa that has accumulated only females and some agent outside of Africa that has selected mostly males, we find this possibility unlikely. Thus, despite the similarity to sexual dimorphism in leopards, it is improbable that sexual dimorphism accounts for the differences between the *Megantereon* populations.

Might the variation in the sample be a result of polytypism normally found in a widely dispersed species? For the morphological traits that we analysed, which clearly separate the *Megantereon* sample, the *P. pardus* sample – which also ranges across Africa and Eurasia – does not cluster into geographically distinct groups.

In almost all analyses of premolar-molar row measurements (e.g. Figs 2–6), the East African *Megantereon* from East Rudolf, the Greek *Megantereon* from Appolonia (Martínez-Navarro & Palmqvist 1996), the Spanish *Megantereon* from Venta Micena (Martínez-Navarro & Palmqvist 1995) and the Dmanisi *Megantereon* from Georgia (Vekua 1995) fall within or close to the range of the African group, indicating that *M. whitei* is the most appropriate identity for these specimens based on current evidence.

Likewise, the Kenyan specimen from South Turkwel (Werdelin & Lewis 2000) is either in the range of, or smaller than the other *M. whitei* specimens in terms of the key variables that warrant the splitting of the genus into an African and non-African species. It must be acknowledged that the morphological features used by Werdelin and Lewis (2000, 2002) to classify the South Turkwel specimen into its own species were not addressed in this paper, and thus all that we can say is that it falls within the range of the African population in terms of the features that we analysed, as suggested by Palmqvist (2002) (but see also Werdelin & Lewis 2002). Thus, while our analysis suggests that *M. whitei* encompasses all African specimens of *Megantereon* and those from Georgia, Greece and Spain, and the other *Megantereon* specimens included in our study should maintain their designation as *M. cultridens*, other non-metric features may be invoked to further parse the sample into more species.

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