ARTICLE

A RE-EVALUATION OF THE DIVERSITY OF *MEGANTEREON* (MAMMALIA, CARNIVORA, MACHAIRODONTINAE) AND THE PROBLEM OF SPECIES IDENTIFICATION IN EXTINCT CARNIVORES

PAUL PALMQVIST,^{*, 1} VANESSA TORREGROSA,¹ JUAN A. PÉREZ-CLAROS,¹ BIENVENIDO MARTÍNEZ-NAVARRO,² and ALAN TURNER³

¹Departamento de Ecología y Geología, Facultad de Ciencias, Universidad de Málaga, 29071-Málaga, Spain, ppb@uma.es, torregrosa@uma.es, johnny@uma.es

²ICREA, Area de Prehistòria, Universitat Rovira i Virgili-IPHES, Plaça Imperial Tarraco 1, 43005-Tarragona, Spain, bienvenido@icrea.es

³School of Biological and Earth Sciences, Liverpool John Moores University, Liverpool L3 3AF, UK, a.turner@livjm.ac.uk

ABSTRACT —In this article, hypotheses about the origin, evolution and dispersal of Megantereon are reviewed using the fossil specimens included in previous comparative studies as well as the remains identified in the late Pliocene site of Fonelas (Spain) and the early Pleistocene localities of Lantian, Lingyi, Longdan, Renzidong (China), and Untermassfeld (Germany). The validity of the two species proposed by Martínez-Navarro and Palmqvist (1995), Megantereon cultridens and M. whitei, is evaluated using tooth measurements and multivariate statistical methods. The hypothesis of sexual dimorphism as an explanation for the morphological variability of Megantereon is tested with a large sample of sexed individuals of Panthera pardus and Panthera leo. Results obtained indicate similar or even smaller differences in tooth dimensions between M. cultridens and M. whitei than between sexes in both leopards and lions, except in the case of the lower fourth premolar. However, in spite of a substantial overlap between both Megantereon species in the size of the upper canine, this tooth reverses the differences found for other tooth measurements, because M. cultridens shows larger cheek teeth on average than M. whitei but smaller sabers. This is confirmed by principal components and discriminant analyses, which reveal that sexual dimorphism in leopards and lions is a matter of tooth size and not of relative proportions and argues against the interpretation of M. cultridens and M. whitei as the sexes (males and females, respectively) of a single species. These results indicate that M. cultridens and M. whitei are valid species, because the differences in tooth measurements exceed those expected from sexual dimorphism and do not reveal the effects of biased sampling. Finally, an analysis of jaw anatomy reveals biomechanical differences between both Megantereon species, related to the relative efficiency of the biting muscles at the level of the lower carnassial.

INTRODUCTION

The origin, evolution and dispersal of the genus Megantereon (Mammalia, Carnivora, Machairodontinae) has been approached in several articles under different taxonomic interpretations. For example, the studies of Ficcareli (1979) and Berta and Galiano (1983) addressed the problem of how many species of this genus lived in Africa, and agreed with Hendey (1974) in considering only one evolutionary lineage for this continent. However, the reviews of the systematics of Megantereon made by Pons-Moyà (1987), Turner (1987), Martínez-Navarro and Palmqvist (1995, 1996), Sardella (1997) and Qiu and colleagues (2004) reached quite different conclusions. Turner (1987) grouped all the specimens of Megantereon in a single lineage, M. cultridens (Cuvier, 1824) (synonyms = M. megantereon, Croizet and Joubert, 1828; M. nihowanensis, Teilhard de Chardin and Piveteau, 1930; M. falconeri, Pomel, 1853; M. sivalensis, Falconer and Cautley, 1868), interpreting the undoubted anatomical and metric variability within the genus that has led to the designation of many species as a reflection of a high level of sexual dimorphism combined with geographic differences.

Martínez-Navarro and Palmqvist (1995, 1996) compared the specimens of *Megantereon* from Africa, Eurasia, and North

America by means of multivariate methods such as principal components and discriminant analysis, using as metric variables the mesiodistal length and buccolingual breadth of the lower cheek teeth and the upper carnassial. The conclusion of these studies was that M. cultridens and M. whitei were the only valid species of the genus. Under this interpretation, M. cultridens would represent the primitive form in the New World and the one found in Eurasia until the Plio-Pleistocene limit (e.g., Les Etouaires, Pardines, Saint-Vallier and Senéze in France; Olivola and Tasso within the Upper Valdarno in Italy; Bugiuliesti in Romania; Fonelas, La Puebla de Valverde and Villarroya in Spain; Figs. 1A-C). Megantereon whitei, the advanced African form (Broom, 1937) (synonyms = M. gracile, Broom and Shepers, 1946; M. eurynodon, Ewer, 1955), would group all the African specimens from the Plio-Pleistocene (Martínez-Navarro and Palmqvist, 1995; Palmqvist, 2002) and those from several early Pleistocene localities in the North of the Mediterranean (vg., Apollonia-1 in Greece, Argentario and Pirro Nord in Italy, Untermassfeld in Germany, Urkút in Hungary, Venta Micena in Spain, Ubeidiya in Israel, and Dmanisi in Georgia). According to Martínez-Navarro and Palmqvist (1995), M. whitei shows a marked reduction in the size of the cheek teeth in relation to M. *cultridens*, particularly the third lower premolar, which translates into the appearance of a diastema between the latter tooth and the fourth lower premolar (Figs. 1F, H). Megantereon whitei

^{*}Corresponding author.



FIGURE 1. Comparison of the craniodental morphology of the two species of *Megantereon, M. cultridens* and *M. whitei*, represented by the cranium and mandible from Senèze (cast), Haute Loire, France (KNM-ER243) (A); cranium and mandible from Perrier, Auvergne, France (unnumbered specimen) (B); cranium from Les Etouaires, Auvergne, France (1094) (C); cranium and mandible from Longdan, Dongxiang, Gansu, China (HMV 1217) (D); cranium from Ileret Area 9 A, Okote Member, Koobi Fora Formation, Kenya (KNM-ER 793) (E); cranium and mandible from Dunanisi, Georgia (skull Nr. 1341; mandible of an unnumbered specimen) (F); mandible from South Turkwel, Turkana Basin, Kenya (KNM-ST 23812) (G); mandible from Ileret Area 9 A, Okote Member, Koobi Fora Formation, Kenya (KNM-ER 793) (H); mandible from Longdan (HMV 1214) (I). Scale bars in centimeters. A–C, E–H: photographs taken by B. Martínez-Navarro. D, I: photographs provided by T. Deng.

ranges in Africa from late Pliocene to early Pleistocene times, arriving at the gates of Europe during the Plio-Pleistocene transition, as evidenced at Dmanisi (Martínez-Navarro and Palmqvist, 1996; Arribas and Palmqvist, 1999; Rook et al., 2004; Martínez-Navarro, 2004).

However, Pons-Moyà (1987) and Sardella (1998) proposed a different evolutionary scenario for *Megantereon* in Europe, which in their opinion would represent an example of anagenetic change. In this way, they interpreted the "advanced form" described as *M. whitei* by Martínez-Navarro and Palmqvist (1995, 1996) as the last step of a European evolutionary trend, convergent to African *M. whitei*, which ended in the earliest Galerian.

Finally, in a recent monograph on the large mammal assemblage from the early Pleistocene locality of Longdan (Dongsiang, Gansu, China), which has provided the best sample of *Megantereon* so far found in Eurasia (Fig. 1D), Qiu and colleagues (2004) review the taxonomy of this genus. They recognize two species in China (*M. nihowanensis*, represented by the specimens from Longdan [Qiu et al., 2004] and Nihowan Loc. 18 [Teilhard de Chardin and Piveteau, 1930], and *M. lantianensis*, identified with the single mandible from Lantian, Gonqwangling [Hu and Qi, 1978]) and another two in Europe (*M. megantereon*, which includes the fossils from Pardines [Heintz et al., 1974], and *M. cultridens*, represented by the skull material from Saint Vallier [Viret, 1954]).

Ewer (1955) first compared the specimens of Megantereon from Kromdraai A (South Africa) with those described from other localities as M. cultridens, concluding that they differed at the species level. In a recent article, Werdelin and Lewis (2000) described a new species, M. ekidoit, from late Pliocene deposits (~3.5 Ma) of the Nachukui Formation south of the Turkwel River in Turkana, northern Kenya, a finding which represents the oldest presence of Megantereon in Africa. The new species was described from a right mandibular ramus (KNM-St 23812) with I₃-M₁ (Fig. 1G). However, Palmqvist (2002) noted that the fourth premolar and the lower carnassial of *M. ekidoit* matched the anatomy and size of the other African specimens of Megantereon, and concluded that it is a primitive form of the lineage of M. whitei. Given the age of the South Turkwel deposits, this specimen would represent the earliest representative of this evolutionary line (however, see Werdelin and Lewis, 2002).

The first reference to the problem of sexual dimorphism in the machairodontines was provided by Viret (1954), who affirmed that the poor fossil record of these hypercarnivores, combined with the anatomical and metric differences between both sexes, made it difficult to compare the specimens from different localities. Turner (1987) performed a comparative study of tooth dimensions in a wide sample of modern leopards, Panthera pardus, concluding that the metric differences recorded in Megantereon do not exceed those derived from sexual dimorphism and geographic variation in this pantherine cat. According to the results obtained by Turner (1987), most African specimens are of smaller size on average and, thus, could be conceived as female individuals of the Eurasian and North American species, M. cultridens. Under this interpretation, the early Pleistocene fossils of Europe attributed to M. whitei by Martínez-Navarro and Palmqvist (1995, 1996) could be also assigned to females of M. cultridens. However, the results obtained by Turner (1987) were based on the size of the lower carnassial, which is the tooth that appears to change less in the evolution of Megantereon (Palmqvist, 2002).

The origin of *Megantereon* is uncertain given the low preservational completeness of its fossil record, as this carnivore is represented in most localities by small numbers of specimens (usually isolated teeth and jaw fragments). In fact, the only exception is the sample of six skulls and three jaws from the rich assemblage from Longdan (Qui et al., 2004). In addition, the bones of the postcranial skeleton are rarely preserved. Berta and Galiano (1983) suggested a North American origin for Megantereon, based on the specimen from the Bone Valley Formation, Florida (~4.5 Ma, Florida), which was initially identified as M. hesperus (Schultz and Martin, 1970) and reclassified by Martínez-Navarro and Palmqvist (1995) as M. cultridens. This is the oldest record of Megantereon, because the earliest occurrence of this genus in Eurasia is dated not older than 3.5 Ma (Les Etouaires, France; Fig. 1C), which indicates that M. cultridens dispersed from North America to the Old World (Qiu, 2003). Europe was the home of *M. cultridens* until the late Pliocene, while this species was probably present in China until the base of the middle Pleistocene (Zhoukoudian Loc. 1, dated with U-series in 0.5-0.4 Ma for the uppermost layers and 0.6–0.8 for the lower strata; Shen *et al.*, 2001), where it was identified as *M. inexpectatus*. In contrast, Turner (1987) pointed to an African origin at ~3.5 Ma, while Sotnikova (1989) considered the Asian continent as the most probable source area for the dispersal event, a suggestion which seems to be corroborated by the presence of *Megantereon* in Pao Te Tsien (loc. 44) at the end of the Miocene. There is also a report on a lower fourth premolar from the late Miocene (~5.7 Ma) of Tugen Hills, Kenya, tentatively attributed to *Dinofelis* that could belong to *Megantereon* in Europe is in the German locality of Untermassfeld, which has a Jaramillo age (~1 Ma).

The nearly complete skeleton from Senéze (France) allows Megantereon to be characterized as a jaguar-sized, short limbed carnivore with a stoutly built postcranial skeleton, in which the robust distal limb bones indicate an ambushing hunting method. This could mean an ability to subdue large prey relative to the size of the predator. The curved, unserrated, elongated and laterally compressed upper canines suggest a hunting technique based on a throat bite to the ungulate prey once immobilized by the robust forelimbs (Turner and Antón, 1997). Biogeochemical data on the abundance of carbon and nitrogen isotopes (δ^{13} C, δ^{15} N) from bone collagen and trace-elements (Sr, Zn) from bioapatite in fossil samples from Venta Micena (Guadix-Baza Basin, southeast Spain) corroborate this anatomically-based conclusion, suggesting that M. whitei ambushed browsing ungulates such as the deer Praemegaceros in forested habitat (Fig. 2), while the sympatric lion-sized, saber-tooth Homotherium latidens pursued large grazing ungulates such as bison and juvenile mammoths in open environments (Palmqvist et al., 2003). It is worth noting, however, that Turner and Antón (1997) argued that male large deer with antlers would not be a suitable prey for Megantereon, because saber-tooths could not get to the neck to make an efficient killing throat bite because the antler would hold the animal in the wrong position. The isotopic data suggest also that the diets of Homotherium and Megantereon show some degree of overlap, because horses were an important prey of both predators (Fig. 2).

In this article, we re-evaluate the systematics of Megantereon, testing the hypothesis of sexual dimorphism as an explanation for the morphological variability of the genus. In addition to those fossil specimens already included in previous comparative studies (e.g., Turner, 1987; Martínez-Navarro and Palmqvist, 1995, 1996; Sardella, 1998; Werdelin and Lewis, 2000, 2002; Palmqvist, 2002), we analyze here the unpublished remains of Megantereon identified in the late Pliocene site of Fonelas P-1 in Spain (Fig. 3) (Arribas et al., 2001, 2004) as well as those from the early Pleistocene localities of Lantian (Hu and Qi, 1978), Lingyi (Chow and Zhou, 1965), Longdan (Qiu et al., 2004), Renzidong (Liu, 2005), and Untermassfeld (Kahlke, 1995; Hemmer, 2001). However, it is worth noting that two specimens assigned to M. whitei in previous studies (jaw fragment KB 5224 from Kromdraai B, South Africa, and cranium OMO 28-67-1075 from Member B, Shungura Formation, Omo) were not included in this analysis because they match the anatomy of Dinofelis (Werdelin and Lewis, 2001).

MATERIAL AND METHODS

This review includes all the specimens of *Megantereon* from the Old and New World that we have directly studied and found in the literature. Table 1 shows the mesiodistal and buccolingual dimensions of teeth (c, p3, p4, m1, C, P3, and P4) of *M. cultridens* and *M. whitei* from localities of Europe (Valdarno [Ficcarelli, 1979], Argentario [Baschieri and Segre, 1958; Sardella, 1994], Pirro Nord [De Giuli et al., 1986; Sardella, 1994; Rook et al., 2004] and Olivola [Forsyth Major, 1890; Ficcarelli,



FIGURE 2. Reconstruction of the predatory behavior of *Megantereon* whitei from the early Pleistocene locality of Venta Micena (Guadix-Baza basin, southeast Spain) on a large deer (*Praemegaceros* aff. obscurus) and a horse (*Equus altidens*). Drawings by Mauricio Antón (modified from Turner and Antón, 1997). Although the reconstruction for *Praemegaceros* illustrates what *Megantereon* would not do with a large male deer bearing antlers, because the antlers would make it difficult to carry out the throat bite, biogeochemical data (δ^{13} C and δ^{15} N ratios in bone collagen and Sr:Zn proportions in bone and enamel hydroxylapatite) of the Venta Micena fauna indicates that megacerine deer form the main prey of *M. whitei* in this paleocommunity (Palmqvist et al., 2003).



FIGURE 3. Right and left mandibular rami (**A**, **B**: specimen FP1-2002-1391 and **C**, **D**: specimen FP1-2002-5001) and left upper canine (**E**, specimen FP1-2001-3G-B°N) of *Megantereon cultridens* from the late Pliocene site of Fonelas P-1 (Guadix-Baza basin, Granada, SE Spain). Scale bar in centimeters. Photographs taken by P. Palmqvist.

1979] in Italy; Saint Vallier [Viret, 1954], Senéze [Schaub, 1925; Sardella, 1994], Pardines and Perrier-Les Etouaires [Heintz et al., 1974; Sardella, 1994] in France; Untermassfeld [Kahlke, 1995; Hemmer, 2001] in Germany; Urkút [Sardella, 1994] in Hungary; Bugiulesti [Radulescu and Sansón, 1991] in Romania; Apollonia-1 [Koufos, 1992; Martínez-Navarro and Palmqvist, 1996] in Greece; Dmanisi [Dzaparidze et al., 1989; Gabunia, 1995; Martínez-Navarro and Palmqvist, 1995; Vekua, 1995] in Georgia; La Puebla de Valverde [Kurtén and Crusafont-Pairó, 1977], Villarroya [Crusafont-Pairó and Kurtén, 1977; Sotnikova, 1989], Venta Micena [Pons-Moyá, 1987; Martínez-Navarro, 1992; Martínez-Navarro and Palmqvist, 1995], and Fonelas [Arribas et al., 2001] in Spain), Ubeidiya in Israel (Ballesio, 1986), Asia (Pao Te Hsien [Zdansky, 1924], Kuruksay 1 [Sharapov, 1986; Sotnikova, 1989], Nihowan [Teilhard De Chardin and Piveteau, 1930], Zhoukoudian [Teilhard De Chardin, 1939], Lantian [Qiu et al., 2004], Lingyi [Chow and Zhou, 1965], Yushé [Teilhard De Chardin and Leroy, 1945] and Renzidong [Liu, 2005]), North America (Broadwater Local Fauna in Nebraska [Shultz and Martin, 1970], Hagerman Local Fauna in Idaho [Gazin, 1933; Bjork, 1970], Rexroad Local Fauna in Kansas [Hibbard, 1937] and Upper Bone Valley Formation in Florida [Berta and Galiano, 1983]) and Africa (Elandsfontein [Turner, 1987], Sterkfontein [Broom and Schepers, 1946; Turner, 1987], Swartkrans [Turner, 1987], Kromdraai A and B [Ewer, 1955; Turner, 1987], Schurveburg [Broom, 1939; Turner, 1987], East Turkana [Leakey, 1976; Turner, 1987], South Turkwel [Werdelin and Lewis, 2000], Omo Shungura [Howell and Peter, 1976], and Ain Brimba [Howell and Peter, 1987]). Table 1 includes four measurements obtained from the scarce mandibles of Megantereon available for this study that were preserved completely. These measurements have proven useful in the biomechanical analysis of jaw geometry for estimating the development of chewing muscles and bite strength in carnivores (Bicknevicius, 1996; Bicknevicius and Leigh, 1997; Bicknevicius and Van Valkenburgh, 1996; Van Valkenburgh and Ruff, 1987) and include: (1) the moment arm of the masseter and pterygoid muscles (MAM, measured from glenoid to angular process); (2) the moment arm of the temporalis muscle (MAT, measured from glenoid to apex of coronoid process); (3) the moment arm of resistance for an object positioned at the canines (MAR, measured from glenoid to lower canine); and (4) jaw depth (JD, measured below the distal end of the lower carnassial), which estimates the resistance of the mandible against dorsoventral loads.

The two alternative hypotheses on the metric variability of Megantereon (i.e., that it could be explained by a high level of sexual dimorphism in a single species, M. cultridens [Turner, 1987], and that it reflects the differences between two separate species, M. cultridens and M. whitei [Martínez-Navarro and Palmqvist, 1995, 1996]) were tested using for comparisons the appropriate tooth measurements from a large sample (N = 126) of sexed individuals of two modern felids, the leopard, Panthera pardus, and the African lion, Panthera leo (unpublished measurements taken by A. Turner and V. Torregrosa). The leopard is a moderately dimorphic carnivore of medium body size (males: 37-90 kg, females: 28-60 kg; Nowak, 1999) while lions are of larger body size and show an extreme degree of sexual dimorphism among extant felids (males: 150-250 kg, females: 82-120 kg; Nowak, 1999). Given that the specimens of both species come from different African and Asian populations, this allows testing for geographic differences in tooth measurements. Extant and extinct felids were compared with the statistical package SPSS (v. 13.0), using methodologies of multivariate analysis such as discriminant analysis and principal components. For each tooth measurement, the degree of sexual dimorphism in leopards and lions was evaluated with the method of Lubischew (Sneath and Sokal, 1973), which allows testing single characters as discriminators. The coefficient of discrimination is K = $(X_{\delta}$ – $(X_{\varphi})^2/2S_x^2$, where X_{σ} is the mean of character X for males, X_{φ} is the corresponding mean for females, and S_x^2 is the pooled vari-ance of character X in both sexes $(S_x^2 = (\sigma_{x\sigma}^2 n_{\sigma} + \sigma_{x\varphi}^2 n_{\varphi})/(n_{\sigma}^2 + n_{\varphi})$, where $\sigma_{x\sigma}^2$ and $\sigma_{x\varphi}^2$ are the variance of character X for make and formulas and $\sigma_{x\varphi}$ are the variance of character X for males and females, and n_{\diamond} and n_{ϕ} are their sample sizes, respectively). Given that the percentage of misclassifications with variable X is approximately the probability that a normal deviate exceeds $\sqrt{K/2}$, the greater K is, the better character X is as a

TABLE 1. Tooth measurements.

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Orkit (6506/20) M. wnitei 18.0 9.5 Romania 18.0 19.5	
Bugulesti M. whitei 21.0 11.0 17.0 8.0 30.0 13.5	
Greece	
Apollonial (APL12) M. whitei 9.2 6.2 5.6 3.4 14.4 6.0 18.1 8.5	26.1
Apollonial (APL13) [*] M. whitei 24.6 11.3	
Georgia	0 27.0
Dmanis (left) M. Writer 222 108 134 62 280 110 40 80 0.0 4.0 10.0 7.7 19.1 5.9 55.4 20.0 150.0 Dmanis (Nr 1341)* M. Writer 222 108 134 62 280 110 40 80) 27.8
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Spain	
La Puebla de Valverde M.cultridens 20.0 12.0	
La Puebla de Valverde M.cultridens 15.3 6.4	
La Puebla de Valverde M.cultridens 15.7 7.2	
La rueba de Valverde M.Cutridens 15.7 7.5	
Villarrow M. cultridens 18.0 9.3 29.7 14.0	
Villarroya (V-135) M.cultridens 17.0 9.9	
Villarroya M.cultridens 19.1 10.0	
Villarroya (V-122) M.cultridens 14.3 6.3	
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Villarroya (V-134) M.cultridens 21.5 11.5	
Vinatroya (1/94m) M.Cutriaters 10.9 4.70 16.2 6.3 19.4 9.4 Vinatroya (1/94m) M.cutriaters 10.9 4.70 16.2 8.3 19.4 9.4 Vinatroya (1/94m) M.cutriaters 17.5 8.3	
Vilariosa (17594) M. dufridens 20.0 —	
Villarroya (1771M) M.cultridens 16.9 —	
Venta Micena (VM-2264)* M. whitei 14.5 6.3 17.8 9.0	27.8
Venta Micena (VM-2265) M. whitei 18.8 8.7	30.0
Venta Micena (VM-2206) M. whitei 19.2 8.7	
Venta Micena (VM-220/1/2005) M. White: 10.5 6.6	
Yours and cra (Ym 22/0) M. Writer 250 11.1 Fonelas Prociso 1 (FP-1 5001) M. cultridens 11.2 10.9 5.8 19.5 9.2 23.7 11.8	33.0
Fonelas Pocico 1 (FP-1 1391) M.cultridens 10.7 5.5 21.5 9.3 24.7 12.4 48.5 30.9 166.1	1 25.0
Fonelas Pocico 1 (FP-1 5004) M.cultridens 25.2 9.3	ı 36.4
Fonelas Pocico 1 (FP-1 5003) M.cultridens 39.2 27.1	1 36.4

(continued on next page)

discriminator. For example, with K = 7.68, 95% of identifications will be correct (two-tailed t-test). This requires the distribution of variable X in males and females to be approximately normal and of equal variance. The coefficient *K* was also used for evaluating the differences in tooth dimensions between *M. cultridens* and *M. whitei*.

- 1	15
- 1	65
- L	0.2

		C1		Р	3	I	24	1	M1	c	;	р	3	р	4	n	n1				
Localities	Species	L	В	L	В	L	В	L	В	L	В	L	В	L	В	L	В	MAT	MAM	MAR	JD
Asia																					
'Ubeidiya [*]	M. whitei									11.1	9.9										
Pao Te Hsien (M7279)	M.cultridens			17.3	7.0	27.7	13.0														
Kuruksay (3120)	M.cultridens	19.9	11.1																		
Kuruksay (3848/73)	M.cultridens													18.0	7.7	19.5	9.4				
Kuruksay (73 459)	M.cultridens									10.8	_	10.4	4.9	18.6	7.2	19.1	8.7				
Nihowan	M.cultridens	28.4	14.3	13.9	7.0	28.0	13.4														
Nihowan	M.cultridens					31.0	15.0														
Nihowan	M.cultridens									15.0	_	9.5	_	19.0	_	24.0			28.5	158.7	30.0
Choukoutien (Local.1)	M.cultridens	25.0	15.0	16.0	7.0	35.0	13.0	5.0	10.0												
Lingyi	M.cultridens	23.0	9.5	14.0	7.0	30.0	12.0														
Yushé	M.cultridens	28.0	14.0	14.0	_	33.0	_														
Yushé	M.cultridens	22.0	_																		
Renzidong (V 13042)	M. cultridens			17.1	6.9	33.0	_														
Renzidong (V 13042)	M. cultridens			16.8	6.8	33.4	_														
Renzidong (V 13043)	M. cultridens													21.4	9.6						
Londang (HMV 1214)	M. cultridens	29	13.5	13.5	6.3	31	13	4.9	7.8	10.3	8.0	8.4	4.9	19.5	8.4	20.8	10.2	41.0	27.5	149.6	28.8
Londang (HMV 1214)	M. cultridens											7.0	4.0								
Londang (HMV 1215)	M. cultridens	23.5(a)	>9	14.2	6.1	29.8	13.2	4.7	8.7												
Londang (HMV 1216)	M. cultridens	()		13.5	6.2	32	13.4														
Londang (HMV 1217)	M. cultridens	25.7	15	13.4	6.9	31.7	14	5	10	11.0	7.8	9.5	5.8	21.5	10.0	24	10.7	37.7		142.7	24.2
Londang (HMV 1218)	M. cultridens							-		12.0	7.5	8.8	4.9	20.0		23.5	11.7				
Londang (HMV 1220)	M. cultridens	27.5	14	12.2	6.0	33.7	13.7	5	11												
Lantian	M. cultridens							-		10.0	6.5	7.5	4.5	18.0	8.0	23.0	10.0				
North America	in cumucio									10.0	0.0	710	112	10.0	0.0	2010	10.0				
Nebraska (UNSM-25494)	M cultridens											10.7	5.6	18.3	72	197	93				
Idaho (USNM 12614)	M cultridens											10.7	510	10.0	7.2	19.8	8.5				25.0
Kansas (USNM 3917)	M cultridens													18.6	9.0	19.0	0.5				25.0
Florida (LE 22890)	M cultridans											12.0	5.6	10.0	8.0	21.0	0.5				28.0
A frica	meannachs											12.0	5.0	17.1	0.0	21.0	2.5				20.9
Kromdraai A (KA 64)	M whitei	25.0	12.0			30.2	10.6							17.0		10.6	0.0	35.7	26.2		33.8
Flandsfontein (F 3060)	M. whitei	25.0	12.0			50.2	10.0							15.0	8 1	20.6	8.0	31.0	20.2		55.6
Sworthrong (STS 1558)	M. whitei													12.2	6.0	10.2	0.9	51.0	21.4		26.0
Swartkrans (S1S-1556)	M. whitei											6.6	2.0	13.5	0.9	19.5	0.5				20.0
Schurveburg (1M-856)	M. whitei											0.0 5 0	3.9	14.5	7.5	17.0	0.0				27.0
Sterktontein (SK-557)	M. whitei	21.5	12.1	0.0		24.0	11.0	4.1	6.4	0.0	7.0	5.8	3.3	14.5	1.5	17.6	0.7	22.1		125.6	27.0
East Lake Turkana (ER-793)	M. whitei	21.5	13.1	9.0	5.5	24.8	11.0	4.1	0.4	9.0	7.0	5.2	4.5	14.5	0.9	17.0	8.7	33.1		135.0	29.7
East Lake Turkana (ER-/01)	M. whitei					27.0	12.5			7.0				145	62	20.0	8.8	24.0	24.2	122.6	25.2
South Turkwei (KNM-ST 23812)	M. whitei					22.7	14.0			7.8	5.5	—	_	14.5	6.3	17.1	8.5	34.8	24.2	132.6	25.2
Ain Brimba (1958-14-163)	M. whitei					32.7	14.2														

L: mesiodistal length, B: buccolingual breadth (in millimeters) of *Megantereon* specimens from the Old and New World. C1: upper canine, P3: third upper premolar, P4: upper carnassial, M1: upper molar, c: lower canine, p3: third lower premolar, p4: fourth lower premolar, m1: lower carnassial, MAT: moment arm for temporalis muscle (measured from glenoid to apex of coronoid process), MAM: moment arm of masseter muscle (measured from glenoid to an object positioned at canines (measured from glenoid to lower canine), JD: jaw depth (measured below the distal end of the lower carnassial).

*Measurements taken by B. Martínez-Navarro; the measurements of the specimens of *M. cultridens* from the late Pliocene locality of Fonelas Pocico 1 were provided by A. Arribas.

RESULTS

Figure 4 shows the bivariate plots for mesiodistal length and buccolingual breadth measurements of selected teeth, which allow estimating the degree of overlap between males and females of modern felids, on the one hand, and between the two *Megantereon* species, *M. cultridens* and *M. whitei*, on the other. It is worth noting that the Chinese specimens classified as *M. nihowanensis* cluster with *M. cultridens*, which confirms that the latter was the only species that lived in Europe and Asia before the arrival in Europe of African *M. whitei* during early Pleistocene times.

Table 2 shows the values obtained for the coefficient K of Lubischew (1962). In general terms, it may be emphasized that lions show a higher degree of sexual dimorphism than leopards, as the degree of overlap between both sexes in the former species is lower than in the latter one for all tooth dimensions except the breadth of the upper carnassial. This is especially true for the size of the upper canines, which are the teeth that show a higher degree of sexual dimorphism among extant felids (see subsequent discussion). Concerning *Megantereon*, the lower fourth premolar is the only tooth whose mesiodistal and buccolingual dimensions show a clear separation between the two species, with the highest values for *M. cultridens* and the lowest ones for *M. whitei*. Specifically, the K test indicates that 87% and 66% of the fossil specimens can be confidently assigned to their respective species using these measurements (Table 2). However, the

degree of overlap between M. cultridens and M. whitei in the length and breadth of the upper and lower carnassial teeth is similar to that found between the distributions of both sexes in leopards and greater than in lions, with the specimens of M. *whitei* showing lower measurements on average than those of *M*. cultridens. In addition, there is a substantial overlap between both Megantereon species in the length and breadth of the upper canine, because these measurements allow correct reclassification of only < 25% and $\sim 20\%$ of individuals, respectively. This overlap is greater than the one observed between sexes in modern felids, as > 60% of leopards and $\sim 80\%$ of lions can be sexed using the length of the upper canine. However, it is worth noting that *M. cultridens*, whose cheek teeth tend to be larger than those of M. whitei, has on average the smallest upper canines, although the sample size and range for *M. cultridens* are greater than for M. whitei. This reverses the trend showed by the fourth lower premolar and the carnassials, arguing strongly against the interpretation of M. cultridens and M. whitei as the sexes (males and females, respectively) of a single species.

A discriminant analysis was also performed using as variables the length of the lower fourth premolar and the breadth of the first lower molar, in order to evaluate in further depth the ability of these measurements to differentiate between *M. cultridens* and *M. whitei*, following the approach suggested by Martínez-Navarro and Palmqvist (1995, 1996). These tooth measurements were selected using a stepwise procedure as the best metric variables for discriminating between both *Megantereon* species. The



FIGURE 4. Bivariate plot for p4, m1, C, and P4 mesiodistal length and buccolingual width (in millimeters) in *Megantereon cultridens* (\bullet), *M. whitei* (\bigcirc), *Panthera leo* males (\blacksquare), *P. leo* females (\square), *Panthera pardus* males (\blacktriangle), and *P. pardus* females (Δ).

discriminant function obtained provides 96.4% of correct reclassifications for the specimens of M. cultridens and M. whitei (Fig. 5). In addition, it is interesting to note that the two variables used in this analysis show factor loadings of opposite sign in the discriminant function, which indicates that the relative dimensions of these teeth are different in both saber-tooths, with M. whitei showing a smaller fourth premolar relative to the size of the lower carnassial than M. cultridens. Similar analyses were performed for discriminating between sexes in leopards and lions. In both cases, however, there is a greater overlap between the scores for males and females on the discriminant functions, which is reflected in the lower percentages of correct allocations obtained, 73.4% for leopards and 80.3% for lions; in the case of leopards, this percentage decreases to 70.3% if the method of cross validations (i.e., the leave-one-out test) is used. In both discriminant functions, the factor loadings of the variables are positive and of similar value, which reveals that sexual dimorphism in these felids is a matter of size and not of relative proportions (i.e., the males show larger premolars and carnassials than the females). This indicates that the differences recorded in tooth measurements between *M. cultridens* and *M. whitei* exceed those expected from sexual dimorphism in large felids and, thus, do not reveal the effects of biased sampling in both populations.

These results are confirmed by a principal components analysis, performed using as variables the logarithms of the length and breadth of the fourth lower premolar and the first lower molar in those mandibles and jaw fragments of *Megantereon* in which the four measurements were available (Table 1), as well as in leopards and lions. The distribution of the specimens analyzed on the first two components (Fig. 6), which jointly account for more than 98.5% of the original variance (Table 3), reveals a substantial morphological overlap between the teeth of both sexes in leopards and lions, which is not the case for the specimens of *M*.

Tooth	Statistics	Megante	ereon	Panther	a pardus	Panthera leo			
Dimensions		M. cultridens	M. whitei	ð	Ŷ		ð	ę	
Clength	μ	22.6	25.1	14.49	12.07	25.77		21.39	
-	σ	3.59	3.84	1.57	0.90	1.74		1.68	
	N	31	9	38	24	31		32	
	√K/2 (%)	0.343 (73	.3%)	0.897	(37.3%)		1.284 (20.4%))	
	[(μ _♂ - μ _♀)/μ _♀]100	10.0%	6	20.	0%		20.5%		
C breadth	μ	11.7	12.52	10.94	9.31	18.40		15.54	
	σ	1.95	1.89	1.22	0.86	1.31		1.15	
	N	28	9	37	24	32		32	
	√K/2 (%)	0.212 (83	3.3%)	0.745	(45.9%)		1.159 (25.1%))	
	[(μ _♂ – μ _♀)/μ _♀]100	6.5%		17.	5%		18.4%		
P4 length	μ	31.4	28.4	24.99	23.30	37.56		34.98	
	σ	2.46	2.32	1.64	1.53	1.51		1.96	
	N W/D (0()	30	12	40	25	32	0 70 4 (46 60)	33	
	$\sqrt{K/2}$ (%)	0.619 (5.	3.9%)	0.528	(59.9%)		0./34 (46.6%))	
D4 has a d4h	$[(\mu_{3} - \mu_{2})/\mu_{2}]100$	12.0	/0	12.10	11 70	10.61	7.4%	16.02	
P4 breadth	μ	13.8	11.9	15.10	11./0	18.01		10.83	
	σ N	1.38	1.10	0.99	0.00	21		1.40	
	$\sqrt{\frac{1}{\frac{1}{\frac{1}{\frac{1}{\frac{1}{\frac{1}{\frac{1}{1$	21 0.720 (A	7.0%)	0.872	(11.10)	51	0 707 (48 2)	55	
	$(\mathbf{K}/2)$ (70)	16.09	/.0 /0) /_	0.623	(41.4 /0) 0%		10.6%		
n4 length	$[(\mu_3 - \mu_{\varphi})/\mu_{\varphi}]_{100}$	10.07	15.13	18.16	16.68	27 49	10.0 /0	24 97	
p4 length	μ σ	1 37	1 13	1 26	1 18	1.00		1 50	
	N	23	11	30	25	32		31	
	$\sqrt{K/2}$ (%)	1 566 (1)	27%)	0.600	(551%)	52	0 925 (35 9%))	
	$[(\mu_{1} - \mu_{2})/\mu_{2}]100$	26.89	6	8 ()%		10.1%	,	
p4 breadth	μ μ	8.50	6.90	8.64	7.97	13.98	10.170	12.59	
protouuti	σ	0.89	0.70	0.70	0.74	0.76		0.98	
	Ň	21	11	39	25	32		31	
	√K/2 (%)	0.966 (34	4.1%)	0.469	(64.1%)		0.794 (43.0%))	
	$[(\mu_{3} - \mu_{9})/\mu_{9}]100$	23.29	6	8.4	Ì%		11.0%	/	
m1 length	μ	21.0	18.8	18.39	17.11	28.50		25.70	
C	σ	2.37	0.94	1.35	1.00	1.31		1.40	
	N	27	17	41	25	34		31	
	√K/2 (%)	0.566 (57	7.4%)	0.520	(60.5%)		1.035 (30.5%))	
	$[(\mu_{3} - \mu_{2})/\mu_{2}]100$	11.79	6	7.5	5%		10.9%		
m1 breadth	μ	9.80	8.70	8.69	7.96	14.32		13.04	
	σ	1.23	0.34	0.73	0.53	0.59		0.80	
	N	26	15	41	25	34		31	
	√K/2 (%)	0.551 (58	8.5%)	0.551	(58.4%)		0.919 (36.2)		
	[(μ _ð – μ _♀)/μ _♀]100	12.6%	/o	9.2	2%		9.8%		

TABLE 2. Comparison of the discriminating power of single tooth measurements in *Megantereon*, leopards and lions (μ : mean, σ : standard deviation, *N*: sample size) using the coefficient K of Lubischew.

For each measurement, the probability (two-tailed t-test) that a normal deviate exceeds $\sqrt{K/2}$ allows estimating the degree of overlap (%) between the two distributions compared (species for *Megantereon*, sexes for both *P. pardus* and *P. leo*). The degree of sexual dimorphism in leopards and lions for each measurement, estimated as the difference between the means for males and females divided by the mean for females, is provided; in the case of *Megantereon*, this percentage is calculated considering the specimens of *M. cultridens* as males and those of *M. whitei* as females.

cultridens and M. whitei. In fact, the factor scores for males and females of P. pardus and P. leo show that the metric differences between the sexes of both species are explained exclusively by the first principal component. Given that all the variables have positive factor loadings on this component, it may be interpreted in an ad hoc manner as a size vector (Reyment and Jöreskog, 1993). This confirms that sexual dimorphism is basically a matter of size differences between sexes in these felids. On the contrary, the scores of the specimens of M. cultridens and M. whitei show non-overlapping distributions on the plot of the first two principal components (Fig. 6). In addition, the factor loadings of the variables measured on the two teeth show different signs on the second component (Table 3), which is the one that separates the specimens of Megantereon from both leopards and lions. Specifically, the length and breadth of the fourth premolar have positive loadings while the corresponding variables of the lower carnassial receive negative ones. For this reason, this component may be interpreted in an *ad hoc* manner as a shape vector (Reyment and Jöreskog, 1993). This result indicates, again, that the metric differences between the cheek teeth of M. cultridens and M. whitei are not merely attributable to size differences between sexes, as could be expected if the specimens of *M. cultridens* and *M. whitei* were predominantly the males and females, respectively, of a single species.

The differences described above are perceived more clearly in Figure 7, which shows the ratio between the average mesiodistal lengths at crown base of the upper canine and the lower fourth premolar in M. cultridens (1.178) and M. whitei (1.659), compared with the corresponding ratios for males and females of P. leo (0.937 and 0.855, respectively) and P. pardus (0.795 and 0.726, respectively). This figure also includes vertical bars that represent the range of values for these ratios (i.e., mean canine length plus one standard deviation divided by mean premolar length minus one standard deviation, and vice versa). The graphs show that the two Megantereon species have distinct tooth proportions, with M. whitei showing an upper canine which is more than 1.5 times longer mesiodistally than the fourth lower premolar, while the ratio obtained for the corresponding measurements in *M. cultridens* shows that both teeth are more similarly proportioned in this species. It is also interesting to note that, for each species, the confidence intervals around the mean ratios do not include the average value of the other. In the case of lions and leopards, however, the two sexes show similar average tooth proportions and a wide overlap between their confidence inter-



FIGURE 5. Linear discriminant functions (Φ) for p4 length and m1 breadth values in *Megantereon*, *P. leo*, and *P. pardus*. R₁ and R₂: group centroids. R₀: limit between groups. χ^2 : chi-square test for independence of variables. D²: Mahalanobis distance between group centroids. The functions are measured in discriminant units. *Megantereon cultridens* (Φ), *M. whitei* (\bigcirc), *Panthera leo* males (\blacksquare), *P. leo* females (\square), *Panthera pardus* males (\blacktriangle), and *P. pardus* females (Δ).

vals, which in both cases include the average ratio of the other sex.

Figure 8 shows the lengths of the two main slicing cusps of the lower carnassial, the paraconid and the protoconid, in *M. cultridens* and *M. whitei*, as well as in leopards and lions. In both pantherine cats, these cusps are more developed in the males than in the females, reflecting the differences in body size related to sexual dimorphism. However, in the case of leopards there is a substantial overlap between both sexes in the dimensions of the protoconid and the paraconid, which is not the case in lions, where these measurements help in differentiating between sexes.

This is in agreement with the higher degree of sexual dimorphism of lions. In the case of *Megantereon*, both species show a similar range of values for the length of the protoconid (i.e., the cusp more posteriorly positioned), but the paraconid (i.e., the cusp more anteriorly positioned) is longer in *M. cultridens* than in *M. whitei*. The shortening of the paraconid in *M. whitei* (Fig. 9) parallels the reduction of the lower premolar teeth in this species relative to *M. cultridens*, indicating that the point of maximum chewing force is placed more posteriorly in the carnassial of the African species, which relates to the greater development of the sabers (see below).



FIGURE 6. Bivariate plot of scores for extant leopards and lions and for *Megantereon* specimens on the first two principal components.

Among modern felids, sexual dimorphism is more marked in the size of the upper canines than in other tooth measurements, exceeding the differences between both sexes in the dimensions of the skull and mandible. Such a degree of sexual dimorphism is not related to diet, body mass or habitat, as the only relevant factor seems to be the breeding system (Van Valkenburgh and Sacco, 2002). For this reason, it is not surprising that the upper canines of a lion are, on average, 20.5% longer and 18.5% wider TABLE 3. Results of principal components analysis of *Megantereon* and modern felids: eigenvalues (λ), percentages of original variance explained by the eigenvectors, and factor loadings of variables in the first two principal components.

	PC1	PC2
λ	3.853	0.092
% variance	96.34	2.30
p4 length	0.984	0.108
p4 width	0.976	0.189
m1 length	0.981	-0.167
m1 width	0.985	-0.129

than those of a lioness, and similar values apply in the case of leopards (Table 2). However, lions and leopards are less sexually dimorphic in the size of the lower fourth premolar and in the dimensions of the upper and lower carnassials, the differences between males and females ranging from only 7% to 12% (Table 2). Similar percentages are obtained when the dimensions of the cheek teeth are compared in M. cultridens and M. whitei, except in the case of the fourth lower premolar, a tooth for which the differences in mean length and breadth between both Megantereon species (26.2% and 23.8%, respectively) exceed amply those found for the corresponding measurements in leopards and lions, and are even greater than the differences in the dimensions of the upper canines between the sexes of these species (Table 2). Obviously, given the extreme reduction of the lower third premolar in M. whitei, as exhibited by the specimen from Dmanisi (Fig. 1F), the differences between both Megantereon species would be maximized if the dimensions of this tooth were used for comparisons. In fact, the third lower premolar may even disappear in *M. whitei*, as in the mandible from South Turkwel (Fig. 1G) (Werdelin and Lewis, 2000; Palmqvist, 2002). However, M. whitei, the species whose cheek teeth show on average a smaller size, has upper canines that are on average more developed than those of *M. cultridens*, by 10% in length and by 6.5% in breadth, an effect that is produced in part by the high measurements of the Pirro Nord specimen. Such difference, although lower than the one found in modern felids between the average dimensions of the upper canines in males and females, is not easily explained by sexual dimorphism, since it is reversed for other teeth such as the lower premolars and the upper and lower carnassials, which follow in part the pattern exhibited by lions and leopards for metric differences between the sexes (Fig. 4, Table 2). Thus, it is difficult to imagine a species in which the males, represented by



FIGURE 7. Ratios of mean mesiodistal lengths of the upper canine and the fourth lower premolar of males and females in *P. pardus* and *P. leo*, and in the species of *Megantereon*. The upper and lower limits of bars represent the ratios of maximum to minimum values and minimum to maximum values, respectively. Drawings by Mauricio Antón.



FIGURE 8. Plot of lower carnassial protoconid and paraconid length (in millimeters) in males and females of *P. pardus* and *P. leo*, and in the species of *Megantereon. Megantereon cultridens* (\bigcirc), *M. whitei* (\bigcirc), *Panthera leo* males (\blacksquare), *P. leo* females (\square), *Panthera pardus* males (\blacktriangle), and *P. pardus* females (\triangle).

the majority of specimens assigned to *M. cultridens*, could have cheek teeth more developed than the females, mostly represented by the specimens attributed to *M. whitei*, but the canines of smaller size on average. In addition, it would be difficult to explain, under the hypothesis of an extreme degree of sexual dimorphism in *Megantereon*, why the metric differences between the specimens attributed to *M. cultridens* and those assigned to *M. whitei* are more pronounced in the lower premolars than in the carnassials, because in the case of leopards and lions the size differences for all these teeth between males and females are similar.

The anatomical differences between the mandibles of M. cultridens and M. whitei imply differences in their biomechanical behavior, affecting the relative efficiency of the biting muscles at the level of the lower fourth premolar and carnassial. This may be analyzed by plotting the moment arm of resistance for an

object positioned at the notch of the lower carnassial (COM1) or at the main cusp of the fourth lower premolar (COP4) on the moment arm of the temporalis muscle (MAT), following the approach developed by Emerson and Radinsky (1980). Given that the relative position of the temporal fossa is similar in the specimens of both species (Fig. 9), the variable MAT (measured as the distance from the condyle to the apex of the coronoid process) is a good estimator of the relative temporalis moment arm for any degree of jaw gape. Thus, other things being equal, the ratio between MAT and COM1 (or COP4) estimates the efficiency of jaw leverage. Figure 10 shows that the slopes of COM1 on MAT for *M. whitei* and *M. cultridens* are statistically different (t = 3.42, P = .011), and this holds also for COP4 on MAT (t = 3.10, P = .021). These results indicate that the two Megantereon species follow different allometric rules. The efficiency of jaw biting at the lower cheek teeth relates directly to the moment arm of temporalis muscle (MAT) and inversely to the moment arm of resistance for an object positioned at the fourth premolar or at the carnassial (i.e., COP4 or COM1, respectively). Figure 10 shows also that the measurements of MAT, COP4 and COM1 in the specimens of M. cultridens result in high values for the ratios MAT:COP4 and MAT:COM1, thus indicating a high biting efficiency for the jaw dimensions of this saber-tooth. Similarly, the ratios for these measurements in the mandibles of M. whitei indicate also that this species maximized the bite force at the lower cheek teeth. However, the regression lines adjusted for both Megantereon species are different, which implies that the mandible of *M. whitei* is not a small-sized version of the one of *M. cultridens*. In fact, if we increase the size of a mandible of M. whitei to the average dimensions of M. cultridens without changing its form, the ratios MAT:COP4 and MAT: COM1 would take lower values than in the latter species, which would translate into a loss of biting efficiency. This holds also if a mandible of *M. cultridens* is isometrically scaled to the smaller size of *M. whitei*, as this design would be less efficient for such dimensions, resulting in a lower bite force than in M. cultridens (i.e., lower MAT:COP4 and MAT:COM1 ratios). These results indicate that both species are equally well adapted, in terms of jaw geometry, to their respective sizes.

DISCUSSION

Once the hypothesis of sexual dimorphism is rejected, it is worth considering the relationship between the differences in tooth measurements between both *Megantereon* species and the European faunal context in which the replacement of *M. cultridens* by *M. whitei* took place if the latter dispersed out of Africa during the late Pliocene as proposed by Martínez-Navarro and Palmqvist (1995, 1996).

The Plio-Pleistocene transition in southwestern Europe is marked by an important faunal turnover, as detected in the late Villafranchian of Italy (Olivola and Tasso faunal units; Azzaroli, 1983, 1995; Azzaroli et al., 1988; Rook and Torre, 1996). The comparative study of the large mammal assemblages from several circummediterranean localities (e.g., Apollonia-1, Dmanisi, Pirro Nord, 'Ubeidiya, Cueva Victoria and Venta Micena) shows the arrival in Europe of African and Asian species during the early Pleistocene (see review in Martínez-Navarro, 2004). Immigrants originating in Asia are basically ruminant species (e.g., the ovibovine Soergelia minor; Martínez-Navarro et al., 2005a), the horse Equus altidens (Guerrero-Alba and Palmqvist, 1997) and three canids, Canis etruscus, C. mosbachensis, and Lycaon lycaonoides (Martínez-Navarro and Rook, 2003). African immigrants include the hippo Hippopotamus antiquus, the giant gelada Theropithecus oswaldi, and saber-tooth M. whitei (Martínez-Navarro and Palmqvist, 1996; Rook et al., 2004). In addition, members of the genus Homo showing anatomical affinities with early African H. habilis are recorded at 1.81 Ma in Dmanisi (Rightmire et al., 2006).



FIGURE 9. Cranial and tooth morphology of *Megantereon whitei* (\mathbf{A} , \mathbf{C}) and *Megantereon cultridens* (\mathbf{B} , \mathbf{D}) based on the crania of Dmanisi and Senèze, respectively. Arrows on the crania indicate the midpoint of the temporal fossa profile. The temporalis fibers have nearly the same orientation in both species. \mathbf{C} and \mathbf{D} represent the upper and lower postcanine teeth, where the tips of cusps are indicated as filled circles and the notches as empty circles. The carnassials (P4, m1) have reciprocally curved blade edges. The lines with arrows indicate the approximate correspondence between the elements of the upper and lower dentition when the jaw is closing. Bu = buccal; Lin = lingual.

Megantereon shows the following craniodental characters, shared with other machairodontines (for review and references on saber-tooth anatomy, see Emerson and Radinsky, 1980; Marean, 1989; Van Valkenburgh and Ruff, 1987; Martin, 1989; Anyonge, 1996; Biknevicius et al., 1996; Antón and Galobart, 1999; Arribas and Palmqvist, 1999; Antón et al., 2004; Salesa et al., 2005): (1) Extremely long and flattened upper canines with unserrated margins. (2) Longer, thicker, more pointed and procumbent upper incisors than in modern felids, and reduced, incisorshaped lower canines, suggesting a functional emphasis on tearing and stripping flesh from carcasses, a task that modern felids perform with the assistance of their stout, conically shaped canines; the extremely large upper canines of Megantereon would probably be ineffective in the manipulation of chunks of flesh. (3) Upper carnassials with the protocone reduced and lowered away from the occlusal surface, a condition present only among extant felids in the hypercarnivorous cheetah, forming a long and thin blade specialized for slicing flesh. (4) A lowered glenoid fossa, a reduced height of the coronoid process, a laterally shifted angular process and a shortened zygomatic arch all allow a wider gape than that of modern felines, but suggest that the temporalis muscle was weaker. However, the temporal fossa was shorter and narrower in Megantereon, which indicates that the temporalis was oriented more vertically and perpendicular to the tooth row, increasing the bite force at the lower carnassial, which was closer to the mandibular condyle. (5) An enlarged, lowered and ventrally extended mastoid process, indicating that the cleidoand sterno-mastoid muscles must have been correspondingly large. In addition, the occiput is higher and narrower than in felines, and the temporomandibular joint is located more ventrally. The mastoid process is rotated further below the skull joint so that the leverage of the neck muscles is increased, thus suggesting that a head-depressing motion was involved in the penetration of the canines. These craniodental features could be thought to indicate that Megantereon and other saber-tooths were able to hunt very large prey relative to their own size (Arribas and Palmqvist, 1999), although recent discussions of the origin of such features suggest that efficiency in killing may have been the more important reason for their development (Antón et al., 2004; Salesa et al., 2005, 2006). In any case, what seems clear is that Megantereon consumed exclusively soft tissues, given its specialized dentition for meat slicing. As a result, this



FIGURE 10. Bilogarithmic plot of the moment arms of resistance of m1 (COM1, values depicted as circles) and p4 (COP4, values depicted as squares) on MAT for several specimens of *Megantereon whitei* and *Megantereon cultridens*. Both species show different allometric relationships, although the lines are approximately parallel for their p4 and m1. The leverages for *M. whitei* and *M. cultridens* at the lower carnassial and fourth premolar, estimated by the ratios MAT/COM1 and MAT/COP4, respectively, have differential efficiency according to their MAT values.

predator left variable amounts of flesh on the carcasses of the ungulates hunted and all within bone nutrients intact. These resources could be subsequently scavenged by hyenas and hominins (Marean, 1989; Turner, 1992; Arribas and Palmqvist, 1999).

The postcranial morphology of Megantereon is similar to extant jaguars (Lewis, 1997), although long distance dragging capabilities and especially tree caching treatment of prey such as we see in leopards are unlikely in animals with such large and mediolaterally flattened canine teeth (Turner and Antón, 1997). Powerfully developed forelimbs suggest that a killing bite in the throat may have been coupled with the immobilization of the prey by the front limbs (Turner and Antón, 1997). Compared with other saber-tooths, Megantereon has a short brachial index (i.e., radius length/humerus length), slightly greater than 80% in M. cultridens (Lewis, 1997; Werdelin and Lewis, 2001). The metapodials, radius and tibia are also shorter than those of large felines, and the tail was also shortened. These features argue for slower speed in Megantereon and point to an ambushing behavior (Turner and Antón, 1998), confirmed by biogeochemical analyses of fossil samples from Venta Micena (Palmqvist et al., 2003).

The European carnivore guild included two saber-tooths during the early Pleistocene, *H. latidens* and *M. whitei*, which presumably maximized the amount of flesh that remained on their kills and, thus, opened broad opportunities of scavenging for

other species such as hyenas and hominins (Turner, 1992; Martínez-Navarro and Palmqvist, 1996). Saber-tooths became extinct in East Africa 1.5 Ma ago, which coincides with the emergence of the Acheulean Industrial Complex, and are replaced by lions and leopards, predators that presumably exploited the carcasses of their prey more fully (Turner, 1990, 1992; Turner and Antón, 1998). The arrival in Europe of the pantherine cats one million years later was followed by the extinction of M. whitei and other large felids such as the European jaguar, Panthera gombaszoegensis, and the giant cheetah, Acinonyx pardinensis, although the scimitar-toothed cat Homotherium seemingly survived in northern Europe until late Pleistocene times (Reumer et al., 2003; Antón et al., 2005). The persistence of saber-tooths in Europe helps to explain the success of the Oldowan tools in this continent, where the Oldowan/Acheulean transition took place later than in Africa, at 0.5 Ma (Palmqvist et al., 2005), since the sharp flakes characteristic of Oldowan assemblages were fully appropriate for scavenging the carcasses partially defleshed by the saber-tooths and the cores would have been useful for breaking the bones for accessing their marrow content (Plummer, 2004). In fact, the marked seasonality that characterized temperate Europe for most of the Pleistocene, with cooler and drier conditions than those of tropical Africa, made the availability of large ungulate carcasses for scavenging a key resource for both hyenas and hominins, and may have assisted the initial dispersal of Homo from Africa (Turner and Antón, 1998; Arribas and Palmqvist, 1999). Presumably, the new pantherine cats that arrived in Europe during middle Pleistocene times exploited their kills more fully than the saber-tooths and giant cheetahs, which resulted in the loss of a regular source of scavengeable carcasses for the bone-cracking hyenas and the hominins. In these new ecological circumstances, the trophic niche that they exploited vanished. The change in the composition of the carnivore guild forced the hominins toward behavioral and technological improvement, which resulted in the development of the Acheulean tools of H. heidelbergensis (Arribas and Palmqvist, 1999). The destiny of the giant hyena Pachycrocuta brevirostris, constrained by an enormous size and a highly specialized anatomy, was extinction, although whether this species was a strict scavenger (Palmqvist et al., 1996; Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001) or a less specialized hunter and scavenger in the manner of the modern spotted hyenas, Crocuta crocuta, that replaced it (Turner and Antón, 1996), is open to question.

The results of this study therefore suggest that one possible explanation for the replacement of European M. cultridens by African M. whitei is that the latter species was more efficient at subduing ungulates of medium size, given its more specialized craniodental anatomy and in particular the comparatively more developed upper canines. The larger sabers of M. whitei would have required a wider gape, however, which was achieved by reducing the height of the coronoid process above the occlusal plane of the cheek teeth, shortening the distance from the mandibular condyle to the carnassials and shifting the angular process laterally. This anatomical reorganization is reflected in the moment arms for the temporalis and masseter muscles (MAT and MAM, respectively), which are shortened in M. whitei. As discussed above, the narrowing of the temporalis muscle poses an unavoidable biomechanical constraint on the point of maximum bite force exerted at the carnassials, a point that is positioned more backwardly in M. whitei than in M. cultridens given the greater elongation of the sabers in the former. As a consequence, M. whitei shows a reduction of the postcanine dentition not related to the slicing function developed by the carnassials. This is seen particularly in the case of the third premolar, which is reduced to a vestigial peg or even lost, as in the specimen from South Turkwel (Palmqvist, 2002), and occurs to a lesser degree in the fourth premolar and even in the paraconid of the carnassial, which are also shortened in relation to the dimensions of these teeth in M. cultridens. The reduction of the premolar tooth row in *M. whitei* translates into a shortening of the mandible, which results in a more vertically oriented mandibular symphysis, whereas in M. cultridens the symphyseal regions is more oblique (Martínez-Navarro and Palmqvist, 1995). This change may relate to strengthening of the symphyseal region (Therrien, 2005), enabling the relatively small lower canines to function together with the large and anteriorly set incisors as a gripping set for initial access to carcasses and for pulling at soft tissues without the involvement of the large upper canines (Turner, 1992; Turner and Antón, 1997). All of these transformations in the craniodental anatomy of M. whitei represent an advance in the saber-tooth grade, allowing this predator to hunt more efficiently. In turn this would have resulted in the availability of relatively large amounts of flesh and all bone nutrients on the carcasses of the ungulates hunted by M. whitei. This provides the ecological connection between the dispersal of M. whitei out of Africa and the first human arrival in Europe, a continent where the survival of hominin populations during the cold season depended on the regular scavenging of ungulate carcasses (Turner, 1992; Martínez-Navarro and Palmqvist, 1996; Arribas and Palmqvist, 1999).

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