

## Chapter 2

# Carnivoran Dispersal Out of Africa During the Early Pleistocene: Relevance for Hominins?

Margaret E. Lewis and Lars Werdelin

**Abstract** Carnivorans and hominins share a long history of interactions. This paper examines some of the evidence for carnivoran migration out of Africa at the same time as the earliest hominin dispersals. Of the two relevant taxa, *Crocota* and *Megantereon*, *Megantereon* is the focus of this paper due to increased interest in this taxon in recent years and to the nature of the earliest records of dispersal of these two taxa, raising several questions related to *Megantereon* and its possible influence on hominins. To answer these questions, a brief summary of the literature on *Megantereon* in Eurasia and Africa is provided. While researchers do not agree on the number of species of *Megantereon* or the evolutionary relationships among those species, most would agree that *Megantereon* is a hypercarnivorous predator capable of grappling with relatively large prey for its body size. Despite the fact that carcasses generated by *Megantereon* were probably of value to hominins, the hypotheses that these carcasses were a major source of food or that they were a major force enabling hominins to migrate out of Africa are rejected. As indicated in the literature on extant carnivorans, kleptoparasitism (= food theft) by dominant members of a carnivore guild exacts a heavy price on lower ranking carnivores. In addition, there is nothing in the African fossil record to suggest a special relationship between *Megantereon* and hominins that did not exist between hominins and other large-bodied carnivorans. The hypothesis that a species of *Megantereon* migrated out of Africa at roughly the same time as early hominins is also considered. While this hypothesis cannot be rejected, alternative hypotheses to explain similarities between later African and Eurasian forms of *Megantereon* are proposed (e.g., shared characters are due to convergence or are symplesiomorphies). In the end, the small number of diverse African species (including hominins) who disperse into Eurasia at the Plio-

Pleistocene transition may have been part of a sweepstakes dispersal where the factors permitting (or driving) dispersal may have differed from species to species.

**Keywords** *Crocota* • *Megantereon* • *Pachycrocota* • Guild • Kleptoparasitism • Machairodont • Sabertooth • Scavenging

## Introduction

The image of the first hominins dispersing from Africa into Eurasia is a compelling one. While the questions surrounding this event can be addressed in numerous ways, it is important to consider species that shared similar adaptations with the dispersing hominins. One group that probably overlapped significantly in diet and habitat with these hominins is the larger members of the Order Carnivora.

The relationship between carnivorans and hominins has changed through time. Early hominins fell prey to large-bodied carnivorans, as numerous lines of evidence attest (e.g., Brain 1981). At some point, hominins encroached upon the carnivore guild within Africa and entered into competitive relationships with large-bodied carnivorans (e.g., Lewis and Werdelin 2007, and all references therein, as well as Turner 1988; Lewis 1997; Brantingham 1998). Since it has been shown that carnivore guilds are tightly constrained in ecological space and that changes in part of this guild affect its entirety (Dayan and Simberloff 1996, 2005; Woodroffe and Ginsberg 2005), understanding the adaptations of any large-bodied carnivore is crucial for reconstructing the potential niche space for all other large-bodied carnivores (including hominins) present at that particular time and place. Changes in the adaptations of larger carnivorans and their dispersal events may yield critical information about factors affecting evolutionary events and dispersal patterns in hominins.

This paper uses the African fossil record to identify carnivoran taxa of relevance to the question of initial hominin dispersal to Eurasia. A literature survey and critical analysis of those taxa is then presented, with reference to the question of hominin dispersal.

---

M.E. Lewis (✉)

School of Mathematical and Natural Sciences (Biology), The Richard Stockton College of New Jersey, PO Box 195, Pomona, NJ 08240-0195, USA

e-mail: margaret.lewis@stockton.edu

L. Werdelin

Department of Palaeozoology, Swedish Museum of Natural History, Box 50007, S-104 05 Stockholm, Sweden

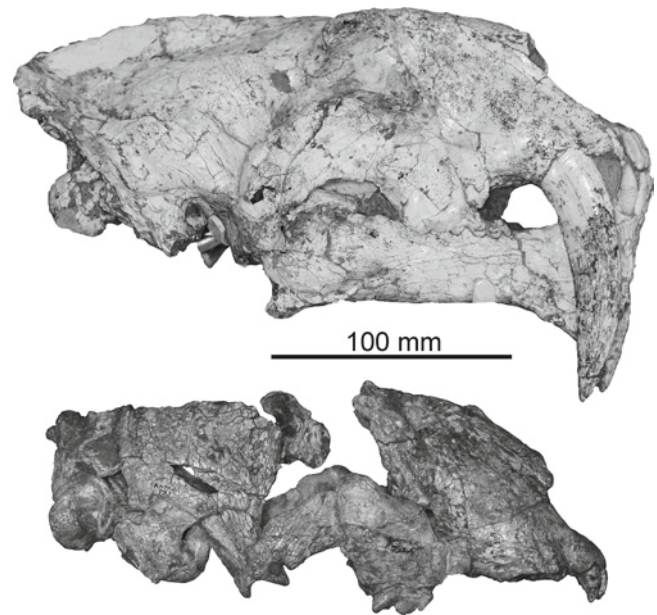
e-mail: werdelin@nrm.se

## The Plio-Pleistocene Carnivoran Guilds of Africa

The carnivoran guilds of Plio-Pleistocene Africa included a higher diversity of genera and species than present today (see Table 2.1). Like *Panthera* today, some genera had more than one species present in a given area at a given time (e.g., *Dinofelis*, *Crocuta*; Werdelin and Lewis 2005; Lewis and Werdelin 2007). In addition, the carnivoran guilds of eastern and southern Africa were composed of different taxa (e.g., Turner 1990; Lewis 1995b, 1997). Within each region, detectable ecomorphological differences occur among congeners (e.g., differences in *Dinofelis* from Olduvai Gorge versus other eastern Africa localities of similar age, Werdelin and Lewis 2001).

Of the taxa listed in Table 2.1, some did not disperse to Eurasia (e.g., *Parahyaena*, but see Arribas et al. 2001). Others may have migrated significantly earlier than hominins (e.g., *Homotherium* and *Acinonyx*) or may be of New World origin (e.g., *Acinonyx*). Members of only two genera may have crossed into Eurasia at the same time as hominins: *Crocuta* and *Megantereon*.

The dietary adaptations and abilities of spotted hyenas (*Crocuta*) make this a very attractive species to study in comparison with tool-using, group-living, hunting hominins. *Crocuta* appears in Europe after 0.8 Ma, but is present in Asia much earlier. Although the dating is not exact, the current best estimate is that *Crocuta* must have entered Eurasia



**Fig. 2.1** Skulls of *Megantereon*. Top: *M. nihowanensis*, unnumbered skull, Hezheng Museum, Gansu, China from the Longdan Basin, Gansu. Bottom: *M. whitei*, KNM-ER 793A, Okote Mb., Koobi Fora Fm., Turkana Basin, Kenya. Note that despite the significantly smaller teeth of the latter specimen, the skull is only very slightly anteroposteriorly shorter (cf. Werdelin and Lewis 2002)

**Table 2.1** Large-bodied carnivoran genera present in Plio-Pleistocene Africa

Family	Genus	Modern survivor
Canidae	<i>Canis</i>	<i>C. pictus</i> – African wild dog
Felidae	<i>Acinonyx</i>	<i>A. jubatus</i> – cheetah
Felidae	<i>Panthera</i>	<i>P. leo</i> (lion) & <i>P. pardus</i> (leopard)
Felidae	<i>Dinofelis</i>	None
Felidae	<i>Homotherium</i>	None
Felidae	<i>Megantereon</i>	None
Hyaenidae	<i>Chasmaporthetes</i>	None
Hyaenidae	<i>Lycyaenops</i>	None
Hyaenidae	<i>Crocuta</i>	<i>C. crocuta</i> – spotted hyena
Hyaenidae	<i>Hyaena</i>	<i>H. hyaena</i> – striped hyena
Hyaenidae	<i>Pachycrocuta</i>	None
Hyaenidae	<i>Parahyaena</i>	<i>P. brunnea</i> – brown hyena

Individual species are not listed due to the sheer number present (see Werdelin and Lewis 2005 for a complete listing). Some genera have multiple species present in the Plio-Pleistocene while others are not well known enough to assess taxonomic diversity. Note that modern survivors are not necessarily equivalent in behavior and ecology to their extinct congeners.

well before 2 Ma. This is attested to primarily by its presence in the Longdan Basin of China, in levels that are dated to ca. 2.2 Ma or even older (Qiu et al. 2004) and possibly in the Pinjor Formation of Indo-Pakistan (see Patnaik and Nanda 2010). Interestingly, and perhaps significantly, *Crocuta* is not recorded from Dmanisi (Vekua 1995). This may be an indication that it used a different dispersal route, possibly via the Indian Subcontinent, than did hominins at ca. 1.8 Ma. Unfortunately, the lack of Asian specimens around the crucial hominin dispersal period makes dispersals of *Crocuta* difficult to evaluate.

Among the African machairodont lineages present during the Plio-Pleistocene of Africa, *Megantereon* (Fig. 2.1) has been identified as being of crucial importance to the understanding of dispersals into Eurasia from Africa at the Plio-Pleistocene transition (e.g., Martínez-Navarro and Palmqvist 1996; Palmqvist et al. 1996; Arribas and Palmqvist 1999; Palmqvist et al. 2007; Martínez-Navarro 2010). Unfortunately, *Megantereon*, as a genus, is the most poorly known Plio-Pleistocene machairodont of Africa. In contrast to *Crocuta*, however, the few specimens of *Megantereon* that have been found are from crucial time periods and sites (see below). The rest of this paper will be confined to evaluating the evidence provided by *Megantereon*.

## Questions Surrounding the Dispersal of *Megantereon*

*Megantereon* has been hypothesized to have migrated from Africa to Eurasia at roughly the same time as the earliest hominin migration (e.g., Martínez-Navarro 2010). This hypothesis is based on the assignment of specimens from 'Ubeidiya (Israel), Dmanisi (Georgia), and other Eurasian sites to the African species *M. whitei* rather than to a new species or to *M. cultridens*, which is found at older Eurasian localities (Martínez-Navarro and Palmqvist 1995, 1996; Palmqvist et al. 1996; Rook et al. 2004; Palmqvist et al. 2007; Martínez-Navarro et al. 2009; Martínez-Navarro 2010). The identification of this later Eurasian form and the Levantine material as being African in origin led to the suggestion that *Megantereon* made the first migration of hominins into Eurasia possible by providing carcasses for them to scavenge (Martínez-Navarro and Palmqvist 1996; Palmqvist et al. 1996, 2007). Such a food source has been suggested to have been sufficient for hominin subsistence, even in the presence of *Pachycrocuta*, which is reconstructed as a "strict scavenger" (Martínez-Navarro and Palmqvist 1996; Palmqvist et al. 1996).

Several questions must therefore be asked:

1. Do the specimens of *Megantereon* found at Venta Micena (Spain), Dmanisi (Georgia), Pirro Nord (Italy), Appolonia-1 (Greece), Untermassfeld (Germany), Argentario (Italy), Urkút (Hungary), Bugiulesti (Romania), and Java (Indonesia) (collectively referred to herein as late Eurasian *Megantereon*) that have been placed in the African species *M. whitei* (Martínez-Navarro and Palmqvist 1995, 1996; Palmqvist et al. 1996; Rook et al. 2004; Palmqvist et al. 2007; Martínez-Navarro et al. 2009; Martínez-Navarro 2010) truly differ from older European specimens of *Megantereon* (referred to herein as *Megantereon cultridens sensu stricto* or early Eurasian *Megantereon*)?
2. If the above specimens are different from *M. cultridens sensu stricto*, do they show similarities to the African lineage of *Megantereon* in general or to a specific African species (e.g., *M. whitei* or *M. ekidoi*)?
3. If they do show similarities to the African lineage or a specific African species, what is the nature of that similarity (i.e., is it due to dispersal from Africa to Eurasia or to convergence)?
4. Where do the affinities of the Levantine *Megantereon* from 'Ubeidiya (Israel) lie and what implications does this material have for understanding the biogeography of *Megantereon*?
5. Regardless of its affinities, could late Eurasian *Megantereon* have been a significant source of carcasses for scavenging by the earliest hominins in Europe even in the presence of the hyaenid *Pachycrocuta*?

Before these questions can be addressed, a discussion of the history of the study of *Megantereon* must be undertaken.

## Brief History of the Taxonomy of *Megantereon*

Controversy over the attribution of specimens within the genus *Megantereon* has a long history. Summaries of the early history of this genus and its numerous species can be found elsewhere (e.g., Ficarelli 1979; Sardella 1998; Palmqvist et al. 2007). Ficarelli (1979) was the first to bring order to the taxonomic chaos that reigned within this genus. His revision identified one Eurasian species of *Megantereon*, *M. cultridens*, which was diagnosed as "small machairodonts with non-crenulated upper canines from both European and Asiatic Villafranchian ..." (1979:18). Although Ficarelli removed a large number of Asian forms from the genus, he considered the rest to be within an acceptable range of variation for the single species *M. cultridens*. Ficarelli summarized the literature on African and North American specimens of *Megantereon*, but refrained from commenting on the taxonomic validity of the various species proposed for these specimens.

The next researcher to tackle the task of sorting out Eurasian and African *Megantereon* was Turner (1987). Turner undertook an exhaustive review of the published diagnoses of all *Megantereon* species known at the time to determine the number of valid taxa in Africa and to evaluate all valid taxa and comment on possible origination and dispersal events. Turner's review identified numerous diagnostic characteristics that were found in more than one African species suggesting to him that all African material then known should be placed within a single taxon. Turner also questioned the validity of diagnoses of Eurasian and North American species. Differences in size were suggested to be due to sexual dimorphism and geographic variation. Based on the problems that he uncovered in the published diagnoses and descriptions, Turner then went a step further than Ficarelli and proposed that there was a single species, *Megantereon cultridens*, to which all North American, African, and Eurasian specimens belonged. Turner has since revised this viewpoint (Palmqvist et al. 2007; see below).

In a study published at roughly the same time as Turner's, Pons-Moya (1987) separated the European and Asian forms into separate subspecies (*M. c. cultridens* and *M. c. adroveri* in the European Villafranchian and Lower Pleistocene, respectively, and *M. c. nihowanensis*, in Asia). Although Pons-Moya reached conclusions that were superficially similar to those of Turner, he did distinguish between early and late forms of European *Megantereon*. More recently, Hemmer (2001) has followed Pons-Moya in using *M. c. adroveri* for



the *Megantereon* found at the Early Pleistocene site of Untermassfeld in Germany.

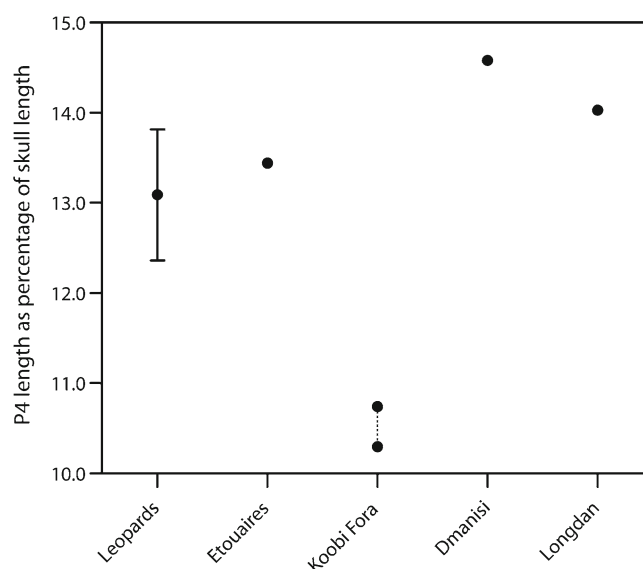
In 1995, Martínez-Navarro and Palmqvist reinstated some of the species of *Megantereon*. Based on analyses of dental measurements, Martínez-Navarro and Palmqvist proposed that there were three species within the genus:

1. *M. cultridens* (Cuvier 1824) found in the North American Lower Pliocene, the Asian Upper Pliocene and Lower and Middle Pleistocene, and the European Upper Pliocene (Villafranchian). See Berta and Galiano (1983) and Turner (1987) for alternate views on the taxonomy of the North American specimens.
2. *M. whitei* (Broom 1937) found in the African Upper Pliocene and Lower Pleistocene and the European and Middle Eastern Lower Pleistocene. Later papers (Rook et al. 2004; Martínez-Navarro et al. 2009) expand the list of non-African sites to include Java and 'Ubeidiya.
3. *M. falconeri* (Pomel 1853) found in the Upper Pliocene of India. This species had been revised previously (Petter and Howell 1982).

This scheme was repeated in subsequent papers (e.g., Arribas and Palmqvist 1999; Martínez-Navarro and Palmqvist 1996; Palmqvist et al. 2007; Martínez-Navarro et al. 2009). These authors suggested that *Megantereon cultridens* arose in the New World (as originally proposed by Berta and Galiano 1983) and dispersed to the Old World approximately 3.5 Ma. *M. cultridens* then evolved into *M. falconeri* on the Indian subcontinent and *M. whitei* in Africa. *M. whitei* later dispersed from Africa to Eurasia. Later papers do not mention *M. falconeri* and only discuss Asian material that they have assigned to *M. cultridens* (Palmqvist et al. 2007). Alternate origins for *Megantereon* in Africa (Turner 1987) and Asia (Sotnikova 1989) have also been proposed.

The assignment of specimens to taxa by Martínez-Navarro, Palmqvist and colleagues was based solely on dental metrics and did not consider non-dental and non-metric characters. In their analyses, these authors assumed that if specimens were not statistically significantly different in dental metrics, then those specimens belonged to the same species. Differences in other measurements or in non-metric characters were ignored as was the potential confounding factor of disparate body sizes amongst species of *Megantereon*.

We performed a simple analysis of dental measurements relative to skull length to test whether the size of the teeth relative to skull size differs even if their absolute length and/or breadth does not (Fig. 2.2). Comparison of the relative proportions of upper carnassial (P4) length to skull condylobasal length demonstrates that the Koobi Fora skull (KNM-ER 793; African *M. whitei*) is considerably different from all of the specimens. The much smaller Dmanisi skull (Nr. 1341; considered to be *M. whitei* by Martínez-Navarro, Palmqvist and colleagues) has the longest upper



**Fig. 2.2** Length of upper carnassial (P4) as a percentage of skull condylobasal length (CBL) for a sample of extant leopards, *Panthera pardus*, from Africa and Asia (left,  $N = 15$ , with 99.9% confidence interval) and some specimens of *Megantereon* species. P4 measurements are from Palmqvist et al. 2007. The lower point for the Koobi Fora specimen uses CBL as determined from Fig. 2.1 in Palmqvist et al. (2007), while the upper point uses the actual CBL as measured by us on the skull. The difference between the Koobi Fora specimen and all other *Megantereon* specimens is much greater than the variation within the sample of leopards

carnassial relative to skull length, while the Koobi Fora specimen has the relatively shortest carnassial. When the range of variation in an extant felid (leopard) is considered, the Koobi Fora specimen can be seen to lie far outside the potential range of the other taxa. While this is just a rough analysis of one difference between the Dmanisi specimen and African *M. whitei*, it demonstrates that, at least in this feature, Dmanisi is substantially different from the African taxon.

In contrast to Martínez-Navarro, Palmqvist and colleagues, Sardella (1998) further subdivided *Megantereon* based on morphometric analyses. Recognizing the incomplete nature of most of the specimens, his classification included both morphotypes and species and lumped all of the following into what he referred to as *Megantereon ex. gr. cultridens*:

1. *Megantereon* sp. 1 (primitive form)

Locality/Age: Baode, China (late Miocene?).

Characters: “P<sup>3</sup> is laterally compressed with an anterior and a posterior cusplet and is, on the whole, more developed than in all the other studied specimens of *Megantereon*. P<sup>4</sup> shows no preparastyle and a strong deuterocone [= protocone]. This tooth is morphologically very similar to that of the more advanced forms of *Megantereon*.” (1998:6) (However, further investigation

strongly suggests that the Baode specimen belongs to a species of *Paramachairodus*, a genus already known from the Baode faunas).

2. *Megantereon* sp. 2 (primitive form)

Locality/Age: Odessa Catacombs, Ukraine (Early Pliocene; Ruscinian).

Characters: moderate reduction of  $P^3$  and  $P_3$ . More recent study, however, has demonstrated that these specimens belong to a species of *Dinofelis* (Sotnikova in litt. to LW 07/02/2004).

3. *M. cultridens* (primitive form)

Locality/Age: Perrier-Les Etouaires (Early Villafranchian).

Characters: “low degree of development of the upper incisors, similar in shape to those of the living felids, while upper canines are well developed like in other dirktoothed cats” (1998:7).

4. *M. cultridens* (typical form)

Locality/Age: Europe (Pardines, Puebla de Valverde, St. Vallier, Senèze, Fontana Acetosa, Olivola, Upper Valdarno) (Early-Late Villafranchian).

Characters: “Machairodont the size of a panther; the skull shows a shortened muzzle; teeth are not crenulated; the incisors are stronger than in modern felids, but are not so developed than in other sabertoothed cats as *Homotherium* and *Machairodus*; the upper canines are not serrated with a very high and curved crown,  $P^3$  and  $P^4$  are very reduced with deutocone variable in size; on the whole, the structure of the upper carnassial is close to modern felids. Very developed mandibular flange.  $C_1$  is weak,  $P_3$  reduced. The neck is long and limb bones are strong, with straight shortened diaphysis” (1998:7–8).

5. *M. cultridens* (advanced form)

Locality/Age: Europe (Pirro Nord, Argentario, Urkút, Venta Micena, Apollonia 1, Dmanisi) (Late Villafranchian).

More derived characters: “(1) very strong incisors; (2) upper canines greatly developed in size; (3) upper carnassial moderately reduced; (4) reduced  $P_4$ ” (1998:9).

6. *Megantereon falconeri* (Pomel)

Locality/Age: Asia (Late Pliocene-Middle Pleistocene)

Late Pliocene forms: very “strong” upper canines and moderately reduced premolars.

Early Pleistocene forms: large-sized specimens with moderately reduced  $P_4$ .

Middle Pleistocene form: large.

7. *Megantereon whitei* (Broom)

Locality/Age: Africa (Plio-Pleistocene).

Characters: reduced  $P^4$  and  $P_4$  and very “strong” upper canines.

Sardella viewed the European morphotypes of *M. cultridens* as part of a single evolutionary lineage through time. Like Turner (1987), Sardella removed the North American specimens from the Bone Valley Formation (4.5 Ma) from

*Megantereon* and thus concluded that *Megantereon* migrated from the Old World into North America. Most interestingly, Sardella concluded that his *M. cultridens* (advanced form) morphotype is related to the African *M. whitei* morphotype, but that the two forms are distinct. However, Sardella has since begun referring to his *M. cultridens* (advanced form) as *M. whitei* and referred material from Monte Argentario, Italy to this species (Sardella et al. 2008). This change in nomenclature was based on the hypothesis of Martínez-Navarro and Palmqvist reaching a “larger consensus” (Sardella et al. 2008:603), which means, presumably, the recent support for this hypothesis by Turner (i.e., Palmqvist et al. 2007). Sardella and colleagues note the anatomical differences between Pliocene *M. cultridens* and Early Pleistocene European *Megantereon*, but do not discuss the morphological justification for combining African *M. whitei* and Early Pleistocene European *Megantereon* into a single species.

In a recent contribution to the taxonomy of *Megantereon*, Liu (2005) made a distinction between two European forms (typified by the material from St. Vallier and Senèze, respectively) listing a series of craniodontal characteristics said to distinguish the two. He then resurrected the name *Megantereon megartereon* for the St. Vallier form, and placed some Chinese material (and implicitly also *M. falconeri*) in this taxon. Evaluation of this perspective must be left for the future, but it is of significance that Liu also acknowledges the specific status of the African *M. whitei*. Younger European material was not included in the analysis.

Recent work by Palmqvist and colleagues (including Martínez-Navarro and Turner; Palmqvist et al. 2007) indicate that size differences among Eurasian and African specimens are not due to sexual dimorphism. This study expanded the number and geographic extent of specimens included in their previous morphometric analyses. No specimens from the Indian subcontinent are included, nor is the validity of *M. falconeri* discussed. In these analyses, specimens were classified a priori as either *M. whitei* (all Africa, European Lower Pleistocene, and 'Ubeidiya) or *M. cultridens* (European Upper Pliocene, Asia, and North America). Within Asia, material is included from China and Tajikistan, but not Java. Analyses of two (discriminant analysis:  $P_4$  length and  $M_1$  breadth) to four variables (principal components analysis: log length and breadth of  $P_4$  and  $M_1$ ) support these a priori classifications, although one might question, in particular, the use of discriminant analysis with only two variables. While measurements of the upper and lower canines, premolars, and molars are presented, only  $P_4$  and  $M_1$  measurements appear to be useful in discriminating these groups. These authors suggest that proportional changes throughout the dentition and concomitant changes in the rest of the skull led to *M. whitei*

being able to hunt “more efficiently” (p. 173) than *M. cultridens*. The removal of Java from the list of sites with *M. whitei* present means that this taxon in their scenario did not penetrate very far into Asia. This study did not search for features that might distinguish sub-groups within these a priori groups or categorize the specimens in a different manner.

Each of the above researchers or research groups used different means of determining the taxonomic status of the various species of *Megantereon* and, not surprisingly, came to different conclusions (see Table 2.2). While there is little consensus among these researchers, there are some points on which most recent studies agree:

1. African and at least some Asian forms differ morphologically from what was originally described as European *M. cultridens* (but see Liu 2005, with respect to Asian forms).
2. There are two forms within Europe (or three, in the case of Liu 2005): the larger, more robust early form (which all agree is *M. cultridens*) and a later form characterized by dental reduction.
3. The latter form within Europe may share some affinity with African forms (although the nature of this affinity is disputed).
4. Differences in size within African *M. whitei*, particularly those in southern Africa, are most likely due to sexual dimorphism (a point made by Turner that has gone unchallenged by all subsequent researchers).

**Table 2.2** Summary of changes in the taxonomy of *Megantereon* through time

Old World Species of <i>Megantereon</i> (valid and invalid)		
Europe	Asia	Africa
<i>M. cultridens</i>	<i>M. falconeri</i>	<i>M. ekidoit</i>
<i>M. c. adroveri</i>	<i>M. inexpectatus</i>	<i>M. eurynodon</i>
<i>M. megantereon</i>	<i>M. lantianensis</i>	<i>M. gracile</i>
	<i>M. nihowanensis</i>	<i>M. whitei</i>
<b>Ficcarelli 1979</b>		
<i>M. cultridens</i>	<i>M. cultridens</i>	No comment
<b>Turner 1987</b>		
<i>M. cultridens</i>	<i>M. cultridens</i>	<i>M. cultridens</i>
<b>Martínez-Navarro and Palmqvist 1995</b>		
<i>M. cultridens</i> (early form)	<i>M. falconeri</i>	<i>M. whitei</i>
<i>M. whitei</i> (late form)		
<b>Sardella 1998</b>		
<i>M. ex gr. cultridens</i>	<i>M. ex gr. cultridens</i>	<i>M. ex gr. cultridens</i>
( <i>M. cultridens</i> primitive form)	( <i>M. falconeri</i> )	( <i>M. whitei</i> )
<i>M. ex gr. cultridens</i>		
( <i>M. cultridens</i> typical form)		
<i>M. ex gr. cultridens</i>		
( <i>M. cultridens</i> advanced form)		
<b>Liu 2005</b>		
<i>M. megantereon</i> (St. Vallier)	<i>M. cf. megantereon</i> <sup>a</sup>	<i>M. whitei</i>
<i>M. cultridens</i> (Senèze)		Did not include later form
Did not include later form		
<b>Palmqvist et al. 2007</b>		
<i>M. cultridens</i> (early form)	<i>M. cultridens</i> (widespread)	<i>M. whitei</i>
<i>M. whitei</i> (late form)	<i>M. whitei</i> (limited)	
<b>Current Paper (after Werdelin and Lewis 2000, 2002)</b>		
<i>M. cultridens</i> (early form)	One or more taxa <sup>b</sup>	<i>M. ekidoit</i> (early form)
<i>M. adroveri</i> (late form; new rank)		<i>M. whitei</i> (late form)

<sup>a</sup>This form belongs to the genus named and has characters that may be compared usefully to the species-level taxon, though it may not actually belong to this species.

<sup>b</sup>While a discussion of Asian *Megantereon* taxonomy is beyond the purview of this paper, we believe the following may be valid species within Asia: *M. falconeri*, *M. inexpectatus*, or *M. nihowanensis*. *M. falconeri* has priority if there is only a single species of *Megantereon* within Asia.

Although numerous sites throughout Eurasia and Africa list *Megantereon* as present, the actual material is often fairly incomplete. As such, it is compelling that different research groups have come to some of the same conclusions, even if they dispute how these conclusions should be interpreted taxonomically.

### A New Species of African *Megantereon*: Significance for Dmanisi

In 2000, a new species of *Megantereon* (*M. ekidoit*) was described from the Kenyan site of South Turkwel (3.5–3.2 Ma) (Werdelin and Lewis 2000). While only a single mandible of this species is known (Fig. 2.3), this specimen clearly belongs to *Megantereon* but differs from known members of the genus. *M. ekidoit* was diagnosed as “a *Megantereon* with a slender mandibular ramus, large salivary gland pit on the anteromedial face of the ramus, small masseteric and mental foramina, and well developed, hookshaped coronoid process” (2000:1173). The individual mandible upon which the description was based lacks the  $P_3$ , a feature that the authors excluded from the diagnosis due to the possibility that it was an individual variation.

The significance of this specimen is that it is the oldest described specimen of this genus from Africa and improves

our understanding of evolution within the African lineage of *Megantereon*. Older material has been reported from Aramis at 4.4 Ma (WoldeGabriel et al. 1994), but has not yet been described. Specimens from the Lukeino Formation in Kenya are most likely to be *Paramachairodus* or a related taxon rather than *Megantereon* as they resemble the Baode material (LW, personal observation). Given the exclusion of the Lukeino material from *Megantereon*, along with the Baode and Odessa material as discussed above, the mandible of *M. ekidoit* is the oldest described specimen of *Megantereon* worldwide.

Not everyone immediately accepted the new species. Palmqvist (2002) attempted to show that the new species fit comfortably within the existing African species, *M. whitei* based on a quantitative analysis of the mandibular dentition and a list of characters shared between the two.

Werdelin and Lewis issued a rebuttal (2002) noting that Palmqvist was correct that *M. ekidoit* and *M. whitei* were similar in the dental proportions mentioned (though not in all dental proportions) and that the diagnosis of the species was based on non-dental characters. In short, some aspects of the dentition within the African lineage of *Megantereon* remained the same while other characters evolved. In our experience, carnivoran teeth, particularly among felids, tend to be fairly conservative in comparison to the rest of the body.

Palmqvist (2002) listed seven characters that he believed synonymized *M. whitei* (including the Dmanisi and other European material) and *M. ekidoit*. Werdelin and Lewis (2002) countered by noting that five of the seven were features shared by *Megantereon* as a genus. Werdelin & Lewis dismissed some of the other characters as misunderstandings (e.g., misreading of the lack of  $P_3$  as separating *M. ekidoit* from *M. whitei* rather than the possibility of individual variation).

Finally, the last characters that Palmqvist stated were shared between the two species are, in fact, shared between *M. ekidoit* and the Dmanisi *Megantereon* (as figured in Vekua 1995), but were not shared with *M. whitei sensu stricto* (i.e., the other African specimens). A feature shared by *M. ekidoit* and the Dmanisi form (but not *M. whitei sensu stricto*) is the presence of a long, shallow masseteric fossa that is developed well anterior to the posterior end of  $M_1$ . Palmqvist’s last character, that of the hook-shaped coronoid process for which *M. ekidoit* was named, was not shared by all three taxa: the coronoid process of *M. whitei* is not hook-shaped, that of the South Turkwel specimen is, and the Dmanisi specimen is intermediate.

The significance of this debate is that like the analysis presented in Fig. 2.2, it casts doubt on the assignation of the Dmanisi material (and by extension other late Eurasian *Megantereon*) material to *M. whitei*. However, the possibility of an African origin of the Dmanisi form cannot be discarded due to the similarities between that form and *M. ekidoit*.



**Fig. 2.3** Right mandibular rami of *Megantereon*. Top: *M. whitei*, KNM-ER 793B, Okote Mb., Koobi Fora Fm., Turkana Basin, Kenya. Bottom: *M. ekidoit*, KNM-ER ST 23812, South Turkwel, West Turkana, Turkana Basin, Kenya. Note that the latter is considerably more slender despite being ontogenetically older (as judged by tooth wear), indicating that *M. whitei* was a craniodentally more robust animal



## Ecomorphology of African *Megantereon*

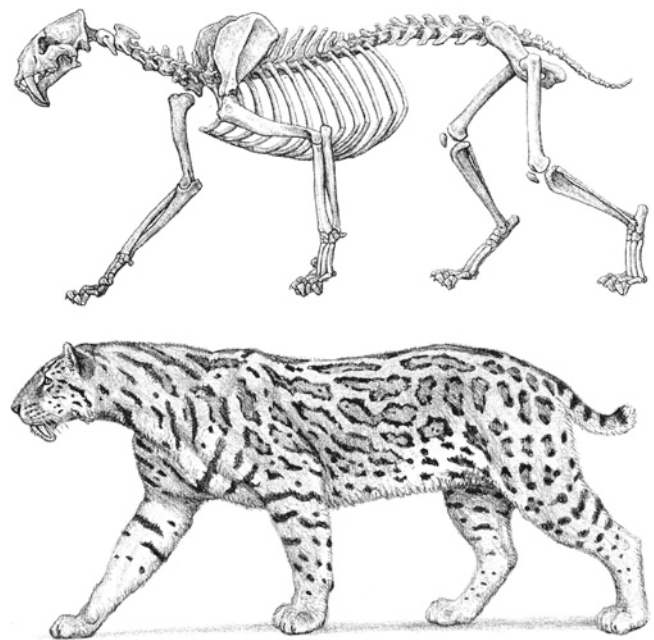
Sabertoothed felids (subfamily Machairodontinae) in the African Plio-Pleistocene include representatives of three different tribes: the Metailurini (e.g., *Dinofelis*), the Homotheriini (e.g., *Homotherium*), and the Smilodontini (e.g., *Megantereon*). Representatives of these tribes are quite different in morphology and presumably behavior.

In comparison to other large-bodied carnivorans found in the African Plio-Pleistocene (e.g., *Dinofelis*, *Crocota*, and *Homotherium*), *Megantereon* is very poorly represented. Craniodental and postcranial specimens are known from both eastern and southern Africa. However, partial skeletons are rare. One partial skeleton has been described from Kromdraai B (Vrba 1981). Associated bits and pieces of postcrania occur at Koobi Fora, but are extremely fragmentary (Lewis 1997; Werdelin and Lewis, in preparation).

The older species, *M. ekidoit*, is currently known only from eastern Africa from approximately 3.5–3.2 Ma. If the Aramis material belongs to this species, this extends its first appearance datum back to 4.4 Ma. Unfortunately, other specimens of *Megantereon* from the Pliocene of eastern Africa (e.g., Shungura Fm. Mbs. B–G) are isolated teeth, making taxonomic identifications below the genus level impossible (Werdelin and Lewis 2005). No postcrania have as yet been assigned to this taxon.

The younger species, *M. whitei*, is present in both eastern and southern Africa. Within eastern Africa, the only definite record of this taxon is in the Okote Mb. of the Koobi Fora Formation (Werdelin and Lewis 2005; Lewis and Werdelin 2007). *Megantereon whitei* is better represented in South Africa than at eastern African sites, with records from Kromdraai Mb. A, Swartkrans Mb. 3, Sterkfontein, Mbs 2, 3, 4, and Coopers (Broom and Schepers 1946; Broom 1948; Ewer 1955; Hendey 1973, 1974; Vrba 1981; Turner 1987, 1993; Lewis 1995a, b, 1997; Hartstone-Rose et al. 2007).

Like their close relative *Smilodon*, members of the genus *Megantereon* in both Europe and Africa have been shown to have extreme strength in the forelimb (Lewis 1995a, b, 1997; Martínez-Navarro and Palmqvist 1996) (see Fig. 2.4). Specimens from Kromdraai, South Africa possess a limb morphology that is more similar to that of extant jaguars than to any of the modern African felid taxa or other African sabertooths, although they were much more heavily muscled than jaguars (Lewis 1995a, b, 1997). As a result, African and European *Megantereon* have been identified as potential providers of large carcasses for hominins (Lewis 1995b, 1997; Martínez-Navarro and Palmqvist 1996; Arribas and Palmqvist 1999). However, based on body size and morphology, Lewis (1995b, 1997) concluded that African *Megantereon* could not have generated carcasses much larger than those generated by extant carnivorans. Thus, it is unclear whether *Megantereon* would have been as important a scavenging



**Fig. 2.4** Skeletal and life reconstructions of *Megantereon*, showing the long, low body, robust and heavily muscled forequarters, and short tail. Illustration by Mauricio Antón. Reprinted with permission from the artist

resource (or, conversely, as much of a threat as a kleptoparasite) as other sabertoothed felids.

One should note that throughout much of the Plio-Pleistocene, *Megantereon* was not the only sabertooth present. In addition to at least one species of *Homotherium*, there were two species of *Dinofelis* living at any given time in eastern Africa, although not necessarily at the same location. One species of *Dinofelis* tended to be relatively larger (e.g., *D. aronoki*) and one tended to be a little smaller with a more crouched posture (e.g., *D. petheri* or *D. piveteaui*) (Werdelin and Lewis 2001; Lewis and Werdelin 2007). Species of *Megantereon*, however, were the smallest of the African machairodonts during this time.

Like *Dinofelis*, *Megantereon* has been suggested to have inhabited mixed/closed habitats (Lewis 1995a, b, 1997) or even dense forest (Marean 1989; Palmqvist et al. 2008) in contrast to *Homotherium*, which has been reconstructed as more open-habitat adapted in both Europe and Africa (e.g., Lewis 1995b, 1997; Palmqvist et al. 2003; Antón et al. 2005). Habitat preference does not mean that a species is limited to that habitat, however, as narrow categorizations of habitat preference cannot be made from carnivoran postcranial morphology (Van Valkenburgh 1987; Taylor 1989). Large, extant carnivorans in Africa may be found in a variety of habitats despite what their postcranial morphology might predict (e.g., lions, leopards, spotted hyenas; see review in Van Valkenburgh 2001). Of course, it is possible that the ability of many extant African carnivorans to inhabit a variety of



habitats successfully is a key component of the suite of adaptations that ensured their survival to the present (Lewis and Werdelin 2007). While the crouched posture of *Megantereon* spp. is indicative of an ambush predator and their size and limb morphology suggest an ability to climb trees (Lewis 1995a, b, 1997; Martínez-Navarro and Palmqvist 1996), this does not mean that they were tied to specific habitats (nor does it mean that they were “partially arboreal” as reported by Hartstone-Rose et al. 2007 in a mis-citation of Lewis 1997). Their forelimb morphology may reflect prey grappling more than scansorial ability regardless of their habitat preference (Lewis 1997). However, carbon- and nitrogen-stable isotope analyses of *Megantereon* from Venta Micena (Spain), have suggested that at least this population focused on browsing and mixed feeding cervids in a closed habitat (Palmqvist et al. 2003, 2008).

Despite being the smallest of the sabertooths known from this time period, even if *Megantereon* spp. did climb trees, they would have been more likely to steal already cached carcasses and feed on them in the trees than to cache carcasses (Lewis 1997; Lewis and Werdelin 2007). Tree-caching a shifting carcass would have been a risky behavior with high potential for damage to the canines (Lewis 1997; Turner and Antón 1997; Lewis and Werdelin 2007).

In sum, the studies cited above have suggested that the various species of *Megantereon* were ambush predators that may have utilized mixed/closed habitats predominantly, although they may have been present in a variety of habitats. Despite their size, all studies have agreed that they could have taken down prey of a large enough size to be of interest to larger scavengers, including hominins. Carcasses generated by *Megantereon* likely had intact within-bone nutrients and varying amounts of flesh present due to its specialized dentition (e.g., Ewer 1973; Marean 1989; Lewis 1995a, b, 1997; Marean and Ehrhardt 1995; Turner 1988; Palmqvist et al. 2007). Nothing in the fossil record of *Megantereon* has suggested the possibility of group hunting, a behavior that would have strongly discouraged kleptoparasitism. However, the robust musculature in combination with the utilization of cover within mixed/closed habitats would have made even a solitary individual of *Megantereon* a formidable foe.

## ***Megantereon* and Hominin Behavior**

Given the morphology of *Megantereon* spp., one can assume that a single individual of this taxon would have been more difficult to dislodge from a carcass or defend oneself from than a single modern leopard or lion. Of course, weapons and grouping behavior would have increased the relative rank of hominins within the carnivore guilds. Successful aggressive behaviors by hominins would also have conferred status.

What could confrontationally scavenging hominins have gained from *Megantereon* kills? If a group of hominins were drawn to a kill site soon after the kill occurred and were able to scare away the cat, there could have been a great benefit. If hominins were passively scavenging (i.e., waiting until the predator abandoned the carcass) or came upon a kill after the cat had finished with it, the story might be quite different. While Martínez-Navarro and Palmqvist have suggested that *Megantereon* would have exploited carcasses to a “small degree” (1996:871) such that there would be enough for hyaenids (e.g., *Pachycrocuta*), behaving as “strict scavengers” and scavenging hominins, not everyone would agree. Based on both an analogy to North American *Smilodon*, which has a large amount of tooth breakage, and the fact that modern big cats use their tongues as files to rasp flesh off bones, Van Valkenburgh (2001) has suggested that African sabertooths were probably quite capable of dismembering the carcass and engaging in bone-cracking. However, despite the fact that *Smilodon* and *Megantereon* are sister taxa, there is no evidence (e.g., broken teeth showing wear) in Africa, at least, to support the idea that *Megantereon* engaged in these behaviors at the level hypothesized for *Smilodon* (Lewis and Werdelin 2007). Given the dental morphology and reduced tooth row in *Megantereon*, and especially *M. whitei*, bone-cracking is highly improbable.

What is clear is that *Megantereon*, like all felids, was hypercarnivorous and probably could quickly deflesh a carcass if it needed to (i.e., if it was living in an area of high competition with marauding groups of hominins and large-bodied hyaenids). Despite debate over bone-cracking, *Megantereon* could not in all likelihood access larger chambers of the skull or bone marrow cavities in larger bones. Thus, if hominins did not arrive early on the scene or were not confrontational scavengers, the remains would still have been useful, but not bountiful. In addition, *Pachycrocuta* could access a wider range of carcass-based resources than *Megantereon*. If this large-bodied hyaenid arrived at a *Megantereon* kill prior to hominins, there might be even less left for hominins. [Note that at the time hominins initially dispersed to Eurasia, African *Pachycrocuta* was rare (southern Africa) or extinct (eastern Africa).]

If hominins scavenged regularly from one resource species, that species would have experienced a great deal of stress and would either have had to adopt new strategies to protect or hide their food or migrate to a hominin-free area to prevent at least local extinction (see Lewis 1997 for similar arguments against regular stealing of tree-cached carcasses by hominins). Kleptoparasitism by high ranking carnivores has been shown to drive populations of lower ranking taxa into suboptimal habitats (Woodroffe and Ginsberg 2005) or even to local extinction (Linnell and Strand 2000; Creel 2001). Given that *Megantereon* continued to be associated with hominins for some time even after hominins dispersed

to Europe, one would surmise that by the time of migration hominins were not stealing carcasses from *Megantereon* at a rate that would cause severe stress. Of course, it is certainly possible that *Megantereon* fled Africa in an attempt to escape hominins with hominins in hot pursuit and that hominins were eventually successful in driving *Megantereon* extinct in both Eurasia and Africa. Given the timing of migration and co-occurrence of the two taxa at multiple sites, this scenario is highly unlikely. Even if hominins could be established as being primarily responsible for the eventual disappearance of *Megantereon*, it is probably not possible to determine whether they out competed *Megantereon* through hunting or through confrontational scavenging or by some combination thereof.

All of this, of course, raises the interesting question of why *Megantereon* kills might be favored over those of other large felids. Could *Megantereon* be the only non-pack living carnivorous large enough to take down prey of a size usable by hominins? This scenario is unlikely as *Dinofelis* would also fall into this category (see Marean and Ehrhardt 1995; Lewis 1997; Van Valkenburgh 2001; Antón et al. 2005, for discussions of pack living and/or hunting in various Eurasian and African carnivores). Could the smaller body size of *Megantereon whitei* individuals make them more susceptible to hominin kleptoparasitism than other machairodonts? What, then, would prevent other carnivores from engaging in kleptoparasitism against *M. whitei*? One must note that there is nothing in the African fossil record that suggests a special relationship between *Megantereon* and *Homo* to the exclusion of other large-bodied carnivores.

While hominins may have benefited from occasional scavenging of *Megantereon* kills, it is unlikely that they could have relied on *Megantereon* as their sole source of meat. Assuming that *Megantereon* dispersed from Africa at the same time (or even slightly before) hominins, the presence of *Megantereon* was probably not the primary motivating factor in hominin dispersal. Ability to scavenge from *Megantereon* would have been useful and may have helped hominins establish themselves in Eurasia, but it seems likely that there were additional factors driving hominin dispersal. While it is possible that they were interested in the same prey species, it is also possible that they were interested in different prey species that happened to be dispersing out of Africa for the same reasons at roughly the same time. Both hypotheses are equally untestable at present.

## Reiteration of Questions Posed Earlier

At this point it is probably useful to return to the five questions posed at the beginning of this paper and make some attempt to answer them. Not all of the questions can be

answered here. Some hypotheses may simply be untestable while others may necessitate the discovery of more fossils.

1. Do the specimens of *Megantereon* found at Venta Micena (Spain), Dmanisi (Georgia), Pirro Nord (Italy), Apollonia-1 (Greece), Untermassfeld (Germany), Argentario (Italy), Urkút (Hungary), Bugiulesti (Romania), and Java (Indonesia) (collectively referred to herein as late Eurasian *Megantereon*) that have been referred to the African species *M. whitei* (Martínez-Navarro and Palmqvist 1995, 1996; Palmqvist et al. 1996; Rook et al. 2004; Palmqvist et al. 2007; Martínez-Navarro 2010) truly differ from older European specimens of *Megantereon* (referred to herein as *Megantereon cultridens sensu stricto* or early Eurasian *Megantereon*)?

Most researchers agree that there are two different morphotypes present in the fossil record of Eurasia (but see Ficcarelli 1979; Turner 1987). Whether one chooses to see them as two subspecies within a larger *M. cultridens* or as two species within *Megantereon*, this works out functionally to the same conclusion: there is a detectable difference in morphology between early and late specimens of *Megantereon*.

One should note, however, that the morphometric analyses do not include all material listed above as being a part of *M. whitei*. In many cases, the material does not preserve the necessary areas of the body. The Javan *Megantereon*, for example, consists exclusively of isolated upper canines, a portion of the skeleton that is not diagnostic at the species level in *Megantereon* (for example, see Fig. 4 and Table 2 in Palmqvist et al. 2007). However, this does not invalidate the argument that there are two species (or morphotypes) present in Eurasia. Eurasian sites stated to have *M. whitei* that are included in various multivariate analyses (Martínez-Navarro and Palmqvist 1996; Palmqvist et al. 2007) are Venta Micena, Dmanisi, Apollonia-1, Argentario, Pirro Nord, Untermassfeld, Urkút, and Bugiulesti. A clear difference can be seen between specimens from those sites and older European material. As such, we support a species-level distinction between early and late Eurasian *Megantereon*, although we do not concur that the later species is *M. whitei* (see next two items). Our understanding of the geographical and temporal extent of the later species will only be enhanced with the discovery and description of new fossils.

2. If the above specimens are different from *M. cultridens sensu stricto*, do they show affinities with the African lineage of *Megantereon* or with a specific African species (e.g., *M. whitei* or *M. ekidoi*)?

Martínez-Navarro and Palmqvist (1995, 1996; Palmqvist et al. 2007) have demonstrated morphometrically that specimens of late Eurasian *Megantereon* fall within the range of the dental proportions of African *M. whitei* rather than *M. cultridens*. Palmqvist (2002) noted that those particular

dental proportions do not change between *M. whitei* and *M. ekidoit*. On the other hand, Werdelin and Lewis (2002) indicate that *M. ekidoit* and at least the Dmanisi specimen share some features to the exclusion of *M. whitei*. These shared features may be primitive (a view favored by the authors of this paper), which raises the interesting question of the timing of origin of the possibly more derived *M. whitei*. Another character of the Dmanisi specimen, coronoid process shape, was intermediate between the morphology of *M. whitei* and *M. ekidoit*. In sum, while the exact relationship between these specimens and the two African species is currently unknown, there is a general consensus that there is an affinity between these specimens and the African forms.

3. If they do show affinities with the African lineage or specific African species, what is the nature of that affinity (i.e., is it due to dispersal from Africa to Eurasia or to convergence)?

Unfortunately, not enough is known about the later group of Eurasian *Megantereon* to rule out convergence with the African forms. More specimens of *M. ekidoit* would also be useful. It is certainly possible that ecological changes enabling hominin migration and/or the appearance of hominins drove Eurasian *Megantereon* to converge on African forms. However, this is not currently a testable hypothesis. The hypothesis that later Eurasian *Megantereon* is derived from *M. ekidoit* also cannot be disproved. Based on the dissimilarity between the Dmanisi specimen and *M. whitei* in some features, we believe that late Eurasian *Megantereon* cannot be referred to *M. whitei*. It may instead be related to the Eurasian *M. cultridens* and, if so, could be placed in *Megantereon adroveri* Pons-Moya 1987 (new rank).

4. Where do the affinities of the Levantine *Megantereon* from 'Ubeidiya (Israel) lie and what implications does this material have for understanding the biogeography of *Megantereon*?

The site of 'Ubeidiya is critical in many ways to the understanding of the dispersal of African taxa into Eurasia (see Belmaker 2006, 2010a,b). The first specimen of *Megantereon* to be described from 'Ubeidiya was a well-preserved upper canine (UB 80) (Haas 1968; Ballesio 1986). While Ballesio (1986) assigned this tooth to *M. cf. cultridens*, he believed that the material was not sufficient to determine its taxonomic and geographic affinities. Martínez-Navarro, Palmqvist and colleagues (e.g., Martínez-Navarro and Palmqvist 1995; Palmqvist et al. 2007) refer the specimen to *M. whitei*, thus supporting their hypothesis that *M. whitei* dispersed from Africa and eventually replaced the larger Eurasian *M. cultridens*.

Two additional 'Ubeidiya specimens have now been assigned to *Megantereon cf. M. whitei* along with UB 80: a lower canine (UB 14) and a middle phalanx (UB 307)

(Martínez-Navarro et al. 2009). Martínez-Navarro and colleagues note that precise identifications of all of the 'Ubeidiya material cannot currently be made due to the nature of the material. Their tentative assignation of the phalanx to *Megantereon cf. M. whitei*, however, is based on its small size and its similarity to an unpublished phalanx from Venta Micena believed to be *M. whitei* (presumably based on the assignation of more diagnostic portions of the skeleton at Venta Micena to this taxon). Measurements of both phalanges are presented in their paper and suggest that they are similar in size and proportion. These authors rule out the possibility that this is *Panthera*, particularly *P. leo* and *P. pardus*, based on the relative elongation of UB 307. However, no data is provided to support this statement. *Panthera cf. P. gombaszoegensis* is found at this site, but no mention is made of what distinguishes UB 307 from this species of *Panthera*.

Interestingly, Palmqvist et al. (2007) list measurements for an unpublished lower canine from 'Ubeidiya (presumably UB 14) and include width and breadth measurements that are larger than some of their *M. cultridens* measurements (thus suggesting their assignments of canines to species are based on something other than size). While they do not include measurements of the upper canine from 'Ubeidiya, their measurements of upper canines do not distinguish *M. cultridens* from *M. whitei* (as they define these two taxa). Measurements of lower canines are not included in the analyses and no mention is made of this specimen within descriptions of their statistical results.

Assignation of the published 'Ubeidiya material was tentative (Martínez-Navarro et al. 2009). We suggest that the 'Ubeidiya material is not complete enough to assign to a specific species. In addition, no new diagnostic material of *Megantereon* was found in the post Ballesio excavations from 1989–1994 and 1997–1999 (Belmaker M., personal communication, 2008). Martínez-Navarro and colleagues have suggested a similarity between the unpublished Venta Micena *Megantereon* phalanx and that from 'Ubeidiya. While it is certainly possible that the 'Ubeidiya material belongs to *M. whitei*, it is also possible that it is *M. cultridens*, *M. ekidoit*, or a completely new species. Until more diagnostic material is recovered, the taxonomic status of the 'Ubeidiya *Megantereon* remains unclear as are the biogeographic implications of this material.

5. Regardless of its affinities, could late Eurasian *Megantereon* have been a significant source of carcasses for scavenging by the earliest hominins in Europe even in the presence of the hyaenid *Pachycrocuta*?

The key word here is “significant”. Given the behavior of modern large-bodied carnivorans, one would expect hominins at this time to attempt to take carcasses from *Megantereon*. How important that resource was to migrating hominins is unknown. It seems doubtful that this would be the only factor



or even the dominant factor enabling hominin migration out of Africa. For reasons mentioned above, regular, confrontational use of this source of carcasses might cause the resource to disappear. While there may have been few species actively dispersing from Africa to Eurasia at this time, there were indigenous species that hominins would have encountered as they moved northwards. While stealing carcasses from *Megantereon* probably occurred occasionally, it is likely that hominins encountered other sources of meat and marrow along their journey.

## Conclusions

The evolution of *Megantereon* is not well enough understood to fully comprehend the nature of dispersals within this genus (see also Leakey and Werdelin 2010). While there are interesting hypotheses linking *Megantereon* and hominins, none are currently testable. Perhaps *Megantereon* dispersed from Africa at roughly the same time as hominins. Perhaps the appearance of hominins in Eurasia and/or ecological changes enabling hominin migration to this region drove later Eurasian *Megantereon* to converge on African forms. Perhaps the later form of *Megantereon* shared primitive features with African forms implying no dispersal and no convergence. We just do not know at present.

We can, however, set the scene in Africa for hominin dispersal. After 1.8 Ma, the carnivore guilds of Africa were decreasing in taxonomic diversity (Werdelin and Lewis 2005) and hominins were becoming increasingly dominant. Effective kleptoparasitic strategies, such as confrontational scavenging, by *Homo* could have destabilized the carnivore guilds, although it is probably not a sufficient explanation for all the species that become extinct during the Early Pleistocene (Lewis and Werdelin 2007). Most importantly, while some hominins migrate to Eurasia, others remain in Africa. These African hominins do not go extinct. What would cause some hominins to disperse while others remain (a question outside the purview of this paper)?

The point is that there are many more issues at play here than the relationship between hominins and carnivores. While we can continue to ask what *Theropithecus oswaldi*, *Hippopotamus antiquus*, *Megantereon* and *Homo erectus* might have in common at the time of dispersal (Martínez-Navarro 2004; Rook et al. 2004; Various papers in this volume, 2010), this may also be the wrong question. Dispersal to Eurasia at this point may have been a Simpsonian sweepstakes event where the factors affecting dispersal may have been different for each taxon and dispersal may not have occurred all at once. The search then becomes much more difficult: a search for the stochastic needle in the paleoenvironmental haystack.

**Acknowledgments** We would like to thank the symposium and workshop organizers and book editors for the invitation to participate. We would also like to thank all of the workshop participants, and especially B. Martínez-Navarro and M. Belmaker, for thoughtful discussions and critical comments on the workshop manuscript. Special thanks to J. Fleagle for editorial comments and B. Martínez-Navarro and two anonymous reviewers for their comments on this manuscript. Thanks also to M. Lague for comments. This research was supported by a grant from the LSB Leakey Foundation to ML and K.E. Reed, NSF grant to ML, Stockton Distinguished Faculty Fellowships to ML, and Swedish Research Council Grants to LW.

## References

- Antón, M., Galobart, A., & Turner, A. (2005). Co-existence of scimitar-toothed cats, lions and hominins in the European Pleistocene. Implications of the post-cranial anatomy of *Homotherium latidens* (Owen) for comparative palaeoecology. *Quaternary Science Reviews*, 24, 1287–1301.
- Arribas, A., & Palmqvist, P. (1999). On the ecological connection between sabre-tooths and hominids: Fauna dispersal events in the Lower Pleistocene and a review of the evidence for the first human arrival in Europe. *Journal of Archaeological Science*, 26, 571–585.
- Arribas, A., Riquelme, J. A., Palmqvist, P., Garrido, G., Hernández, R., Laplana, C., et al. (2001). Un nuevo yacimiento de grandes mamíferos villafranchienses en la Cuenca de Guadix-Baza (Granada): Fonelas P-1, primer registro de una fauna próxima al límite Plio-Pleistoceno en la Península Ibérica. *Boletín Geológico y Minero*, 112, 3–34.
- Ballesio, R. (1986). Les Carnivores du gisement Pléistocène d'Oubeidiyeh (Israël). *Mémoires et Travaux du Centre de Recherche Français de Jerusalem*, 5, 63–92.
- Belmaker, M. (2006). *Community structure through time: 'Ubeidiya, a Lower Pleistocene site as a case study*. Ph.D. dissertation, Hebrew University, Jerusalem.
- Belmaker, M. (2010a). The presence of a large cercopithecine (cf. *Theropithecus* sp.) in the 'Ubeidiya formation (Early Pleistocene, Israel). *Journal of Human Evolution* 58, 79–89.
- Belmaker, M. (2010b). Early Pleistocene faunal connections between Africa and Eurasia: an ecological perspective. In J. G. Fleagle, J. J. Shea, F. E. Grine, A. L. Baden, R. E. Leakey (Eds.), *Out of Africa I: the first hominin colonization of Eurasia* (pp. 183–205). Dordrecht: Springer.
- Berta, A., & Galiano, H. (1983). *Megantereon hesperus* from the late Hemphillian of Florida with remarks on the phylogenetic relationships of machairodonts (Mammalia, Felidae, Machairodontinae). *Journal of Paleontology*, 57, 892–899.
- Brain, C. K. (1981). *The hunters or the hunted? An introduction to African cave taphonomy*. Chicago: University of Chicago Press.
- Brantingham, P. J. (1998). Hominid-carnivore coevolution and invasion of the predatory guild. *Journal of Anthropological Archaeology*, 17, 327–353.
- Broom, R. (1937). On some new Pleistocene mammals from limestone caves of the Transvaal. *South African Journal of Science*, 33, 750–768.
- Broom, R. (1948). Some South African Pliocene and Pleistocene mammals. *Annals of the Transvaal Museum*, 21, 1–38.
- Broom, R., & Schepers, G. (1946). The South African fossil ape men: The Australopithecinae. *Transvaal Museum Memoirs*, 2, 1–272.
- Creel, S. (2001). Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. *Conservation Biology*, 15, 271–274.
- Cuvier, G. (1824). Recherches sur les ossements fossiles, où l'on rétablit les caractères de plusieurs animaux dont les révolutions du globe ont détruit les espèces. Paris.

- Dayan, T., & Simberloff, D. (1996). Patterns of size separation in carnivore communities. In J. L. Gittleman (Ed.), *Carnivore behavior, ecology, and evolution* (Vol. 2, pp. 243–266). Ithaca, NY: Cornell University Press.
- Dayan, T., & Simberloff, D. (2005). Ecological and community-wide character displacement: the next generation. *Ecology Letters*, 8, 875–894.
- Ewer, R. (1955). The fossil carnivores of the Transvaal caves: Machairodontinae. *Proceedings of the Zoological Society, London*, 125, 587–615.
- Ewer, R. (1973). *The carnivores*. New York: Cornell University Press.
- Ficcarelli, G. (1979). The Villafranchian machairodonts of Tuscany. *Palaeontographia Italica*, 79, 17–26.
- Haas, G. (1968). *On the fauna of 'Ubeidiya*. Jerusalem: The Israel Academy of Science and Humanities.
- Hartstone-Rose, A., De Ruiter, D. J., Berger, L. R., & Churchill, S. E. (2007). A sabre-toothed felid from Coopers cave (Gauteng, South Africa) and its implications for *Megantereon* (Felidae: Machairodontinae) taxonomy. *Palaeontologia Africana*, 42, 99–108.
- Hemmer, H. (2001). Die Felidae aus dem Epivillafranchium von Untermassfeld. *Monographien des Römisch-Germanischen Zentralmuseum*, 40, 699–782.
- Hendey, Q. (1973). Carnivore remains from the Kromdraai australopithecine site (Mammalia: Carnivora). *Annals of the Transvaal Museum*, 28, 99–112.
- Hendey, Q. (1974). The late Cenozoic Carnivora of the south-western Cape Province. *Annals of the South African Museum*, 63, 1–369.
- Leakey, M. G. & Werdelin, L. (2010). Early Pleistocene mammals of Africa: Background to dispersal. In J. G. Fleagle, J. J. Shea, F. E. Grine, A. L. Baden, & R. E. Leakey (Eds.) *Out of Africa I: The first hominin colonization of Eurasia* (pp. 3–11). Dordrecht, The Netherlands: Springer.
- Lewis, M. E. (1995a). Functional morphology of the sabertoothed felid *Megantereon* from Kromdraai, South Africa. *Journal of Vertebrate Paleontology*, 15, 40A.
- Lewis, M. E. (1995b). *Plio-Pleistocene carnivoran guilds: Implications for hominid paleoecology*. Ph.D. thesis, State University of New York, Stony Brook.
- Lewis, M. E. (1997). Carnivoran paleoguilds of Africa: Implications for hominid food procurement strategies. *Journal of Human Evolution*, 32, 257–288.
- Lewis, M. E., & Werdelin, L. (2007). Patterns of change in the Plio-Pleistocene carnivorans of eastern Africa: Implications for hominin evolution. In R. Bobe, Z. Alemseged, & A. K. Behrensmeyer (Eds.), *Hominin environments in the East African Pliocene: An assessment of the faunal evidence* (pp. 77–106). Dordrecht, The Netherlands: Springer.
- Linnell, J. D. C., & Strand, O. (2000). Interference interactions, coexistence and conservation of mammalian carnivores. *Diversity and Distributions*, 6, 169–176.
- Liu, J.-Y. (2005). *Megantereon* fossil remains from Renzidong Cave, Fanchang County, Anhui Province, China. *Vertebrata Palasiatica*, 43, 122–134.
- Marean, C. W. (1989). Sabertooth cats and their relevance for early hominid diet and evolution. *Journal of Human Evolution*, 18, 559–582.
- Marean, C. W., & Ehrhardt, C. L. (1995). Paleoanthropological and paleoecological implications of the taphonomy of a sabertooth's den. *Journal of Human Evolution*, 29, 515–547.
- Martínez-Navarro, B. (2004). Hippos, pigs, bovids, sabertoothed tigers, monkeys and hominids dispersals during late Pliocene and early Pleistocene times through the Levantine corridor. In: N.L. Goren-Inbar, & J. D. Speth (Eds.), *Proceedings of the Conference entitled "Human Paleocology in the Levantine Corridor," Jerusalem July 2002* (pp. 37–51). London: Oxbow Books.
- Martínez-Navarro, B. (2010). Early Pleistocene faunas of Eurasia and hominin dispersals. In J. G. Fleagle, J. J. Shea, F. E. Grine, A. L. Baden, R. E. Leakey (Eds.), *Out of Africa I: the first hominin colonization of Eurasia* (pp. 207–224). Dordrecht: Springer.
- Martínez-Navarro, B., & Palmqvist, P. (1995). Presence of the African machairodont *Megantereon whitei* (Broom, 1937) (Felidae, Carnivora, Mammalia) in the Lower Pleistocene site of Venta Micena (Orce, Granada, Spain), with some considerations on the origin, evolution and dispersal of the genus. *Journal of Archaeological Science*, 22, 569–582.
- Martínez-Navarro, B., & Palmqvist, P. (1996). Presence of the African saber-toothed felid *Megantereon whitei* (Broom, 1937) (Mammalia, Carnivora, Machairodontinae) in Apollonia-1 (Mygdonia Basin, Macedonia, Greece). *Journal of Archaeological Science*, 23, 869–872.
- Martínez-Navarro, B., Belmaker, M., & Bar-Yosef, O. (2009). The large carnivores from 'Ubeidiya (early Pleistocene, Israel): Biochronological and biogeographical implications. *Journal of Human Evolution*, 56, 514–524.
- Palmqvist, P. (2002). On the presence of *Megantereon whitei* at the South Turkwel Hominid Site, northern Kenya. *Journal of Paleontology*, 76, 928–930.
- Palmqvist, P., Martínez-Navarro, B., & Arribas, A. (1996). Prey selection by terrestrial carnivores in a Lower Pleistocene community. *Paleobiology*, 22, 514–534.
- Palmqvist, P., Gröcke, D. R., Arribas, A., & Fariña, R. A. (2003). Paleocological reconstruction of a lower Pleistocene large mammal community using biogeochemical ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ,  $\delta^{18}\text{O}$ , Sr:Zn) and ecomorphological approaches. *Paleobiology*, 29, 205–229.
- Palmqvist, P., Torregrosa, V., Pérez-Claros, J. A., Martínez-Navarro, B., & Turner, A. (2007). A re-evaluation of the diversity of *Megantereon* (Mammalia, Carnivora, Machairodontinae) and the problem of species identification in extinct carnivores. *Journal of Vertebrate Paleontology*, 27, 160–175.
- Palmqvist, P., Pérez-Claros, J. A., Janis, C. M., Figueirido, B., Torregrosa, V., & Gröcke, D. R. (2008). Biogeochemical and ecomorphological inferences on prey selection and resource partitioning among mammalian carnivores in an Early Pleistocene community. *Palaaios*, 23, 724–737.
- Patnaik, R., & Nanda, A. C. (2010). Early Pleistocene mammalian faunas of India and evidence of connections with other parts of the world. In J. G. Fleagle, J. J. Shea, F. E. Grine, A. L. Baden, R. E. Leakey (Eds.), *Out of Africa I: the first hominin colonization of Eurasia* (pp. 129–143). Dordrecht: Springer.
- Petter, G., & Howell, F. C. (1982). Un Féliné machairodonte des formations plio-pleistocènes des Siwaliks: *Megantereon falconeri* Pomel/ = *M. sivalensis* (F. et C.). (Mammalia. Carnivora. Felidae). *Comptes Rendus de l'Académie des Sciences, Paris, Série II* 295, 281–284.
- Pomel, M. (1853). Catalogue méthodique et descriptif des Vertébrés fossiles. Paris.
- Pons-Moya, J. (1987). Los carnívoros (Mammalia) de Venta Micena (Granada, España). *Paleontología i Evolució, Mem. Esp.*, 1, 109–128.
- Qiu, Z., Deng, T., & Wang, B. (2004). Early Pleistocene mammalian fauna from Longdan, Dongxiang, Gansu, China. *Palaeontologia Sinica*, 191, 1–198.
- Rook, L., Martínez Navarro, B., & Howell, F. C. (2004). Occurrence of *Theropithecus* sp. in the Late Villafranchian of Southern Italy and implications for Early Pleistocene "out of Africa" dispersals. *Journal of Human Evolution*, 47, 267–277.
- Sardella, R. (1998). The Plio-Pleistocene Old World dirk toothed cat *Megantereon* ex gr. *cultridens* (Mammalia, Felidae, Machairodontinae), with comments on taxonomy, origin and evolution. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 207, 1–36.
- Sardella, R., Petrucci, M., & Rook, L. (2008). The African species *Megantereon whitei* from the Early Pleistocene of Monte Argentario (South Tuscany, Central Italy). *Comptes Rendus Palevol*, 7, 601–606.

- Sotnikova, M. V. (1989). Late Pliocene-Early Pleistocene Carnivora: Stratigraphic significance. *Trudy, Akademia Nauk, SSSR*, 440, 1–123 (in Russian).
- Taylor, M. E. (1989). Locomotor adaptations by carnivores. In J. L. Gittleman (Ed.), *Carnivore behavior, ecology, and evolution* (pp. 382–409). New York: Cornell University Press.
- Turner, A. (1987). *Megantereon cultridens* (Cuvier) (Mammalia, Felidae, Machairodontinae) from Plio-Pleistocene deposits in Africa and Eurasia, with comments on the possibility of a New World origin. *Journal of Paleontology*, 61, 1256–1268.
- Turner, A. (1988). Relative scavenging opportunities for east and south African Plio-Pleistocene hominids. *Journal of Archaeological Science*, 15, 327–341.
- Turner, A. (1990). The evolution of the guild of larger terrestrial carnivores during the Plio-Pleistocene in Africa. *Geobios*, 23, 349–368.
- Turner, A. (1993). New fossil carnivore remains from Swartkrans. In: C. K. Brain (Ed.), *Swartkrans: A cave's chronicle of early man* (pp. 161–165). Transvaal Museum Monograph No. 8. Pretoria: Transvaal Museum.
- Turner, A., & Antón, M. (1997). *The big cats and their fossil relatives: An illustrated guide to their evolution and natural history*. New York: Columbia University Press. 234 pp.
- Van Valkenburgh, B. (1987). Skeletal indicators of locomotor behavior in living and extinct carnivores. *Journal of Vertebrate Paleontology*, 7, 162–182.
- Van Valkenburgh, B. (2001). The dog-eat-dog world of carnivores: A review of past and present carnivore community dynamics. In C. B. Stanford & H. T. Bunn (Eds.), *Meat-eating and human evolution* (pp. 101–121). Oxford: Oxford University Press.
- Vekua, A. K. (1995). Die Wirbeltierfauna des Villafranchium von Dmanisi und ihre biostratigraphische Bedeutung. *Jahrbuch des Römisch-Deutschen Zentralmuseums, Mainz*, 42, 77–180.
- Vrba, E. S. (1981). The Kromdraai australopithecine site revisited in 1980; Recent investigations and results. *Annals of the Transvaal Museum*, 33, 17–59.
- Werdelin, L., & Lewis, M. E. (2000). Carnivora from the South Turkwel hominid site, northern Kenya. *Journal of Paleontology*, 74, 1173–1180.
- Werdelin, L., & Lewis, M. E. (2001). A revision of the genus *Dinofelis* (Mammalia, Felidae). *Zoological Journal of the Linnean Society*, 132, 147–258.
- Werdelin, L., & Lewis, M. E. (2002). Species identification in *Megantereon*: A reply to Palmqvist. *Journal of Paleontology*, 76, 931–933.
- Werdelin, L., & Lewis, M. E. (2005). Plio-Pleistocene Carnivora of eastern Africa: Species richness and turnover patterns. *Zoological Journal of the Linnean Society*, 144, 121–144.
- Werdelin, L., & Lewis, M. E. (in prep). *Koobi Fora Research Project, volume 6: The fossil carnivora*. San Francisco: California Academy of Sciences.
- WoldeGabriel, G., White, T. D., Suwa, G., Renne, P., de Heinzelin, J., Hart, W. K., et al. (1994). Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia. *Nature*, 371, 330–333.
- Woodroffe, R., & Ginsberg, J. R. (2005). King of the beasts? Evidence for guild redundancy among large mammalian carnivores. In J. C. Ray, K. H. Redford, R. S. Steneck, & J. Berger (Eds.), *Large carnivores and the conservation of biodiversity* (pp. 154–178). Washington, DC: Island Press.



Out of Africa I

The First Hominin Colonization of Eurasia

(Eds.) J.G. Fleagle; J.J. Shea; F.E. Grine; A.L. Baden; R.E.

Leakey

2010, X, 294 p., Hardcover

ISBN: 978-90-481-9035-5