Out of Africa I

Vertebrate Paleobiology and Paleoanthropology Series

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Out of Africa I

The First Hominin Colonization of Eurasia

Contributions from the Second Stony Brook
Human Evolution Symposium and Workshop, September 27–30, 2005

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Preface

Today, humans are the most cosmopolitan of all primates, and one of the most widespread of all living mammals. Our lineage has not always been so geographically widespread. For over two-thirds of our evolutionary history, from our divergence from chimpanzees more than 6 million years ago, until as recently as 2 million years ago, hominins were an endemic African group. Sometime near the beginning of the Pleistocene, just under 2 million years ago, this all changed, and archeological and paleontological evidence of early hominins appears in many parts of Eurasia. The papers in this volume address the many facets of the first hominin range expansion from Africa into Eurasia.

These include not just the obvious issues of when hominins first appear in Eurasia and the type of evidence indicating their presence, but a whole series of broader questions about the nature of this initial hominin intercontinental dispersal. Why did hominins first leave Africa in the Early Pleistocene and no earlier? What do we know about the adaptations of the hominins that dispersed – their diet, locomotor abilities, cultural abilities? Was there a single dispersal event or several? Did this initial dispersal lead to successful colonization of Eurasia, or were they just temporary excursions? Was the hominin dispersal part of a broader faunal expansion of African mammals northward, or is there something unique about our lineage? What route or routes did dispersing populations take? Why do we have evidence of Early Pleistocene hominins in western and eastern Asia, but nothing in between?

In order to address these and many other issues regarding the initial dispersal of hominins out of Africa, we organized the Second Stony Brook Human Evolution Symposium and Workshop in 2005. An international group of scholars assembled in Stony Brook for 5 days of presentations and discussions to explore our current understanding of this aspect of human evolution and to identify priorities for future research. This volume is the result of that meeting. Since the mid-1980s, the lower boundary of the Pleistocene Epoch (i.e., the beginning of the Quaternary Period) has been regarded as corresponding with the base of the Calabrian stratotype, at 1.81 Ma. Recently, however, the International Union of Geological Sciences has recognized the base of the Gelasian stratotype, which corresponds to the Matuyama (C2r) chronozone, or the Gauss-Matuyama boundary, as defining the Pliocene-Pleistocene boundary at 2.588 Ma. Because many of the papers were submitted before that change, in this volume, the older convention has been followed with the base of the Pleistocene at 1.8 Ma.

The workshop was sponsored by Stony Brook University and the Turkana Basin Institute, with important contributions by Kay Harrigan Woods, Bill and Kathy Cleary, Jim and Marilyn Simons, The Richard and Rhoda Goldman Fund, The Leakey Foundation and the Office of the Provost, Stony Brook University. The President of Stony Brook, Dr. Shirley Strum Kenny, kindly offered her home at Sunwood for the workshop. In addition to the contributors to this volume, Susan Antón, Karen Baab, Amanuel Beyin, Paul Bingham, Ari Grossman, Lawrence Martin, James Rossie, Danielle Royer, Matthew Sisk, Fred Spoor, Kathryn Twiss, and Frank Brown. Elizabeth Wilson contributed to the success of the symposium and workshop in many ways.

The chapters in this volume underwent extensive peer-review. We thank our many colleagues who contributed their time, effort, and wisdom to the review process. Luci Betti-Nash, Amanuel Beyin, Chris Gilbert, Jessica Lodwick, and Brandon Wheeler provided extensive assistance in the editing of this volume. We thank Eric Delson and Eric Sargis, senior co-editors of the Vertebrate Paleontology and Paleoanthropology Series for their endless support, encouragement, and especially their patience in seeing this volume through to publication.

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Part I
The African Background

Introduction

The papers in this first part discuss the aspects of geography, climate, faunal composition and hominin culture that enabled or led to the initial dispersal of hominins into Eurasia.

In “Early Pleistocene Mammals of Africa: Background to Dispersal”, Meave Leakey and Lars Werdelin place the evolution and dispersal of hominins in the broader context of the evolution of anthropoid primates in Africa and their patterns of dispersal over the past 20 million years. In particular, they compare the ecology of early *Homo* with that of *Theropithecus,* another widely dispersing catarrhine from the Plio-Pleistocene. They also review patterns of African carnivore evolution and dispersal from the Miocene through the Pleistocene. They argue that with the advent of culture, in the form of stone tools, hominins moved into a new feeding niche and became part of the carnivore guild, with the added ability to also exploit plant resources. This would have affected many aspects of their ecology, including home range size and dispersal abilities, and also affected the ecology and survival within the diverse carnivore communities of the Pliocene and Early Pleistocene. They also review the herbivore communities of the Pliocene and Pleistocene, noting that the hominin shift to a carnivore feeding niche took place in the context of a diverse assemblage of large herbivores that were potential prey. Cut marks on a broad size range of taxa support the view that Early Pleistocene hominins did indeed exploit a diversity of taxa for meat.

Much of the discussion regarding the initial dispersal of hominins from Africa to Eurasia in the earliest Pleistocene centers around the role of synchronic carnivores, especially the genus *Megantereon*, both as a co-disperser and as a potential competitor. In “Carnivoran Dispersal Out of Africa During the Early Pleistocene: Relevance for Hominins”, Margaret Lewis and Lars Werdelin review the diverse carnivores in the Pliocene and Pleistocene of Africa. They then summarize the complex taxonomic history of the genus *Megantereon* and questions surrounding the intercontinental dispersal of various species within that genus, including the identity of the species of *Megantereon* from the site of Dmanisi. Finally, they review the nature of the likely ecological relationships and possible interactions between hominins and *Megantereon*.

In “Saharan Corridors and Their Role in the Evolutionary Geography of ‘Out of Africa I’”, Marta Mirazón Lahr observes that dispersal of hominins out of Africa must have first involved dispersal within Africa since the fossil record of early hominin evolution is almost exclusively from sub-Saharan Africa. Accordingly, she points out that questions of dispersal can be examined at very different scales, such as species or populations and continents or ecological zones. It is at the latter scales that evolution takes place. In a review of the paleontological and archeological record of North Africa, she finds that evidence of a hominin presence is very rare before the Early and Middle Pleistocene, and the earliest record, at Ain Hanech in Algeria, corresponds to the timing of the colonization of Eurasia. Thus, trans-Saharan dispersal was very rare, and hominin presence in North Africa was probably ephemeral prior to the Middle Pleistocene. She argues that it is most likely that the initial hominin dispersal into Eurasia was across the Bab-el-Mandeb Strait from the Horn of

Africa to the Arabian Peninsula. Ironically, Early Pleistocene hominin dispersals into Eurasia were apparently more successful and more long-lived than those into North Africa.

It is generally accepted that the development of culture represented by the manufacture and use of stone tools was one of the most important factors that enabled hominins to successfully disperse into Eurasia and the remains of these artifacts are often the primary evidence we have of early hominin presence. In "Stone Age Visiting Cards Revisited: A Strategic Perspective on the Lithic Technology of Early Hominin Dispersal", John Shea investigates what differences in stone tool technology tell us about the identity and behavior of the hominins that made them. Shea notes that efforts to link specific lithic technologies uniquely with one taxon of hominin have repeatedly failed, and the lack of correspondence is increasing with increased diversity in hominin phylogeny. Most notably, pebble core tools such as those that characterize the Oldowan industries persist from the late Pliocene to the present. He suggests that a more profitable approach might be to look at different technologies from a strategic perspective. Following an examination of the likely costs and benefits of the production and use of pebble cores such as those characterizing Oldowan industries, and Large Cutting Tool (LCT) core technology, he argues that the former are likely characteristic of low density, mobile, colonizing populations, while LCT technologies are more characteristic of larger, stable populations.

The Editors

Chapter 1
Early Pleistocene Mammals of Africa: Background to Dispersal

Meave Leakey and Lars Werdelin

Abstract The initial dispersal of humans out of Africa was a significant event in human evolution raising many questions. Why did this happen at this particular time? Was it part of a major migration of mammals out of Africa and did any species move into Africa at the same time? Were climate and habitat changes taking place that might have been contributing factors? With the advent of culture at 2.6 Ma, hominins moved from the primate to the carnivore feeding niche, thus avoiding constraints that had previously determined their distribution. Here we look at fossil carnivores and cercopithecids for factors that provide a background to this significant event in our evolutionary history and we also look at herbivore diversity as a potential source of prey for meat-eating hominins.

Keywords Carnivore • Dispersal • Catarrhine • *Homo erectus*

Introduction

Until the first evidence of culture in the hominin record, the geographic distribution of human ancestors was subjected to life history constraints common to all higher primates. Catarrhines today are largely restricted to tropical and subtropical forests and woodlands that provide relatively high quality foods that are largely available year round. The few extant African catarrhines found outside these habitats, such as baboons (*Papio* sp.) and vervet monkeys (*Chlorocebus aethiops*), are semi-terrestrial eclectic feeders tolerant of extreme seasonal variations in their food supply. The ability to utilize and manufacture stone tools was the first in a series of adaptations that enabled hominins to shift feeding strategy and compete with carnivores with increasing success. In the absence of constraints that had previously limited hominin distribution, hominins migrated into habitats from which other catarrhines were excluded, and ultimately to latitudes far removed from the tropics.

To fully understand the relative significance of the factors influencing this event, it is essential to assess whether the dispersal of *Homo erectus* (*sensu lato*; see Antón 2003 for discussion; and Spoor et al. 2007 for use of *Homo erectus* for African specimens previously referred to as *Homo ergaster*) out of Africa 1.8 million years ago was part of a major migration event affecting many species, was restricted to a very few species with similar life histories and diets, or was unique to *H. erectus*. To explore possible scenarios we first look at anthropoid evolutionary history in the Miocene, Pliocene and Pleistocene as a background to hominin evolution prior to the advent of culture, when early hominins were an integral part of the fossil catarrhine assemblages and subject to similar constraints on their distribution. We then examine patterns of cercopithecid and carnivore dispersal in the critical time interval, and particularly at or near 1.8 Ma to assess whether other species moved out of Africa at this time. We then discuss the Early Pleistocene carnivore guilds and how these might have influenced meat eating hominin food procurement strategies. Finally, we look at Early Pleistocene herbivore faunal assemblages as a potential food resource for the newly emerged meat eating hominins.

The Turkana Basin, Kenya, is a source for much of this discussion since it documents a particularly rich record over the appropriate time interval. The many archeological sites at Olduvai Gorge, Tanzania, and the fossil assemblages of the Transvaal caves in South Africa are also important sources of evidence.

Anthropoid Faunal Assemblages

With the notable exception of *Homo*, the distribution of anthropoids today is largely constrained to the tropics; apes and most monkeys are found in tropical and subtropical forests and woodlands where food resources are relatively

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reliable and year round. Whereas in Africa today apes are rare and represented by few species inhabiting limited areas of tropical forest, monkeys in contrast are more common, widely dispersed and diverse, largely inhabiting low latitude tropical and riparian forests and closed woodlands across central Africa. The difference in ape and monkey distributions may reflect the preference of apes for higher quality foods, especially fruits, in less seasonal environments, and their more protracted reproductive schedules (Jablonski et al. 2000). Alternatively the switch from ape dominance and diversity in the Late Miocene to monkey dominance today may have been related to climate and habitat changes during the Late Miocene of Africa and Europe (Fleagle 1999).

Although Pliocene and Pleistocene fossil apes are virtually unknown (McBrearty and Jablonski 2005), the cercopithecid fossil record at this time is good and monkeys were relatively common in the faunal assemblages (Table 1.1). Surprisingly, in the past, African cercopithecids were less restricted in their distribution than today, occurring widely in eastern, southern and northern Africa. The majority of modern African cercopithecid species are not representative either of their fossil precursors or of the majority of their Asian cousins in either distribution or diet.

Cercopithecid diversity stems from small bodied semi-terrestrial papionins and colobines common in woodland and well watered habitats in the Late Miocene (Frost 2001, 2002; Leakey et al. 2003). The morphology of the dentition of these early cercopithecid monkeys suggests that they had similar diets with a high proportion of seeds (Leakey et al. 2003) and their locomotor adaptations indicate that they were more terrestrial than their modern counterparts. Their success may relate to an ability to adapt to the seasonality that increasingly came to dominate open country habitats.

Monkeys underwent a significant radiation between 3.5 and 2.0 Ma, most clearly seen in the colobines. In contrast to the relatively small-bodied, arboreal, leaf-eating modern colobines found in forests and closed woodlands, the Plio-Pleistocene colobines are represented by three genera (*Rhinocolobus, Paracolobus* and *Cercopithecoides*, including several species) of large-bodied, comparatively terrestrial monkeys inhabiting open woodlands and savannas. In many aspects of their morphology, these extinct African colobines most closely resemble the larger extant colobines from Asia; the "temple langurs" (*Semnopithecus entellus*) and the "odd-nosed colobines" (*Rhinopithecus*, *Pygathrix*, and *Nasalis*), which today are widely distributed in more open habitats (Jablonski and Leakey 2008). The general perception that colobines are and have always been arboreal species confined to forests is erroneous.

Table 1.1 The cercopithecoid faunal assemblage from the Upper Burgi and KBS Members of the Koobi Fora Formation, Omo Group deposits, Turkana Basin Kenya. *Theropithecus oswaldi* (in bold) far outnumbers any other species, being represented by over 200 specimens in contrast to all other species which are represented by less than 25 specimens

Parapapio sp. indet. A	*Colobus freedmani*
Parapapio sp. indet. B	*Rhinocolobus turkanaensis*
Lophocebus cf. *L. albigena*	*Cercopithecoides kimeui*
Theropithecus oswaldi	*Cercopithecoides williamsi*
Cercopithecus sp. indet. A	*Paracolobus mutiwa*

The most common genus of monkey in the Plio-Pleistocene was *Theropithecus*. Although today the single remaining species of *Theropithecus, T. gelada*, is confined to the Ethiopian highlands, where it maintains a tenuous hold on this small locality in Africa, in the past this genus was widespread and the most common cercopithecid in the Plio-Pleistocene. First appearing approximately 3.5 Ma ago (Leakey et al. 2001), it derives from a papionin ancestor that diverged to specialize in a graminivorous diet. The evolution of *Theropithecus*, with its increasingly marked dental adaptations towards exclusive graminivory, is well documented (Jolly 1985; Jablonski 1993b; Leakey 1993). *Theropithecus brumpti*, the common gelada in the Late Pliocene, inhabited more closed woodland habitats than its successor *Theropithecus oswaldi*, which replaced *T. brumpti* about 2.5 Ma ago (Eck 1987a; Eck and Jablonski 1987; Leakey 1993; Jablonski and Leakey 2008). This unusual, highly specialized grass eating monkey was extremely successful, surviving for 2 million years, from 2.5 Ma until its extinction in the last 500,000 years. Its known occurrences are widespread; fossil *T. oswaldi* have been recorded from sites in eastern, southern, and northern Africa (Jablonski 1993a), the Levant (Belmaker 2002, 2009), Italy (Rook et al. 2004; but see Patel et al. 2007), and Spain (Gibert et al. 1995) (the phalanx CV-O, ascribed to *Homo* by Gibert and co-workers has recently been reclassified as *Theropithecus* in Martínez-Navarro et al. 2005), in Europe, and the Siwaliks in India (Gupta and Sahni 1981; Delson 1993). *Theropithecus* was the most widespread cercopithecid known in the Late Pliocene and Early to Middle Pleistocene.

Competition from *Theropithecus* and the large bodied colobines between 3.0 and 1.5 Ma appears to have led to a reduction in the earlier papionin diversity in eastern Africa where, at this time papionins are rather uncommon. It was only in the last 1.0 Ma that *Papio* became more common and today this genus is the most widespread cercopithecid in Africa. In the Plio-Pleistocene Transvaal cave deposits of South Africa, where there is less diversity among fossil colobines, with only *Cercopithecoides williamsi* (the most terrestrial of the African fossil colobines) represented (Freedman 1957), papionins were common throughout this time (Freedman 1976; Freedman and Brain 1977). Fossil guenons (*Cercopithecus* sp.) were rare in the East African fossil record; few specimens are known from the Pliocene and few have been recovered from the Early Pleistocene of the Turkana Basin (Leakey 1988; Eck 1987b; Jablonski and Leakey 2008). Although molecular studies indicate that

Cercopithecus originated in the Late Miocene and that the major subdivisions of the genus are Pliocene in age (Tosi et al. 2005), it is not until the last 1.5 Ma that there is fossil evidence that might suggest the beginning of the radiation that led to their modern status as the most common and diverse African genus of monkeys, largely inhabiting tropical forests in central Africa. The modern, rather restricted distribution of African monkeys is thus in direct contrast to that in the Plio-Pleistocene, when cercopithecid species were taxonomically diverse and geographically widespread, frequenting diverse habitats ranging from riparian woodlands, grasslands and relatively open country. Although the most common monkeys today are the guenons, the majority of which inhabit tropical forests (Gautier-Hion et al. 1988), the most widespread species are the baboons (species of *Papio*) and vervets (*Chlorocebus aethiops*), eclectic feeders that are able to utilize fall-back foods in times of drought and food shortages (Kingdon 1997).

Hominins too have a well documented fossil record and their early occurrences frequently coincide with those of cercopithecids. Hominins were almost as widely dispersed geographically in the Pliocene and Early Pleistocene as the most widespread monkeys, although they were less common. Although the earliest hominins are known from the Late Miocene (Brunet et al. 2002; Haile-Selassie 2001; Senut et al. 2001), it is not until 3.5 Ma that there is evidence of diversity in the fossil record (Leakey et al. 2001). Between 2.5 and 1.8 Ma, when hominins shared their habitat with a diverse cercopithecid assemblage including three genera of colobines and one species of *Theropithecus*, they came to increasingly externalize their food procurement functions in the form of stone tools.

Patterns of Catarrhine Dispersal

What is it that determines the distribution of catarrhines and, as the closest relatives of hominins, what can the distribution of past cercopithecid and hominoid assemblages tell us about the dispersal of hominins? Cercopithecid migrations in the past appear to have been exclusively out of Africa (Fleagle and Gilbert 2006). The earliest evidence for the divergence of the modern subfamilies is in Africa with the presence of colobines at 11 Ma in the Baringo Basin in Kenya (Benefit and Pickford 1986). Colobines are first found in Europe soon after this with the appearance of *Mesopithecus* (Delson 1973, 1975a, b, 1994), they first appear in Asia (northern India and Pakistan) by the Late Miocene between 7 and 5 Ma (Barry 1987), and in the latest Miocene of China (Delson 1994). The earliest known cercopithecines are from the latest Miocene, dated to approximately 7 Ma (Delson 1973, 1975a, b; Szalay and Delson 1979; Leakey et al. 1996, 2003). At about this time, cercopithecines are recognized in Europe; *Procynocephalus* appears in the latest Miocene, *Dolichopithecus* appears in the early Middle Pliocene and *Paradolichopithecus* appears in the Middle Pliocene. There is no evidence of anthropoid faunal exchange in the Pliocene, and in the Pleistocene, the only cercopithecid known to have spread out of Africa is *Theropithecus*. The earliest recorded *Theropithecus* out of Africa is from Pirro Nord in Italy, which has an estimated biochronological date of 1.6–1.3 Ma (Rook et al. 2004). However, the ocurrence at Pirro Nord has been questioned by Patel et al. (2007) who also note the absence of *Theropithecus* from any other Plio-Pleistocene sites outside of Africa and the Levant (including Dmanisi). It is thus possible that *Theropithecus* migrated out of Africa at a similar time to *Homo erectus*, even though the genus is not present at localities such as Dmanisi that include *H. erectus* or Venta Micena and Appolonia-1 that (along with Dmanisi) include *Megantereon*, another putative African migrant (see below).

The earliest evidence of fossil "apes" outside Africa is between 16.5 and 17 Ma from southern Germany and they are also recorded at Paşalar in Turkey (Mourtzou and Andrews 2008). Hominoids are widespread in Eurasia in the Middle Miocene in contrast to Africa where they are very rare. Hominoids disappeared from Europe in the Late Miocene. The earliest fossil hominins appeared in the Late Miocene of Africa, but the evidence is inconclusive as to whether extant African apes and humans originated in Africa or from the Middle Miocene hominoid diversity of Eurasia; two contrasting schools of thought currently pertain to this problem (Kordos and Begun 2002). Fossil hominins are relatively abundant in eastern and southern Africa in the Pliocene, but the earliest evidence of migration of hominins out of Africa is that of *Homo erectus* at ~1.7 Ma (Antón et al. 2002).

In order to assess parameters determining the distribution of the Catarrhini, Jablonski et al. (2000) examined the impact of environmental change in the Late Pliocene and Pleistocene in China. During this time there were decreases in the extent of tropical and subtropical ecozones as a result of southward latitudinal shifts. The responses of the major catarrhine genera to these habitat shifts were diverse, but dietary selectivity and life history parameters were noted to be strong predictors of the type and magnitude of responses of individual taxa. Relative to apes, monkeys can survive on a wider variety of vegetation in extreme seasonal habitats and have shorter gestation times, weaning periods and interbirth intervals. Apes have a preference for high quality foods, especially ripe fruits, in less seasonal environments and more protracted reproductive schedules and lower intrinsic rates of population increase. Apes, including gibbons, orang-utans and *Gigantopithecus*, were found to be more sensitive to environmental change than monkeys, including macaques and langurs (Jablonski et al. 2000).

Hominins, like apes, have an advanced age for onset of reproduction, long gestation and weaning periods and long interbirth intervals. They are an extreme example of “K-selection” reproductive strategy in which high parental investment in low numbers of offspring per lifetime yield a low intrinsic rate of population increase (Pianka 1978). They are therefore expected to conform to the ape pattern. Jablonski et al. (2000) found this to be generally true, with the exception of early *Homo sapiens*, because advanced culture enabled this species to colonize highly seasonal habitats including tundra, which were unavailable to other catarrhines.

Antón et al. (2002) note that rate of dispersal, like foraging strategy, is influenced by home range size and body size. These factors likely also contributed to the wide Pleistocene dispersal of *Theropithecus oswaldi*. In contrast to the relatively small home range sizes of modern forest dwelling monkeys, extant *Theropithecus gelada* has a relatively extensive home range in which the exceptionally large troops forage for limited food resources. This was presumably also true for the large bodied *Theropithecus oswaldi* in the Plio-Pleistocene. Carnivores have increased home range sizes relative to herbivores, so that the home range size of early *Homo* would have increased with the shift to meat eating. Indeed archeological evidence indicates large home range sizes for early hominins; the distribution of archeological sites within Africa at this time shows increasing complexity of the archeological record and increasing distance from lithic raw material sources (Cachel and Harris 1995; Delagnes and Roche 2005). The rapid rates of dispersal of *Homo erectus* appear to have been promoted by changes in foraging strategy that led to increases in home range size and body size facilitated by changes in ecosystem structure during the Plio-Pleistocene (Antón et al. 2002). But what were the factors that may have affected hominin success as they changed foraging strategy?

Patterns of Carnivore Dispersal

The dispersal of mammalian species into new geographical areas requires corridors of appropriate habitats with access to water and suitable food. Species that require specific but limited feeding niches are less likely to be widely distributed than those more tolerant of variations in their food supply. Carnivores are thus generally more widely distributed than herbivores, since suitable food is widely distributed.

In contrast to catarrhines, carnivore dispersal in the Miocene was almost exclusively from Eurasia into Africa (Werdelin 2006, unpublished data). It was not until the very end of the Miocene that this pattern changed. Between 5.5 and 4.0 Ma, carnivores continued to move into Africa and the first migrations out of Africa took place. After this time, carnivore migration has been almost exclusively out of Africa, involving taxa of medium to large (>10 kg) body size.

Out of 31 carnivoran species that were present in East Africa between 2.1 and 1.8 Ma (of which 18–19 including *Mellivora*, were large and terrestrial), only one (*Megantereon whitei*) possibly migrated out of Africa at this time. *M. whitei* can be parsimoniously regarded as present in some southern European sites (e.g., Venta Micena, Dmanisi, Appolonia-1) dated 1.8–1.5 Ma, though this identification is not unproblematic (Werdelin and Lewis 2002; Lewis and Werdelin 2007). *Crocuta* left Africa some time prior to 2 Ma, as the current FAD for this genus in China is ~2.2 Ma (Qiu et al. 2003), while the FAD for Europe is <0.8 Ma.

In contrast, diverse carnivoran taxa appear to migrate out of Africa at various times before and after 2.1–1.8 Ma. Both *Megantereon* and *Homotherium* may have migrated from Africa at ca. 3.5 Ma or earlier. *Panthera* and *Acinonyx* also have FADs in Europe at ca. 3 Ma, which is later than in Africa. *P. leo* reaches Eurasia from Africa ca. 0.5 Ma. With all these data, there is no evidence among carnivore taxa for a peak of migrations at a time corresponding to the timing of the first appearance of *Homo* outside Africa.

The composition of the carnivore faunal assemblages changes with time, which may be partly a result of the influence of hominins. Up to the end of the Pliocene, carnivore assemblages include numerous large-bodied specialists, some of which were undoubtedly preying on early australopithecines. The time interval 2–1.5 Ma is the time of extinction of these large, specialist carnivores, while after this the majority of remaining carnivores in Africa can be considered ecological generalists (Table 1.2; Lewis and Werdelin 2007;

Table 1.2 The carnivoran faunal assemblage from eastern and southern Africa dated between 2 and 1.5 Ma ago. Large-bodied specialist taxa are in bold; extinct species not replaced by closely related taxa are starred

Caracal caracal
Chasmaporthetes nitidula*
Crocuta dietrichi
Crocuta ultra
Crossarchus transvaalensis
Cynictis penicillata
Dinofelis aronoki*
Dinofelis barlowi*
Dinofelis piveteaui*
Dinofelis **sp. (Olduvai)***
Felis sp.
Galerella debilis
Galerella primitivus
Genetta genetta
Genetta tigrina
Helogale hirtula
Herpestes ichneumon
Homotherium **sp.***
Hyaena hyaena
Hyaena makapani
Ichneumia albicauda
Lycyaenops silberbergi*
Megantereon whitei*
Mellivora capensis
Mungos dietrichi
Mungos minutus
*Nyctereutes terblanchei**
*Pachycrocuta brevirostris**
Panthera leo
Panthera pardus
Parahyaena brunnea
Proteles amplidentus
Prototocyon recki
Pseudocivetta ingens*
Sivaonyx **sp.***
Suricata suricatta
Torolutra ougandensis
Vulpes chama
Vulpes pulcher

Peters et al. 2008). This sequence of events is clearly correlated with the time when hominins evolved new dietary strategies and began directly competing with carnivorans for prey (Lewis and Werdelin 2007). Increased competition from hominins, as well as increased seasonality may have led to times of acute food shortages that were unlikely to have been present earlier and may have affected the survival of specialist species.

The Early Pleistocene Carnivore Guild

Werdelin and Lewis (2005) examined carnivore species diversity through the African Plio-Pleistocene. Carnivore species richness in the last 4 Ma reaches a maximum between 3.9 and 3.6 Ma, with a further peak between 2.1 and 1.8 Ma. This corresponds to a high rate of originations and extinctions of taxa at 4.0–3.5 Ma and another peak of origination between 2.0–1.5 Ma. This latter peak was, however, outstripped by a higher rate of extinction that continues to the present day, resulting in the modern relatively depauperate carnivore assemblages. It is likely that a large proportion of these extinctions were the direct result of increasing competition from hominins.

Lewis (1997) examined the functional anatomy of extant and extinct fossil carnivorans to assess their impact on carcass availability for early meat eating hominins. Her analysis shows that Plio-Pleistocene carnivorans as a group engaged in a wider range of behaviors than their modern counterparts, largely due to the presence of sabertooth cats, which are hypothesized to have been providers of large carcasses for hominin scavenging (Blumenschine 1987; Marean 1989; Van Valkenburgh et al. 1990). The largest carcasses would have been provided by the sabertooth *Homotherium*, while *Dinofeli*s and *Megantereon* probably fed from carcasses of similar size to those killed by lions and leopards today (Lewis 1997).

The advent of culture placed hominins in a new feeding niche. Whereas previously human ancestors were carnivore prey (Brain 1981) they now had a way of accessing meat and became part of the carnivore guild. Cut-marked bones, and bones smashed to extract marrow attest to the adoption of meat eating strategies as early as 2.6 Ma (Semaw et al. 1997). The method of procurement of meat is not known, but it is likely that hominins initially scavenged carcasses left by other predators and only later improved their skills to become active hunters. Early butchery sites are not common but at Olduvai Gorge, an elephant skeleton in Bed 1 at FLK North and a *Deinotherium* skeleton just above the base of Bed II were both found with artifacts (Leakey 1971). Although it is not clear how the animals died, these occurrences show that, between 1.8 and 1.6 Ma hominids butchered the carcasses of large mammals. Early hominins would have directly competed with other large carnivores, especially hyaenas, for their meat and marrow. Subsequent carnivoran extinction events between 2 and 1 million years ago would have had a substantial effect on carcass availability for hominins. But it may have been the hunting skills perfected by the hominins that precipitated these extinctions. Certainly, as hominins became proficient hunters, they would have increasingly occupied the niches of the large predators, particularly *Homotherium*. This is reflected in the elevated extinction rate of carnivores in eastern Africa 2–1.5 Ma (Lewis and Werdelin 2007).

It should not be forgotten that hominins, like apes, are not exclusively carnivorous and a wide variety of edible plant resources would have offered a rich source of alternative foods. Because no evidence of plant remains is preserved in archeological sites, it is not possible to assess the importance of plant foods to these early hominins, and indeed this aspect of their diet is often ignored. However, plant resources would certainly have added to their dietary flexibility and ability to move widely through diverse habitats. The combination of access to high calorie meat and marrow together with the ability to utilize plant resources when meat became scarce would have made these early hominins opportunistic flexible feeders with a wide range of dietary options, including many large herbivorous mammals.

Early Pleistocene Herbivores: Proboscideans, Perissodactyls and Artiodactyls

As with the large bodied carnivores, the large bodied herbivores were more diverse in the eastern African Pliocene and Pleistocene than today, even when the faunal assemblages from a wide range of modern habitats are combined. In the Early Pleistocene, the large herbivore species in a single geographic area in the Turkana basin included three proboscideans, three hippos, and three giraffids, where only one species of each of these taxa is known in the wider region of East Africa today; six suids and six equids where only two and three respectively are known today; and a great diversity of large bovids which included two species of *Pelorovis* and two of *Megalotragus*, all now extinct (Table 1.3) (Harris 1983, 1991; Harris et al. 1988; Bobe et al. 2007).

The composition of the herbivore assemblages varied through time reflecting increased climatic variability and seasonality as the environments became more open and more arid through the Late Pliocene and Early Pleistocene. Between 2.3 and 2.1 Ma, bovid abundance and diversity increased in the Shungura Formation, lower Omo Valley, in the Turkana Basin (Bobe and Eck 2001); this was apparently related to greater environmental heterogeneity at the initiation of glacial cycles in the north and to a drier climate in the tropics of Africa. An analysis that included all the major

Table 1.3 The Bovidae faunal assemblage from the Omo Group deposits, Turkana Basin, Kenya, including the Upper Burgi and KBS Members of the Koobi Fora Formation, the Kalachoro and Kaitio Members of the Nachukui Formation and Member G unit 24 through to Member J of the Shungura Formation (from Bobe et al. 2007). The dominant species (represented by 50 or more specimens) are in bold

Aepyceros shungurae-melampus
Beatragus antiquus
Connochaetes gentryi
Damaliscus (Parmularius) eppsi
Megalotragus isaaci
Parmularius altidens
Antidorcas recki
Gazella cf. *granti*
Gazella janenschi
Gazella praethomsoni
Pelorovis oldowayensis
Pelorovis turkanensis
Syncerus acoelotus
Cephalophus sp.
Hippotragus gigas
Oryx sp.
Madoqua sp.
Raphicerus sp.
Kobus ancystrocera
Kobus ellipsiprymnus
Kobus kob
Kobus aff. *leche*
Kobus sigmoidalis
Menelikia lyrocera
Tragelaphus gaudryi
Tragelaphus nakuae
Tragelaphus strepsiceros

Table 1.4 Species identified in archeological sites in the KBS and Okote Members of the Koobi Fora Formation, East Turkana (From Bunn 1997)

Rodentia	*Thryonomys* sp.
	Hystrix sp.
	Rodentia indet.
Primates	*Papio* sp
	Cercopithecus sp.
	Theropithecus oswaldi
	Colobus sp.
	Cercocebus sp.
	Australopithecus boisei
	Homo sp.
Carnivora	*Viverridae* indet.
	Felidae indet.
	Canis mesomelas
Proboscidea	*Elephas recki*
Equidae	*Equus tabeti*
	Hipparion aethiopicus
Rhinocerotidae	*Ceratotherium simum*
	Diceros bicornis
Hippopotamidae	*Hexaprotodon karumensis*
	Hippopotamus gorgops
Suidae	*Metridiochoerus andrewsi*
	Kolpochoerus limnetes
Giraffidae	*Giraffa jumae*
Bovidae	*Aepyceros* sp.
	Antidorcus recki
	Gazella granti
	Kobus ellipsyprymnus
	Megalotragus isaaci
	Parmularius altidens
	Pelorovis sp.
	Sivatherium maurusium
	Tragelaphus strepsiceros
Pisces	*Polypterus*
	Clarius sp.
	Cichlidae indet.
Chelonia	*Trionyx* sp.
	Chelonia indet.
Squamata	Squamata indet.
Aves	Aves indet.
Crocodylidae	*Euthecodon* sp.
	Crocodylidae indet.

families of large to medium sized mammals collected from the Shungura Formation (Bobe et al. 2007) shows changes in dominance of three of the most common families, the Suidae, Cercopithecidae and Bovidae and increased faunal variability after 2.5 Ma, with the relative numbers of species favoring closed woodland and forested environments higher at some intervals and those associated with open grassland environments dominating at others. These short term fluctuations are superimposed on a long term trend from more forested to more open arid woodland and bushland environments.

Analyses of a more comprehensive data set from the Omo-Turkana Basin, that includes the Shungura, Nachukui and Koobi Fora Formations indicates three peaks of bovid diversity in the time interval between 4 and 2 Ma that occurred at about 3.8–3.4 Ma, 2.8–2.4 Ma and 2.0–1.4 Ma (Bobe et al. 2007). The last two peaks correspond to previously identified periods of high faunal turnover in the Turkana Basin at 2.4–2.2 and 2.0–1.8 Ma (Bobe and Behrensmeyer 2002, 2004), and the last peak was also a time of diversification of grazing bovids inhabiting the expanding grasslands which included the species *Pelorovis oldowayensis, Megalotragus isaaci* and *Beatragus antiquus* (Bobe and Behrensmeyer 2004). Three tribes (Alcelaphini, Antilopini and Hippotragini) that are strongly indicative of open seasonally arid grasslands and bushlands increase in relative abundance during this time. These patterns in faunal distribution and abundance are consistent with the known record of climate change derived from marine sediments (deMenocal 1995; deMenocal and Bloemendal 1995; Dupont and Leroy 1995; Denton 1999).

It appears that at the time that early *Homo* was adapting to an increasingly carnivorous life style, the bovid assemblages were diverse, rich in open country bushland species and variable in species composition reflecting the climatic variability that increasingly came to dominate the opening bushlands and grasslands. The diverse assemblage of large herbivores thus provided a plentiful and diverse potential meat resource for early hominins which they appear to have fully utilized. Vertebrate taxa identified from archeological sites in the KBS and Okote Members at East Turkana (Bunn 1997), some showing cut marks, are listed in Table 1.4. Similarly an extraordinary diversity of vertebrate taxa ranging in size from micromammals and frogs to elephants, rhinos and hippos has been recovered from the many Bed 1 and Lower Bed II sites at Olduvai; these too were utilized by early hominins (see Appendix B by Margaret Leakey in Leakey 1971).

These faunal assemblages excavated from living floors show diversity in both the taxa and the body size of the animals represented. Furthermore, the composition and diversity of the taxa represented as well as the body parts preserved (with a high representation of limb bone elements), indicate that these sites are unlikely to be kill sites but rather that the hominins were transporting selected meaty parts of carcasses to central locations and there systematically processing these parts for marrow and meat. Cut marks have been found on bones ranging in size from small gazelles to large hippos, giraffes and even elephants, and the disposition of the cut marks indicates systematic butchery procedures for carcass skinning, joint disarticulation and meat removal as well as extensive breakage for marrow (Bunn 1997).

Conclusions

The almost simultaneous appearance of *Homo erectus* in geographically widespread sites, including Dmanisi in Georgia (Rightmire and Lordkipanidze 2010) and Perning (Mojokerto) in Java (Antón 2003), at approximately the same time that this species is first recognized in Africa, raises many questions. Evidence from Pliocene and Pleistocene faunal assemblages from eastern and southern Africa provide a background to this event. In this paper we have looked at African anthropoid, carnivoran and herbivore fossil faunal assemblages in order to explore possible influences that may have led to the initial dispersal of hominins out of Africa ~1.8 Ma ago.

Prior to the appearance of stone tools 2.6 Ma ago, hominins were subject to constraints on their dispersal and distribution that are common to all higher primates and relate to life history parameters and dietary selectivity; hominins were an integral component of primate faunal assemblages and were as widely dispersed as the most widespread cercopithecids. The most successful cercopithecids in the long term were those that could adapt to the increasingly dry open conditions and flexibility in dietary choice seems to have been the key adaptation that led to the success of early *Homo* at this time. The ability to combine plant and meat resources gave the Early Pleistocene hominins considerable dietary flexibility and the potential to exploit a wide variety of food sources in seasonal habitats. With this dietary shift, the constraints on the distribution of pre-meat eating hominins were largely removed and hominins were no longer confined to relatively tropical and subtropical habitats.

With the advent of culture, and this shift to meat eating, hominins came into direct competition with a diversity of large carnivores that shared their habitats. The carnivore guild, of which they became part, was more diverse than that in eastern Africa today and would have provided early hominins with many opportunities for scavenging meat from carcasses. The large herbivores show a corresponding high taxonomic diversity particularly among the largest taxa. Although it is not known whether hominins hunted their own prey or scavenged meat from carnivore kills, evidence from archeological sites at East Turkana and Olduvai dated between 1.8 and 1.5 Ma show that hominins were taking meat from herbivores of all body sizes, from small gazelles and rodents to rhinos, elephants and giraffe, and were transporting selected meaty parts of carcasses found elsewhere to central areas for consumption (Table 1.4).

To fully understand the relative significance of the factors discussed above, it is essential to assess whether the dispersal of *Homo erectus* out of Africa 1.8 million years ago was part of a major migration affecting many species, was restricted to very few species with similar life history and diets, or was unique to *H. erectus*. In order to attain a full understanding of this question, a number of aspects have to be approached in detail. The Plio-Pleistocene fauna of Africa, especially eastern Africa, which is the probable source area for *H. erectus* must be fully investigated so that possible migrants can be identified. The Plio-Pleistocene fauna of Eurasia must be similarly studied. This will allow possible African immigrants to be detected, as well as possible ancestors of such immigrants, should allopatric speciation have occurred rapidly. The pattern of migrations throughout the Plio-Pleistocene or even further back should be investigated, to determine whether there are any features unique to the 2.0–1.5 Ma time interval when *H. erectus* reached Eurasia. Finally, the ecological characteristics of the identified migrants must be understood, so that the causes of migration of each species can (ideally) be determined and compared with those inferred for *H. erectus*, to show whether possible coincident migrations were due to similar factors or were entirely fortuitous. At present, our assessment based on fossil carnivore and cercopithecid assemblages suggests that there were few if any migration events out of Africa contemporaneous with that of *H. erectus* and that those that may have occurred (*Megantereon, Hippopotamus, Theropithecus*; Rook et al. 2004, Martínez-Navarro 2004) could have been due to factors distinct from those that led to the dispersal of *H. erectus*.

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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, *Crocuta* 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 *Crocuta* • *Megantereon* • *Pachycrocuta* • 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.

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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 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.

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

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

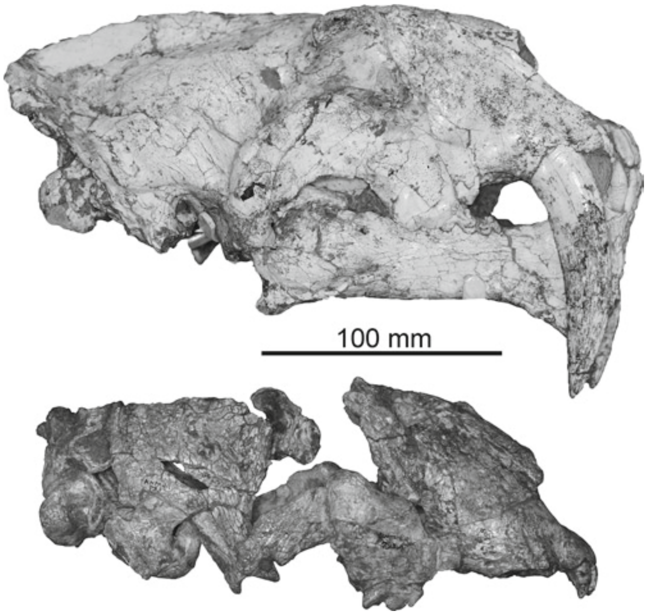

Fig. 2.1 Skulls of *Megantereon*. *Top*: *M. nihowanensis*, unnumbered skull, Hezheng Museum, Gansu, China from the Longdan Basin, Gansu. *Bottom*: *M. whitei*, KNM-ER 793A, Okote Mb., Koobi Fora Fm., Turkana Basin, Kenya. Note that despite the significantly smaller teeth of the latter specimen, the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

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. ekidoit*)?
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., Ficcarelli 1979; Sardella 1998; Palmqvist et al. 2007). Ficcarelli (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 Ficcarelli 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*. Ficcarelli 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 Ficcarelli 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 assignation 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 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.

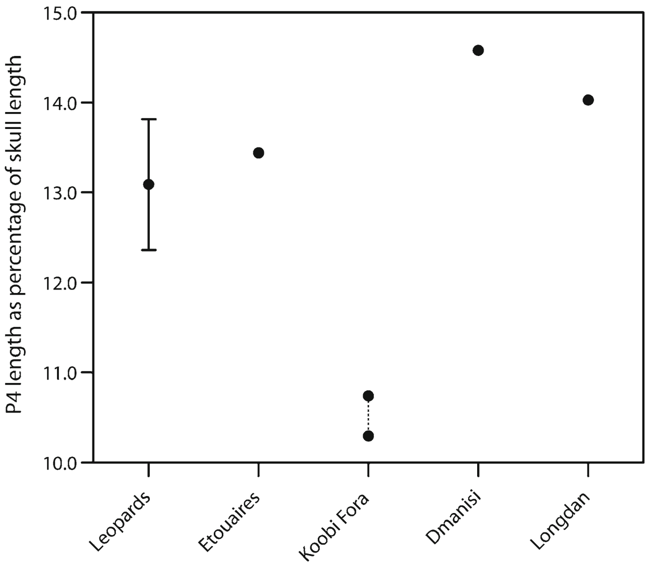

Fig. 2.2 Length of upper carnassial (P4) as a percentage of skull condylobasal length (CBL) for a sample of extant leopards, *Panthera pardus*, from Africa and Asia (left, $N = 15$, with 99.9% confidence interval) and some specimens of *Megantereon* species. P4 measurements are from Palmqvist et al. 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

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^3 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^4 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 deuterocone 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 craniodental characteristics said to distinguish the two. He then resurrected the name *Megantereon megantereon* 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 *Megantereon* (valid and invalid)		
Europe	Asia	Africa
M. cultridens	*M. falconeri*	*M. ekidoit*
M. c. adroveri	*M. inexpectatus*	*M. eurynodon*
M. megantereon	*M. lantianensis*	*M. gracile*
	M. nihowanensis	*M. whitei*
Ficcarelli 1979		
M. cultridens	*M. cultridens*	No comment
Turner 1987		
M. cultridens	*M. cultridens*	*M. cultridens*
Martínez-Navarro and Palmqvist 1995		
M. cultridens (early form)	*M. falconeri*	*M. whitei*
M. whitei (late form)		
Sardella 1998		
M. ex gr. cultridens	*M. ex gr. cultridens*	*M. ex gr. cultridens*
(*M. cultridens* primitive form)	(*M. falconeri*)	(*M. whitei*)
M. ex gr. cultridens		
(*M. cultridens* typical form)		
M. ex gr. cultridens		
(*M. cultridens* advanced form)		
Liu 2005		
M. megantereon (St. Vallier)	*M. cf. megantereon*[a]	*M. whitei*
M. cultridens (Senèze)		Did not include later form
Did not include later form		
Palmqvist et al. 2007		
M. cultridens (early form)	*M. cultridens* (widespread)	*M. whitei*
M. whitei (late form)	*M. whitei* (limited)	
Current Paper (after Werdelin and Lewis 2000, 2002)		
M. cultridens (early form)	One or more taxa[b]	*M. ekidoit* (early form)
M. adroveri (late form; new rank)		*M. whitei* (late form)

[a] 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.

[b] 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.

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 Turkwell, 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

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*.

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

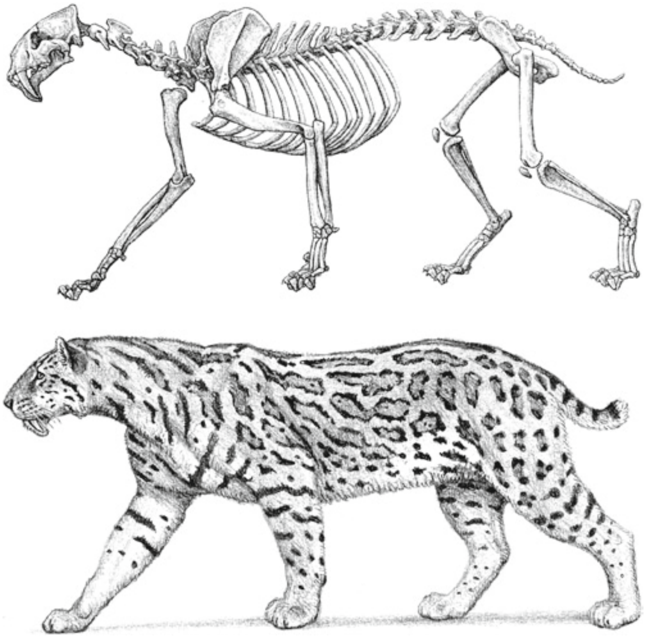

Fig. 2.4 Skeletal and life reconstructions of *Megantereon*, showing the long, low body, robust and heavily muscled forequarters, and short tail. Illustration by Mauricio Antón. Reprinted with permission from the artist

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. petteri* 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