J. Paleont., 76(5), 2002, pp. 928–930

0022-3360/02/0076-928$03.00

ON THE PRESENCE OF *MEGANTEREON WHITEI* AT THE SOUTH TURKWEL HOMINID SITE, NORTHERN KENYA

PAUL PALMQVIST
Departamento de Geología y Ecología (Área de Paleontología), Facultad de Ciencias, Universidad de Málaga. 29071 Málaga, Spain, <Paul.Palmqvist@uma.es>

INTRODUCTION

WERDELIN AND LEWIS (2000) recently described a new species of the saber-tooth genus *Megantereon* (Mammalia, Carnivora, Felidae) from Late Pliocene (∼3.5 Ma) deposits of the Nachukui Formation south of the Turkwel River in Turkana, northern Kenya (Ward et al., 1999). The new species, *Megantereon ekidoit*, is said to represent the earliest occurrence of this genus in Africa. It was described from a right mandibular ramus (KNM-St 23812) with i3–m1. As discussed below, the post-canine diastema is longer than the cheek-tooth row, since there does not appear to have been a third premolar (p3), and the coronoid process is relatively well developed, showing a hook-shaped morphology (Werdelin and Lewis, 2000: Fig. 1). The fourth premolar (p4) and the lower carnassial tooth (m1) show considerable wear.

Two major reviews on the origin, evolution and dispersal of *Megantereon* have been published by Turner (1987) and by Martínez-Navarro and Palmqvist (1995), respectively; surprisingly, neither of these articles were cited by Werdelin and Lewis (2000).

The saber-tooth genus *Megantereon* shares much in common with *Smilodon*, and both genera form the tribe Smilodontini. The earliest presence of *Megantereon* is recorded at 4.5 Ma in the Bone Valley Formation (Florida), where it is represented by *Megantereon cultridens*. This species dispersed from North America before 3.5 Ma, to extend all over the Old World. Europe was also home to *M. cultridens* until the lower Pleistocene, and in China it lingered well into the middle Pleistocene (e.g., at Choukoutien Locality I).

In a comprehensive review of the systematics of *Megantereon* in the New and Old World, Turner (1987) considered *M. cultridens* to be the only valid species for this genus; however, his analysis was based on the morphology and dimensions of the lower carnassial, the tooth that shows least interpopulational variability and greatest conservatism in the evolution of the genus. The comparative study by Martínez-Navarro and Palmqvist (1995) of *Megantereon* remains followed a multivariate approach using both principal component and discriminant analyses of tooth measurements. The results of the their study showed that *M. cultridens* gave rise in Africa to a new species, *Megantereon whitei*, characterized by a reduction in the size of both the maxillary carnassial (P4) and the mandibular premolars, particularly p3; the extreme reduction of the latter tooth is reflected in the appearance of a diastema between p3 and p4. *M. whitei* survived in Africa until 1.5 Ma (Turner, 1990), and is recorded at South Africa (Sterkfontein, Elandsfontein, Schurveburg, Kromdraai, Swartkrans) and East Africa (Omo, East Turkana, Koobi Fora) (Martínez-Navarro and Palmqvist, 1995). The time range of *M. whitei* in Africa comprises from ∼3 Ma (Sterkfontein Member 2) to ∼1 Ma (Swartkrans Member 3) (Martínez-Navarro and Palmqvist, 1995).

Megantereon whitei dispersed to Eurasia at the Plio-Pleistocene boundary, as recorded at Orce (Guadix-Baza Basin, Spain), Apollonia (Mygdonia Basin, Greece) and Dmanisi (East Georgia, Caucasus) (Martínez-Navarro and Palmqvist, 1995, 1996). The arrival of this machairodont in Eurasia may well have played a significant role in facilitating the dispersal out of Africa of the giant, short-faced hyena *Pachycrocuta* and the first representatives of the genus *Homo*, since *Megantereon* seems to have been an ambush-predator with great killing capability in relation to its nutritional requirements (Arribas and Palmqvist, 1999). Presumably it left relatively large amounts of flesh and all nutrients within bones in the carcasses of its ungulate prey; such resources could be subsequently scavenged by both hyenas and hominids (Palmqvist et al., 1996; Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001).

The goal of this article is to show that mandibular ramus KNM-St 23812, attributed by Werdelin and Lewis (2000) to *M. ekidoit*, is not a new species of *Megantereon*, and that this specimen can be confidently assigned to *M. whitei*.

DISCUSSION

Figure 1.1 shows the mesiodistal length of p4 and m1 in *Megantereon* specimens from the New and Old World (data from Turner, 1987; Martínez-Navarro and Palmqvist, 1995, 1996). The length of these teeth in the holotype of *M. ekidoit* (Lp4 = 14.5 mm, Lm1 = 17.1 mm; data from Werdelin and Lewis, 2000) place it very close to several specimens of *M. whitei*, such as TM-856 (Schurveburg, South Africa), ER-793 (East Turkana), VM-2264 (Venta Micena, Spain), and APL-12 (Apollonia, Greece). Figure 1.2 plots length against width for p4 in *Megantereon;* a clear-cut morphospatial discontinuity is seen between *M. whitei* and *M. cultridens*. The corresponding measurements for this tooth in the South Turkwel specimen (Wp4 = 6.3 mm; data from Werdelin and Lewis, 2000) are similar to those of African *M. whitei*, which show a lower Lp4/Wp4 ratio than Eurasian and North American *M. cultridens*.

Martínez-Navarro and Palmqvist (1995, 1996) presented linear discriminant functions between *M. cultridens* and *M. whitei*, using as variables the length and width of the fourth premolar, and the length of the lower carnassial. The function that combines the length of p4 and m1 ($\phi = 2.568 \times Lp4 - 0.385 \times Lm1$) yields a value for the South Turkwel specimen (30.7) that clearly places it within the group formed by the African forms, very close to the bivariate mean of *M. whitei* populations (group centroid for *M. whitei* = 30.9, range of values = 26.7–36.1; group centroid for *M. cultridens* = 41.9, range = 37.7–48.4; limit between groups = 36.4), underlining its affinity with them. Similarly, the discriminant function for the dimensions of the fourth premolar ($\phi = 3.943 \times Lp4 - 3.226 \times Wp4$) gives a value for South Turkwel (36.9) which is within the confidence interval around the bivariate mean of *M. whitei* (centroid = 33.1, range = 30.1–37.5)

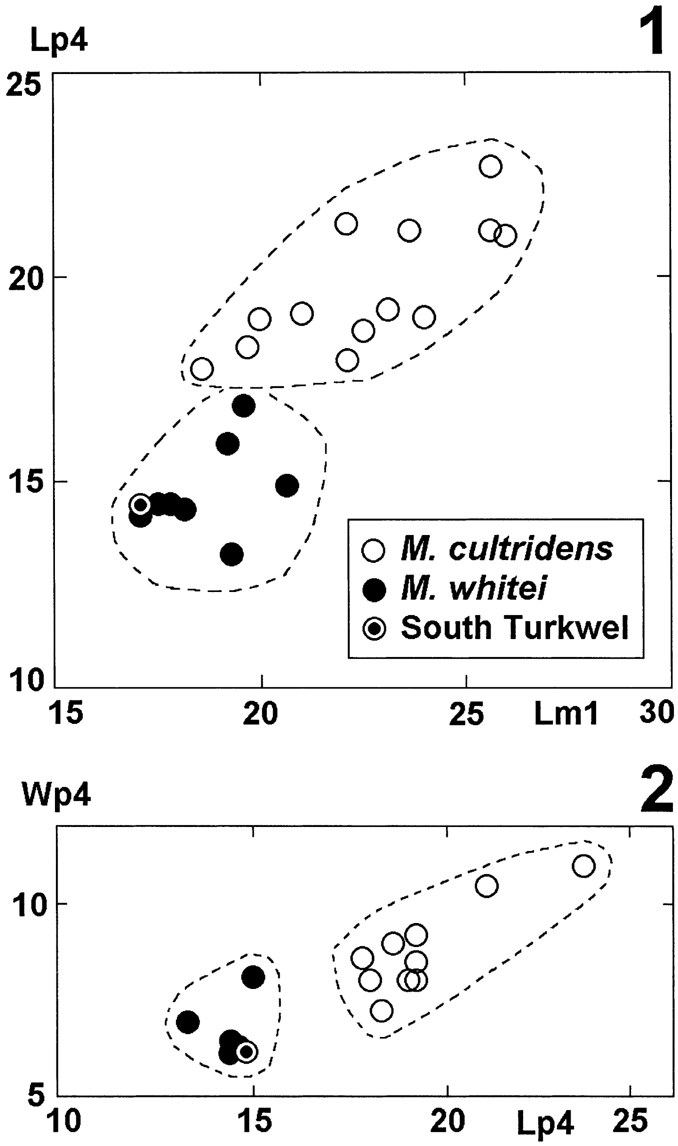

FIGURE *1*—Scatter-plot of *1,* lower carnassial length (Lm1) and lower fourth premolar length (Lp4), and *2,* lower fourth premolar length and width (Wp4) for specimens of *Megantereon* (Eurasian and North American *M. cultridens,* African *M. whitei*; data from Turner, 1987; Martínez-Navarro and Palmqvist, 1995, 1996). The corresponding measurements for mandible KNM-St 23812, the holotype of *M. ekidoit,* are also shown (data from Werdelin and Lewis, 2000).

and distant from the corresponding value for *M. cultridens* (centroid = 48.0, range = 42.4–57.2; limit = 40.6). These results suggest clearly that the mandibular ramus KNM-St 23812 belonged to *M. whitei*.

In addition, anatomical characteristics of the South Turkwel fossil corroborate this statistically-based conclusion. Although complete mandibles of *Megantereon* are rare, the mandibular ramii of *M. whitei* preserved at Dmanisi and East Turkana (Martínez-Navarro and Palmqvist, 1995: Fig. 6) show a remarkable similarity with the South Turkwel specimen. These features include, among others cited by Werdelin and Lewis (2000), the following: 1) a nearly vertical symphyseal region, as a consequence of the reduction in size of the lower premolar teeth, that forms a large anteroventral mandibular flange; 2) a lower canine small, slender and nearly incisiform in shape; 3) a single mental foramen beneath the anterior part of the postcanine diastema, approximately level with the ventral border of the main body of the ramus; 4) a shallow and long masseteric fossa, developed well anterior to the posterior end of m1, with a quite small masseteric foramen; 5) a mandibular condyle set well below the level of the cheek tooth row; 6) a postcanine diastema that angles downwards from the incisors to the cheek tooth row; and 7) a coronoid process curving backwards in a hook shape, which is particularly evident in the case of the Dmanisi mandible.

Werdelin and Lewis (2000) consider that the absence of p3 precludes the South Turkwel specimen of belonging to African *M. whitei,* in which this tooth is greatly reduced in size relative to Eurasian and North American *M. cultridens* (Martínez-Navarro and Palmqvist, 1995), although they also open the possibility that the absence of p3 could represent an individual variant in the trend for an extreme reduction of this tooth; in such a case, Werdelin and Lewis (2000) consider that the reduction of p3 would be a synapomorphy uniting *M. ekidoit* with *M. whitei*. Alternatively, the absence of p3 could be due to the loss of this tooth during the life of the animal (which reached a relatively advanced age given the considerable degree of wearing in both p4 and m1), and the subsequent obliteration of the alveolus by bony overgrowth; this situation is found in some specimens of *M. whitei* such as mandibular ramus VM-2264 from Venta Micena (Martínez-Navarro and Palmqvist, 1995, fig. 8), in which p3 is absent and the dental alveolus shows moderate resorption.

There has been a general trend during the last decades for oversplitting in the systematics of large carnivores, particularly in the case of *Megantereon* and other machairodonts, in part due to the poor and biased nature of their fossil record, their rarity in the assemblages of large mammals derived of the extremely low population densities as top predators in the paleocommunities; as a result, many new species have been described from fragmentary specimens and isolated teeth, which in some instances were heavily worn. This is so for *M. eurynodon*, *M. falconeri*, *M. gracile, M. hesperus*, *M. inexpectatus*, *M. megantereon*, *M. nihowanensis,* and *M. sivalensis*, among others (see review in Martínez-Navarro and Palmqvist, 1995). However, the comparative analysis of metric measurements for lower and upper cheek teeth made by Martínez-Navarro and Palmqvist (1995) showed only two valid species for this genus, *M. cultridens* and *M. whitei*. The dimensions of the lower fourth premolar and lower carnassial tooth as well as the morphology of the mandibular ramus of the specimen from South Turkwel unequivocally identify it as an earlier representative of *M. whitei*. Thus, these results indicate that *M. ekidoit*, the new species proposed by Werdelin and Lewis (2000) for the South Turkwel finding, is not a valid species and must be synonimized with *M. whitei*; given the age of deposits at this locality (~3.5 Ma), this specimen represents the earliest occurrence of *M. whitei* in Africa.

ACKNOWLEDGMENTS

I thank J. M. González-Donoso and two anonymous reviewers for their insightful comments and helpful criticism of the manuscript.

REFERENCES

ARRIBAS, A., AND P. PALMQVIST. 1998. Taphonomy and palaeoecology of an assemblage of large mammals: hyaenid activity in the lower Pleistocene site at Venta Micena (Orce, Guadix-Baza Basin, Granada, Spain). Geobios, 31(suppl.):3–47.

ARRIBAS, A., AND P. PALMQVIST. 1999. On the ecological connection between sabre-tooths and hominids: faunal 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.

Martínez-Navarro, B., and P. Palmqvist. 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., and P. Palmqvist. 1996. Presence of the African saber-toothed felid *Megantereon whitei* (Broom, 1937) (Mammalia, Carnivora, Machairodontidae) in Apollonia-1 (Mygdonia Basin, Macedonia, Greece). Journal of Archaeological Science, 23:869–872.

Palmqvist, P., and A. Arribas. 2001. Taphonomic decoding of the paleobiological information locked in a lower Pleistocene assemblage of large mammals. Paleobiology, 27:512–530.

Palmqvist, P., B. Martínez-Navarro, and A. Arribas. 1996. Prey selection by terrestrial carnivores in a lower Pleistocene paleocommunity. Paleobiology, 22:514–534.

Turner, A. 1987. *Megantereon cultridens* (Cuvier) (Mammalia. Felidae, Machairodontinae) from Plio-Pleistocene deposits in Africa and Eurasia, with comments on dispersal and the possibility of a New World origin. Journal of Paleontology, 61:1256–1268.

Turner, A. 1990. The evolution of the guild of larger terrestrial carnivores in the Plio-Pleistocene of Africa. Geobios, 23:349–368.

Ward, C. V., M. G. Leakey, B. Brown, F. Brown, J. Harris, and A. Walker. 1999. South Turkwel: a new Pliocene hominid site in Kenya. Journal of Human Evolution, 36:69–95.

Werdelin, L., and M. E. Lewis. 2000. Carnivora from the South Turkwell hominid site, Northern Kenya. Journal of Paleontology, 74:1173–1180.

Accepted 2 October 2001