Presence of the African Saber-toothed Felid *Megantereon whitei* (Broom, 1937) (Mammalia, Carnivora, Machairodontinae) in Apollonia-1 (Mygdonia Basin, Macedonia, Greece)

Bienvenido Martínez-Navarro

Museo de Prehistoria y Paleontología 'J. Gibert' & Casa de Oficios "Palacio de los Segura II", 18858-Orce, Granada, Spain

Paul Palmqvist

Departamento de Geología y Ecología, Área de Paleontología, Facultad de Ciencias, Universidad de Málaga, Facultad de Ciencas, 29071-Malaga, Spain

We have made a multivariate morphometric study of the fossils of *Megantereon* from the Apollonia-1 site at the Mygdonia Basin (Macedonia, Greece), using discriminant functions. Results obtained indicate that these specimens belong to the African species *Megantereon whitei* Broom, which is also found in the Lower Pleistocene of Dmanisi (East Georgia, Caucasus) and Orce (Southern Spain). Morphofunctional studies of *M. whitei* suggest that this saber-toothed felid was an ambush predator with great killing capability in relation to its food requirements, thus leaving enough meat to be scavenged by both hyaenas and hominids. *M. whitei* may have played an important ecological role making the first dispersal of *Homo* to Eurasia the Lower Pleistocene possible.

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In a recently published article, Martínez-Navarro and Palmqvist (1995) studied the specimens of *Megantereon* from the Lower Pleistocene site of Venta Micena (Orce, Granada, Southeastern Spain) and compared them with African, Eurasian and North American samples, by using standard methods of multivariate morphometrics—namely, principal components and discriminant analysis on dental measurements. The results obtained clearly indicated the existence of three distinct lineages *of Megantereon:* (1) *M. cultridens* (Cuvier), indigenous to North America from the Lower Pliocene onwards, which colonized Eurasia and survived until the Middle Pleistocene in China; (2) *M. falconeri* Pomel, originating from *M. cultridens* in the Indian subcontinent during the Upper Pliocene; and (3) *M. whitei* Broom, descendant of *M. cultridens* in Africa, which colonized Europe as far north as the 40th parallel at the Plio-Pleistocene boundary, reaching Dmanisi (East Georgia) via the Near East and the southern part of the Iberian Peninsula, probably across the Straits of Gibraltar.

A previous study of the systematics and dispersal of *Megantereon* by Turner (1987) considered *M. cultridens* as the only valid species for this genus, although this analysis was highly biased, because (a) it was based only in the lower carnassial (M_1), the tooth which shows the greatest conservatism and least size variability in the evolution of *Megantereon*, and (b) the Venta Micena and Dmanisi specimens were not included in the study.

Koufos (1992) found *Megantereon* in Apollonia-1 at the Mygdonia Basin (Macedonia, Greece) (Figure 1), which he named as *M. cultridens*, following the lumping and conservative taxonomy of the genus, although he finds these fossils similar to those from Venta Micena. The objective of this note is to use the discriminant functions developed by Martínez-Navarro and Palmqvist (1995) to investigate whether these specimens belonged to the Eurasian or African species. The fossils include an upper left C^1 (*APL-13*) (L=24·6 mm, W=11·3 mm), and a right mandibular ramus (*APL-12*) with I_1 (L=4·7, W=2·5), I_2 (L=5·5, W=3·7), I_3 (L=6·4, W=5·2), C_1 (L=8·5, W=5·1), P_3 (L=5·6, W=3·4), P_4 (L=14·4, W=6·0) and M_1 (L=18·1, W=8·5).

The value obtained (37·4) for the *APL-12* specimen in the discriminant function between *M. cultridens* and

(a)

Discriminant function:
$\Phi = 2.568\text{LP}/4 - 0.385\text{M}/1$
$D^2 = 11.07$
$F_{2.15} = 18.74 \; (P < 0.001)$

Nihowan

Saint Vallier

Val d'Arno

Megantereon cultridens

Megantereon whitei

☆ Venta Micena
◆ Dmanisi
■ Apollonia
● Africa
○ Europe
△ China
◇ Siwaliks
□ North America

Elandsfontein

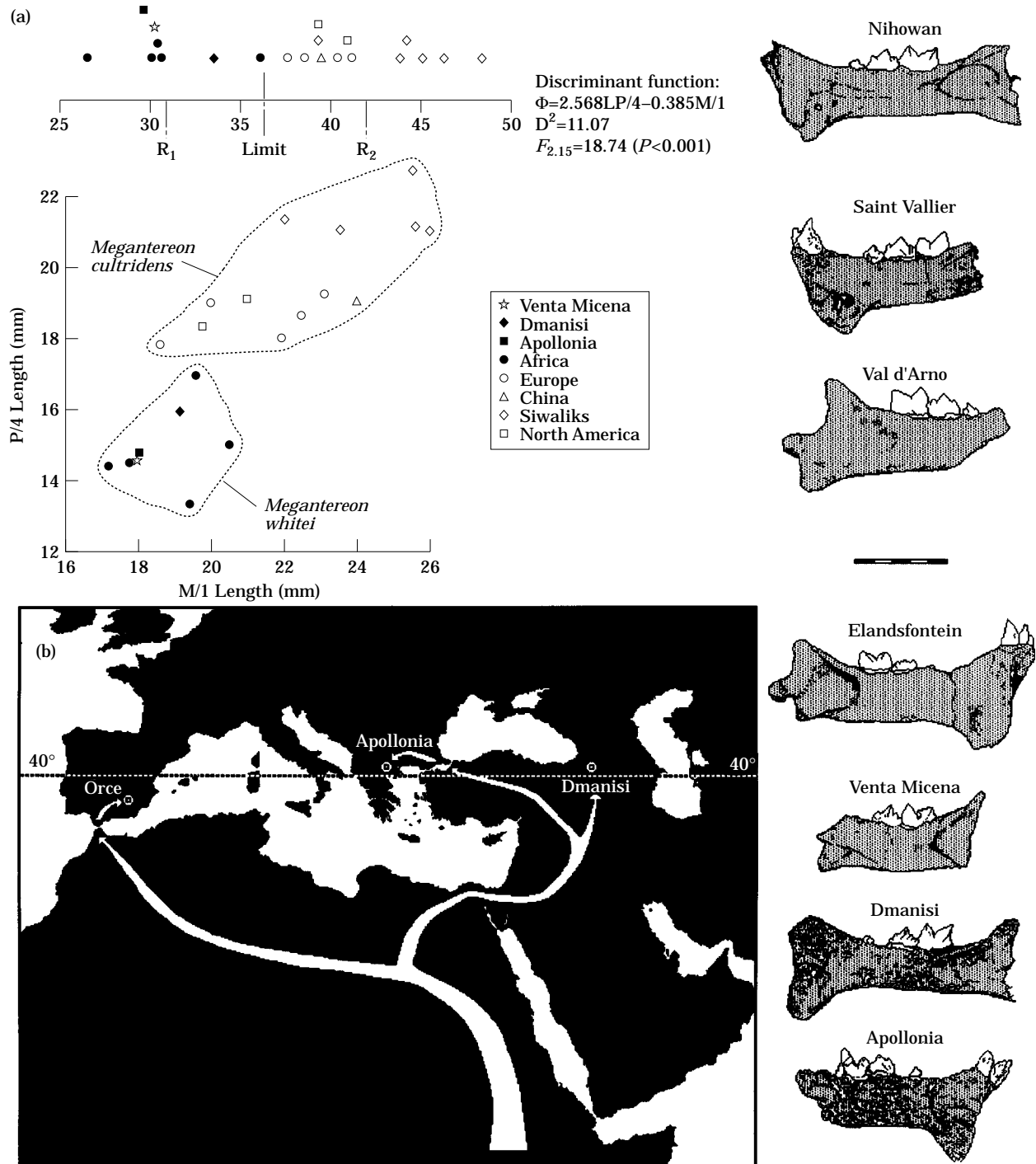Venta Micena

Dmanisi

Apollonia

(b)

Figure 1. (a) Bivariate plot of M_1 length and P_4 length and linear discriminant analysis between African machairodont *Megantereon whitei* BROOM and North American and Eurasian *Megantereon cultridens* CUVIER (redrawn from Martínez-Navarro & Palmqvist, 1995: figure 4). The values obtained for the Venta Micena, Dmanisi and Apollonia specimens in the discriminant function are also shown. (b) Dispersal of African *M. whitei* to Eurasia in the Plio-Pleistocene limit and geographic distribution of North Mediterranean Lower Pleistocene sites with presence of *M. whitei* (Apollonia, Greece; Venta Micena, Orce, Spain; Dmanisi, Georgia). The right mandibular ramus from Apollonia-1 (*APL-12*) was drawn from a photograph in Koufos (1992); the other specimens were redrawn after Martínez-Navarro and Palmqvist (1995; figure 6). Specimens of the genus *Homo* have been found in two localities (Venta Micena and Dmanisi).

M. whitei for P_4 dimensions ($\Phi = 3.943 \times \text{LP}_4 - 3.226 \times \text{WP}_4$) places it in the group formed by Venta Micena and the African forms (group centroid for *M. whitei* = 33·1; range = 30·2–36·1; group centroid for *M. cultridens* = 48·0; range 42·4–57·2; limit between groups = 40·6). When the discriminant function for both P_4 and M_1

lengths ($\Phi = 2 \cdot 568 \times \mathbf{LP_4} - 0 \cdot 385 \times \mathbf{LM_1}$) is applied, the value obtained ($30 \cdot 0$) places it very close to the bivariate mean of *M. whitei* populations (group centroid for *M. whitei* $= 30 \cdot 9$; range $= 26 \cdot 7 – 36 \cdot 1$; group centroid for *M. cultridens* $= 41 \cdot 9$; range $= 37 \cdot 7 – 48 \cdot 4$; limit between groups $= 36 \cdot 4$), underlining its affinity to them (Figure 1(a)). Anatomical characteristics of the fossils corroborate this morphometrically-based conclusion. It is interesting to note that the value obtained ($33 \cdot 7$) in the latter discriminant function for the Dmanisi specimen ($\mathrm{LP_4} = 16$ mm, $\mathrm{LM_1} = 19 \cdot 2$ mm; measurements kindly provided by Prof. Leo Gabunia) classifies it as *M. whitei*.

M. whitei was accompanied in Greece at the Plio-Pleistocene boundary by some species of ungulates probably originating in Asia—which were also present at Venta Micena—such as *Soergelia* sp., Caprinae indet. and *Megaloceros (Megaceroides)* sp. (Kostopoulos & Koufos, 1994). This assemblage marks a faunal break at the end of the Villafranchian, and is related to the first arrival of *Homo* to Europe, a migration indicated by the finding of (1) a human cranial fragment and a humeral diaphysis at Venta Micena (Gibert & Palmqvist, 1995; Gibert *et al.*, 1994), (2) lithic industries and stone manuports associated with the same fauna of Venta Micena at Fuente Nueva-3, Barranco del Paso and Barranco León (Orce) (Tixier *et al.*, 1995), (3) a human phalanx at the Lower Pleistocene karstic site of Cueva Victoria (Murcia, Southern Spain) (Gibert & Pérez-Pérez, 1989; Palmqvist *et al.*, 1996), and (4) a human mandible and lithic industries in the Lower Pleistocene of Dmanisi (Dzaparidze *et al.*, 1992; Gabunia & Vekua, 1995).

According to the data presented above, it could be possible to find *Homo* remains in the near future at Apollonia-1 or other localities of Lower Pleistocene age at the Mygdonia Basin, which—it should be borne in mind—is located in the Balkan Peninsula at a latitude similar to Venta Micena and Dmanisi, and near the Bosphorous Strait (Figure 1(b)).

Morphofunctional studies currently in progress of *M. whitei* suggest that the dimensions that can be calculated for this machairodont differ markedly depending on whether they are estimated from the teeth or from the postcranial skeleton (Palmqvist *et al.*, 1996). When body size is calculated with minimum squares regression analysis (Van Valkenburg, 1990) of lower carnassial tooth (M_1) length on body weight in modern species of felids, the value obtained is of approximately 55 kg. This suggests that this species was leopard-sized (Martínez-Navarro & Palmqvist, 1995). On the other hand, surface area of the diaphyseal cross section of the humerus in this species (523 mm^2) is approximately half that in the great scimitar cat *Homotherium latidens* (1052 mm^2), suggesting a weight of at least 100 kg for *M. whitei*. However, the width of the distal epiphysis of the humerus, which articulates with the radius, is greater in this species ($47 \cdot 5$ mm) than in a leopard ($38 \cdot 5$ mm; Walker, 1985) or even in the lion (46 mm), which suggests that the animal was larger than this latter species (around 200 kg). These three independent estimates differ widely, although the most reliable estimate is probably that obtained from the diaphysis of the humerus, given that the section of this long bone bears the weight of the forepart of the body. If we consider this estimate correct, we are then dealing with a predator of about 100 kg, whose killing capability (estimated from the width of the distal epiphysis of the humerus, which indicates the strength of *M. whitei* for immobilizing prey while it used its elongated canines to kill) was four-fold greater than would be suggested by its food requirements or the speed at which it could eat (deduced from its markedly reduced carnassials).

We therefore have a picture of a hypercarnivorous felid which would generate large amounts of carrion, since it would exploit the carcasses of its prey to a small degree, leaving enough meat for the hyaenas (which behaved in Venta Micena as strict scavengers; Palmqvist *et al.*, 1996), as well as for hominids. In the light of this likely situation, the recent discoveries of *Homo* both at Venta Micena and Dmanisi associated with African *M. whitei* (Martínez-Navarro & Palmqvist, 1995) are not surprising, since this latter species would have made the first dispersal of hominids to Eurasia in the Lower Pleistocene possible (Figure 1(b)).

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