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

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We have made a comparative analysis of dental morphometries of the *Megantereon* specimens found in the Lower Pleistocene site at Venta Micena (Orce, Granada, Southeastern Spain) with representatives of the genus throughout the Old and New World. The methodologies used in the study include discriminant functions and principal component analysis. The results obtained point to the presence of three distinct species of this genus: *M. cultridens* (Cuvier), indigenous to North America from the Lower Pliocene onwards, which in the Indian subcontinent gave rise to the larger sized species *M. falconeri* Pomel during the Upper Pliocene. *M. cultridens* survived until the Middle Pleistocene in China, and its African descendant *M. whitei* Broom colonized Europe at the time of the Plio-Pleistocene boundary, reaching Dmanisi via the Near East and southern part of the Iberian Peninsula at Venta Micena via the Strait of Gibraltar. © 1995 Academic Press Limited

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Introduction

The Venta Micena site lies in the northeastern sector of the Guadix-Baza basin in the southeast of the Iberian Peninsula (for information of the geology, sedimentology and stratigraphy of the basin, readers are referred to Vera *et al.*, 1985; Anadón *et al.*, 1987; Soria *et al.*, 1987 and Gibert *et al.*, 1992*a*). The Venta Micena site is dated to 1·65 my BP on both faunal and palaeomagnetic grounds (Martínez Navarro, 1991; Gibert *et al.*, 1992*a*; Gibert & Palmqvist, 1994; Gibert *et al.*, 1994). This article concentrates on aspects of the large carnivores.

The rich, fossil-bearing, horizontal layer, 0·75–0·80 m thick, can be followed for over 2·5 km in the low escarpment around the present dry valley at Venta Micena. Fundamentally, this layer is a soft calcrete. Beneath it, a well-cemented hardpan can also readily be followed around the scarp, and its slightly undulating surface points to former local ponding on it in an ephemeral lacustrine or swampy environment. Once the ponds had filled with micrite sediment, water rising through it carried calcium carbonate upwards to be deposited as a soft caliche-type calcrete around the vertebrate bones. The variable length of time which elapsed before their complete burial was attained no doubt explains the variable state of preservation of the bones (Gibert, Caporicci & Martínez Navarro, 1990; Gibert *et al.*, 1992*b*). Absence of preferential patterns in their spatial arrangement, as well as of any sedimentary structures, precludes attributing the accumulation to geological mechanisms; hence biological agents seem to be implicated, perhaps carnivores, rodents, or even hominids (Agustí *et al.*, 1985; Gibert & Caporicci, 1989; Gibert *et al.*, 1990; Gibert *et al.*, 1992*b*; Palmqvist, Gibert & Martínez Navarro, 1993).

Analysis of size/abundance ratios for bones of various ungulates identified at the site shows that there is virtually no taphonomic bias other than greater surface weathering on bones of small bodied species (Palmqvist, Gibert & Martínez Navarro, 1992). Comparison of the relative frequency of occurrence of

different types of bones found at the site (skulls, mandibles, vertebra, ribs, long bones, etc.), with that at known carnivore dens, open lairs, or human settlements (Palmqvist *et al.*, 1993), by a factor analysis of correspondences, indicates hyaenas as the main collecting agency of bones at Venta Micena (Mendoza *et al.*, 1993).

Systematic revision and quantitative analysis of the large mammals (Martínez Navarro, 1991; 1992*a-c*) shows the presence of a typical European Lower Pleistocene fauna, neither Villafranchian nor Middle Pleistocene in type, representing the merged evolutionary trajectories of three faunal assemblages with separate histories, namely:
(1) Authocthonous Villafranchian developments (*Mammuthus meridionalis, Dicerorhinus etruscus brachycephalus*, Homotherium latidens* and *Ursus etruscus*).
(2) Asiatic inmigrants (*Praeovibos* sp., *Bubalus* sp., *Soergelia minor, Capra alba*, Cervidae gen. et sp. indet. and *Praemegaceros solilhacus*); and
(3) African inmigrants (*Megantereon whitei, Pachycrocuta brevirostris, Canis falconeri, Hippopotamus amphibius antiquus* and *Homo* sp.).

The faunal break at the Plio-Pleistocene boundary marked by the appearance of *Canis etruscus* has been termed "The Wolf Event" (Azzaroli, 1983; Azzaroli *et al.*, 1988).

It should be mentioned here that, although the attribution of Venta Micena cranial fragment (VM-0) to *Homo* has been queried (Agustí & Moyà-Solà, 1987), support for it comes from several quarters—comparative anatomy (Gibert *et al.*, 1989; 1992*e*; Campillo, 1992), morphometric fractal analysis of sagittal and lambdoid sutural patterns (Gibert & Palmqvist, 1994) and paleoimmunological identification of human albumin using monoclonal antibody techniques (Borja *et al.*, 1992; as well as by Professor Jerold Lowenstein, unpubl. data). Apart from VM-0, two further hominid fossils—namely, a complete humeral shaft (VM-1960) and part of another (VM-3691)—have been published from Venta Micena together with humeral fragments found in another hyaena den 150 km to the east in Lower Pleistocene bone breccia at the karstic site of Cueva Victoria (Cartagena, Spain) (Gibert & Martínez Navarro, 1992; Gibert *et al.*, 1992*e*; Gibert *et al.*, in press), where a human middle phalangeal bone was also found (Gibert & Pérez-Pérez, 1989). Furthermore, at Venta Micena, as well as at other sites at Orce, evidence of Lower Pleistocene human activity is provided not only by stone manuports and flaking (Gibert *et al.*, 1992*d*), but also by patterns of anthropic breakage of long bones (Gibert *et al.*, 1992*c*), and cut-marks on them (Gibert & Jiménez, 1991).

Paleoecological and paleoethological studies have been published (Martínez Navarro, 1992*c*; Mendoza *et al.*, 1993). Both cenogrames and multivariate statistical comparison of the taxonomic composition of the fossil community with that found nowadays in the different African biomes, indicate an association of large mammals typical of a dry biotope, such as savanna with spiny trees and tall grass. Analyses of both equine dental-wear patterns and ungulate infant/adult ratios, point clearly to prey selection by predators for young and elderly individuals, especially of larger body-size species.

It is particularly important to review the systematics of the genus *Megantereon* in order to determine which species was present at Venta Micena. To this end, morphological and metrical comparisons are offered with representatives of that genus from Europe, Asia, Africa and North America, using principal component and discriminant function analyses (cf. Reyment, Blackith & Campbell, 1984; Davis, 1986; Reyment & Jöreskog, 1993). The variates taken for comparison include mandible, posterior mandibular dentition and maxillary carnassial tooth (P4/) (notably, their length and width), given the absence of complete skulls of this genus at Venta Micena and their extreme scarcity at other sites. Wearing or poor preservation of fossil teeth and bones counselled rejection, following preliminary tests, of more advanced morphometric approaches (Bookstein, 1991; Reyment, 1991; Gibert & Palmqvist, 1995), such as analysis of outlines using Fourier series, eigenshape analysis, mean axes, fractal analysis, etc., or geometric morphometry of shape coordinates for landmarks, with principal and relative warp analyses. Only Type II homologous reference points, or their equivalents, can be defined for such material (Bookstein, 1991), apart from vague pseudo-landmarks quite lacking in anatomical precision given the slight nature of changes in curvature on cusps or between them.

Systematic Background

The Venta Micena carnivores were published by Pons-Moyà (1987) who, in addition to the Machairodont species *Homotherium latidens* (Owen, 1846), named a new subspecies, namely, *Megantereon cultridens adroveri* for which Venta Micena is the type-station. The basis for this was (*ibidem*: 218): a left mandibular fragment between P/4 and M/1, a left mandibular fragment between M/1 and the boundary between the root of P/3 and alveolus of P/4, a mandibular fragment at C, a mandibular fragment at M/1, a fragment of P/4 and a small fragment of maxillary C. The anatomical description and metrical analysis of the Venta Micena P/4 (L=14·5, W=6·5) pointed to a smaller size than that of Villafranchian specimens (L=18·8, W=8·0) from Puebla de Valverde (cf. Kurtén & Crusafont, 1977) or Val d'Arno (cf. Ficarelli, 1979), in support of the subspecific differentiation of *Megantereon cultridens adroveri*. Pons-Moyà (1987) regarded three subspecies as inhabiting Eurasia, namely, *M. cultridens cultridens* (the European Villafranchian

Table 1. Tooth measurements (length and width, in mm) of Megantereon from the Old and New World

Sites	C/1 L	C/1 W	P/3 L	P/3 W	P/4 L	P/4 W	M/1 L	M/1 W	P4/ L	P4/ W
European										
Italy (Ficarelli, 1979)										
IGF-827					19·2	9·2	23·1	11·0		
IGF-826							23·0	10·4		
IGF-829							18·4	9·3		
IGF-12485					18·0	8·0	22·1	10·0		
IGF-4711					19·2	8·5				
IGF-4709					19·0	8·0	20·0	9·5		
IGF-827									35·4	14·2
IGF-830									31·9	12·2
IGF-4712									35·5	11·8
IGF-15355									30·0	14·5
France (Turner, 1987)										
QSV-146	10·2	7·0	12·4	6·5	17·8	8·6	18·6	8·7		
QSV-145									29·8	14·6
QSV-1150									29·5	14·0
Spain (Kurtén & Crusafont, 1977; Turner, 1987)										
La Puebla de Valverde							19·6	9·1		
Villarroya									29·7	14·0
Asiatic										
Nihovan (Teilhard de Chardin & Piveteau, 1930; Teilhard de Chardin, 1939)										
Skull									31·0	15·0
Skull									38·0	
Mandible	15·0		9·5		19·0		24·0			
Choukoutien, Local. 1 (Teilhard de Chardin, 1939)										
									35·0	13·0
Siwaliks (Pilgrim, 1931; Petter & Howell, 1982)										
(mandibles BM-16557,					18·7		22·5			
BM-15554, BM-48929,					21·3		22·1			
DM-49 and GSI-D-100)					21·1		23·6			
					21·1		25·6			
					22·7		25·6			
BM-48436					23·5	11·0				
BM-39730									33·0	12·5
BM-16557							24·5	11·0		
GSI-D-100			8·0	6·3	21·0	10·5	26·0	13·0		
North American										
Nebraska (Berta & Galiano, 1983)			10·7	5·6	18·3	7·2	19·7	9·3		
Idaho (Berta & Galiano, 1983)							19·8	8·5		
Kansas (Berta & Galiano, 1983)					18·6	9·0				
Florida (Berta & Galiano, 1983)			12·0	5·6	19·1	8·0	21·0	9·5		
African										
South Africa (Turner, 1987)										
KA-64					17·0		19·6	9·0	30·2	10·6
E-3060					15·0	8·1	20·6	8·9		
STS-1558					13·3	6·9	19·3	8·3		
TM-856			6·6	3·9	14·5		17·6	8·5		
SK-337			5·8	3·5		7·5				
KB-5224							24·5	11·7		
East Lake Turkana (Kenya) (Leakey, 1976; Turner, 1987)										
ER-793	10·0	7·0			14·4	6·4	17·1	8·1	24·7	13·3
ER-701							20·0	8·8	27·0	12·5
Venta Micena (Martínez Navarro, 1991, 1992a,b)										
VM-2264					14·5	6·3	17·8	9·0		
VM-2265							18·8	8·7		
VM-2266							19·2	8·7		
VM-2267/2268	10·5	6·6								
VM-2270									25·6	11·1

form), *M. cultridens nihowanensis (the Asiatic form) and M. cultridens adroveri* (a European Lower Pleistocene form).

This is supported by our revision (Martínez Navarro, 1991, 1992*a,b*) of Venta Micena *Megantereon* sp., both the specimens studied by Pons-Moyà and also
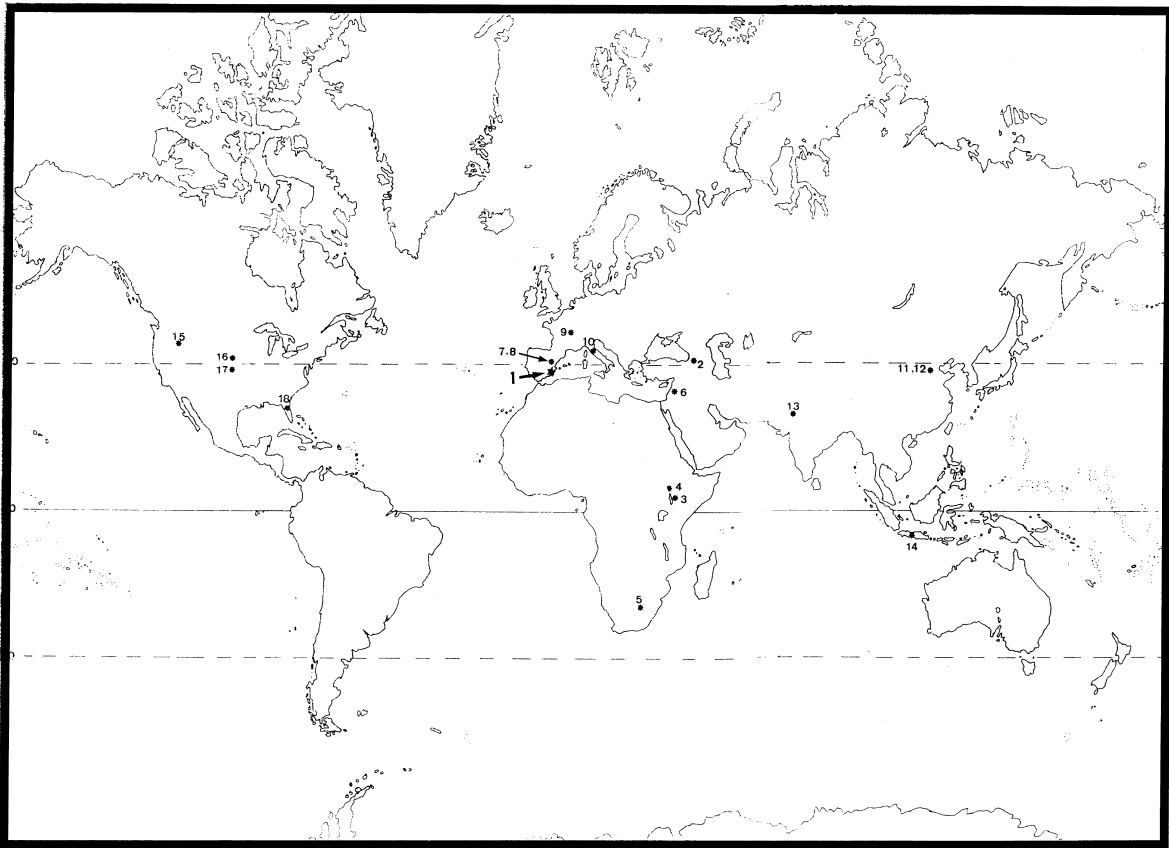
Figure 1. Geographic distribution of Pliocene and Pleistocene sites with *Megantereon* in the Old and New World. 1: Venta Micena (Orce, Spain); 2: Dmanisi (Georgia) (Dzparidze and others, 1989); 3: East Turkana (Kenya) (Leakey, 1976; Turner, 1987); 4: Omo (Ethiopia) (Howell & Petter, 1976); 5: Elandsfontein, Sterkfontein, Swartkrans, Kromdraai A and B, and Schueveburg (South Africa) (Turner, 1987); 6: Ubediya (Israel) (Ballesio, 1986); 7: Puebla de Valverde (Spain) (Kurtén & Crusafont, 1977); 8: Villarroya (Spain) (Turner, 1987); 9: Saint Vallier (France) (Turner, 1987); 10: Upper Val D'Arno (Italy) (Ficcarelli, 1979); 11: Nihowan (China) (Teilhard de Chardin, 1939); 12: Choukoutien (China) (Teilhard de Chardin, 1939); 13: Siwaliks (Pakistan) (Pilgrim, 1932; Petter & Howell, 1982); 14: Sangiran (Java) (De Vos & Aziz, 1987); 15: Hagerman (Idaho, U.S.A.) (Gazin, 1933; Bjork, 1970); 16: Broadwater (Nebraska, U.S.A.) (Schulz & Martin, 1970); 17: Rexroad (Kansas, U.S.A.) (Hibbard, 1937); 18: Bone Valley (Florida, U.S.A.) (Berta & Galiano, 1983).

a maxillary carnassial (P4/) (Figure 8) which highlights the difference between Venta Micena and other Eurasian forms. Nevertheless, it also shows the Venta Micena form to be closely related to eastern and southern African forms (cf. Turner, 1987). The inference must be drawn, pace Turner, that more than one species of *Megantereon, M. cultridens* (Cuvier, 1824), was present in the Old World; it is very likely that there were both a Eurasian species and an African one.

The findings published by Martínez Navarro will be compared with European, African, Asiatic, and North American data. The European data are from Upper Val d'Arno and Olivola in Italy (Ficarelli, 1979), Saint Vallier in France (Turner, 1987), and the Spanish stations of Puebla de Valverde (Kurtén & Crusafont, 1977). African data come from the South African stations of Elandsfontein, Sterkfontein, Swartkrans, Kromdraai A and B, and Schueveburg (Turner, 1987), and East Turkana in Kenya (Leakey, 1976; Turner, 1987). In Asia, there are data from the Chinese stations

of Nihowan (Teilhard de Chardin & Piveteau, 1930) and Choukoutien (Teilhard de Chardin, 1939), and from the Siwalik Hills in Pakistan (Pilgrim, 1932; Petter & Howell, 1982—whose data are used here). North American data come from the Hagerman Local Fauna in Idaho (Gazin, 1933; Bjork, 1970), the Rexroad Local Fauna in Kansas (Hibbard, 1937), the Broadwater Local Fauna in Nebraska (Schultz & Martin, 1970), and the Upper Bone Valley Formation in central Florida (Berta & Galiano, 1983—from which all the North American data used here have been taken; Table 1). Unfortunately, absence of a scale in the photograph has precluded use of material from Dmanisi in the Caucasian Republic of Georgia (Dzaparidze *et al.*, 1989). Nor could use be made of the maxillary canine from Ubediya in Israel (Ballesio, 1986) or the two maxillary canines from Sangiran in Java (De Vos & Aziz, 1987). Lack of published metrical data likewise prevented us from using the sample of maxillary dentition from Omo in Ethiopia (Howell & Petter, 1976) (Figure 1 and Table 1).
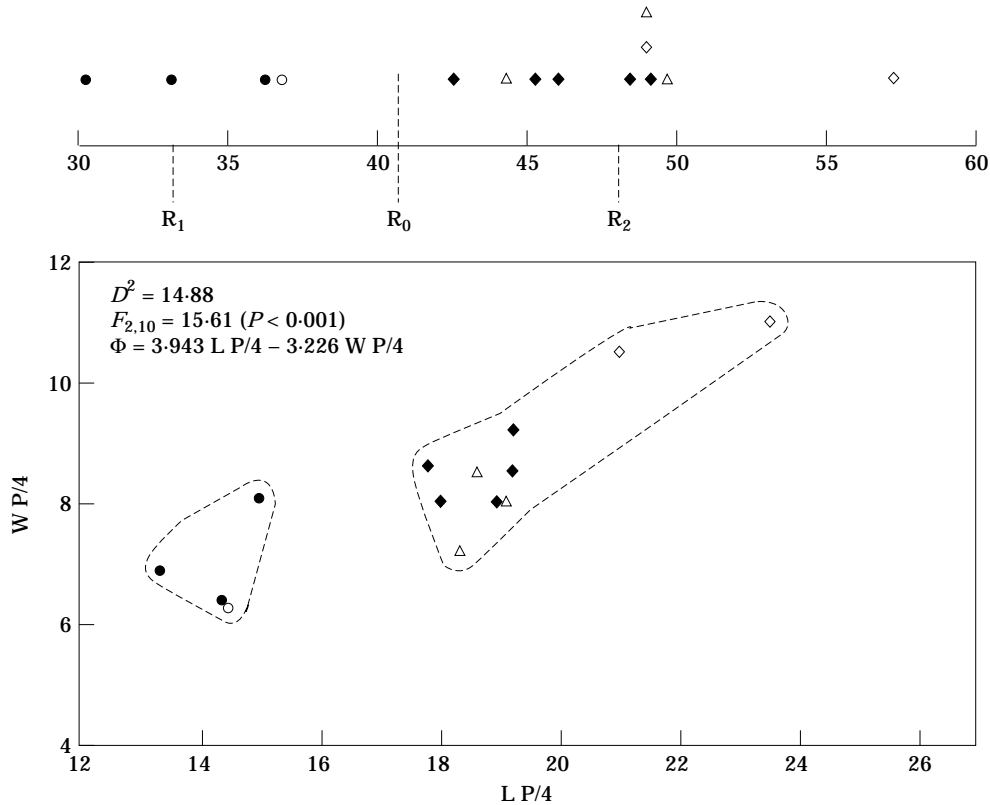
Figure 2. Bivariate plot and linear discriminant function (Φ) for L P/4 and W P/4 values (mm) in *Megantereon*. R_1: centroid of African specimens; R_2: centroid of Eurasian and North American specimens; R_0: limit between groups; D^2: Mahalanobis distance between group centroids; F: Snedecor's test for equality of bivariate means. The function is measured in discriminant units. ($\bigcirc$): Venta Micena; ($\bullet$): Africa; ($\blacklozenge$): Europe; ($\diamond$): Siwaliks; ($\triangle$): North America; ($\blacktriangle$): China.

Discussion

Although the Venta Micena subspecies *M. cultridens adroveri* was shown to differ from Asiatic and European Villafranchian forms (Pons-Moyà, 1987), a lumping taxonomy for the genus *Megantereon* proposes a very different conclusion of extreme sexual dimorphism and within-species geographic variability (Turner, 1987, based on a comparison between the metrical variability of M/1 length and width measurements in both sexes of modern African *Panthera pardus* from south-west Cape Province, Transvaal, and Malawi, and that of the same measurements on *Megantereon* from eastern and southern Africa and Europe excluding Venta Micena).

This conclusion is, however, based on the tooth which shows the least size differences in *Megantereon*, namely, mandibular M/1 which shows greatest conservatism throughout the evolution of the genus as well as considerable overlap of dimensions, although generally speaking African fossils tend to be small, apart from KB-5224 from South Africa which has values in excess of any North American or Eurasian ones other than those from the Siwaliks.

When other teeth are compared from the various forms of *Megantereon* from the Old and New Worlds,

differences important enough to indicate the presence of separate species within the genus can most certainly be seen.

(1) Both P/3 and P/4 are relatively small in African and Venta Micena fossils, which thereby form a homogeneous group. Figure 2 plots length against width values for P/4 (given in Table 1) and a clear-cut morphospatial discontinuity is seen which separates, on the one hand, the fossils from Africa and Venta Micena, from those from Eurasia and North America, on the other. The same figure also includes results of a linear discriminant-function analysis which separates African fossils from the rest: the discriminant function correctly reassigns each specimen to its respective group. Snedecor's F test ($F_{2,10}=15\cdot61$) for the Mahalanobis distance between the bivariant centroids of the groups ($D^2=14\cdot88$) permits the inference of a statistically significant difference between their respective means ($P<0\cdot001$). According to the magnitude of the factor loadings of the variates which make up the discriminant function ($\Phi=3\cdot943$ L P/4$-3\cdot226$ W P/4), P/4 length accounts for 63·9% of the total variance of the function and its width for the remaining 36·1%, while the signs of the factor loadings indicate high positive values for the (L P/4:W P/4) ratio in both Eurasian and North American specimens, and much
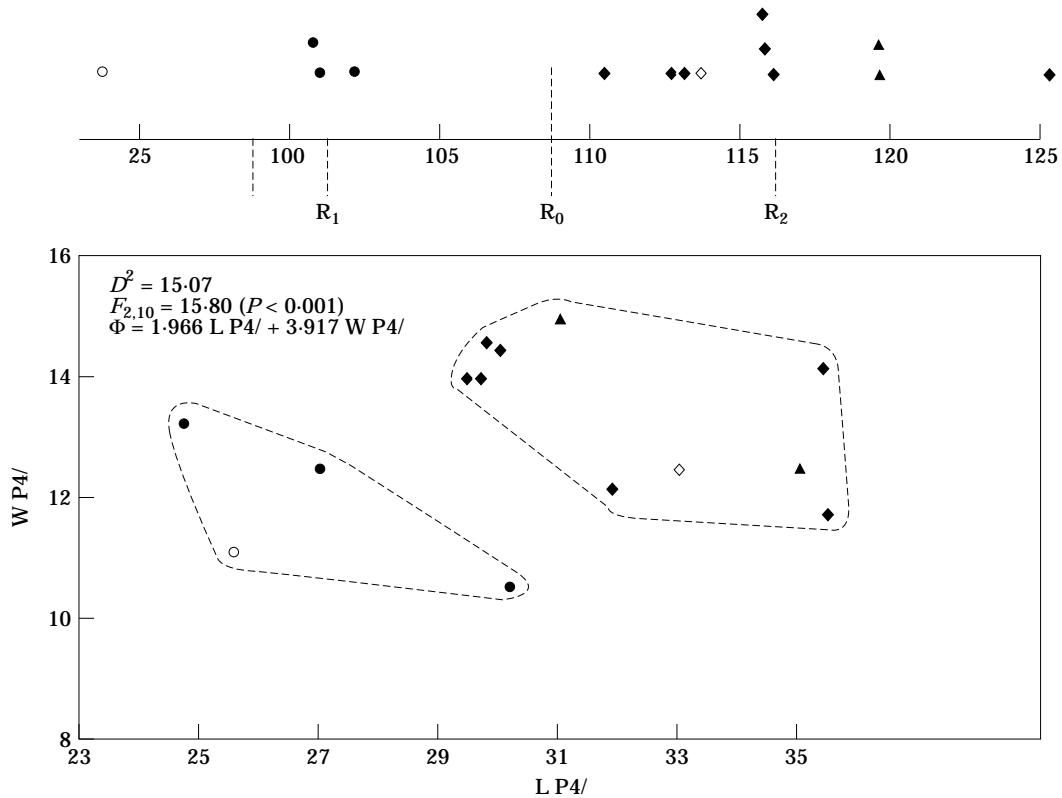
Figure 3. Bivariate plot and linear discriminant function (Φ) for L P4/ and W P4/ values (mm) in *Megantereon*. R_1: centroid of African specimens; R_2: centroid of Eurasian and North American specimens; R_0: limit between groups; D^2: Mahalanobis distance between group centroids; F: Snedecor's test for equality of bivariate means. The function is measured in discriminant units. Key as in Figure 2.

lower values in the case of African ones; when the discriminant function is applied to the Venta Micena specimen, it is unmistakably assigned to the African group.

(2) A diastema between P/3 and P/4 in African specimens is correlated with their reduced mandibular premolar length and width dimensions (particularly marked in modern forms) and this also occurs at Venta Micena. An Eurasian Villafranchian specimen from Nihowan also has a diastema (Teilhard de Chardin & Piveteau, 1930), albeit of trivial proportions as the high values of the premolar dimensions would lead us to expect.

(3) The maxillary carnassial (P4/) of the African specimens (Figure 3) is smaller than in Eurasian ones, and the sole Venta Micena specimen is smaller still. Figure 3 shows length and width dimensions for this tooth, and discontinuity between the two groups is clear-cut. Discriminant-function analysis gives 100% correct reassignment once again, maintaining the same degree as before for the bivariate contrast between the mean values of the two groups ($D^2 = 15.07$; $F_{2,10} = 15.80$; $P < 0.001$). In this case, the proportion of the variance of the function ($\Phi = 1.966$ L P4/ $+ 3.917$ W P4/) accounted for by the variates is 62.4% and 37.6%, respectively. Given that both of them have the same

sign in the discriminant function, the higher values for the function given by the Eurasian specimens indicate their greater length and width than those of the African specimens; when the Venta Micena specimen is considered, it gives even lower values than the African ones.

(4) In order to include the Siwalik data in the comparison, Figure 4 plots the length of the mandibular carnassial (M/1) against that of mandibular P/4 and clearly shows the presence of three groups with only slight overlap. Most of the Siwalik specimens show high values, with thoses from Africa and Venta Micena showing the lowest ones, and European, Chinese, and North American specimens occupying intermediate positions. The same figure includes the discriminant function for the two variates ($\Phi = 2.568$ L P/4 $- 0.385$ L M/1) and shows clear separation between the African and the other two groups. The sign of the variates in the function shows that both North American and Eurasian forms have a higher (L P/4:L M/1) ratio than African ones. Put another way, African and Venta Micena specimens have P/4 dimensions which are relatively lower than those of M/1. Here again there is a statistically significant contrast between the two bivariate means ($D^2 = 11.07$; $F_{2,15} = 18.74$; $P < 0.001$) and the proportion of the variance accounted for by the
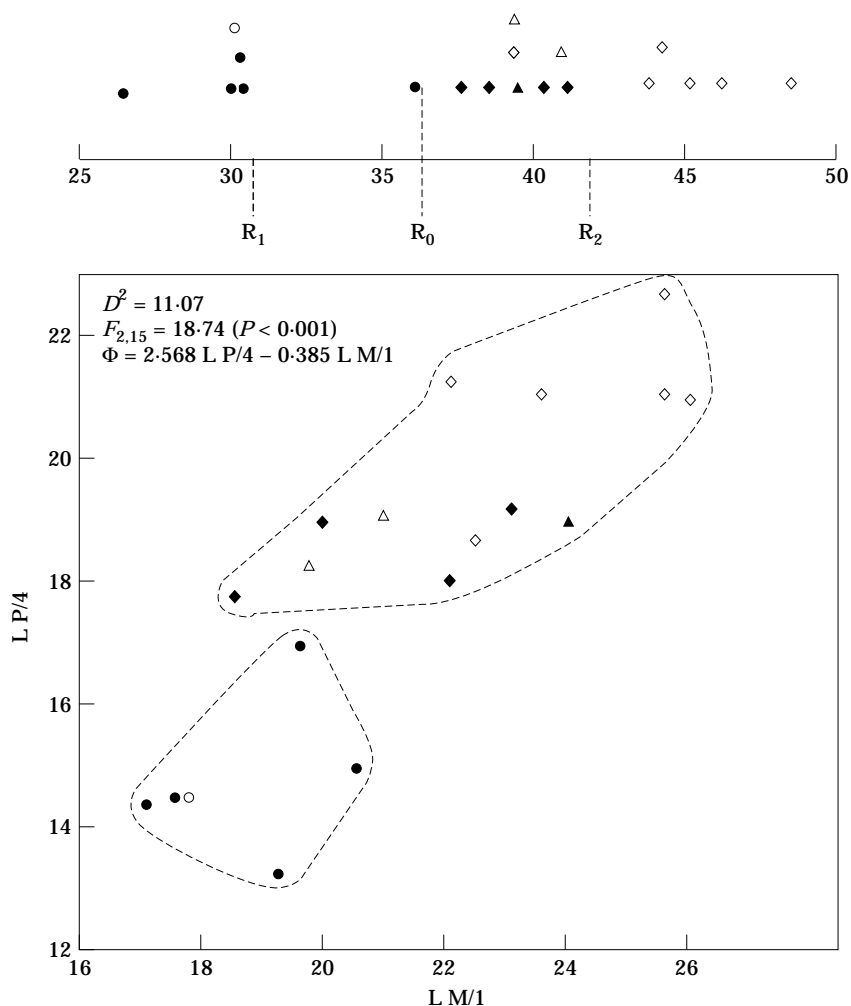
Figure 4. Bivariate plot and linear discriminant function (Φ) for L M/1 and L P/4 values (mm) in *Megantereon*. R_1: centroid of African specimens; R_2: centroid of Eurasian and North American specimens; R_0: limit between groups; D^2: Mahalanobis distance between group centroids; F: Snedecor's test for equality of bivariate means. The function is measured in discriminant units. Key as in Figure 2.
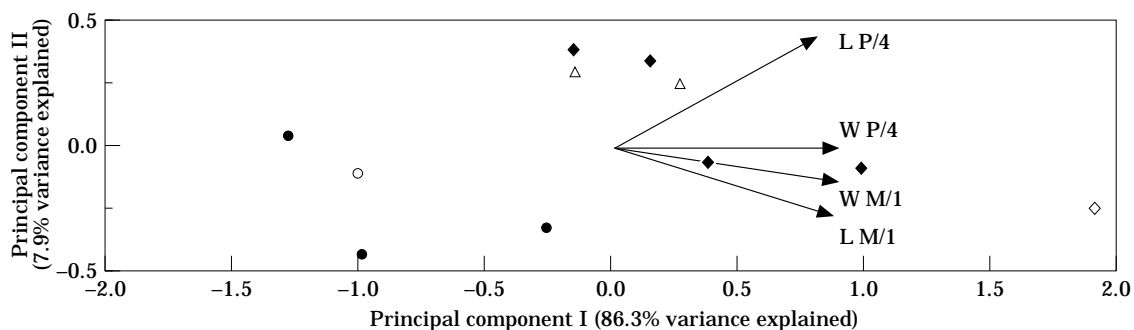

Figure 5. R-mode principal component analysis of *Megantereon*, plot of specimens on eigenvectors I and II, extracted from the correlation matrix of logarithmically transformed variates L M/1, W M/1, L P/4, and W P/4. Key as in Figure 2.

variates is 86·9% for L P/4 and 13·1% for L M/1, which rather suggest the conservative nature of the evolution of M/1 in the genus. When the discriminant function is applied to Venta Micena a value is obtained close to the centroid for African forms, underlining its affinity to them.

(5) In order to compare this last-mentioned finding in a broader multivariate statistical context, an *R*-mode
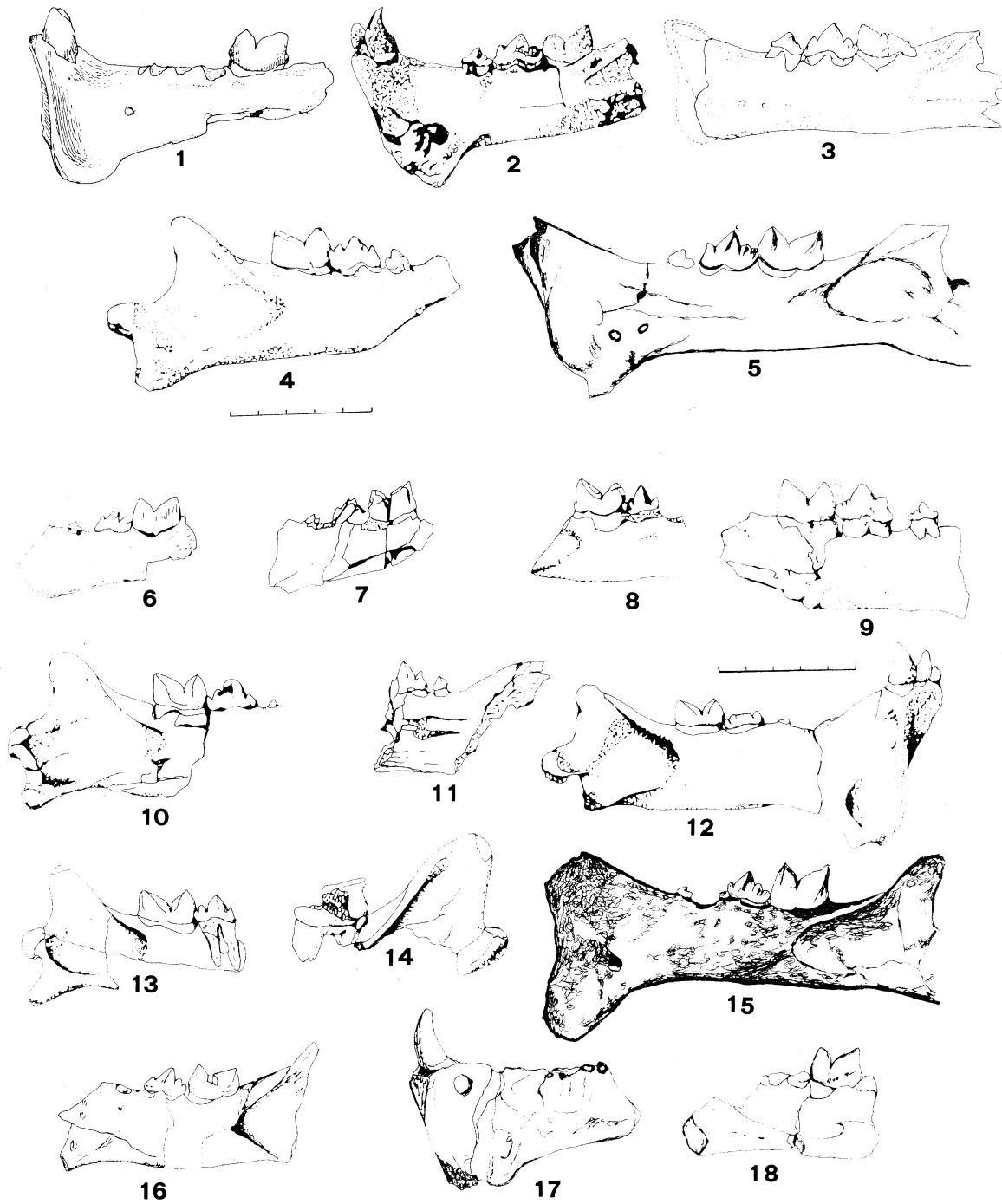
Figure 6. Old and New World specimens of *Megantereon* discussed in the text. 1–5 are *M. cultridens* and 6–18 are *M. whitei*. 1: UNSM-25494, Broadwater Formation of Nebraska (redrawn after Berta & Galiano, 1983); 2: QSV-146, Saint Vallier (France) (redrawn after Turner, 1987); 3: UF-22890, Bone Valley Formation of Florida (redrawn after B. & G.); 4: IGF-827, Valdarno (Italy) (redrawn after Turner); 5: unnumbered specimen from Nihowan (China) (drawn from a photograph in Teilhard de Chardin & Piveteau, 1930); 6: TM-856, Schurveburg (South Africa) (redrawn after Broom, 1936, in Turner, 1987); 7: TM-856 (redrawn after Turner); 8: STS-1558, Sterkfontein (South Africa) (redrawn after Turner); 9: unnumbered specimen from Afar (redrawn after Ficcarelli, 1979); 10: KA-64, Kromdraai A (South Africa) (redrawn after Turner); 11: SK-337, Swartkrans (South Africa) (redrawn after Turner); 12: ER-793, East Turkana (Kenya) (redrawn after Turner from a cast); 13: E-3060, Elandsfontein (South Africa) (redrawn after Turner); 14: BE3-5224, Kromdraai B (South Africa) (redrawn after Turner); 15: unnumbered specimen from Dmanisi (Georgia) (drawn from a photograph in Dzparidze *et al.*, 1989); 16: VM-2264; 17: VM-2267/VM-2268; 18: VM-2265.
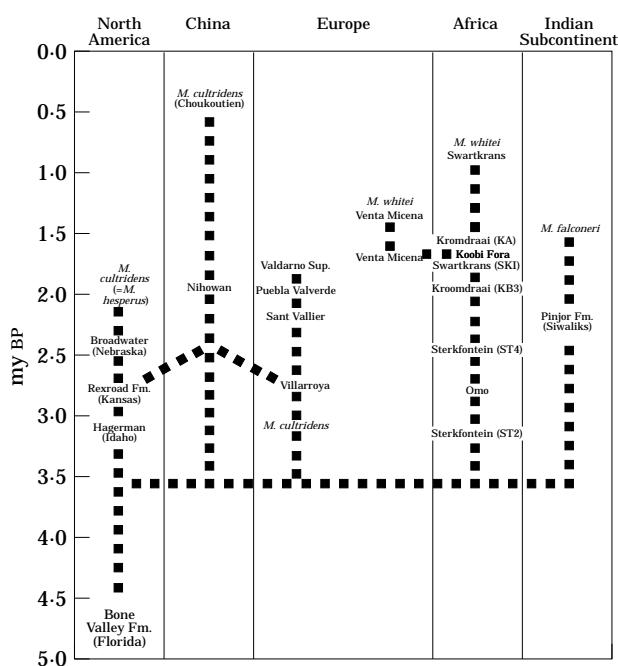
Figure 7. Proposed hypothesis for the origin, dispersal routes and speciation events of *Megantereon* in the New and Old Worlds.

principal component analysis was performed on the correlation matrix of the variates L P/4, W P/4, L M/1, and W M/1, following their logarithmic transformation. The results are shown in Figure 5 which indicates the factor scores for the specimens corresponding to the first two eigenvectors, which account for almost 95% of the total variance of the four variates. Also plotted in this figure are the loadings of the variates on the orthogonal principal components, all with positive values on the first axis which may be regarded as a size-vector (Reyment *et al.*, 1984), whereas on the second one L P/4 and L M/1 have, respectively, positive and negative values, and the other two variates have values close to zero, which suggest that this component can be regarded as a shape-vector, with positive values for those P/4 teeth, which are relatively large compared to M/1, and negative values for P/4, which are relatively small compared to M/1. Whereas Eurasian and North American specimens take up situations on the factorial plot which tend towards positive values for both principal components, African specimens, together with that from Venta Micena, tend towards negative values on both.

(6) The symphyseal region of the mandible tends to be vertical in the specimens from Africa, Dmanisi, and Venta Micena, as a consequence of the reduction in size of the lower premolar teeth, whereas in other specimens from Europe and those from China this region has a more prognathous cross-section. In North American specimens, it is more primitive and its anatomical characteristics are less developed (Figure 6).

(7) Body size estimates were calculated for specimens of *Megantereon* using allometric regression of weight on lower carnassial tooth length from the following equation, adjusted with modern field data (Van Valkenburg, 1990), which has an average error of 28% in the predictions: log W=3·05 log L M/1–2·15. The mean body weight obtained for the Venta Micena sample (52·8 kg) is close to the corresponding value estimated for African specimens (66·6 kg). The mean for both groups considered together (62·5 kg; S.D.=23·1; minimum=40·8; maximum=122·2) is smaller than those estimated for both specimens from Eurasia (79·9 ± 24·8; 51·0–114·7) and Siwaliks (120·0 ± 23·2; 89·2–146·4). These means are significantly different according to a *t*-test, especially in the case of Venta Micena and African samples with respect to specimens from Siwaliks (*t*=5·235; *P*<0·001); this latter difference (African and Venta Micena specimens of *Megantereon* weigh, on average, half what those from the Siwaliks do) fully exceeds the sexual dimorphism of modern *Panthera pardus* (mean weight of 60 kg for males, ranging between 37 and 90, and 50 in the case of females, with a range of 28–60; Kingdon, 1977). Body weights estimated for North American specimens (67·7 ± 7·2; 62·8–76·3) are similar to those of *Megantereon* in Africa and Venta Micena.

The foregoing data show that *Megantereon* at Venta Micena resembles African specimens of the genus and differs from North American and Eurasian specimens, apart perhaps from Dmanisi. African affinity is suggested by the photograph published for Dmanisi, despite absence of scale and dimensions (Dzaparidze *et al.*, 1989). This can be seen in Figure 6, which brings together several fossils from both the Old World (Teilhard de Chardin & Piveteau, 1930; Turner, 1987) and the New (Berta & Galiano, 1983). The precise form of the Ubediya specimen of *Megantereon* cf. *cultridens* cannot be determined from the publication (Ballesio, 1986), although the faunal association at the site might suggest an African affinity for it. We cannot determine the species from Java (De Vos & Aziz, 1987).

Systematics, Origin, and Dispersal of the Genus *Megantereon*

The findings presented above point to probably three species of *Megantereon* (Figure 7), rather than a single species favoured by Turner (1987). These are:

(1) *Megantereon cultridens* (Cuvier, 1824), synonymies: *M. megantereon* (Croizet & Joubert, 1828); *M. nihowanensis* (Teilhard de Chardin & Piveteau, 1930); *M. hesperus* (Gazin, 1933); and *M. inexpectatus* (Teilhard de Chardin, 1939). Dispersal of this species covers the North American Lower Pliocene, the Asian Upper Pliocene and Lower and Middle Pleistocene, and the European Upper Pliocene (Villafranchian).
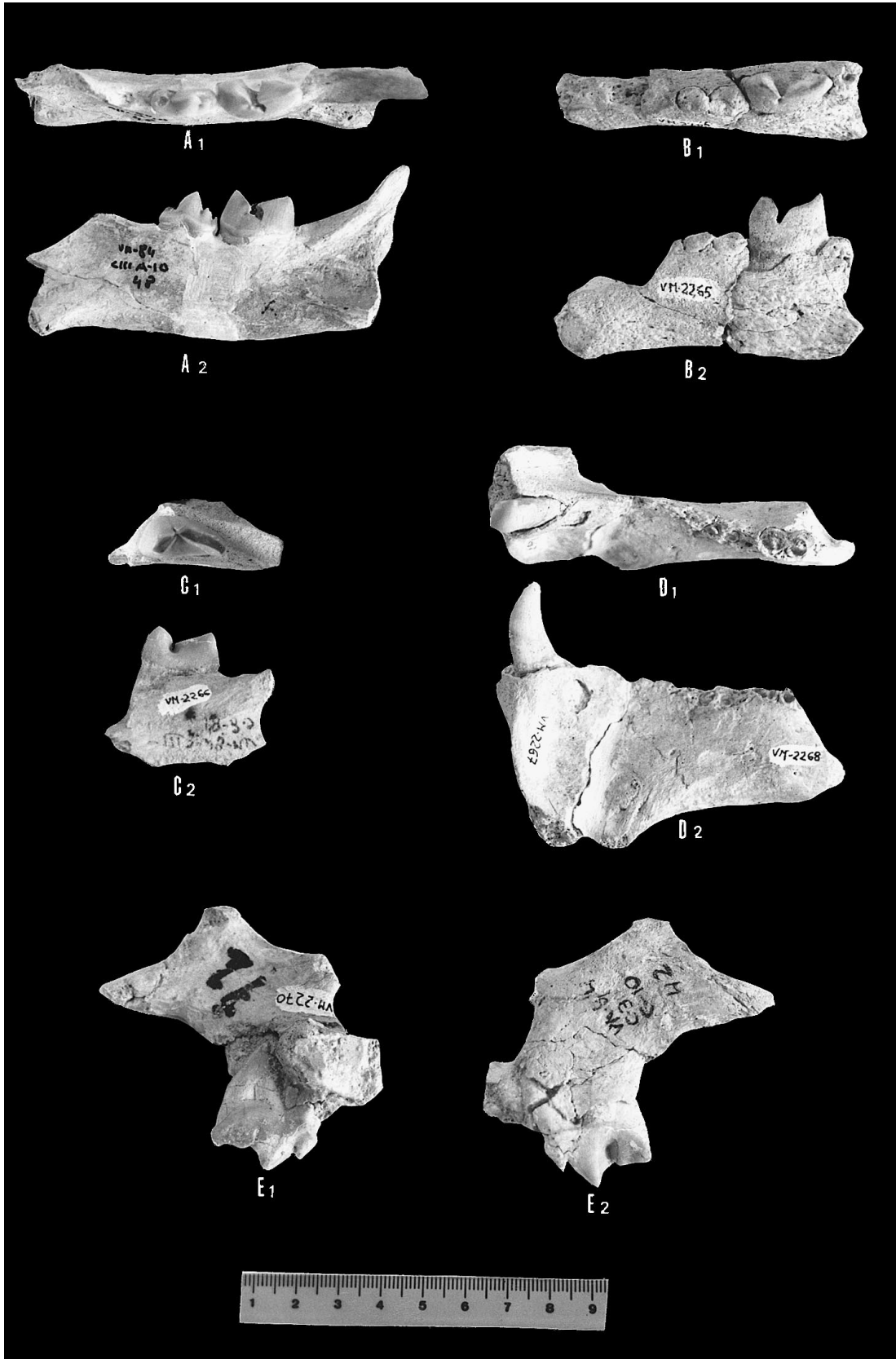
Figure 8. Megantereon whitei from Venta Micena (Orce, Granada, southeastern Spain). A, left hemimandible VM-2264 (A1: occlusal view; A2: buccal view); B: left hemimandible VM-2265 (B1: occlusal view; B2: buccal view); C: right hemimandible VM-2266 (C1: occlusal view; C2: lingual view); D: left hemimandible VM-2267/VM-2268 (D1: occlusal view); E: left maxillar fragment VM-2270 (E1: lingual view; E2: buccal view).

(2) *Megantereon whitei* (Broom, 1937), synonymies: *M. gracile* (Broom & Schepers, 1946); and *M. eurynodon* (Ewer, 1955). As explained by Hendey (1974) and Leakey (1976), its dispersal covers the African Upper Pliocene and Lower Pleistocene, and the European and Middle East Lower Pleistocene.

(3) *Megantereon falconeri* (Pomel, 1853), synonymies: *M. sivalensis* (Falconer & Cautley, 1868). Its dispersal covers the Indian Upper Pliocene.

The genus *Megantereon* shares much in common with the genus *Smilodon* (Schaub, 1925; Kurtén, 1963; Repenning, 1967; Thenius, 1967; Shultz & Martin, 1970; Beaumont, 1978; Martin, 1980; Berta & Galiano, 1983). The two genera form the tribe Smilodontini (Kurtén, 1963). Berta & Galiano (1983) deploy anatomical characteristics in an exemplary cladistic scheme which separates the tribe Smilodontini from other Machairodontines, and the genus *Smilodon* from that of *Megantereon*. These authors put the earliest presence of *Megantereon* at 4·5 my BP in the Bone Valley Formation of Florida which provided a fragmentary mandible with P/3, P/4 and fragmentary M/1 (Figure 6). They assigned it to *M. hesperus* (Gazin, 1933). This species was described from the North American Blancan deposits, probably dating from 3·4 my BP, and is regarded by Kurtén & Anderson (1980) as very closely related to *M. cultridens* (Cuvier, 1824), with which it is here considered to be synonymous.

However, Turner (1987) holds that the Bone Valley Formation specimen is not *Megantereon*, but could be related, instead, to be the genus *Dinofelis*—similar to that from the South African Lower Pliocene at Langebaanweg (Hendey, 1974)—which was also present in the North American Pliocene (Kurtén, 1973; Kurtén & Anderson, 1980). Another possibility noted by Turner is that the mandible might correspond to *Paramachairodus* (Pilgrim, 1913), synonymous with *Pontosmilus* (Kretzoi, 1929) from the Greek Upper Miocene at Pikermi. The hypothesis that *Paramachairodus/Pontosmilus* might have been ancestral to *Megantereon*, put forward by Beaumont (1978), is rejected by Berta & Galiano (1983) on the ground that whereas *Pontosmilus* shows dental serrations, their absence in *Megantereon* should be seen as retention by it, of the primitive state, and they regard the nearest genus to it as being *Metailurus* (Zdansky, 1924) from Eurasian and African Miocene stations. They consider that *Megantereon* arose in North America with *M. hesperus* (Gazin).

In agreement with Berta & Galiano, it is considered here that the *Megantereon* genus, whose oldest species is *M. cultridens* Cuvier (=*M. hesperus* Gazin), originates from the Mio-Pliocene boundary in North America, as a response to the climatic Messinian crisis on the world-wide scale. Between 3·5 and 3·0 my BP this species emigrates from North America and expands all over the Old World.

In Africa it will give rise to the new species of *Megantereon whitei* Broom (=*M. gracile* Broom & Schepers, =*M. eurynodon* Ewer), which survives in this continent until the Lower-Middle Pleistocene boundary.

The findings presented above suggest that the Indian species *M. falconeri* (=*M. sivalensis*, Falconer & Cautley) was also probably derived from North American forms, evolving to become rather larger in size and surviving until the Plio-Pleistocene boundary, although an African origin for it was proposed by Barry, Lindsay & Jacobs (1982) and supported by Turner (1987).

Europe was also home to the North American form until the Plio-Pleistocene boundary, and in China it lingered well into the Middle Pleistocene, c. 0·5–0·4 my BP at Choukoutien Locality I (Zhao *et al.*, 1980 and Shilun *et al.*, 1980, cited by Berta & Galiano, 1983).

What distinguishes Europe at the Plio-Pleistocene boundary (1·8–1·6 my BP) is the arrival from Africa of *Megantereon whitei* (Broom) to replace *M. cultridens* (Cuvier), which is seen at Venta Micena and Dmanisi. The European Villafranchian draws to a close with the arrival of ruminants from Asia and *Hippopotamus*, large carnivores (including *Megantereon whitei*), and primates (including *Homo*) from Africa (Martínez Navarro, 1991, 1992*a*, 1992*b*, 1992*c*).

Conclusions

Comparative dental morphometrics of the various representatives of the genus *Megantereon* throughout the Old and New World point to the presence of three species (Figure 7). These were *M. cultridens* (Cuvier), indigenous to North America from the Lower Pliocene onwards, which in the Indian subcontinent gives rise to *M. falconeri* Pomel during the Upper Pliocene. *M. cultridens* survived until the Middle Pleistocene in China, and its African descendant *M. whitei* Broom colonized Europe as far north as the 40th parallel at the time of the Plio-Pleistocene boundary, reaching Dmanisi via the Near East and southern part of the Iberian Peninsula maybe via an ephemeral land-bridge across the Strait of Gibraltar, where the shallowest ridge is nowadays submerged at 250 m below sea level, although it should be borne in mind that the region has been tectonically active throughout the Neogene.

The spread of *Megantereon whitei*—and other African species—to Spain and Georgia at the Plio-Pleistocene boundary is probably related to the first arrival of *Homo* in Eurasia (Gibert & Palmqvist, 1995), a migration hitherto believed to have had eastern Asia as its only destination in a fundamentally Middle, rather than Lower, Pleistocene context.

*The rhinocerotid species present at Venta Micena was quoted by Santafé & Casanovas (1987) as being *Dicerorhinus etruscus brachycephalus*, but recently it has been reclassified as *Stephanorhinus etruscus* (Cerdeño, 1993).

Acknowledgements

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