Late Villafranchian Mammuthus meridionalis (Nesti, 1825) from the Iberian Peninsula: Dentognathic remains from Incarcal-I (Crespià, Girona) and Venta Micena (Orce, Granada)

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a b s t r a c t

The late Early Pleistocene (Late Villafranchian) paleontological sites of Incarcal-I (Crespià, Catalonia, Spain) and Venta Micena (Orce, Andalusia, Spain), which are approximately 800 km apart, preserve a rich fossil record of proboscideans, corresponding to the species Mammuthus meridionalis. The remains from Incarcal-I have been described as an evolved form of the species. However, their comparison with the mandible of the same species from Venta Micena (with an approximate age of 1.4e1.6 Ma) and other specimens from different sites in Europe and Asia shows that the fossils from Incarcal-I and Venta Micena are very similar in morphology and metric data. Research suggests that the Catalonian specimens correspond to a form of the former species, which according to their morphology probably have a chronology closer to that of the Venta Micena specimens.

1. Introduction

The late Early Pleistocene Incarcal site complex (Crespià, Banyoles-Besalú Basin, Catalonia, Spain) (Fig. 1) is composed of a series of karst cavities developed in the Pliocene lacustrine lime- stone Formation of the same name, which are filled by an alternation of travertines, calcarenites and calcilutites (Ros and Palomar, 2003; Galobart, 2003). This karst complex was discovered at the sixties of the last century, when the works in the Cal Taco quarry started.

Later, geological surveys and subsequent systematic excavations since 1984 showed that these sedimentary infillings preserve an important assemblage of large mammals of Late Villafranchian age (Juliá and Villalta, 1984; Maroto et al., 2003). Systematic excavations were mainly focused in the last twenty five years in one of the cavities, Incarcal-I, which has provided excellent specimens of the following taxa (Galobart and Maroto, 2003): Homotherium latidens, Pachycrocuta brevirostris, Canidae indet., Mammuthus meridionalis, Stephanorhinus etruscus, Hippopotamus antiquus, Bovini indet., Megacerini indet., cf. Capreolus, Oryctolagus sp., Prolagus cf. calpensis, Apodemus aff. mystacinus, Allophaiomys sp., Mimomys cf. blanci, Sorex cf. minutus, cf. Aquila chrysaëtos, Aves indet., Bufo bufo., Testudini indet., Anguilla anguilla, Osteichthyes indet., Juglans sp.

The site of Venta Micena (Orce, Guadix-Baza Basin, Andalusia, Spain) (Fig.1) corresponds to a horizontal layer which has an extentof more than 2.5 km. According to the taxonomic diversity, the abun- dance of specimens and their excellent preservation, Venta Micena is a key-site in the European Quaternary (Anadón et al.,1987; Martínez-Navarro,1991,1992; Palmqvist et al.,1996, 2003, 2011; Palmqvist and Arribas, 2001; Martínez-Navarro et al., 2011a,b, and references therein). The site chronology, based on magnetostratigraphic and biochrological data, is situated around 1.5e1.6 Ma (Martínez-Navarro, 1991). This estimate is reinforced by the presence of the vole Allo- phaiomys pliocaenicus, a former synonym of Allophaiomys ruffoi (Agustí, 2009). However, numerical dating carried out in this locality using the US-ESR methodyielded anage estimate slightly youngerfor the layer studied, 1.37 ± 0.24 Ma (Duval et al., 2011).

The faunal list of Venta Micena (Palmqvist et al., 2005; Abbazzi, 2010; Martínez-Navarro et al., 2010, 2011b, and references therein) is composed of: Homotherium latidens, Megantereon whitei, Panthera cf. gombaszoegensis, Lynx sp., Pachycrocuta brevirostris, Lycaon lycao- noides, Canis mosbachensis, Vulpes praeglacialis, Ursus etruscus, Meles sp., M. meridionalis, Stephanorhinus aff. hundsheimensis, Equus altidens, Hippopotamus antiquus, Bison sp., Hemibos sp. aff. Hemibos gracilis, Hemitragus albus, Praeovibos sp., Soergelia minor, Praemega- ceros cf. verticornis, Metacervocerus rhenanus, Prolagus calpensis, Oryctolagus cf. lacosti, Hystrix mayor, Allophaiomys pliocaenicus, Apodemus aff. mystacinus, Castillomys crusafonti, Eliomys intermedius, Desmana sp., Testudo sp., Lacerta sp., Ophidea indet., Rana sp., Char- adriiformes indet. (aff. Laridae), Aves indet.

Fig. 1. Geographic location and panoramic views of the sites of Incarcal-I (Crespià, Banyoles-Besalú Basin, Catalonia, Spain) and Venta Micena (Orce, Guadix-Baza Basin, Andalusia, Spain).

2. Systematic Paleontology

ORDER PROBOSCIDEA Illiger, 1811
FAMILY ELEPHANTIDAE Gray, 1821
GENUS Mammuthus Brookes, 1828
SPECIES M. meridionalis (Nesti, 1825)

2.1. Referred specimens

The material described in this paper was recovered from the locality of Incarcal-I (Crespià, Catalonia, Spain) and is housed at the Museu Arqueològic Comarcal de Banyoles: IN-I-930, a mandible with both M/3 (Fig. 2A1 and A2) (previously figured as described in Mazo et al., 2003: Fig. 1). We also describe here material from the Venta Micena locality (Orce, Andalucía, Spain), housed at the Museo de Prehistoria y Paleontología of Orce: VM-4103, a partial mandible displaying the left M/3 (Fig. 2B1 and B2).

2.2. Description and measurements 2.2.1. Incarcal (IN-I-930)

A mostly complete, well preserved mandible that shows several fractures. It is large sized, high and robust, and preserves both third molars, the corpus, the coronoid process, the left condile, part of the right condile, and the symphyseal process (Fig. 2A1). Both mandibular corpi are straight. The robustness at the posterior angle of the mandible is small. The mentonian foramens are not visible, probably as a consequence of the fractures. The symphyseal beak is elongated and narrow. The masseteric basins are wide and well preserved, the coronoid processes are straight and parallel between them, and the condyles are well developed (Mazo et al., 2003). The molars are well preserved, but the mesial region is slightly fractured in both specimens and their mesial talons are absent (Fig. 2A2; (Table 1). They preserve eight plates, including the distal talon, although the degree of wear suggests that these molars lost at least 2 or 3 mesial plates, which means that the complete total number of plates would have been originally of at least 10 or 11. The first anterior preserved plate of the right molar is not complete, and the left specimen shows eight complete plates. All the plates are worn, but wearing is more accentuated in the mesial region (i.e., the tooth portion that was first erupted), and it is possible to see the individualized enamel cones in the distal one. The enamel is not thin and appears a little folded. The cement is abundant. The frequency of plates is low, and the mesio-distal interplate distance is equal or slightly greater than plate width. The distal talon is straight. In the occlusal view of the distal plates, it may be observed that the enamel has a large and round central figure, with two narrower and elongated figures in the labial and lingual regions.

Given these anatomical data, the mandible would correspond to an adult individual that died at an age older than 50 years. According to the shape of the symphyseal beak, which is elongated, this individual was probably a female, because this feature is commonly found in modern female elephants (Maccagno, 1962). The age estimate provided and the one that appears below are both based on tooth wearing patterns in living elephants published by Haynes (1991) and also on unpublished data of molar teeth collected by the first author of this study.

Fig. 2. Mandibles from Incarcal-I IN-I-930 (A1 and A2) and Venta Micena VM-4103 (B1 and B2).

2.2.2. Venta Micena (VM 4103)

A mostly complete mandible with the left M/3 (Fig. 2B1). It is not well preserved, as it is slightly deformed and tilted inside. It preserves both mandibular corpi, the left coronoid process and the left third lower molar. It is also possible to see the alveolus in the right corpus. The symphyseal beak is elongated and narrow. It is not possible to measure with accuracy the height and width of the hemimandibles due to diagenetic compaction.

The third lower molar is mostly complete, but the first mesial plate is broken in its middle part (Fig. 2B2; Table 1). It preserves eight plates, all of them worn, but wearing is less accentuated in the distal region, where the cones can be seen showing a thick and folded enamel. As in the preceding case, the degree of tooth wearing suggests that this molar lost at least 1 or 2 mesial plates.

The cement is abundant. The mesio-distal interplate distance is smaller than plate width. The occlusal morphology of the plates is typical of the genus Mammuthus. All these data suggest that this mandible corresponds to an individual older than 45 years. As in the case of the Incarcal specimen, it shows an elongated symphy- seal beak, suggesting that probably it was also a female.

Table 1 Measurements of the molars from the mandibles IN-I-930 and VM-4103, and average values for Mammuthus meridionalis after Maglio (1973), in mm. MDD: mesio-distal diameter; MD_FD: mesio-distal functional diameter; BLD: bucco-lingual diameter; BL_FD: bucco-lingual functional diameter; LF: laminar frequency in 10 cm; PT: total number of plates; PU: used plates; E_{MAX}: maximum thickness of enamel; E_{MIN}: minimum thickness of enamel; E: mean value of enamel thickness.

3. Discussion

The genus Mammuthus is recorded in Eurasia from the Late Pliocene (3.2 Ma, Early Villafranchian) to the Holocene. The Euro- pean record of Mammuthus has been divided traditionally in four successive chronospecies (following Lister and Van Essen, 2003; Maglio, 1973) that cover the whole chronological distribution of this genus in Europe: Mammuthus rumanus for the Early Villa- franchian; M. meridionalis for the Early Pleistocene (Middle and Late Villafranchian); Mammuthus trogontherii, recorded in China since the beginning of the Late Villafranchian around 1.6e1.7 Ma (Lister, 2004) and in Europe as an immigrant present during the first half of the Middle Pleistocene (Galerian); and Mammuthus primigenius for the second half of the Middle PleistoceneeHolocene.

These four species differ basically in the morphology of the molars. The changes from the Pliocene forms to the Late PleistoceneeHolocene ones comprise an increase in both the number of enamel plates and the level of hypsodonty, on the one hand, and a decrease in the enamel thickness, on the other. These morphological changes are associated with a change to a more grazing diet, which was probably induced by the progressive climatic instability and drier conditions that characterized the Middle and Late Pleistocene (Lister and Sher, 2001), The same evolutionary trend can be observed, but on a smaller scale, from the earlier specimens to the later ones of the species M. meridionalis, because three different forms (i.e., primitive, intermediate and evolved) can be

recognized in this intra-specific morphological trend. Specifically, the average number of enamel plates increases in M. meridionalis from a minimum of 13 to a maximum of 19 in the transition from M. meridionalis to M. trogontherii (Lister et al., 2005), whereas the mean value of enamel thickness decreases from 4.5 mm in the most primitive specimens to 3e2.7 mm in the most derived ones. Fig. 3 shows a scatter diagram with the values of laminar frequency (X-axis) and enamel thickness (Y-axis) for the M/3 specimens from Incarcal-I and Venta Micena, together with other M. meridionalis molars from several localities of Europe and Asia, including Fuente Nueva 3 in Orce (Ros-Montoya, 2010), a site from the Prados-Guaten Basin, Madrid, both in Spain (Silva et al., 1999), Upper Valdarno, Monte Tenda, Rio Pradella, Ligniti di Lumena, Torrente Crostolo and Pietrafitta, in Italy (Ferretti, 1999; Palombo and Ferretti, 2005), Malouteyre and Pranlary in the Central Massif, France (Ros-Montoya, 2010), Ubeidiya, Israel (Beden, 1986), and three Georgian sites in the Caucasus, Dedoplisjaro, Dmanisi and Taribana (Ros-Montoya, 2010) (Table 2). The anatomical data and the scatter diagram show that the specimens from Venta Micena and Incarcal-I fall within the range of variability of M. meridionalis.

Fig. 3. Scatter plot showing the laminar frequency values (LF, horizontal axis) and the average values of enamel thickness of the M/3 (E, vertical axis) in the specimens from Incarcal-I and Venta Micena, with a representation of other third molars of M. meridionalis from Europe and Asia.

Table 2 Measurements (in mm) of the third lower molars of Mammuthus meridionalis from different Early Pleistocene sites of Eurasia (for abbreviations, see Table 1).

Fig. 4. Results of PCA in the lower third molars of M. meridionalis. The graph shows the scatter of the specimens' scores on the first two components, which describes a horseshoe pattern (Gutmann effect), reflecting a marked morphological gradient in the data analyzed. According to the factor loadings of the metric variables in these axes (Table 2), the first component correlates positively with the bucco-lingual diameter of the third molar and the average thickness of the enamel crests, and negatively with the laminar frequency. In contrast, the variables that contribute more to the second component are the mesio-distal diameter and the total number of plates, both with positive loadings. According to the distribution of the specimens and their chronologies, there is a well marked gradient in the morphology of the lower third molars between the tooth remains from the older localities (>1.8 Ma), which score positively on the first component and negatively on the second one, and those from the younger sites, which tend to take the opposite scores.

The specimens from Incarcal-I and Venta Micena show a striking similarity in their metric values, which suggests a similar chro- nology for them, older than Fuente Nueva-3 and younger than both the Upper Valdarno and Dmanisi localities.

Principal components analysis (PCA) was used for a more in depth comparison of the specimens from Incarcal-I and Venta Micena with the remains from other sites, using as variables the mesio-distal and bucco-lingual diameters of the lower third molar, the total number of plates along this tooth, the laminar frequency (i.e., number of plates per 10 cm of mesio-distal length) and the average thickness of the enamel crests.

Fig. 4 shows the factor scores on the first two components, which jointly account for nearly 80% of the variance explained by the original variables (Table 3). Inspection of the distribution of the specimens analyzed shows that although the three groups that may be distinguished according to their chronology (i.e., Late Pliocene to early Early Pleistocene, >1.8 Ma; middle Early Pleistocene, 1.8e1.0 Ma; late Early Pleistocene, <1.0 Ma) overlap to some extent, they tend to scatter on different regions of the morphospace, specially in which concerns their scores on the first component.

Specifically, the older specimens tend to show lower third molars that are relatively short and wide, have thick enamel crests and show a low laminar frequency. In contrast, the younger specimens have the opposite condition, with lower third molars that are comparatively longer and narrower, showing more densely packed plates and thinner enamel crests. Interestingly, the fossil teeth from those sites with an intermediate chronology have also an inter- mediate morphology. This is the case of the specimens from Incarcal-I, which cluster among the specimens that have a middle Early Pleistocene age. However, the fossil tooth from Venta Micena takes and intermediate position in the morphospace between the specimens from Late Pliocene to early Early Pleistocene sites, on the one hand, and those collected in middle Early Pleistocene localities, on the other. This suggests that the remains of M. meridionalis from the latter site may be somewhat older than those from Incarcal-I.

Table 3 Results of principal component analysis.

4. Conclusions

The comparative morphological and metric study of the proboscidean dental specimens from the Late Villafranchian localities of Incarcal-I and Venta Micena shows that they are very similar and must be ascribed to an intermediate form of M. mer- idionalis. This suggests that the chronology for both sites must be very close to around 1.4e1.6 Ma, perhaps slightly older in the case of Venta Micena than in Incarcal-I.

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