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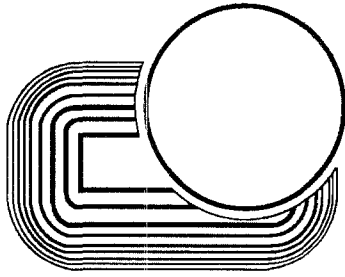


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TAPHONOMY AND PALAEOECOLOGY OF AN ASSEMBLAGE OF LARGE MAMMALS: HYAENID ACTIVITY IN THE LOWER PLEISTOCENE SITE AT VENTA MICENA (ORCE, GUADIX-BAZA BASIN, GRANADA, SPAIN)

ALFONSO ARRIBAS & PAUL PALMQVIST

ARRIBAS A. & PALMQVIST P. 1998. Taphonomy and palaeoecology of an assemblage of large mammals: hyaenid activity in the Lower Pleistocene site at Venta Micena (Orce, Guadix-Baza, Granada, Spain). [Taphonomie et paléocologie d'un assemblage de grands mammifères: activité des hyènes dans un site du Pléistocène inférieur à Venta Micena (Orce, bassin de Guadix-Baza, Grenade, Espagne)]. [Tafonomía y paleoecología de una asociación de grandes mamíferos: actividad de hienidos en el Pleistoceno inferior de Venta Micena (Orce, Cuenca de Guadix-Baza, Granada, España)]. *GEOBIOS*, **31**, **3**, **supplément**: 3-47. Villeurbanne, le 30.06.1998.

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ABSTRACT - We report taphonomic and palaeoecologic data on the rich, diverse and well preserved assemblage of large mammals from lower Pleistocene deposits at Venta Micena (Orce, Granada, south-east Spain). The biostratigraphic and diagenetic characteristics of the assemblage are congruous with the sedimentary context deduced from the study of the site, and both confirm that: (i) the assemblage represents an accumulated taphonomic stage, (ii) it was formed by demic, autochthonous palaeobiologic entities, which were preserved and recorded in situ, and (iii) it is the result of biological processes and agents. Interspecific analysis of size/abundance patterns in ungulates shows that the main taphonomic bias affecting the bones was produced by biological destruction before burial, and that the loss of information was greater for species of smaller body size. Factor correspondence analysis was used to compare the frequencies at which some groups of postcranial elements are represented in several recent and archaeological bone assemblages accumulated by carnivores, rodents and hominids. The results obtained strongly suggest that the bones from Venta Micena were collected mainly by hyaenids, which deposited them near shallow dens excavated around the ponds that surrounded the Pleistocene lake of Orce. An analysis of the abundance of major long bones has shown that differential fragmentation was produced by hyaenas as a function of their structural density and mean marrow content. All these data allow to formulate a descriptive-quantitative model for the characterization of bone assemblages generated from hyaenid activity, in which Venta Micena is an example of bone concentration and modification activities by *Pachycrocuta brevirostris*. Strong selection of prey by carnivores (which killed preferably juveniles, females and individuals with diminished locomotive capabilities among ungulate prey species of larger body size) is indicated by (i) the abundance of juvenile individuals with deciduous teeth in relation to the average weight estimated for adults in each ungulate species, by (ii) the U-shaped attritional mortality profiles deduced from crown height measurements, by (iii) the presence of many metapodials with different osteopathologies, and by (iv) a biased sexual ratio deduced from the metacarpals of large bovids. Comparison between the frequencies in which modern African carnivores kill and scavenge ungulates from different size classes and the abundance of these size categories in the assemblage suggests that the Venta Micena hyaena was a bone-cracking scavenger which fed largely on carcasses of ungulates preyed upon and partially consumed by flesh-eating carnivores such as saber-toothed felids and wild dogs.

KEYWORDS: BONE ASSEMBLAGE, TAPHONOMY, PALAEOECOLOGY, MULTIVARIATE ANALYSIS, LOWER PLEISTOCENE, SPAIN.

RÉSUMÉ - Ce travail est l'étude taphonomique et paléocologique d'un assemblage abondant et diversifié de grands mammifères provenant du gisement de Venta Micena (Pléistocène inférieur, Orce, Grenade, Sud-Est de l'Espagne). Les caractéristiques biostratigraphiques et diagénétiques de l'assemblage s'accordent avec le contexte sédimentaire déduit de l'étude du gisement, les deux approches confirmant (1) que l'assemblage représente un ensemble taphonomique d'accumulation, (2) qu'il fut formé par des entités paléobiologiques autochtones et démiques, préservées et enregistrées in situ et (3) qu'il est le résultat d'agents et de processus biologiques. L'examen interspécifique des données, taille/abondance des espèces d'ongulés, montre que les principaux biais taphonomiques sont dus à une destruction biologique avant l'ensevelissement et concernent principalement les espèces de petite taille. L'analyse factorielle des correspondances est utilisée pour comparer les fréquences des différents groupes d'éléments du squelette post-crânien rencontrés dans des ensembles récents ou archéologiques d'ossements accumulés par les carnivores, les rongeurs et les hommes. Les résultats obtenus suggèrent que les restes de Venta Micena ont été récoltés principalement par des hyènes qui les ont déposés autour de l'entrée de leurs repaires peu profonds, creusés près

des mares qui bordaient le lac pléistocène d'Orce. L'étude de l'abondance des principaux os longs conservés dans l'assemblage montre que les hyènes réalisaient une fragmentation différentielle des os en fonction de leur densité minérale et de leur contenu moyen en moëlle osseuse. Avec ces données, nous pouvons présenter un modèle descriptif-quantitatif pour la caractérisation des assemblages osseux résultant de l'activité des hyènes dont Venta Micena est un exemple de concentration et de modification résultant de l'action de *Pachycrocuta brevirostris*. L'importante sélection des proies par des carnivores qui chassaient principalement des individus jeunes, des femelles et des sujets à capacité locomotrice réduite dans le cas d'ongulés de grande taille, est démontrée par (1) l'abondance des individus jeunes (présence de la dentition déciduale) et la relation avec le poids estimée pour les adultes de chaque espèce; (2) par la courbe de mortalité en U obtenue à partir des mesures de hauteur de la couronne dentaire; (3) de la présence de nombreux métapodes avec diverses ostéopathologies; (4) de la proportion des sexes déduite de la morphométrie des métacarpiens des grands bovidés. Finalement, la comparaison entre la fréquence observée chez les carnivores africains actuels chasseurs et charognards d'ongulés de diverses classes de taille et l'abondance de ces catégories de taille dans l'assemblage fossile suggère que la hyène de Venta Micena avait un comportement de charognard, s'appropriant les cadavres consommés pour partie par les autres carnivores, tels les félidés à dents de sabre et les chiens sauvages.

MOTS-CLÉS: ASSEMBLAGE OSSEUX, TAPHONOMIE, PALÉOÉCOLOGIE, ANALYSE MULTIVARIÉE, PLÉISTOCÈNE INFÉRIEUR, VENTA MICENA.

RESUMEN - En este trabajo se efectúa un estudio tafonómico y paleoecológico de la abundante y diversa asociación de grandes mamíferos proveniente del yacimiento de Venta Micena (Pleistoceno inferior; Orce, Granada, sureste de España). Las características bioestratigráficas y diagenéticas de la asociación fósil son congruentes con el contexto sedimentario deducido del estudio del yacimiento, confirmando ambas que: (i) la asociación presenta un estado tafonómico de acumulado, (ii) se encuentra formada por entidades paleobiológicas démicas, por entidades conservadas autóctonas y por entidades registradas in situ, y (iii) es el resultado de la acción de procesos y agentes biológicos. El análisis interespecífico de los patrones de tamaño/abundancia en las especies de ungulados ha puesto de manifiesto que los principales sesgos tafonómicos se produjeron como consecuencia de la destrucción por agentes biológicos de los restos óseos en la etapa previa a su enterramiento, afectando la pérdida de información más a las especies con dimensiones corporales reducidas. El análisis factorial de correspondencias se usó para comparar las frecuencias en que distintos grupos de elementos esqueléticos postcraneales se encuentran representados en asociaciones recientes y arqueológicas de huesos acumulados por carnívoros, roedores y homínidos. Los resultados obtenidos sugieren que los restos de Venta Micena fueron recolectados principalmente por las hienas, quienes los depositaron en torno a la entrada de cubiles poco profundos, excavados cerca de las charcas que bordeaban el lago pleistoceno de Orce. Un análisis de la abundancia de los principales huesos largos preservados en la asociación ha mostrado que las hienas produjeron una fragmentación diferencial de acuerdo con su densidad mineral y su contenido medio en médula ósea. Todo ello permite presentar un modelo descriptivo-cuantitativo para la caracterización de asociaciones óseas generadas por la actividad de los hiénidos, pudiendo ser Venta Micena el ejemplo de actividad concentradora-modificadora de los representantes de la especie *Pachycrocuta brevirostris*. Se ha podido deducir una intensa selección de presas por parte de los carnívoros, los cuales cazaban preferentemente individuos jóvenes, hembras y ejemplares con capacidad locomotriz disminuida en el caso de las especies de ungulados con mayor tamaño. Las evidencias que apoyan este modelo son: (i) la abundancia de individuos jóvenes, con dentición decidua, en relación al peso estimado para los adultos de cada especie; (ii) los perfiles de mortandad gradual con forma de U, inferibles de las medidas de altura de la corona dentaria; (iii) la presencia de abundantes metapodios que muestran diversas osteopatologías; y (iv) la proporción de sexos deducible a partir de los metacarpienos de los grandes bóvidos. Finalmente, la comparación entre la frecuencia en que los carnívoros modernos africanos cazan y carroñean ungulados de diferentes clases de tamaño y la abundancia de estas categorías en la asociación fósil sugiere que la hiena de Venta Micena era básicamente carroñera, aprovechando los cadáveres de presas cazadas y consumidas en parte por otros carnívoros comedores de carne y no fracturadores de huesos, tales como los félidés con dientes en forma de sable y los perros salvajes.

PALABRAS CLAVE: ASOCIACIÓN ÓSEA, TAFONOMÍA, PALEOECOLOGÍA, ANÁLISIS MULTIVARIANTE, PLEISTOCENO INFERIOR, VENTA MICENA.

INTRODUCTION AND BACKGROUND

The Venta Micena site (Orce, Granada, south-east Spain) is located in the eastern sector of the Guadix-Baza basin (Fig. 1). This basin was endorheic until upper Pleistocene times, thus facilitating an exceptional record of the Plio-Quaternary taphocoenoses of large mammals, which were pre-

served in swampy and lacustrine sediments. Previous studies indicate that the Venta Micena assemblage is included in 90-98% pure micritic limestone, which precipitated in freshwater ponds emplaced on a caliche paleosol of diagenetic origin. This paleosol surrounded a more or less stable and shallow lake with swampy marginal zones that existed in the valley of Orce during the

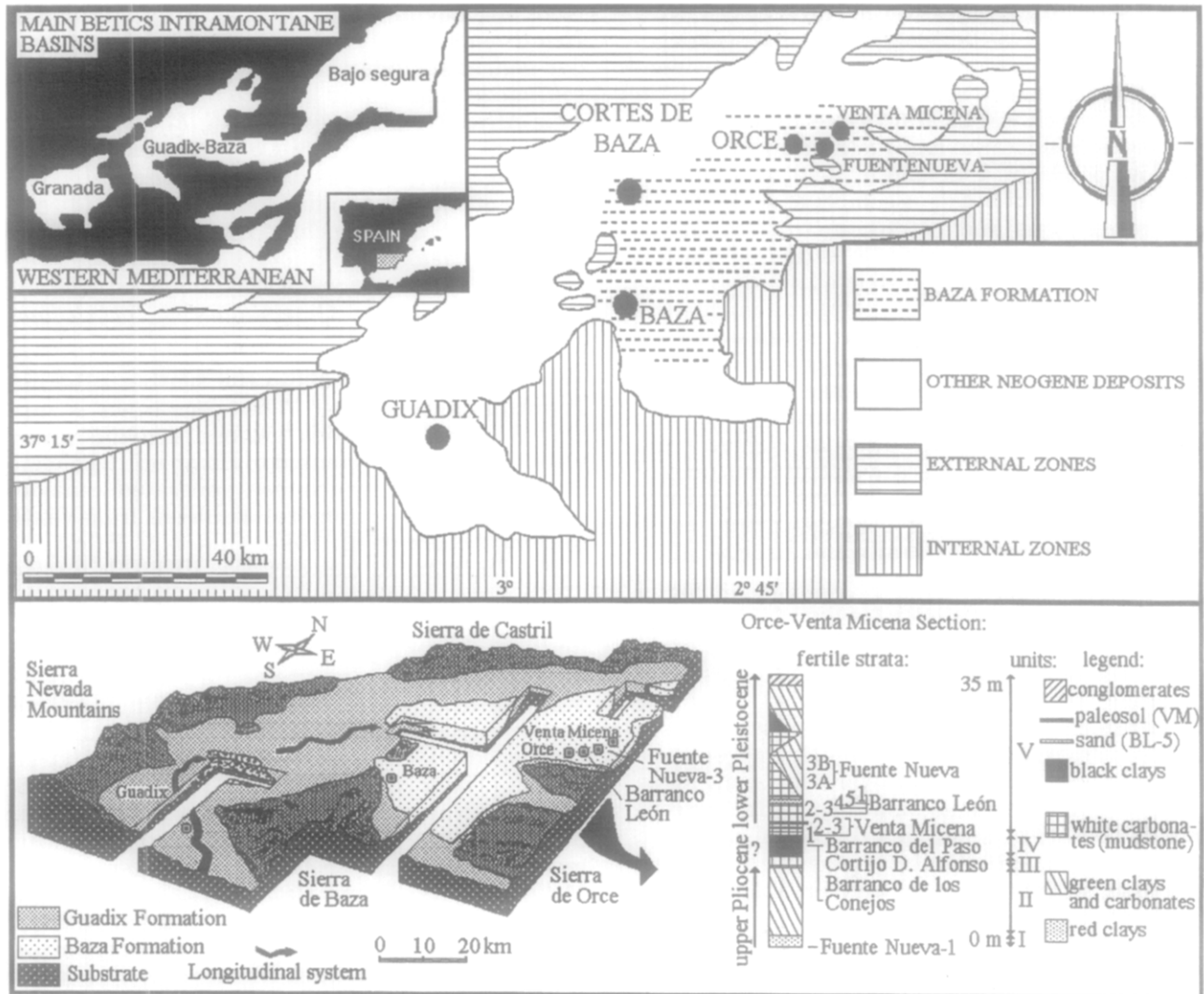


FIGURE 1 - Geological location of Venta Micena and Orce in the intramountainous basin of Guadix-Baza (province of Granada, Southeast Spain), and stratigraphic sections of the Plio-Pleistocene deposits in the Orce-Fuente Nueva-Venta Micena sector. *Localisation géologique de Venta Micena et d'Orce dans le bassin intramontagneux de Guadix-Baza (province de Grenade, Sud-Est de l'Espagne) et succession stratigraphique des dépôts plio-pléistocènes dans le secteur d'Orce-Fuente Nueva-Venta Micena.*

Plio-Pleistocene (Vera et al. 1985; Soria et al. 1987). Biostratigraphic analyses of the faunal assemblage (Martínez-Navarro 1991, 1992a; Martínez-Navarro & Palmqvist 1995; Turq et al. 1996; Martínez-Navarro et al. 1997) place this site in the lower Pleistocene, with an estimated age of 1.2 ± 0.2 Ma.

The 80-120 cm thick Venta Micena stratum is one of the various fossiliferous units with macromammals in the Plio-Pleistocene sedimentary sequence of Orce, whose surface can be followed along 2.5 km approximately, and stands out topographically in the ravines of the region. All the fertile strata from the Orce-Venta Micena sector are found within a carbonate sequence with mean thickness

of 15 m, horizontal stratification undisturbed by tectonic activity, without breaks or discordances, and with a cartographic extension of approximately 16 km². This sequence shows the following vertical sedimentary evolution: white clayey marly facies with carbonate concretions of diagenetic origin and freshwater invertebrates (swamp in central facies); clayey muddy facies with mud-cracks, abundant coal and bony mammal remains (swamp in marginal facies); white carbonate facies (mudstone) with paleosols, carbonate concretions and abundant skeletal remains of fossil mammals (lake with various periods of partial desiccation, during one of which the Venta Micena assemblage was formed).

The fossils from Venta Micena are placed on a paleosol which was developed on sediments deposited during a first lacustrine stage, thus evidencing a generalized descent of the water table in the lake, which was characterized by wide emerged zones (mudcracks and rootmarks) with small shallow ponds (< 1 m depth, 2-20 m diameter) (Gibert et al. 1992). The assemblage is embedded in homogeneous and porous micrite sediments, which precipitated during a period of partial expansion of the ponds (restricted swampy biotope of carbonate facies, with plants colonizing the border of the ponds), and it was closed over by a massive precipitation of micrite produced during an immediately subsequent phase of uprising of the water table in the lake (lacustrine stage two). This welling was rather slow, as suggests the absence of terrigenous, erosive structures, and of any evidence of sediment traction. The micrite which precipitated during both lacustrine stages is very similar, both texturally and structurally.

The accumulation of skeletal remains in Venta Micena (Gibert & Caporicci 1989; Gibert et al. 1992; Palmqvist et al. 1992, 1993) was exclusively due to the biotic factors. Geologic processes, such as fluvial transport, can be excluded, since the bones are randomly oriented, and show no traces of abrasion from rolling or similar movements. Furthermore, many bones were for some time exposed to the elements, and a very high percentage of specimens show clear marks of carnivore damage (with almost total dismembering of all elements, and bite marks and breakage in the most vulnerable places).

The palaeoecological analyses of this fossil community (Martínez-Navarro 1991, 1992b; Mendoza et al. 1993) have been based both on cenogram methodology (Valverde 1967; Legendre 1986) and on multivariate comparisons with several types of modern mammalian communities (Reed 1997). The results obtained suggest that the composition of the palaeocommunity of Venta Micena, in terms of the relative abundance of groups of species established according to their size and with the type of trophic resources used, was similar to that of present day communities of large mammals inhabiting African savannas with tall grass and spiny trees.

The systematic study of macromammals (Martínez-Navarro 1991, 1992a; Martínez-Navarro & Palmqvist 1995, 1996; Palmqvist et al. 1996a) reveals three faunal components in the fossil assemblage: 1) Species present in Western Europe during the upper Pliocene (*Mammuthus meridionalis*, *Stephanorhinus etruscus*, *Homotherium latidens*, *Lynx* aff. *issiodorensis*, cf. *Meles* sp. and *Ursus etruscus*), 2) immigrants from Asia (*Praeo-*

vibos sp., Bovini cf. *Dmanisibos*, *Soergelia minor*, *Hemitragus alba*, Caprini gen. et sp. indet., Cervidae gen. et sp. indet., *Megaloceros* [*Megaceroides*] *solilhacus* and *Canis etruscus*), and 3) species from Africa (*Megantereon whitei*, *Equus altidens*, *Pachycrocuta brevirostris*, *Canis* [*Xenocyon*] *falconeri* and *Hippopotamus amphibius antiquus*). The species of small mammals found at Venta Micena (Agustí et al. 1987) include *Desmana* sp., *Apodemus* aff. *mystacinus*, *Eliomys intermedius*, *Allophaiomys pliocaenicus*, *Castillomys crusafonti* ssp., *Hystrix major*, *Oryctolagus* cf. *lacosti* and *Prolagus calpensis*.

The presence of humans in the southern Iberian Peninsula during lower Pleistocene times is supported by the finding of a few fossil remains which were tentatively attributed to *Homo* sp. (a polemic cranial fragment which has generated considerable debate and a humeral diaphysis from Venta Micena; Gibert et al. 1994; Gibert & Palmqvist 1995; Zihlman & Lowenstein 1996; Palmqvist 1997; a medial phalanx from the karstic site at Cueva Victoria; Palmqvist et al. 1996b), and by undoubted stone artefacts found in situ in the lower Pleistocene site at Fuente Nueva-3a (1.07 Ma), which show a very simple technology not essentially different from the Oldowan and Developed Oldowan types found in sub-Saharan Africa (Tixier et al. 1995; Turq et al. 1996; Martínez-Navarro et al. 1997). It is interesting to point out that the human mandible and lithic industries found in the lower Pleistocene (> 1.6 Ma) deposits from Dmanisi, East Georgia (Gabunia & Vekua 1995) are associated with *M. whitei*, the African machairodont also present in Venta Micena (Martínez-Navarro & Palmqvist 1995, 1996), what indicates extensive faunal dispersal from Africa to Eurasia in the lower Pleistocene.

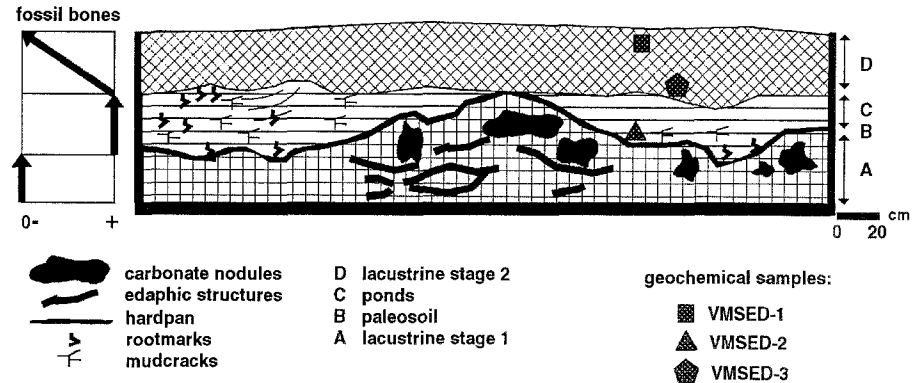
The objectives of this study are: (i) to determine whether the faunal assemblage preserved the structure of the original palaeobiocoenoses; (ii) to identify more accurately the biological agents responsible for the modification and accumulation of the assemblage; and (iii) to study the interspecific relationships that existed in the palaeocommunity, such as those produced by the predatory activity of carnivores.

THE VENTA MICENA STRATUM

The Venta Micena stratum has a mean thickness of 1 m and presents the following vertical structure from bottom to top (Fig. 2):

- A basal level (lacustrine stage 1) whose thickness is between one third and half of the stratum, formed by homogeneous micrite sediments with

FIGURE 2 - Idealized stratigraphic profile of Venta Micena. *Profil stratigraphique schématisé de Venta Micena.*



some carbonate nodules (5-20 cm thick), small mud banks and microscopic fossil shells of freshwater mollusks (among them, *Melanoides tuberculata*, an eurythermal species which colonizes a wide range of biotopes according to Anadón et al. 1987).

- A 4-15 mm thick calcrete paleosol (hardpan), which forms an irregular surface, subparallel to the bedding plane, and is thicker at the highest topographic heights.

- A new level of homogeneous and porous micrite sediments (lacustrine stage 2), which continues up to the top of the stratum, showing numerous rootmarks and mudcracks, which are more abundant in its lower part, and a high density of fossil bones of large mammals; this very restricted vertical interval in the distribution of fossils, marks the palaeontological site at Venta Micena.

The macroscopic, petrographic, geochemical and mineralogic analyses of the stratigraphic levels have yielded the following results: The basal carbonate deposits are rich in mollusks but sterile in vertebrate fossils, thus attesting to a first generalized lacustrine stage in the region, in which the micrite was precipitated under a constant, but variable in depth, water sheet (Soria et al. 1987), in a shallow and well oxygenated environment, since it is suggested by the absence of both pyrite and carbonate facies rich in organic matter that the lake was not subject to eutrophic conditions (Wells 1983). The fossils of terrestrial vertebrates preserved at Venta Micena are located exclusively above the calcrete level, which is interpreted as being a paleosol, developed on the surface of the micrite sediments previously deposited during the first lacustrine stage. The distribution of fossils follows the pre-existing limnic microtopography. This surface defines a stratigraphic unconformity, which was developed after a period of generalized retraction of the Pleistocene lake (Gibert et al. 1992). The calcrete paleosol thus indicates the emergence of the micrite deposits, which were then exposed to subaerial paedogene-

sis in an arid climate with high evaporation rate (Plaziat 1984). The low percentage of iron oxides (0.6% Fe_2O_3) suggests that these sediments were hardly affected by the oscillations in the phreatic level.

The Pleistocene lake of Orce had rather limited dimensions both in expanse and depth during the lacustrine stages described above, since the carbonate deposits are restricted in the large lakes to the borders, while in those of minor size they can extend over all the bottom (Kukal 1971), as happened in the studied region (Vera et al. 1985; Soria et al. 1987). The traditional connection between lakes, swamps and calcrete/sebkha (which may be masked by subaerial paedogenesis of marshy and lacustrine deposits, in which the evaporation plays an essential role and modifies the original sediments; Plaziat 1984) is transformed in the Orce-Venta Micena sector in the following sequence: swamps (Plio-Pleistocene), lake (lacustrine stage 1, lower Pleistocene), emergence and swampy ponds (paleosol formation; stratigraphic unconformity), lake (lacustrine stage 2) (Arribas 1995). In this case the calcrete type paedogenesis does not hide the sedimentary origin of the studied stratum, but allows the distinction of various sedimentary environments and to identify the inner surfaces which have chronological utility in the region, one of which is the local isochron of Venta Micena (Arribas et al. 1994).

GEOCHEMICAL ANALYSES AND DIAGENETIC SETTING

Geochemical analyses have been performed on bony samples obtained from ten metacarpals of *Equus altidens* which were unearthed in different grids of the Venta Micena quarry. The samples (VME-1 to VME-10) were removed from the cortical bone at half of the diaphysis. Three samples of sediment (Fig. 2), obtained from the bottom of the fertile level of the Venta Micena stratum (VMSSED-1, lacustrine stage 2), from the calcreous scab (VMSSED-2, emerged environment) and

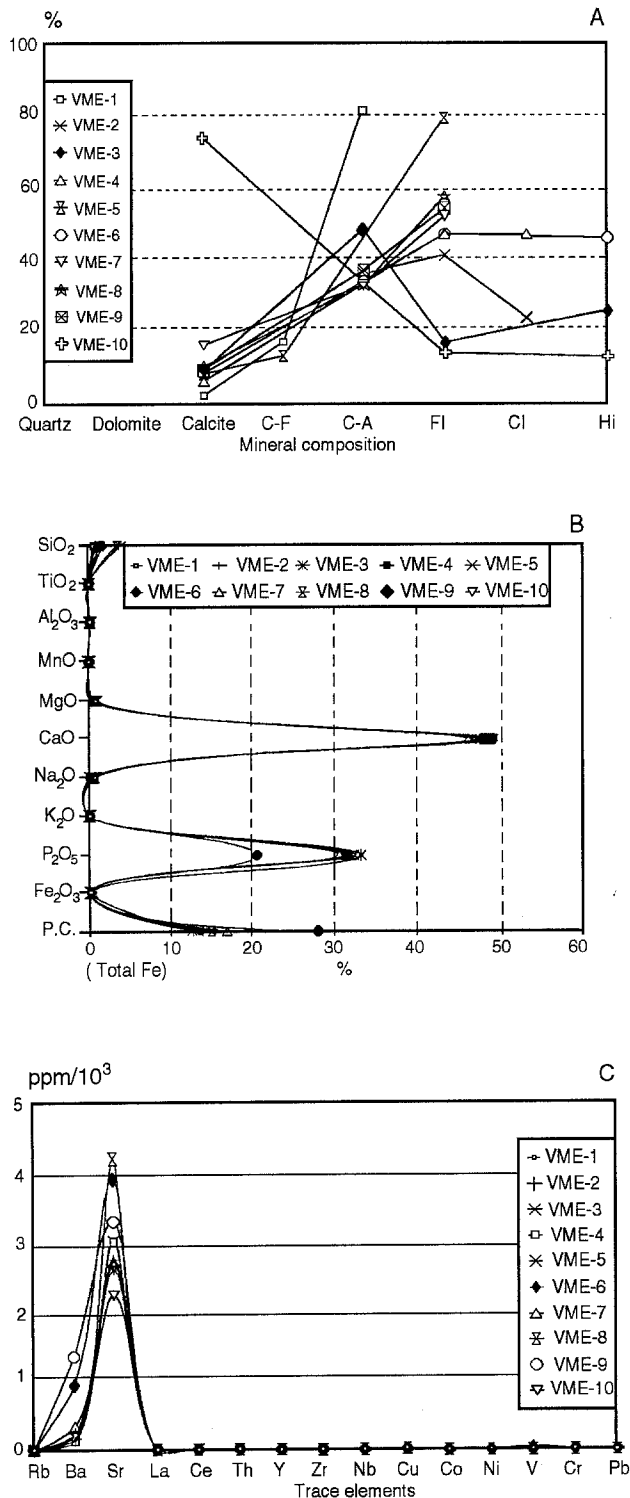


FIGURE 3 - Percentages of mineral phases (A; C-F: carbonate-fluoroapatite; C-A: carbonate-apatite; Fl: fluorine-apatite; Cl: chlorine-apatite; Hi: hydroxyapatite), weight of oxides (B), and abundance (ppm) of trace elements (C) in ten samples (VME-1 to VME-10) of equid bones from Venta Micena.

from a calcareous nodule (VMSED-3, ponds) were also analysed.

The mineral phases (Fig. 3) which predominated in all the bony samples analysed were fluorine-apatite (0-79%) and carbonate-apatite (0-81%); chlorine-apatite was detected in two samples (VME-2,4; 24 and 47%, respectively) and hydroxyapatite in another three (VME-3,6,10; 26, 46 and 13%, respectively). Calcite was found in low percentages (2-16%) in all samples, except VME-10, in which this mineral was very abundant (73%). The prevailing oxides were CaO (46-49%) and P₂O₅ (20-33%); SiO₂ was found in low proportions (0.5-4.2%), TiO₂ was only present in four samples (VME-4,5,6,8) in very low proportions (0.01-0.05%), K₂O was detected in two samples (VME-7,8; 0.02 and 0.01%, respectively), Fe₂O₃ was present in all of them but in minor proportions (<0.4%) and MnO was absent. The predominant trace elements were Sr (2243-4198 ppm) and Ba (121-1348 ppm), followed by V (2-39 ppm), Cu (13-19 ppm), Cr (2-12 ppm), Th (1-11 ppm), Ce (0-10 ppm), Co (0-7 ppm), Ni (0-2 ppm) and La (0-2 ppm).

The comparison between the geochemical results obtained from the fossil samples and those from the sediment ones (Fig. 4) revealed the following differences and similarities:

Mineral composition: the three samples of sediment showed great mineral homogeneity (98-99% calcite, 1% quartz), and the sample from the calcareous paleosol also presented dolomite (1%) as a new mineral phase. On the contrary, the mineralogy of the samples obtained from equid fossils was more heterogeneous, since although both the fluorine-apatite and the carbonate-apatite were the prevailing mineral phases, another three phosphatic mineral phases such as carbonate-fluoroapatite, chlorine-apatite and hydroxyapatite were also present, as well as low proportions of calcite.

Abundance of oxides: the percentages in weight for oxides were similar in all the samples analysed from the sediment, showing no significant differences among them. The oxide content of the fossil samples was also homogeneous, with the exception of VME-9 and VME-10, in which P₂O₅ constituted about 20%, and their SiO₂ (0.5-4.2%) content was lower and more variable than in the sediment samples (8.6-9.1%).

Abundance of trace elements: the trace elements which predominated in both the sediment and the

Pourcentages des phases minérales (A; C-F: carbonate-fluoroapatite; C-A: carbonate-apatite; Cl: chlorapatite; Hi: hydroxyapatite, poids des oxydes (B) et abondance (ppm) des éléments traces pour dix échantillons (VME-1 à VME-10) d'os d'équidés de Venta Micena.

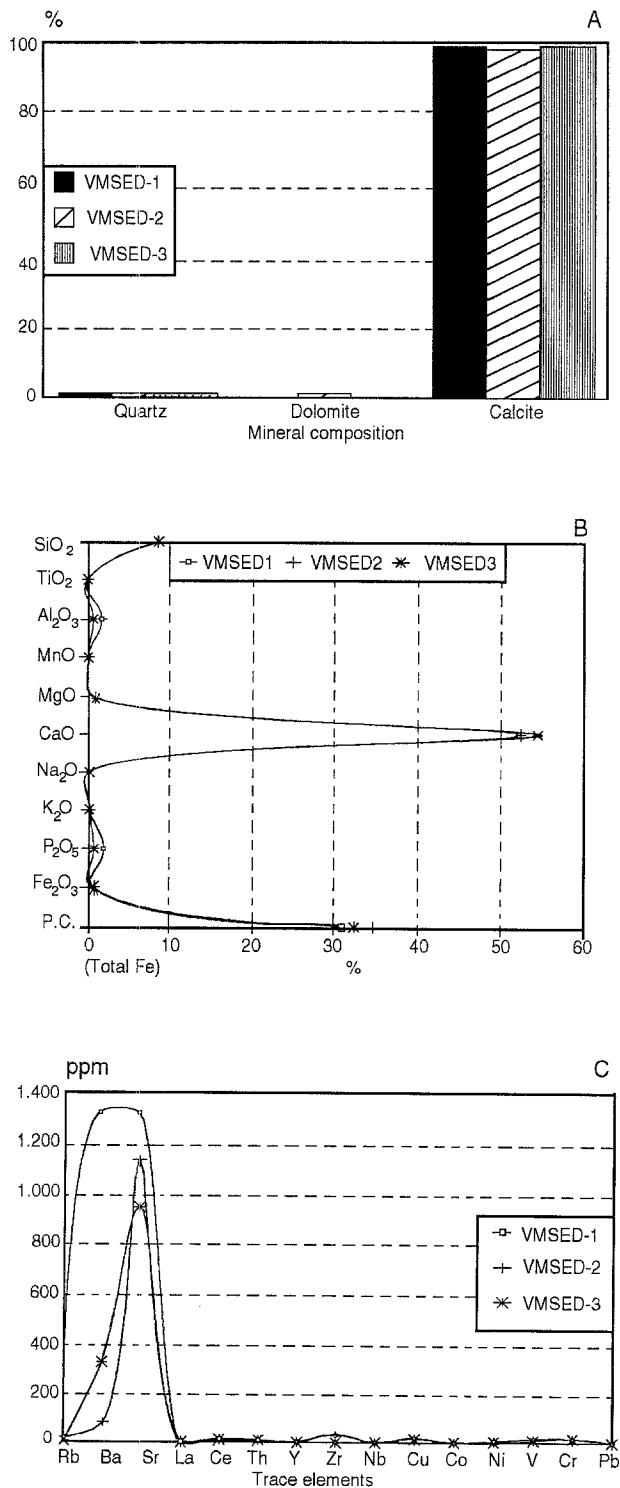


FIGURE 4 - Percentages of mineral phases (A), weight of oxides (B), and abundance (ppm) of trace elements (C) in three samples from the Venta Micena stratum (VMSED-1: micrite from lacustrine stage 2; VMSED-2: calcrete paleosol; VMSED-3: micrite from a calcareous nodule in the ponds).

fossils were Sr and Ba. Both elements showed similar proportions in the sample from the sediment precipitated during the second lacustrine stage, while Sr prevailed over Ba in the samples from the bottom of the fossiliferous level (calcrete paleosol), from the carbonate nodules, and from the equid fossils. Ba was detected both in the bones and in the sediment in similar quantities (121-1348 ppm and 79-1328 ppm, respectively), but Sr was less abundant in the sediment (945-1325 ppm) than in the fossils (2243-4198 ppm).

Inorganic matter represents approximately 70% of bone and dentine, which is usually composed of hydroxyapatite [$\text{Ca}_{10}(\text{PO}_4)_6 \cdot 2\text{OH}$], and the remaining 30% is organic matter constituted in its majority by collagen, which can also vary in its chemical composition (Francillon-Vieillot et al. 1990). The fossils from Venta Micena showed a mineralogic composition in which the original phase, the hydroxyapatite, had disappeared in 7 out of 10 samples, and its abundance was very low in the other 3 samples. The diagenetic processes seem to have produced an enrichment in calcite of the bony structure and a chemical modification of the organic apatite into other phases of the apatite group, as a function of the higher or lower substitution of the Ca, P and OH groups by different trace elements or by oxides, which were assimilated from the surrounding sediment. P was in part replaced by Si within the bony structure, and the incorporation of this element could have been produced by chemical substitution during the diagenesis or during the life of the animals, from the silicophytolites of the herbs that they consumed. Si was not found in the bones as a mineral phase (quartz) but in minerals from the apatite group, what seems to indicate that its incorporation into the bone tissue was produced during the life of the animals. In fact, the important amount of SiO_2 detected in the micrite sediment (8.6-9.1%), which was generated by chemical precipitation of carbonates, could be due to the concentration in the sediment of the organic silica from the herbs that covered the plains surrounding the paleolake of Orce (Mendoza et al. 1993). The same interpretation is adequate for the enrichment in Sr and Ba, minor elements substituting Ca in the hydroxyapatite, which were more abundant in the fossils than in the sediment. On the other hand, several trace elements such as Rb, La, Y, Zr, Nb and Ni have been detected in the sediment, but they were hardly incorporated in the bones.

The X-ray diffraction spectra of the samples analysed and their comparison with those obtained in

Pourcentages des phases minérales (A), poids des oxydes (B) et abondance (ppm) des éléments traces (C) dans trois échantillons de la couche de Venta Micena (VMSED-1: micrite de l'étage lacustre 2; VMSED-2: calcrète de paléosol; VMSED-3: micrite d'un nodule calcaire des mares).

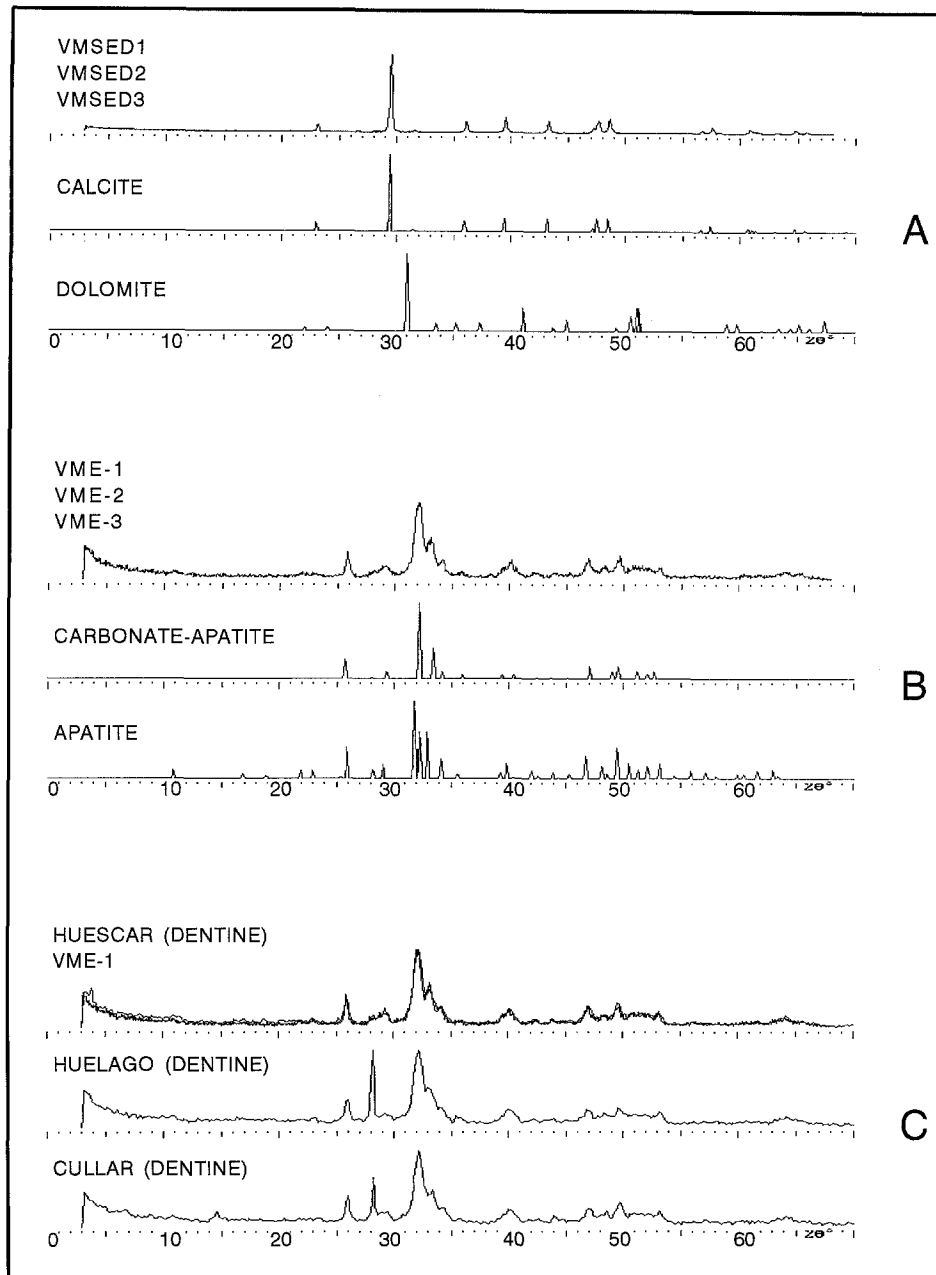


FIGURE 5 - X-ray diffraction spectra of the samples from Venta Micena. **A**, comparison of the three samples of sediment with samples of pure calcite and dolomite, what shows the homogeneity in the crystallinity of the spectra from the site, as indicated by their perfect overlap. **B**, representation of three bone samples (VME-1 to VME-3) which show great cristaline homogeneity, compared with the spectra for the two mineral phases of the apatite group with which they show a higher similarity. **C**, comparison between the bone from Venta Micena (VME-1) and the dentine of equid teeth from Huéscar; both show analogous composition and similar differences with the spectra of equid dentine from the palaeontological sites at Huélago and Cúllar de Baza (which have a new cristaline phase, and are very similar to each other). X-ray diffraction measurements were carried out on powdered bone and tooth samples by means of a Philips diffractometer monochromatized to Cu-k radiation ($\lambda=1540\text{\AA}$). *Spectre de diffraction X pour des échantillons de Venta Micena. A, comparaison de trois échantillons de sédiment avec des échantillons de calcite et de dolomite pures montrant l'homogénéité de cristallinité du spectre du site comme l'indique leur recouvrement parfait. B, représentation de trois échantillons d'os (VME-1 à VME-3) montrant la grande homogénéité cristalline, comparée avec les spectres de deux phases minérales du groupe de l'apatite avec lesquels ils montrent la plus haute similarité. C, comparaison d'un os de Venta Micena (VME-1) et la dentine de dents d'équidé de Huéscar; les deux montrent une composition analogue et des différences similaires avec le spectre de dentine d'équidé des sites paléontologiques de Huélago et Cøllar de Baza (qui ont une nouvelle phase cristalline et sont très similaires entre eux). Les mesures de diffraction X sont réalisées sur de l'os en poudre et des échantillons de dents à l'aide d'un diffractomètre monochromatique Philips en radiation Cu-k ($\lambda= 1540\text{\AA}$).*

samples from other sites in the Baza Formation of the basin (Alberdi & Ruiz Bustos 1989), show interesting results (Fig. 5). The spectrograms of the equid bones from Venta Micena are similar to the spectrum for the sample of tooth dentine obtained from equids of the middle Pleistocene site at Huéscar-1. Both spectra differ from those obtained for the tooth dentine of equids from two other sites in the basin, the upper Pliocene site at Huélago (*Equus stenorhis livenzovensis*) and the middle Pleistocene site at Cúllar de Baza-1, whose samples are very similar. Venta Micena and Huéscar-1 are very close geographically within the carbonate Baza Formation (Vera 1970a, 1970b), while Huélago and Cúllar de Baza-1 are located quite distant (several dozens of km) from the former sites, although both belong to the same basin, and the former is located in the Guadix Formation, which shows clastic characteristics. These comparisons suggest that the mineral composition of the fossilized bony tissue (excluding enamel, which presents both structural and compositional properties clearly different from those of the bone and dentine) does not rely on the taxonomic filiation or on the age of the fossils, but on the lithologic characteristics and the hydrogeological evolution of the different formations in which the palaeontological sites are emplaced.

The sedimentary infilling affects only those bones which have biostratinomic fractures (spiral and longitudinal fractures, as discussed below). The bones which were preserved complete lack any sediment in their inner surface, even in those areas which are close to large nutrient foramina, what indicates that the bones were buried with the periosteum intact. The sedimentary infilling has the same micrite composition as that of the stratum, and is only present in the medullary cavity of the fractured bones, in form of small mud flows which disappear towards the interior of the specimens. This type of infilling is not found in the complete bones.

All the major long bones which were preserved complete, show one or more diagenetic fractures, orthogonal to their longitudinal axes, which are located either at half of the diaphyses or at their ends. These fractures could have been produced following two distinct processes: during the diagenetic compaction, as a result of the superposition of some elements on others (more than 90% of the bones of the assemblage are in contact with other bones) or due to the decompression produced as a consequence of the erosion of the sediments which covered the stratum. These orthogonal fractures are in all cases delimited by bone (i.e., there is no fracture defining the end of one specimen), what helps to clarify the taphonomic state of the assem-

blage (accumulated, resedimented or reworked), since the finding of bone fragments, isolated and delimited by this type of fractures, would imply taphonomic reorganization (i.e., burial + mineralization + diagenetic breakage + unearthing by erosion + displacement, dispersal and/or destruction of certain bones + burial of different specimens from the same bone). When these processes take place, the bone assemblage is, at least in part, mixed diagenetically (i.e., reorganized), which precludes the possibility of making detailed palaeoecological analyses, since the bones may have different age and may come from different environments. Clearly, this is not the case here.

BIOSTRATINOMY OF THE ASSEMBLAGE: VARIATES, PROCESSES AND AGENTS

We have analysed different biostratinomic variates in order to characterize the macrovertebrate assemblage from Venta Micena. Previous approaches to the taphonomic study of this site (Gibert et al. 1992; Palmqvist et al. 1992) include the comparative study of the preservational state of the surface of the bones, and the evidence of the taphonomic bias experienced by the whole assemblage, respectively. In this study we have followed in part the procedure described by Behrensmeyer (1991) for the biostratinomic characterization of vertebrate assemblages.

DIVERSITY, SPECIES ABUNDANCE, AGE CLASSES AND SIZE ESTIMATES

The Venta Micena collection is composed of 6453 identifiable skeletal remains of 19 macromammalian species (≥ 5 kg) and more than 10,000 unidentifiable bone shafts. Table 1 summarizes the raw data on the abundance of species (NISP: number of dental and non dental identifiable specimens; MNI: minimal number of individuals; updated from Martínez-Navarro 1991, 1992a).

The palaeontological sample from this site increases each year during systematic excavations. Up to the present moment, the macromammalian assemblage is composed of 19 taxa, which belong to the orders Proboscidea, Artiodactyla, Perissodactyla and Carnivora, represented by the following families: Elephantidae, Bovidae, Cervidae, Hippopotamidae, Equidae, Rhinocerotidae, Canidae, Felidae, Hyaenidae and Ursidae. The presence of two other mammalian species of small size, the badger (*Meles* sp.) and the porcupine (*Hystrix major*), has been cited in this site, although we have found no fossil remains of the former within the macrovertebrate assemblage. The first species would indicate the presence of mustelids in the palaeocommunity, and the porcupine (which is represented by an isolated maxilla)

Species	NISP (teeth/bones)	A* (%)	MNI (inf./ad.)	% infant.	Wmean (range)	Ir (%)
<i>Mammuthus meridionalis</i>	48 (16/32)	48.0 (0.1)	5 (4/1)	80.0	6033.8 (3713.1-9746.9)	4.26
<i>Hippopotamus amphibius antiquus</i>	58 (19/39)	90.6 (0.2)	5 (3/2)	60.0	3131.4 (2408.7-3978.8)	4.47
Bovini cf <i>Dmanisibos</i>	775 (382/393)	4532.2 (8.2)	27 (16/11)	59.3	449.4 (371.4-745.0)	15.02
<i>Soergelia minor</i>	334 (215/129)	3102.2 (5.6)	13 (3/10)	23.1	227.6 (127.6-324.0)	13.45
<i>Praeovibos</i> sp.	6 (3/3)		1 (0/1)	0.0	316.4 (195.2-388.8)	3.14
<i>Hemitragus alba</i>	305 (209/96)	6015.6 (10.8)	14 (2/12)	14.3	75.2 (57.2-119.4)	11.40
Caprini gen. et sp. indet.	1(0/1)		1(0/1)	0.0	8.0-10.0	
<i>Megaloceros (Megaceroides) solilhacus</i>	962 (557/405)	6263.0 (11.3)	36 (15/21)	41.7	383.8 (269.0-567.8)	13.99
Cervidae gen. et sp. indet.	417 (231/186)	7010.9 (12.6)	20 (3/17)	15.0	95.1 (63.5-170.6)	10.91
artiodactyla indet., size 2	12 (0/12)					
artiodactyla indet., size 2-3	9 (0/9)					
artiodactyla indet., size 3	91 (0/91)					
<i>Stephanorhinus etruscus</i>	90 (55/35)	229.7 (0.4)	6 (2/4)	33.3	1521.1 (1074.0-2176.0)	5.90
<i>Equus altidens</i>	2562 (1183/1379)	17 622.1 (31.7)	70 (32/38)	45.7	354.0 (243.8-486.7)	17.34
herbivore indet., size 2-3	11 (0/11)					
herbivore indet., size 3	357 (0/357)					
herbivore indet., size 3-4	20 (0/20)					
herbivore indet., size 4-5	15 (0/15)					
herbivore indet., size 5-6	6 (0/6)					
<i>Vulpes praeglacialis</i>	24 (19/5)	3480.3 (63)	1 (0/1)	0.0	3.0-5.0 8.24	
<i>Canis falconeri</i>	65 (40/25)	2748.4 (4.9)	3 (0/3)	0.0	29.8 (24.7-34.7)	7.44
<i>Canis etruscus</i>	33 (20/13)	1789.0 (3.2)	4 (0/4)	0.0	9.9 (9.3-11.5) 2.83	
<i>Lynx aff. issiodorensis</i>	6 (2/4)	501.3 (0.9)	1 (0/1)	0.0	8.0-10.0 2.13	
<i>Megantereon whitei</i>	16 (7/9)	400.8 (0.7)	3 (0/3)	0.0	52.9 (46.1-58.1)	1.89
<i>Homotherium latidens</i>	7 (6/1)	62.0 (0.1)	2 (0/2)	0.0	243.9 (183.5-338.0)	1.24
Felidae indet., size 2-3	24 (0/24)					
<i>Pachycrocuta brevirostris</i>	62 (34/28)	1364.6 (2.5)	10 (4/6)	40.0	64.0 (57.8-70.7)	2.46
<i>Ursus etruscus</i>	27 (15/12)	178.6 (03)	3 (1/2)	333	374.9 (309.2-451.6)	3.04
carnivore indet., size 1	2 (0/2)					
carnivore indet., size 2-3	21 (0/21)					
mammal indet., size 1	4 (0/4)					
mammal indet., size 2	11 (0/11)					
mammal indet., size 2-3	73 (0/73)					

TABLE 1 - Abundance of the macromammal species (≥ 5 kg) identified in the Venta Micena assemblage (updated from Martínez-Navarro 1991, 1992a). NISP: number of identifiable specimens (teeth/bones). A*: abundance corrected for taphonomic biases. MNI: minimum number of individuals (juveniles/adults). W: estimated body weight (in kg) for the adult individuals (mean and range) I: index of representation of skeletal parts. *Abondance des espèces de macromammifères (≥ 5 kg) identifiées dans l'assemblage de Venta Micena (mise à jour de Martínez-Navarro 1991, 1992a). NISP: nombre de spécimens identifiables (dents/os). A*: abondance corrigée des biais taphonomiques. MNI: nombre minimum d'individus (juvéniles/adultes). W: poids corporel estimé (en kg) pour des individus adultes (moyenne et extension). I: indice de présence des parties squelettiques.*

stands out since it could be one of the biological collecting agencies of bones.

If we compare the taxonomic composition of the Venta Micena assemblage with those of another three Plio-Pleistocene lacustrine sites from the Guadix-Baza basin (Alberdi et al. 1989), we see that Venta Micena shows the highest diversity of large mammals, since each of the sites at Huélago (upper Pliocene), Huéscar-1 (early middle Pleistocene) and Cúllar de Baza-1 (middle Pleistocene) only present 10 macromamalian species. The first of these sites lacks carnivores (which constitutes an anomalous peculiarity within the palaeomastologic record from Spain, probably due to the special taphonomic characteristics of this site), has one proboscidean (cf. *Mammuthus meridionalis*), two perissodactyls (*Equus stenorhis livenzovensis* and *Stephanorhinus* cf. *etruscus*), four bovids (*Leptobos* cf. *elatus*, *Gazella borbonica*, *Gazello-spira torticornis* and cf. *Hesperidoceras merlae*),

and three cervids (*Criozetoceros ramosus*, *Eucladoceros* cf. *senezensis* and Cervidae indet.); the assemblage from Huéscar-1 has four species of carnivores (*Canis etruscus*, *Panthera gombaszogensis*, *Homotherium* sp. and Hyaenidae indet.), one proboscidean (*Elephas antiquus*), three perissodactyls (*Equus stenorhis* interm. *granatensis/altidens*, *Equus sussenbornensis* and *Stephanorhinus etruscus*), one cervid (*Megaloceros [Megaceroides] cf. solilhacus*) and one hippopotamid (*Hippopotamus major*); finally, the assemblage from Cúllar de Baza-1 has two carnivores (*Canis etruscus* and *Crocuta crocuta*), one proboscidean (*Mammuthus trogontherii*), three perissodactyls (*Equus altidens*, *Equus sussenbornensis* and *Stephanorhinus etruscus*), two bovids (*Bison* sp. and *Capra* sp.), one cervid (*Dolichodoryceros savi-ni*) and one suid (*Sus* cf. *scrofa*). These three sites are also located on sediments which were deposited in swampy and lacustrine environments, under similar conditions to those of Venta Micena

(without evidence of subaerial exposure in the assemblages). The main difference between the assemblage from Venta Micena and those recovered from other sites in the Guadix-Baza basin is the high diversity of carnivore species preserved in the former assemblage, which has all ecological niches of carnivores represented (from opportunistic scavengers to top predators). On the other hand, the taxonomic richness of large mammals in Venta Micena is the same as that recorded in a modern hyaena den (*Crocuta crocuta*) from the Amboseli National Park (Kenya), which was also developed on a calcrete paleosol (Hill 1981, 1984), in which the skeletal remains from 16 to 18 taxa were represented.

Table 1 shows that the herbivore species are those best represented in the Venta Micena assemblage by both NISP and MNI counts, with the following rank abundance: *Equus altidens*, *Megaloceros* (*Megaceroides*) *solilhacus*, Bovini cf. *Dmanisibos*, Cervidae gen. et sp. indet., *Soergelia minor*, *Hemitragus alba*, *Stephanorhinus etruscus*, *Hippopotamus amphibius antiquus*, and *Mammuthus meridionalis*. The worst represented species are carnivores, in which the most abundant species according to their NISP values are *Pachycrocuta brevirostris* and *Canis* (*Xenocyon*) *falconeri* (of which the hyaenid stands out if we also consider its high MNI value).

The index of skeletal representation ($I_r = [NISP_i \times 100] / [NE_i \times MNI_i]$, where $NISP_i$ is the minimal number of identifiable specimens recovered from the "i" species, NE_i is the number of osseous elements found in the skeleton of a living individual of this species, and MNI_i is the minimal number of individuals estimated for species "i" in the assemblage) indicates for each species the percentage of skeletal elements which were preserved in relation to the sum of the total number of elements for all individuals identified in the assemblage (i.e., preservational completeness), and thus provides information about the extent of the taphonomic biases which affected the composition of the assemblage. For example, if an assemblage was produced by a catastrophic or mass mortality event, followed by immediate burial, the I_r index would then take the maximum value (100%) for each species, since all skeletal elements would have been preserved if the diagenetic conditions were not destructive. However, the species in Venta Micena are represented by less than 20% of potentially preservable elements (Fig. 6). The herbivore species may be ordered by decreasing I_r values as follows (Table 1): *Equus altidens*, Bovini cf. *Dmanisibos*, *Megaloceros* (*Megaceroides*) *solilhacus*, *Soergelia minor*, *Hemitragus alba*, Cervidae gen. et sp. indet., *Stephanorhinus etruscus*, *Hippopotamus amphibius antiquus*, *Mammuthus*

meridionalis and *Praeovibos* sp. The main difference between this ordering and the previous one is that the individuals of Bovini cf. *Dmanisibos* are better represented by skeletal remains than those of *Megaloceros*, although the latter species has higher NISP and MNI values, and the same difference is found between *Hemitragus* and Cervidae indet., respectively. Carnivores are poorly represented in the Venta Micena assemblage, since most of these species have <5% values in the I_r index, with the exception of the fox (*Vulpes prae-glacialis*) and the large canid (*Canis* [*Xenocyon*] *falconeri*), which are represented mainly by cranial elements.

The age estimated for the individuals preserved in the assemblage has been classified within two major groups: immature or juvenile individuals with deciduous teeth, and adults with fully erupted permanent dentition. Inspection of data in Table 1 on the distribution of each species by juvenile and adult individuals reveals that: the species of largest body size (elephant, hippo and buffalo) are mainly represented by juvenile individuals, with the exception of the rhino; the species which are better represented by their NISP and MNI values (horse and large deer) also show high percentages of juvenile individuals (>40%); the carnivore species are represented exclusively by adult individuals, with the exception of the hyaenid and the ursid (40% of the individuals of *Pachycrocuta brevirostris* are juveniles, which are represented by deciduous teeth not isolated from the maxilla or mandible, which indicates that these cranial ele-

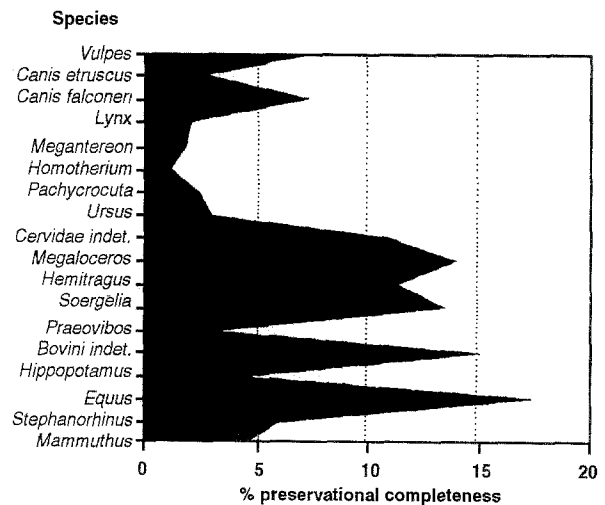


FIGURE 6 - Index of representation (I_r : percentage of preserved skeletal elements in relation to the original number of bones estimated from MNI counts) for the species of large mammals identified at Venta Micena. *Indice de présence (I_r : pourcentage d'éléments squelettiques préservés en fonction du nombre estimés d'os par décomptes MNI) pour les espèces de grands mammifères identifiées à Venta Micena.*

ments were not produced by tooth replacement, but as a consequence of the death of very young individuals).

Body weights (W , in kg) for adults of each species (mean and range) were calculated from several regression equations of weight on craniodental/postcranial variates in recent species (Janis 1990; Roth 1990; Scott 1990; Van Valkenburg 1990). The mean value estimated for each species and the widest range of weight estimations (i.e., the minimum and the maximum of all values obtained with these regressions for craniodental and postcranial remains of a given species) have been included in Table 1. These estimates indicate that the Venta Micena assemblage comprises species weighing between 3-5 kg (fox) and 6000 kg (elephant, approximated range: 3500-10,000 kg), which constitutes a total range of body sizes in the palaeocommunity of more than three orders of magnitude.

BONE ORIENTATION, SPATIAL DENSITY AND SKELETAL ARTICULATION

The distribution in a rose diagram of the directions of the longitudinal axes of long bones in Venta Micena shows no preferred orientation or alignment (Gibert & Caporicci 1989), which suggests a random pattern in the distribution (Shipman 1981). However, two factors must be borne in mind in the analysis of bone orientation: the presence of a water sheet in the environment in which the assemblage was accumulated, and the fact that the skeletal elements could or could not experience free movements aligning with the direction of the currents (as a function of bone density and size, type of depositional interphase, microtopography, grain size and sediment density; Frison & Todds 1986). In Venta Micena the stratigraphic evidence indicates the absence of channelled currents in the area in which the site was formed, which was the plains that surrounded a lake, with numerous ponds emplaced on a paleosol where the majority of the fossils were concentrated. The marked microtopography, with height differences of up to 40 cm, must have determined the position of the bones on the substrate, as well as their possibilities to be displaced by water currents (of which there is no objective evidence in the sediment) or by trampling. Therefore, the bones at Venta Micena had fewer opportunities to experience free movements, since their position is determined by the geomorphology of the palaeorelief and the high density of osseous elements preserved in the site, which form an intricate mixture which is very difficult to excavate. The absence of preferred orientations in the bone assemblage is thus determined by the original characteristics of the substrate.

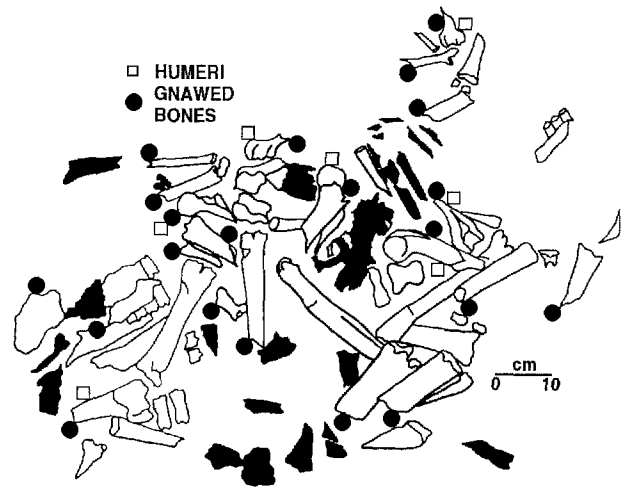
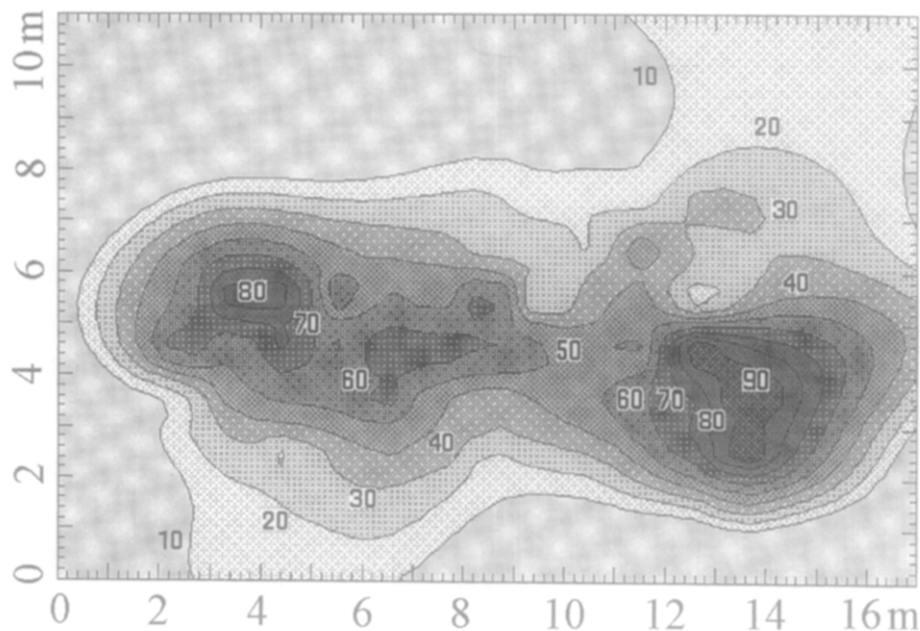


FIGURE 7 - Bones outcropping at high density in one grid (3D8-1993) of the surface excavated in Venta Micena. Affleurement d'os à forte densité sur un élément du quadrillage (3D8-993) de la surface excavée à Venta Micena.

As was explained before, the concentration of bones in this site is very high, and more than 90% of the skeletal elements are in contact with other elements (Fig. 7). The assemblage shows a low degree of horizontal dispersion, with groups of disarticulated but associated elements (i.e., skulls with mandibles, metapodials and phalanges), which represent 80% of all bones, and groups of articulated elements in a lower proportion (approximately 20%). The articulations more frequently preserved are those formed by tibiae-tarsal-metatarsal-phalanges, humerus-radius/ulna, radius-carpal-metacarpal-phalanges and articulated vertebrae.

The Venta Micena site has provided a large amount of skeletal elements. The density plot for the distribution of fossils on the excavated surface of the quarry (number of bones and teeth recovered from each m^2) shows that the mean density of elements is approximately $60/m^2$ (Fig. 8, obtained using the SYSTAT program, version 5.0), although two well defined areas have 80 or even 90 bones/ m^2 of up to 50 cm of length (i.e., tibiae of *Equus* and metapodials of *Megaloceros*). The number of elements per m^2 is in part a function of their size, since the density of elements reaches higher values in the squares which show a majority of postcranial bones (2-50 cm length), while the spatial density is lower in those squares in which cranial elements (60-80 cm length) predominate, because they have greater surface and volume than the former bones, although the surface of these squares is also almost completely covered by fossils.

FIGURE 8 - Density plot for the abundance of skeletal remains (number of bones and teeth per square meter) in the Venta Micena excavation area. *Plan de densité pour l'abondance des restes squelettiques (nombre d'os et de dents par mètre carré) sur la surface excavée de Venta Micena.*



REPRESENTATION OF SKELETAL PARTS AND BONE MODIFICATION

The palaeontological collection recovered from Venta Micena is composed of 6453 identifiable skeletal elements of large mammals, in which all range sizes of complete elements and bone fragments are represented (i.e., from premolars and third phalanges of *Vulpes* to complete mandibles of *Mammuthus*). Fossil remains of micromammals, including teeth and elements from the axial skeleton, are also present in this site, although their study is not included in this work.

Descriptive taphonomic analysis of the Venta Micena assemblage was based on a well restored sample of 1339 specimens housed at the Museum of Paleontology of Orce, which represents a random sample of the Venta Micena collection (Palmqvist et al. 1996a). Isolated teeth represent 12.5%, and 1.4% are fragments of deer antlers. In the sample of bone remains (N = 1152; Fig. 9), limb bones dominate (64.7%), followed by vertebrae (15.5%), cranial elements (10.4%), phalanges (6.3%), and ribs (3.1%). The most abundant post-cranial bones (Fig. 10) are metapodials (>20%), tibiae and humeri (6-8%), calcanei and astragali (3-5%), escapuli, radii, femori, first and second phalanges (2-3%), pelvis fragments and third phalanges (4.3%), and ulnae (<1%). Scapuli are basically represented by proximal fragments; fragments of diaphyses predominate among fossil humeri; the most complete elements are radii; femori are mainly represented by fragments of diaphyses and tibiae by distal epiphyses; the pelvis is only represented by fragments which preserve the acetabulum (Fig. 11).

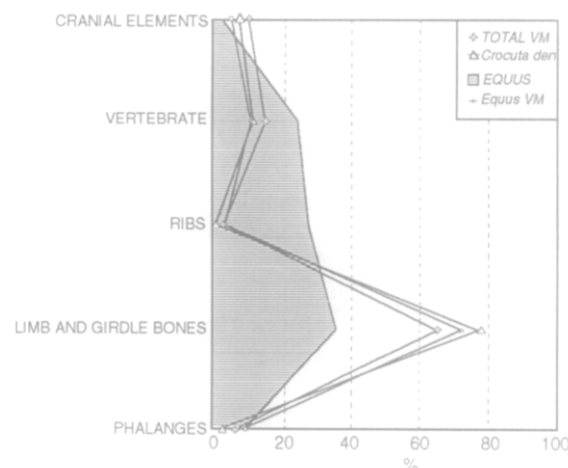
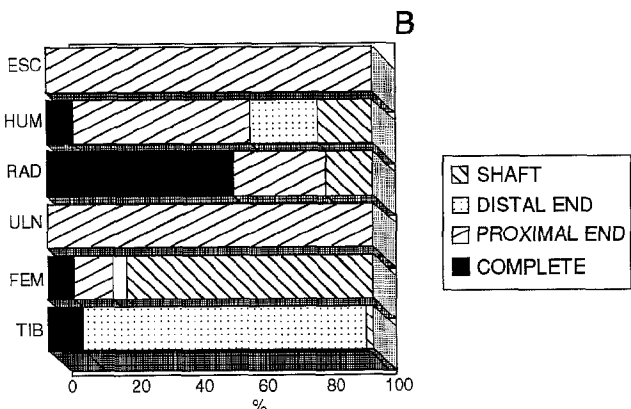
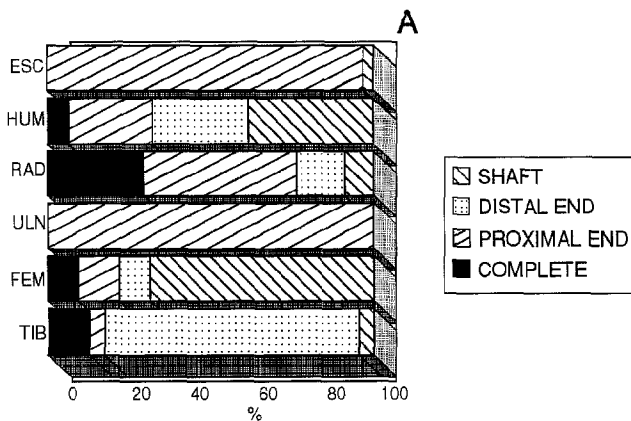
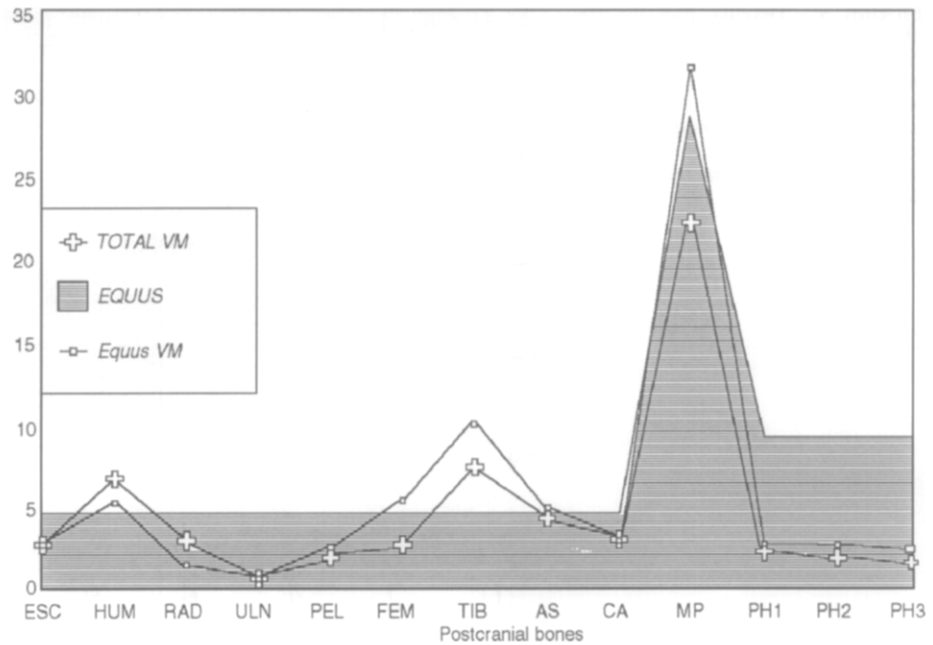


FIGURE 9 - Representation of different types of bones in the Venta Micena equid and in the assemblage of large mammals (shaded area: abundance of these elements in a horse skeleton), compared with data obtained from six modern dens of *Crocuta* (Timbavati, South Africa; Brain 1981). *Représentation des différents types d'os de l'équidé de Venta Micena dans l'assemblage de grands mammifères (surface hachurée: abondance de ces éléments d'un squelette de cheval), comparée avec les données obtenues pour six repaires modernes de *Crocuta* (Timbavati, Afrique du Sud, Brain 1981).*

The surfaces of the bones seem to have been exposed to the effects of subaerial weathering for a short time: 89.3% of the skeletal elements show weathering stage 0 (Behrensmeyer 1978), and only 10.7% of the bones (of which two thirds are metapodials) present weathering stage 1, with few, shallow and small split line cracks due to insolation (1-8 in each bone), and without flaking of their outer surface. These results indicate that subaerial weathering was relatively unimportant.

FIGURE 10 - Representation of limb and girdle bones in the Venta Micena equid and in the assemblage of large mammals; shaded area: abundance of these bones in a horse skeleton (ESC: escapuli, HUM: humeri, RAD: radii, ULN: ulnae, FEM: femori, TIB: tibiae, AS: astragali, CA: calcanei, MP: metapodials, PH1-PH3: phalanges). *Représentation des os de membres et de ceintures de l'équidé de Venta Micena et dans l'assemblage de grands mammifères; surface hachurée: abondance de ces os dans un squelette de cheval (ESC: scapulaires, HUM: humérus, RAD: radius, ULN: ulnaires, FEM: fémurs, TIB: tibias, AS: astragales, CA: calcaneums, ME: métapodiaux, PH1-PH3: phalanges).*

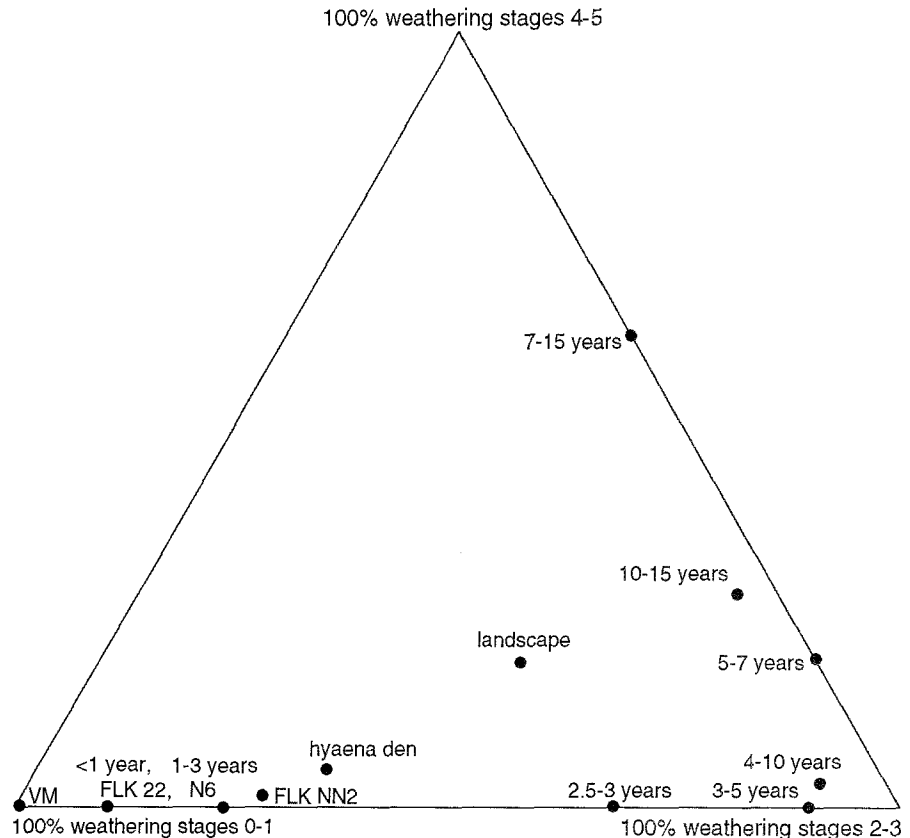


The bones which were preserved complete, lack sedimentary filling, even in those areas of the medullary cavity which are close to nutrient foramina, which indicates that the bones were buried with the periosteum intact. Figure 12 shows the distribution of percentages of bones per weathering stages in Venta Micena and in several control bone assemblages and carcasses of known age since death (Behrensmeyer 1978; Gifford 1977, 1984). The position of Venta Micena in this diagram is close to those of the least weathered assemblages, thus indicating a very short period of subaerial exposure before burial (<1 year).

Horse (*E. altidens*) remains (N = 457) are not well dispersed horizontally: groups of articulated elements represent nearly 20% of this sample, and the remaining 80% of non-articulated bones are found

FIGURE 11 - Relative abundance of several limb bone fragments (diaphyses, distal epiphyses and proximal epiphyses) and complete elements (ESC: escapuli, HUM: humeri, RAD: radii, ULN: ulnae, FEM: femori, TIB: tibiae) in the Venta Micena assemblage (A), compared with their frequencies in the sample of equid bones (B). The first graph includes the bones from carnivores and herbivores, while the second one shows only those skeletal elements of one herbivore species; the latter graph differs substantially from the former in the greater abundance of proximal humeri, femoral diaphyses and distal tibiae. *Abondance relative de plusieurs fragments d'os de membres (diaphyses, épiphyses distales et épiphyses proximales) et d'éléments complets (ESC: scapulaires; HUM: humérus, RAD: radius, ULN: ulnaires, FEM: fémurs, TIB: tibias) dans l'assemblage de Venta Micena (A) comparée avec leur fréquence dans l'échantillon des os d'équidé (B). Le premier graphe comporte les os de carnivores et d'herbivores alors que le second montre seulement des éléments squelettiques d'une espèce d'herbivore; ce graphe diffère sensiblement du premier par l'abondance plus grande de parties proximales d'humérus, de diaphyses fémorales et de parties distales de tibias.*

FIGURE 12 - Frequency distribution of percentages of bones per weathering stages in Venta Micena (data from Palmqvist et al. 1996a), Olduvai Gorge (data from Potts 1982) and several control bone assemblages and carcasses of known number of years since death (data from Behrenmeyer 1978; Gifford 1977, 1984). *Distribution de fréquence des pourcentages d'os dans les couches altérées de Venta Micena (données d'après Palmqvist et al. 1996), la gorge d'Olduvai (données d'après Potts 1982) et plusieurs assemblages d'os et de carcasses de contrôle pour lesquels le nombre d'années depuis la mort est connu (données d'après Behrenmeyer 1978; Gifford 1977, 1984).*



associated. Biostratinomic fractures are abundant (Figs 13-15): only 29.1% (73/251) of major long bones are complete (most of them metapodials), and Type II spiral fractures (Shipman 1981; Lyman 1994) are predominant (100% of fragmented humeri, femuri and radii, 74.4% of tibiae); other types are longitudinal fractures (25.6% of tibiae), undifferentiated fractures (all ribs and vertebrae, with the exception of several vertebrae which only lack their apophyses) and isolated maxilla with both cheek tooth rows (33.3% of cranial elements). On the one hand, the outer surface of the bones is well preserved: no one bone shows signs of abrasion or polish (with the exception of four out of six petrosus bones), and only four elements of the sample (0.9%) are slightly dissolved. On the other hand, gnawing marks are very frequent (Figs 16-18): all cranial fragments, scapuli, humeri, radii, pelvis, femori and tibiae show striations and biting marks produced by carnivores, the preserved epiphyses have furrows and punctures, and the diaphyses, as well as the skull bones, show scoring and pitting. These marks are also observed in all other taxa identified at Venta Micena. Coprolites are relatively common in Venta Micena, preserved as isolated lobes with diameters between 3 and 6 cm.

The results presented up to this moment, allow us to deduce that the very rich and diverse palaeon-

ological site at Venta Micena was formed in the dessicated border of a lake, and that the geological agents may be excluded from the bone accumulation process. The geochemical data from the samples obtained in the sediment and in the fossils, as well as the diagenetic information obtained from the analyses of the fossils, are both in keeping with each other, thus corroborating the initial impression that the assemblage represents an accumulated taphonomic stage, without objective evidence of taphonomic reworking. The bone assemblage is composed of demic palaeobiological entities (hyaenids, as it will be shown later) and autochthonous preserved entities (the remaining species), which were recorded in situ (sensu Fernández-López 1991). The results obtained in all biostratinomic analyses indicate clearly that this assemblage shows a differential bias in the representation of certain anatomical parts and bones in relation to others, and that the accumulation of bones was generated by the activity of scavenger carnivores, presumably hyaenids, being buried in a short period of time.

QUANTITATIVE TAPHONOMY

The quantitative taphonomic study of the Venta Micena assemblage was based on three different approaches: the analysis of size/abundance pat-

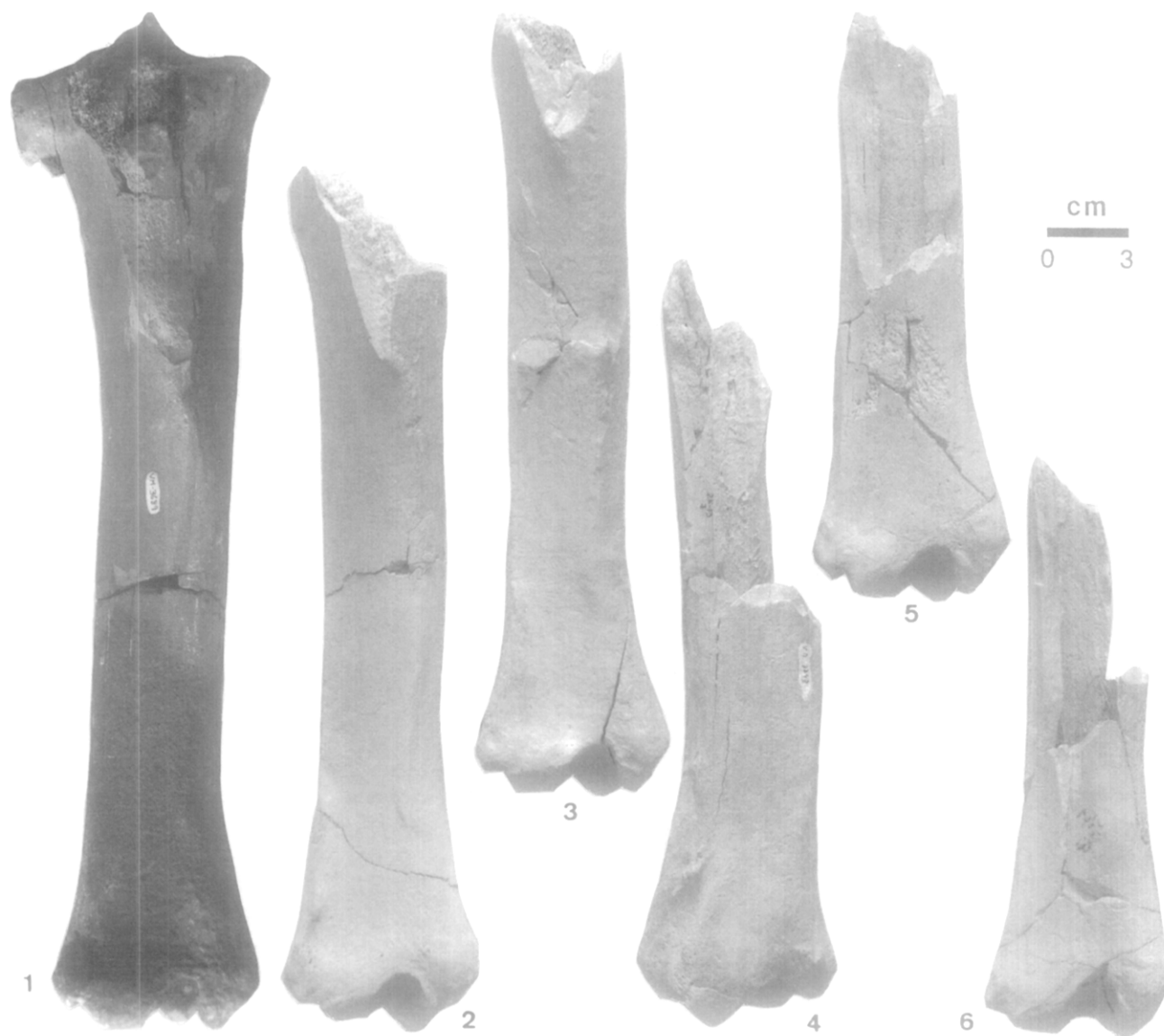


FIGURE 14 - Sequence of consumption by hyaenids of tibiae (1-6) of *Equus altidens*, showing gnawing of epiphyses, spiral and longitudinal fractures. *Séquence de la consommation par des hyènes de tibias (1-6) d'Equus altidens montrant le rongement des épiphyses et des fractures spirales et longitudinales.*

tancy at birth (Western 1979, 1980; Damuth 1982; Peters 1983; Calder 1982, 1984) are allometrically related to species body size, with a slope of around -0.3:

$$\text{Tr} = K_2 W^{-0.3}$$

As a function of both equations, the original abundance (A) of bones from the different species present in a fossil assemblage is determined by:

$$A = D \text{Tr} = K_1 W^{-0.75} K_2 W^{-0.3} = K_3 W^{-1.05},$$

with a 95% confidence interval for the slope ranging between -0.8 and -1.3 (Damuth 1982).

If the value of the slope that relates A with W in a fossil assemblage is included within this interval (-1.05 ± 0.25), it could be then concluded that the assemblage had not experienced significant taphonomic biases with respect to the quantitative composition of the original palaeobiocoenoses, and that the community structure was preserved during fossilization. If, on the contrary, the value obtained for the slope lies well outside the confidence interval, it should be then deduced that the relative frequencies of the species represented in the bony accumulation do not fit the size/abundance relationship that characterizes recent communities, and that the original composition of the



FIGURE 15 - Third metacarpal (4) and metatarsals (1-3, 5, 6) of *Equus altidens*, complete and fractured by hyaenas, showing orthogonal diagenetic fractures in the diaphyses (1-5), breakage by sediment pressure (4), and longitudinal (5) and spiral (6) fractures made by hyaenid crushing. *Troisième métacarpien (4) et métatarsiens (1-3, 5, 6), complets et fracturés par des hyènes, montrant des fractures diagénétiques orthogonales sur les diaphyses (1-5), la cassure par la pression du sédiment (4) et des fractures longitudinales (5) et spirales (6) faites par le broyage des hyènes.*

assemblage was then biased by taphonomic processes (or by other factors, such as sampling or curating errors).

Body size is one of the factors that seems to have the greatest influence on the fossilization potential of terrestrial vertebrates (Behrensmeyer et al. 1979; Behrensmeyer & Dechant Boaz 1980; Damuth 1982), since the bones of large-bodied species are more resistant to processes of physico-chemical weathering and biological destruction (i.e., exposure to sun radiation, salt precipitation, changes in relative humidity, trampling by ungulates, carnivore gnawing, root growth, etc), due to their smaller relative surface (the ratio of their outer surface to the enclosed volume). To correct for taphonomic loss due

to these processes during the period when the bones were exposed on the surface before their definitive burial, the value $d_i = 0.68[\text{Log}(W_m) - \text{Log}(W_i)]$ should be calculated, where W_i is the body weight estimated for species "i", and W_m is the weight of the largest species in the assemblage. In this way, the amended original abundance (A_i^*) of each species will be estimated (Damuth 1982) as:

$$\text{Log}(A_i^*) = \text{Log}(A_i) + d_i.$$

Before the model can be used for the quantitative taphonomic analysis of the Venta Micena palaeo-community, some considerations are in order. Firstly, the analysis must be restricted to a single trophic level, since the population densities decrea-

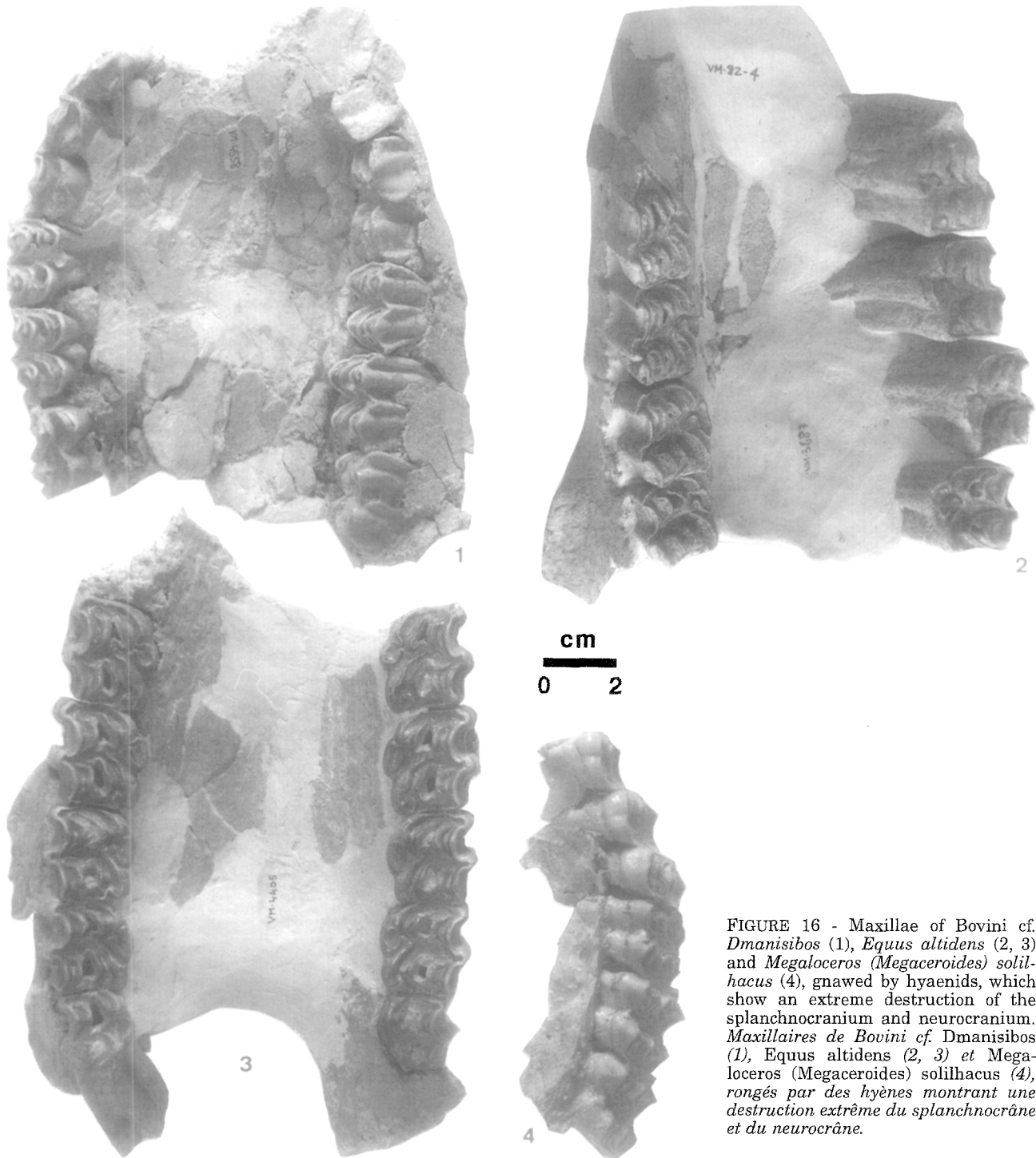


FIGURE 16 - Maxillae of Bovini cf. *Dmanisibos* (1), *Equus altidens* (2, 3) and *Megaloceros (Megaceroides) solilhacus* (4), gnawed by hyaenids, which show an extreme destruction of the splanchnocranium and neurocranium. *Maxillaires de Bovini cf. Dmanisibos* (1), *Equus altidens* (2, 3) et *Megaloceros (Megaceroides) solilhacus* (4), rongés par des hyènes montrant une destruction extrême du splanchnocrâne et du neurocrâne.

se for a given body size as height in the energetic or ecological pyramid increases. Primary consumer species are, as a rule, the most suitable for this analysis, since they are abundant in communities, are highly diverse, and differ considerably in size (at least two orders of magnitude in size differences are necessary to obtain a statistically reliable fit to the

model). In the Venta Micena assemblage 5558 dental and non-dental remains have been identified from 11 species of herbivorous macromammals, whose estimated weights range from approximately 8 to 6000 kg. Carnivores are less relevant for this analysis, as a function of their scarcity in the original communities and, as a consequence, in the fossil