



New material of the goat *Capra? alba* from the Lower Pleistocene of Quibas (Spain); notes on sexual dimorphism, stratigraphic distribution and systematics

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ABSTRACT - Continuing excavations at the Early Pleistocene locality of Quibas (Murcia, Spain) greatly increased the material of *Capra? alba*. The generic attribution of this rare goat is under discussion; some authors prefer to place it in the genus *Hemitragus*.

A larger number of specimens confirms that the metacarpals are more gracile than in other species of *Capra* and *Hemitragus*, including the very early species *Capra primaeva*. Robust metacarpals are an adaptation to mountainous or rocky environments and *Capra? alba* seems to be less adapted to such an environment than *Hemitragus*, *Capra ibex*, *C. pyrenaica*.

A marked sexual dimorphism is noted in the horn cores, which are similar to those of many species of *Capra*. The horn cores of the Pliocene *Sinocapra* are similar to those of *Hemitragus*, while those of *Capra? alba* resemble those of other species of *Capra*. Both lines of evidence suggest that *Capra? alba* is not particularly related to *Hemitragus*, but more work on morphology is needed.

A horn core from Huéscar, which was assigned to *Capra sp.*, represents a female *Capra? alba*, extending the temporal range of the species so that it overlaps with that of *Hemitragus bonali*.

RIASSUNTO - [Nuovi resti della capra *Capra? alba* dal Pleistocene Inferiore di Quibas (Spagna); note sul dimorfismo sessuale, la distribuzione stratigrafica e la sistematica] - Nuove campagne di scavo nel Pleistocene Inferiore di Quibas (Murcia, Spagna) hanno portato alla scoperta di una notevole quantità di materiale attribuibile a *Capra? alba* (Bovidae, Artiodactyla, Mammalia). L'attribuzione generica di questo raro caprino è tuttora oggetto di discussione; alcuni autori ne preferiscono l'attribuzione al genere *Hemitragus*.

I numerosi nuovi resti scoperti nel giacimento di Quibas confermano che i metacarpali di *Capra? alba* sono più gracili che nelle altre specie del genere *Capra* (compresa la specie primitiva *Capra primaeva*) ed in *Hemitragus*. I metacarpali robusti indicano un adattamento ad ambienti montuosi o rocciosi, quindi *Capra? alba* sembra essere meno adattata a tali ambienti rispetto a *Hemitragus*, *Capra ibex* e *C. pyrenaica*.

In *Capra? alba* è possibile notare un marcato dimorfismo sessuale dei cavicchi ossei delle corna, la cui morfologia corrisponde a quella tipica del genere *Capra*. I cavicchi ossei delle corna di *Hemitragus* non mostrano dimorfismo sessuale e sono molto simili a quelli di *Sinocapra* del Pliocene della Cina e del Pliocene inferiore del Nord America. Tali osservazioni sembrano escludere che *Capra? alba* sia una forma vicina a *Hemitragus*. *Capra? alba* potrebbe essere piuttosto un rappresentante primitivo del clade che conduce a *Capra* o appartenere ad una linea evolutiva più primitiva, ed essere quindi più prossima ai generi *Pseudois* o *Ammotragus*. Ulteriori studi sulla morfologia di *Capra? alba* potranno sciogliere questo dubbio.

Un nucleo di corno trovato a Huéscar, in passato attribuito a *Capra sp.*, rappresenta in realtà una femmina di *Capra? alba*. Tale segnalazione estende la distribuzione temporale della specie.

INTRODUCTION

The species *Capra alba* Moyà Solà, 1987 was named on the basis of material from the Early Pleistocene locality of Venta Micena (Granada, Spain). This author also suggested that material from the localities Fuente Nueva 2 and Barranco León 2-3, which are nearby and close in age, and the locality Cueva Victoria in Murcia and of disputed Early or Middle Pleistocene age might belong to the same species. Azanza & Morales (1989) described some material from Huéscar and Cullar de Baza and noted resemblances to *Capra? alba*, but assigned the material to *Capra sp.* Crégut Bonnoure (1999) revised the material from Venta Micena, noted that several bones of the species are morphologically closer to *Hemitragus* than to *Capra* and transferred the species to *Hemitragus*. She also revised material from Cueva

Victoria and assigned it to *Hemitragus bonali*. Material from Quibas was briefly described and assigned to *Capra sp. aff. Capra alba* (Montoya et al., 1999, 2001), later the material was assigned without restriction to *Capra alba* (Carlos Calero et al., 2007). Today, the species is still known from only few localities and there are but few descriptions of material. Whereas we assign here the species to the genus *Capra*, as was done in the original description, we note that a detailed study and comparison with other Caprinae is needed to assess its phylogenetic position within that subfamily and consequently its generic affinities.

The majority of the large mammal remains collected in Quibas belong to this caprine and tend to have an excellent state of preservation. The locality of Quibas (Figs. 1-2) was first described by Montoya et al. (1999, 2001), who suggested an age close to that of Venta Micena



Fig. 1 - Geographic position of the localities with *Capra? alba*: 1) Quibas; 2) Huéscar-1; 3) Venta Micena.

and between 1.0 and 1.3 Ma. The first collections were made from the rubble in the entry of the cave (Fig. 2B). Since 2002 work at the locality was restarted with studies on the geology, geophysics, geomagnetics, palynology and stable oxygen and carbon isotopes (Rodríguez Estrella et al., 2004). Four excavation campaigns yielded some 500 new fossils, including new specimens of *Macaca* and adding Suidae, Felidae, and Canidae (genus *Vulpes*) to the faunal list (Carlos Calero et al., 2004). Initially material *in situ* was collected from the rocks at the left of the entry (including the skull of the male *Capra? alba*) of the cave and cave floor at the entry (including the skull of a female *Capra? alba*). Later a scaffolding was erected to have access to the fissure filling in the north wall of the quarry (Fig. 2A) and fossils were extracted at three levels, which also yielded caprines. The updated faunal list of all sites or levels at the locality is at present: Mollusca: *Pomatias sulcatus* (Draparnaud, 1805), *Chondrina farinesii* (Des Moulins, 1835), *Jaminia (Jaminia) quadridens* (Müller, 1774), *Rumina decollata* (Linnaeus, 1758), *Palaeoglandina montenati* (Truc, 1972), *Oxychilus (Ortizius) mercadoli* (Gasull, 1969), *Sphincterochila (Albea) candidissima* (Draparnaud, 1801), *Trochoidea (Xerocrassa) murcica* (Guirao in Rossmüssler, 1854), *Iberus gualtieranus* (Linnaeus, 1758); Arthropoda: Diplopoda indet.; Amphibia: *Bufo bufo* (Linnaeus, 1758); Reptiles: Testudinoidea indet., *Tarenrola mauritanica* (Linnaeus, 1758), *Lacerta lepida* (Daudin, 1802), *Psammmodromus algirus* (Linnaeus, 1758), Lacertidae indet., *Blanus* sp., *Elaphe* cf. *E. scalaris* (Schinz, 1822), *Natrix* sp., *Vipera* sp., Serpentes indet.; Aves: *Geronicus eremita* (Linnaeus, 1758), *Gypaetus barbatus* (Hablizl, 1783), *Coturnix coturnix* (Linnaeus, 1758), *Columba livia* (Gmelin, 1789), *Cuculus canorus* (Linnaeus, 1758), *Athene noctua* (Scopoli, 1769), *Delichon urbica* (Linnaeus, 1758), *Anthus pratensis* (Linnaeus, 1758), *Phoenicurus ochruros* (Gmelin, 1774), *Saxicola torquata* (Linnaeus, 1766), *Oenanthe hispanica* (Linnaeus, 1758), *Parus major* (Linnaeus, 1758), *Carduelis chloris* (Linnaeus, 1758), *Carduelis carduelis* (Linnaeus, 1758); Mammalia: *Neomys anomalus* (Cabrera, 1907), *Crociodura* sp. aff.

C. suaveolens (Pallas, 1811), *Rhinolophus ferrumequinum* (Schreber, 1774), *Rhinolophus* sp. aff. *R. euryale* (Blasius, 1853), *Myotis* sp., *Macaca sylvanus* (L., 1758), *Arvicola deucalion* (Kretzoi, 1969), *Apodemus* sp., *Castillomys rivas rivas* (Martín Suárez & Mein, 1991), *Eliomys intermedius* (Friant, 1953), *Hystrix refossa* (Gervais, 1852), *Prolagus calpensis* (Major, 1905), *Oryctolagus* sp., *Lynx pardinus* (Temminck, 1827), Felidae indet., *Vulpes* sp., *Equus altidens* (Reichenau, 1915), *Sus* sp., *Capra? alba* Moya-Sola, 1987, Ovibovini indet. cf. *Praeovibos* sp., Cervidae indet. cf. *Dama nestii vallonnetensis*.

While continuing excavations at Quibas are yielding more material of *Capra? alba*, a detailed study of the morphology of the species and its phylogenetic position is under way. It is the intention of this paper to present some preliminary results and describe and interpret sexual dimorphism, some aspects of the locomotory apparatus and the stratigraphic distribution. With the latter aim in mind, we will discuss material from Huéscar and Cullár de Baza.

MATERIAL AND METHODS

The material studied is kept in institutes that are indicated here with the following acronyms:

AUT - Aristotle University of Thessaloniki
GSM - Georgian State Museum, Tbilisi.
IPGAS - Institute of Palaeobiology, Georgian Academy of Sciences, Tbilisi.
IPUW - Institut für Paläontologie der Universität, Wien.
IQW - Institut für Quartärpaläontologie, Weimar.
LPT - Laboratoire de Préhistoire de Tautavel, Université de Perpignan.
MAC - Museo de Arqueología de Cartagena.
MAMA - Museu Arqueològic Municipal "Camil Visedo Moltó", Alcoy.
MBAC - Museo de Bellas Artes, Castellón.
MCP - Musée Crozatier, Le Puy-en-Velay.
MNCN - Museo Nacional de Ciencias Naturales, Madrid.
MPRM - Musée de Préhistoire Régionale, Menton.
MRA - Museum Requien, Avignon.
MUB - Medical University, Baku.
NHM - Natural History Museum, London.
NMB - Naturhistorisches Museum, Basel.
UM - Universidad de Murcia.

Measurements are in mm. The way of measuring is conventional and the measurements are indicated with the following abbreviations:

DAP = antero-posterior diameter
DAPb = DAP measured at the base of the crown in a tooth or at the base of the horn core
DAPo = DAP measured at the occlusal surface of a tooth
DT = transverse diameter
DTa = DT of the anterior lobe of a tooth
DTb = DT of the base of the horn core
DTd = DT measured at the distal articulation of a metapodial
DTp = DT of the posterior lobe of a tooth
L = length



Fig. 2 - The locality of Quibas: A) view to the north; B) view to the north-east.

DESCRIPTION OF THE NEW MATERIAL FROM QUIBAS

The original description of *Capra? alba* included some relatively large horn cores (Moyà Solà, 1987). The horn cores described by Montoya et al. (1999) from Quibas were relatively small. Now there is more material, including some specimens which are clearly larger and which are even larger than those from Venta Micena (Fig. 3). There appear to be two size groups in the horn cores of *Capra? alba* and this is also the case for *Capra ibex* and *C. pyrenaica*. There is a skull fragment with large horn cores and another one with small horn cores (Pl. 1, figs. 1-2).

The section of the horn cores is oval in the case of the smaller specimens, while the somewhat larger specimens tend to have a more or less triangular section with rounded corners and a wide anterior side. This is a common morphology in *Capra*, whereas in *Hemitragus* and *Sinocapra* the horn cores are flattened with a rounded back and a sharp keel at the anterior side. The flattening in the horn cores is well noted in the index 100 DAPb/DTb (Fig. 4). The horn cores of *Capra ibex* and *C. pyrenaica* tend to be very wide, those of *Capra? alba* are more flattened, and those of *Capra primaeva* and *Hemitragus* tend to be flattened.

None of the horn cores from Quibas is complete, but what is preserved suggests that the horn cores of both types were long, while the horn cores of *Hemitragus* and *Sinocapra* are short (Daxner, 1968; Bonifay, 1975; Chen, 1991).

The metapodials of *Capra? alba* from Venta Micena were described by Moyà Solà (1987). Montoya et al. (1999) figured some metacarpals and gave a very short description. However, more specimens became available since that time. It is even more clear than before that the metacarpals from Quibas and Venta Micena group together. These specimens have a similar degree of gracility to those of *Rupicapra*, *Procamptoceras*, and *Ovis* (Fig. 5) and are much more gracile than those of other species of Caprini, like *Capra ibex*, *C. pyrenaica*, *C. primaeva*, and *Ammotragus lervia*. They are even more gracile compared to the metacarpals of *Hemitragus bonali*, *Capra cylindricornis* (the smallest of the four specimens in Fig. 5) and other material from the Caucasus that is assigned to *Capra* (e.g. Vekua, 1986).

The metatarsals of *Capra? alba* from Quibas and Venta Micena have a similar degree of robusticity as those of *C. pyrenaica*, which is surprising, since the metacarpals are more gracile in the former species. While in the metacarpals *Capra? alba* has a similar degree of robusticity as *Ovis antiqua* and domestic *Ovis*, the metatarsal in the former is much more robust than in the latter. Compared to *Hemitragus bonali*, the *Capra? alba* metacarpals are on average much longer, but in the metatarsals this is not the case. The same occurs with the metapodials of *Capra ibex* from Petralona (the larger Mc, with lengths >140 mm) compared to those of *Hemitragus bonali*. The *Sinocapra* metatarsal is close to *Capra? alba*.

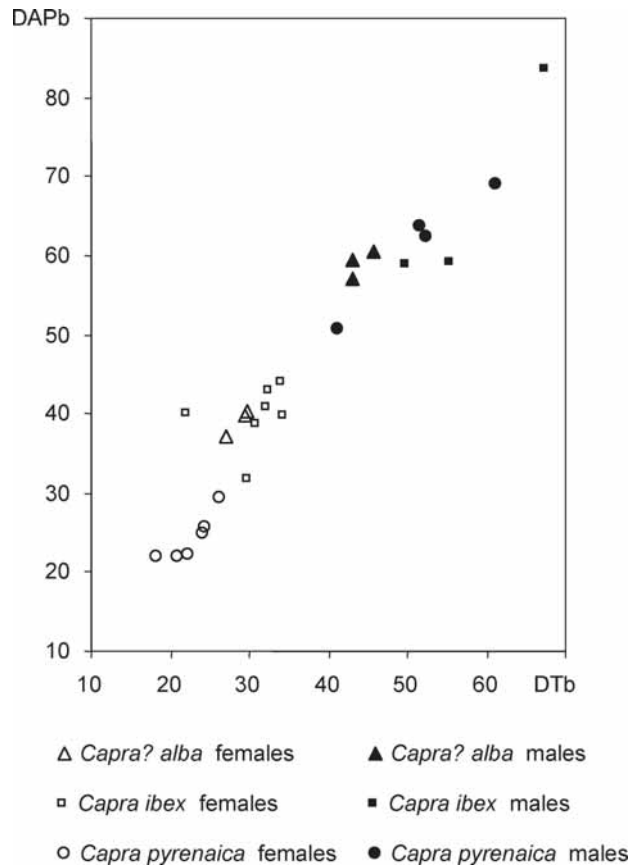


Fig. 3 - Bivariate plot of basal section of the horn cores of selected species of Caprinae: *Capra pyrenaica* from Molí Mató (MAMA), Ares (MBAC) and Recent (MNCN), *Capra ibex* from Petralona (AUT) and Camburg (IQW), *Capra? alba* from Venta Micena (Moyà Solà, 1987) and from Quibas (UM; MUPE).

MATERIAL FROM HUÉSCAR

A horn core from Huéscar (MNCN 19299 = H-26175 = 1335; Plate 1, fig. 3) was described and figured by Azanza & Morales (1989) as *Capra* sp. The specimen was believed to represent a female and resemblances were noted with *Capra? alba* and even more with *Capra primaeva* from the Upper Pliocene of North Africa (Arambourg, 1979). The horn core lacks the base and the tip (Pl. 1, fig. 3). What remains indicates that it was long, unlike in *Hemitragus bonali*. It is curved backwards. The section is oval and relatively compressed. The DAP and DT at the lower end of the fragment are 32.2 and 18.6 mm. It is expected that these measurements at the base would have been slightly more. The specimen is a little smaller than the group of small specimens of *Capra? alba*. In its oval section the horn core resembles these smaller specimens.

In addition to the horn core there are three isolated teeth with the common morphology for the Caprinae (kept under number MNCN 19787). One is a right lower molar, probably a M_1 (Hu1 186 = A922; Pl. 1, fig. 4). The measurements are $DAPo = 14.1$, $DAPb = 13.8$, $DTa = 7.9$, $DTp = 8.9$, $Ta = 0.5$. Another specimen is a right upper molar (Hu1 86 = B16; Pl. 1, fig. 5), probably a M^2 , with the following measurements: $DAPo > 16.4$, $DAPb > 14.9$, $DTa = 11.7$, $DTp =$ —. A left P^2 (Hu1 86 = B553; Pl. 1, fig. 6) measures: $DAP = 8.6$, $DAPb = 8.1$, $DT = 7.6$. The specimens have a size that is similar to specimens of *Capra? alba* and *Hemitragus bonali*. However, the size does not add much information, since most fossil species

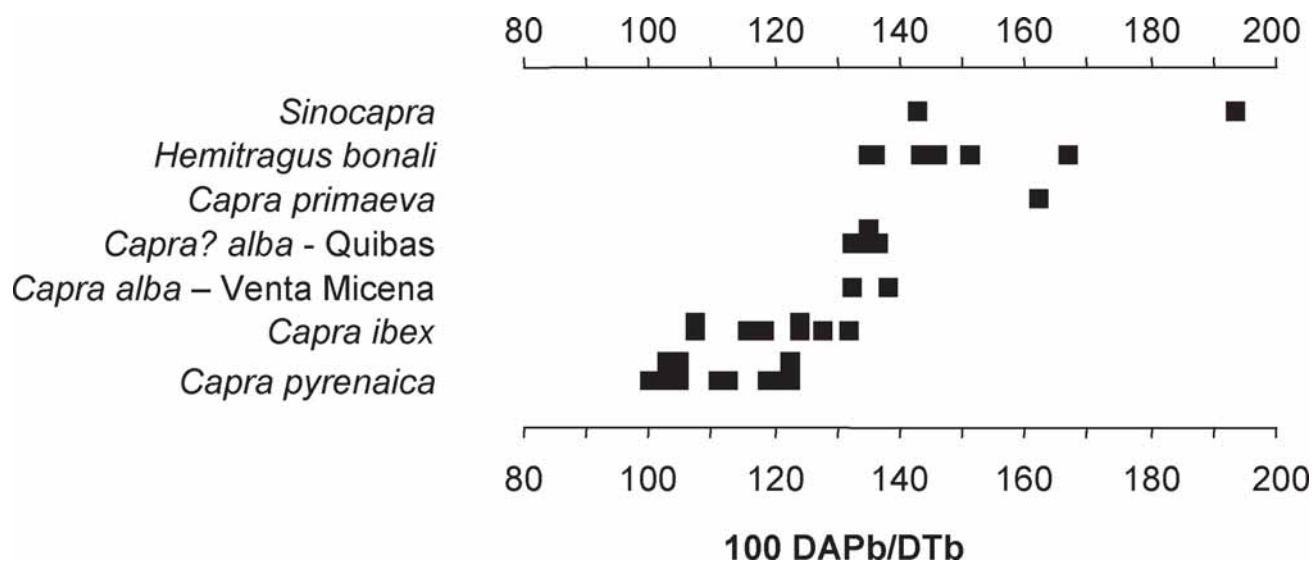


Fig. 4 - Flattening of the horn cores as shown by the index $100 DAPb/DTb$ of the horn cores of selected species of Caprinae: *Capra pyrenaica* from Molí Mató (?; MAMA), Ares (MBAC) and Recent (MNCN), *Capra ibex* from Petralona (AUT) and Camburg (IQW), *Capra? alba* from Venta Micena (Moyà Solà, 1987) and from Quibas (UM; MUPE), *Capra primaeva* from Ain Brimba (Arambourg, 1979), *Hemitragus bonali* from Hundsheim (IPUW) and L'Escaie (Bonifay, 1975), and *Sinocapra* (Chen, 1991).

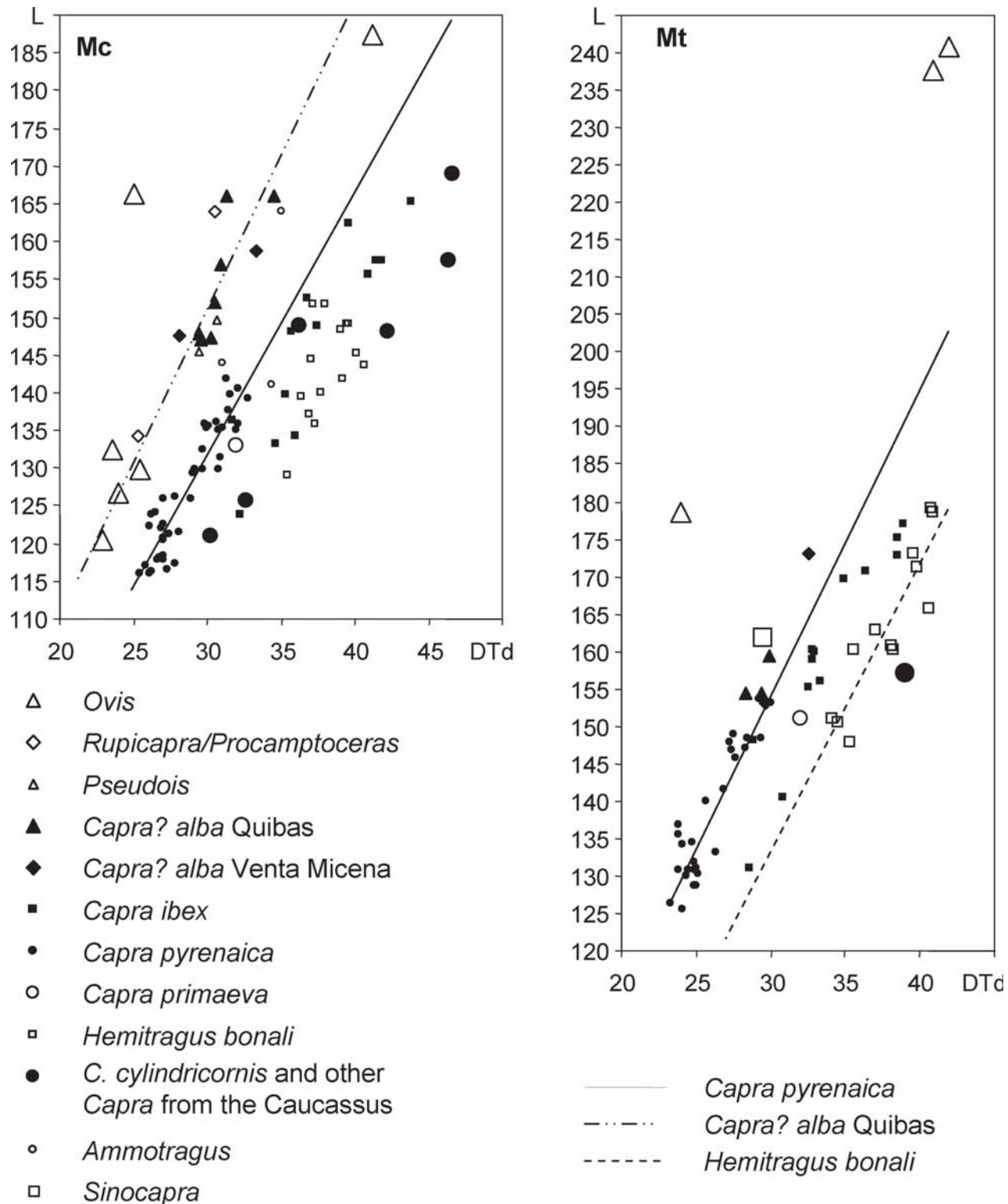


Fig. 5 - Bivariate plot of the distal width (DTd) and length (L) of the metacarpal of selected species of Caprinae: *Capra? alba* from Quibas (UM; MUPE), *Capra? alba* from Venta Micena (Moyà Solà, 1987), *Capra ibex* from Petralona (AUT) and Recent (NHM, LPT), recent *Capra pyrenaica* (MNCN), and *Hemitragus bonali* from Hundsheim (IPUW) and L'Escafe (two Mc from units B-base and D, and means of the Mc of the units B and G; Bonifay, 1975), *Ovis antiqua* from Cueva Victoria (large; MAC), recent *Ovis vignei* (middle; NNML) and subfossil domestic *Ovis* from Valkenburg (small; NNML), recent *Pseudois nayaur* (NHM), *Capra? caucasica* from Azykh V (MUB), Tsona (GSM), Akhalkalaki (IPGAS), recent *Capra caucasica* (small; NNML), recent *Capra cylindricornis* (small; GSM), *Ammotragus lervia* (Daxner, 1968), *Capra primaeva* from Ain Brimba (Arambourg, 1979), *Rupicapra* from Grotte des Cèdres (small; MRA) and *Procampnoceras* from Senèze (large; NMB).

Bivariate plot of the metatarsal. Provenance as in metacarpal except for: *Capra ibex* from Petralona (AUT) and Recent (NNML), *Capra? caucasica* from Akhalkalaki (IPGAS), *Hemitragus bonali* from Hundsheim (IPUW), Vallonnet (MPRM) and Soleilhac (MCP), *Ovis antiqua* from Bammenthal (SMNK) and Arago (LPT) and *Ovis vignei* (small; NNML), *Sinocapra willdownsi* from the Panaca Fm. (Mead & Taylor, 2005). The lines represent regression lines calculated with Excel.

of *Capra* and *Hemitragus* are close in size.

MATERIAL FROM CÚLLAR DE BAZA

Azanza & Morales (1989) described and figured a mandible from Cúllar de Baza and assigned it to *Capra* sp. There is a second specimen in the MNCN. Both specimens are very similar in morphology and size to both *Hemitragus bonali* and *Capra? alba*. However, the specimens are in the known temporal range of the former species and outside the known ranges of any other species of *Capra* or *Hemitragus* in western Europe, but an assignation to any species based on morphology remains problematic.

DISCUSSION

Taxonomic assignation

The increased number of metapodials and horn cores from Quibas strengthens the similarities between the caprines from this locality and Venta Micena. Now there is a larger sample of horn cores from Quibas, a separation in two groups is seen and the apparent difference that was noted between the small horn cores from Quibas and the larger ones from Venta Micena appears to have been due to sampling bias. Both sexes of the different species of *Capra* have horns, but the horns in the males are much larger. This is reflected in the size of the horn cores of *Capra ibex* and *Capra pyrenaica* (Fig. 4). The different size groups in horn cores of *Capra? alba* from Quibas are interpreted here as due to sexual dimorphism and we attribute the two skull fragments from Quibas to a male and to a female. This allows us to confirm the assignation by Azanza & Morales (1989) of the horn core from Huescar to a female. The material from Quibas and Huescar is assigned here without any restriction to *Capra? alba*.

Stratigraphic range

The assignation of the material from Huescar to *Capra? alba* extends the range of the species till above the Jaramillo. The age of this locality was subject to debate; some authors placed it in the early Middle Pleistocene (e.g. Alberdi et al., 1989; Cuenca-Bescós et al., 1999; Ortiz et al., 2000), while others placed in the Early Pleistocene, but above or in the Jaramillo (e.g. Mazo et al., 1985; Agustí et al., 1987; Sesé et al., 2001). A recent palaeomagnetic study has shown the locality to be situated in sediments below the Brunhes-Matuyama boundary and above the Jaramillo Event (Gibert et al., 2007). Material from deposits of Jaramillo age from Vallonnet was assigned to *Hemitragus bonali* (Moullé, 1998). This implies that the temporal distribution of the two forms must have overlapped (Fig. 6). During the late Middle Pleistocene, the temporal ranges of *Hemitragus* and *Capra* overlapped, while during the Late Pleistocene, after the local extinction of *Hemitragus*, a second species of *Capra* appeared in Europe. Apparently, the presence in Europe of two species of *Capra* or *Hemitragus* is normal.

Horn cores

Horn core morphology and size has ecological and

ethological implications. The species of the Bovidae are grouped according to ecology and social structure (Jarman, 1974; Estes, 1974). The smaller species tend to be browsers, which live in smaller social groups, the males tend to have small horn cores and the females tend to be hornless. These species tend to be more territorial and less migratory. The larger species tend to be grazers, less territorial and more migratory, live in larger social groups, both males and females tend to have large horns. The anti-predator behaviour changes from run-and-hide in small solitary forms to out run the predators in larger forms, and defence in still larger forms that occur in larger groups. It is in the intermediate Class C of Jarman that the greatest sexual dimorphism occurs with large horns with a complex morphology in the males and no horns in the females. In these species, a part of the males hold a territory during all or part of the year, and tries to herd as many females as possible into his territory, where he has exclusive mating rights. These groups of females tend to be much larger than in the species of Class B. However, in Class C also the species of the genus *Gazella* are included and in many of these species the females have small horns, while in Classes D and E, females tend to have horns that are nearly as big as those of the males. The afore mentioned studies did not include Caprinae.

In all living Caprinae, the females have horns. Both males and females tend to have simple and small horns in *Hemitragus*, *Rupicapra*, *Capricornis*, *Nemorhaedus*, and *Oreamnos*, and in *Ovibos* and *Budorcas* both sexes tend to have relatively large horns. The males tend to have very large horns and the females small ones in the species of *Capra*, *Ammotragus*, *Pseudois*, and *Ovis*, which is reflected in an important sexual dimorphism and bimodality in the horn cores. In this respect *Capra? alba* belongs to the latter group. We expect a relationship between social structure and the degree of sexual dimorphism, but we did not see a very clear relationship between horn core morphology and the ethological data we collected up to now. In general, the species with strong sexual dimorphism seem to prefer open habitats, whereas the species with a lesser degree of sexual dimorphism may prefer either closed or open habitats.

Metapodials

Robust metacarpals are an adaptation to mountainous habitats. The Caprinae live in mountainous or rocky habitats, and the species that are found in higher mountains or more rocky terrain tend to have more robust metapodials. In this character, *Capra? alba* is apparently less adapted to such habitats than other species of *Capra*, including *Capra primaeva*, known from the Upper Pliocene of Aïn Brimba, and *Hemitragus*. In this respect it resembles *Pseudois*, *Ammotragus*, *Rupicapra*, *Procamptoceras*, and *Ovis*. Either it represents a primitive clade that never acquired very robust metacarpals, or it has become secondarily more gracile.

Capra? alba has the metacarpals more elongate than those of *Capra pyrenaica*, but the metatarsals of both species have a similar degree of robusticity. Though the metapodials of *Capra ibex* and *Hemitragus bonali* are more robust, the same phenomenon is observed in the comparison with *C.? alba*: the latter species has particularly gracile metacarpals. The proportions of the

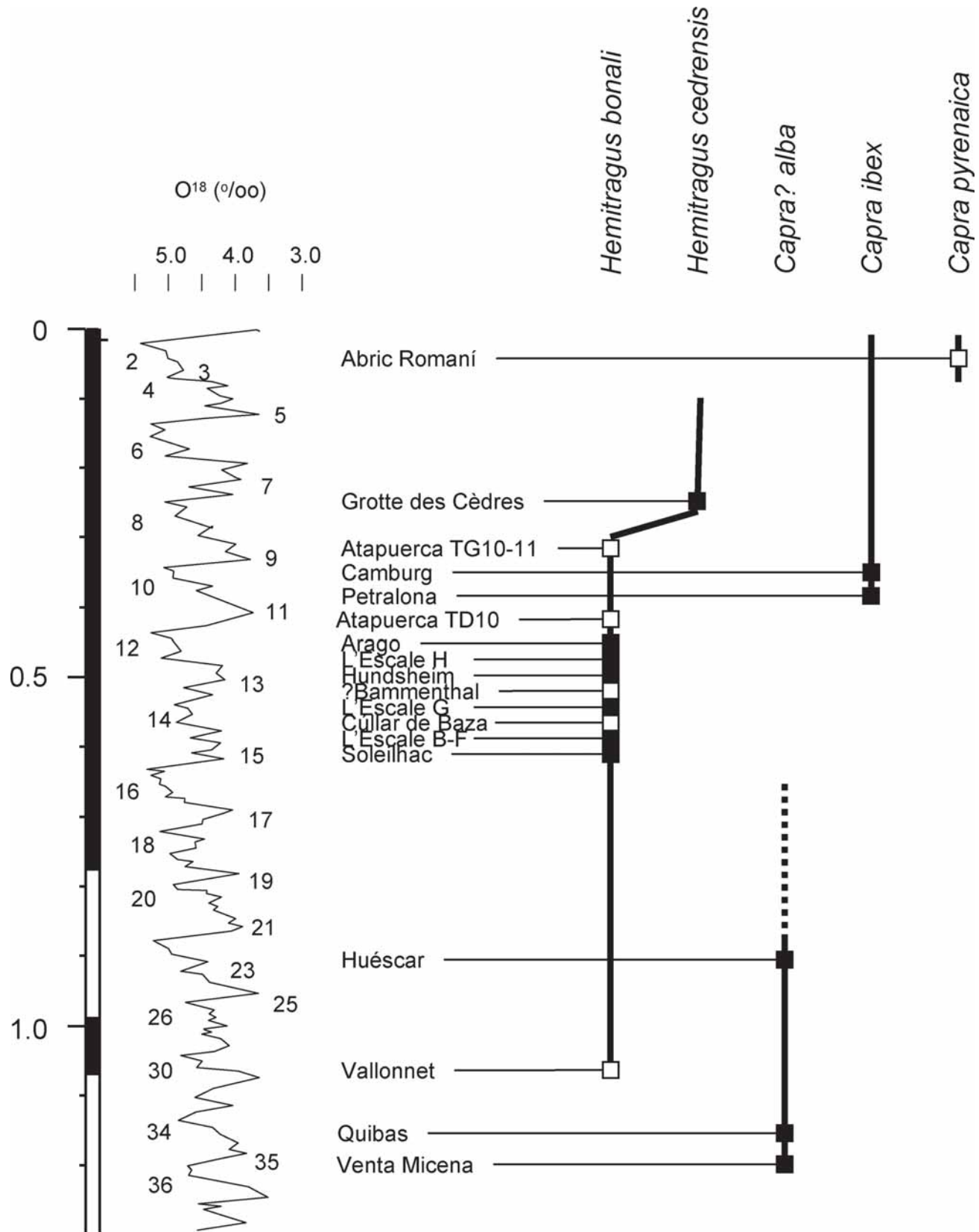


Fig. 6 - The European species of *Capra* and *Hemitragus* and their approximate stratigraphic ranges (adapted from Crégut Bonnoire, 1992, 1989; stratigraphy after Van der Made, 2001, 2005; Van der Made et al., 2004; additional information from Kahlke, 1995, Moullé, 2005, Tsoukala, 1989; Crégut-Bonnoire & Tsoukala, 2003). The position of the localities is approximate, especially if preceded by "?". Presence of a species is indicated by a solid square, while less secure determinations like "sp.", "aff.", "cf." and "?" are indicated by open squares. Isotope curve after Shackleton (1995).

lengths of the metacarpals and metatarsals in *Capra? alba* is similar to that of the other two species of *Capra*, but all three have relatively long metacarpals with respect to the metatarsals compared to *Hemitragus bonali*. The two living species of *Capra* differ thus in robusticity of the metapodials, but *Capra? alba* differs from them in having particularly gracile metapodials, and *Hemitragus* in having particularly large metatarsals.

Such differences in proportions probably reflect locomotory adaptations. Antelopes that are adapted to flat open landscapes tend to have metacarpals and metatarsals that are close in length. However, these animals tend to have much more gracile metapodials. The question arises, whether the locomotory system of *Capra? alba*, with relatively gracile metacarpals, reflects a primitive grade in adaptation to mountainous or rocky environments, while that of *Hemitragus*, with very robust metapodials and relatively short metacarpals, reflects the most advanced grade of adaptation. In this context it may be of interest that the metatarsal of *Capra? alba* has proportions that are very close to a specimen of *Sinocapra* from the Panaca Fm, with an age between 4.95 and 4.50 Ma (Mead & Taylor, 2005), which is possibly both early and primitive. Also the proportions between other limb bones and the shapes of the articular facets are subject to locomotory adaptations. A more detailed study is in course.

Phylogenetic position of *Capra? alba*

Crégut-Bonnoure & Spassov (2002) described the species *Hemitragus orientalis* from the Upper Pliocene of Bulgaria and Hungary. The material consists mainly of teeth, which showed a resemblance with the teeth of *Capra? alba* from Venta Micena. No horn cores or complete metacarpals were described. The authors concluded that the new species is ancestral to the caprine from Venta Micena and that these forms belong in *Hemitragus*, but represent a different lineage from *Hemitragus bonali*.

Recently, the new species *Capra dali* was described from Dmanisi (Bukhsianidze & Vekua, 2006), which is large with outwards curving horn cores (DAP and DT at the base of the horn core, 91.4 and 89.7 respectively). A similar caprine seems to be present in the latest Pliocene

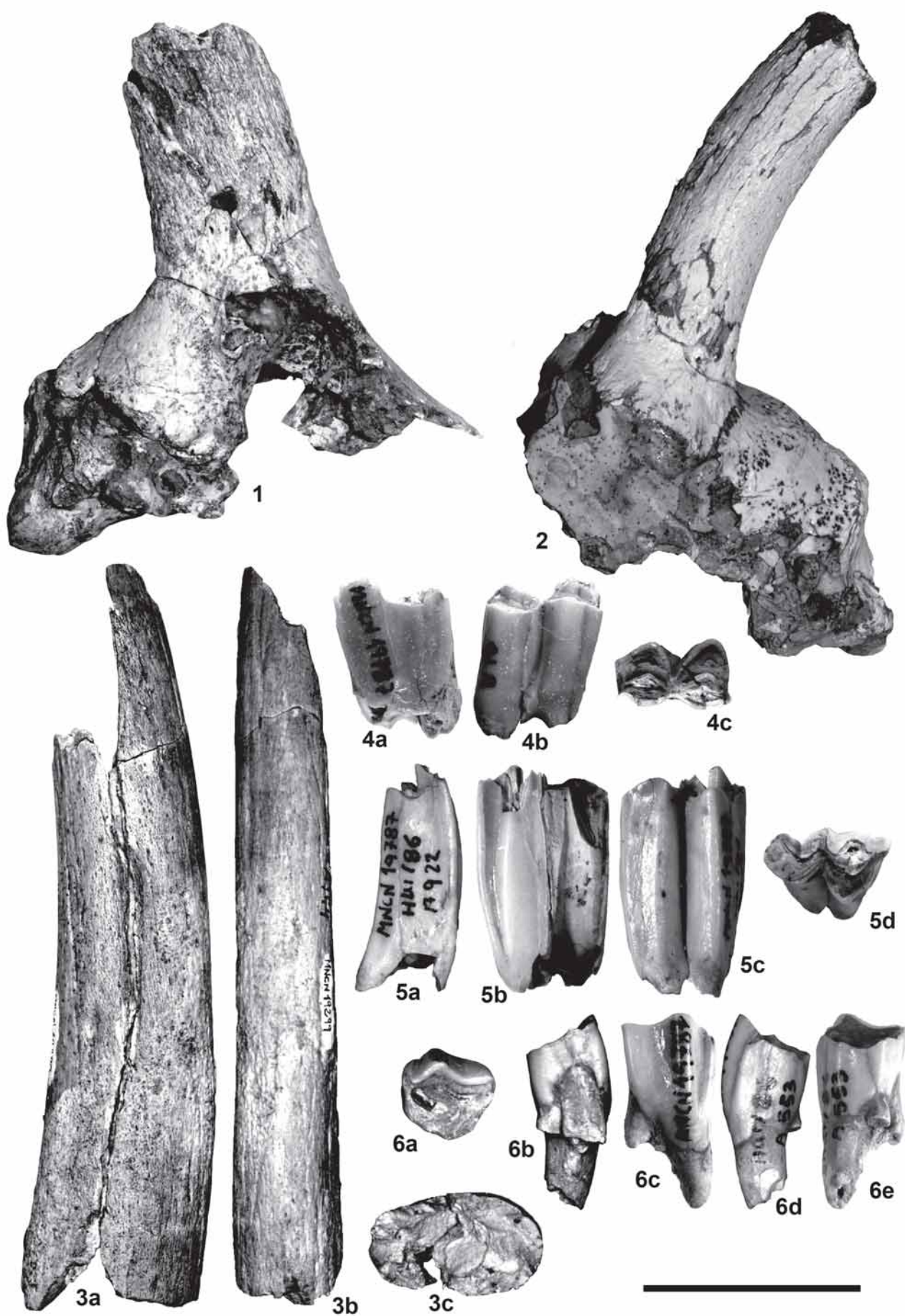
of Fonelas. *Caprovis savini* Newton, 1882 is a rare bovid, with large outward curving horn cores (DAP x DT at the base of the type horn core 54.5 x 72.9 - cast NMB), to which recently some more material was tentatively assigned (De Wilde, 2006 ; Mol & Post, 2007). All this caprine material is of latest Pliocene or Early Pleistocene age and may well belong to a single species. The age of all this material is close to that of *Hemitragus orientalis*. The horn cores cannot be compared, because they are not known in the latter species, though various similarities in the dentition were noted between *H. orientalis* and *C. dali* (Bukhsianidze & Vekua, 2006).

The horn cores of the Pliocene *Sinocapra* and Pleistocene to Recent *Hemitragus* are very similar in being short and in having an anterior keel (Chen, 1991; Mead & Taylor, 2005; Daxner, 1968; Bonifay, 1975). Work on the DNA of the Caprinae suggests a close relationship between *Capra* and *Hemitragus* (Hassanin et al., 1998; Hassanin & Douzery, 1999), which broadly coincides with morphology. More recent work suggested a separation between both genera around 5 Ma ago, which separated around 6.6 Ma ago from *Pseudois* and still earlier from *Ammotragus* (Ropiquet & Hassanin, 2004). The American *Sinocapra willdownsi*, with an age between 4.95 and 4.50 Ma, was interpreted to be an immigrant from Asia (Mead & Taylor, 2005). Though in general, the DNA ages are surprisingly old, they are consistent with the idea of an old *Sinocapra-Hemitragus* clade as suggested by fossil horn cores.

The horn cores of *Capra? alba* and most other species of *Capra* are similar in being long and without anterior keel, which would suggest affinity (which in fact was assumed by Moyà-Solà, 1987). The degree of flattening of the horn cores in *Capra? alba*, which is intermediate between those of other species of *Capra* and *Hemitragus* (Fig. 4), may well be a primitive character, whereas both the flattened horn cores in *Hemitragus* and *Sinocapra* and the wide horn cores in later species of *Capra* may be derived characters. The slender metacarpals of *Capra? alba* might be primitive, while robust metacarpals were present already in *C. primaeva* from Aïn Brimba, with an approximate age of 2.5 Ma. *Capra? alba* seems thus to have characters that are primitive with respect to other

EXPLANATION OF PLATE 1

- figs. 1-2 - *Capra? alba* from Quibas.
 1 - UM Q04 – Ei-D2-27. Skull of a male, lateral view. Scale bar = 8 cm.
 2 - UM Q04 – Ec-A0-16. Skull of a female, lateral view. Scale bar = 8 cm.
- figs. 3-6 - *Capra? alba* from Huéscar 1.
 3 - MNCN19299 (=H-26175, 1335). Right (?) horn core of a female; a) medial (?) view; b) anterior view; c) basal section. Scale bar = 4 cm.
 4 - MNCN19787 (=N26151, Hu1 86, B16). Right M₁; a) lingual view; b) buccal view; c) occlusal view. Scale bar = 2.7 cm.
 5 - MNCN19787 (=N26151, Hu1 186, A922). Right M₂; a) anterior view; b) buccal view; c) lingual view; d) occlusal view. Scale bar = 2.7 cm.
 6 - MNCN19787 (=N26151). Left P₂; a) occlusal view; b) posterior view; c) buccal view; d) anterior view; e) lingual view. Scale bar = 2 cm.



species attributed to *Capra* and *Hemitragus*, even if these are geologically older.

At least some of the morphological characters discussed here, must have developed in parallel. Given these uncertainties, there are various possible positions of *Capra? alba* in the phylogeny of the Caprinae: 1) it might be a primitive species of *Capra*, as suggested by Moyà-Solà (1987); 2) it might be more closely related to *Hemitragus*, as suggested by Cregut-Bonnoure (1999); 3) it might not belong to the *Capra-Hemitragus* clade, but be more closely related to *Pseudois* or *Ammotragus*. Similarly, the latest Pliocene-earliest Pleistocene *Capra-Hemitragus orientalis-Caprovius* material should be studied with an open eye for alternative possibilities. Work on the morphology of the Caprinae in progress, aims to fit *Capra? alba* more reliably into the phylogeny of this group.

CONCLUSIONS

The study and comparison of the increased collections of *Capra? alba* from Quibas lead to the following conclusions:

1) The material from Quibas and Huéscar is assigned without restriction to the species *Capra? alba*, while that from Cullar de Baza might belong to *Hemitragus bonali*.

2) *Capra? alba* is a rare species known from few localities: its first record is in Venta Micena and Quibas (probably around 1.2 Ma) and the last record is in Huéscar (probably in the range 0.78-0.99 Ma). This species was contemporaneous with *Hemitragus bonali*, which appeared in Vallonnet (0.99-1.07 Ma).

3) Like in living species of *Capra*, *Ammotragus*, *Pseudois*, and *Ovis*, the males of *Capra? alba* had large horn cores (and thus large horns) and the females had small horn cores, while in *Hemitragus*, *Rupicapra*, *Capricornis*, *Nemorhaedus*, *Oreamnos*, *Ovibos*, and *Budorcas*, the females have horn cores that approach those of the males in size. These differences are expected to be related to certain aspects of ecology and ethology.

4) *Capra? alba* has metacarpals that are particularly gracile, more so than the metatarsals. This probably reflects a lesser degree of adaptation to mountainous environments, and might be primitive within the Caprini.

5) Various hypotheses have been forwarded on the affinities of *Capra? alba* within the *Capra-Hemitragus* clade, however its affinities should be studied within the wider context of the Caprini.

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REFERENCES

- Agustí J., Moyà-Solà S. & Pons-Moyà J. (1987). La sucesión de Mamíferos en el Pleistoceno inferior de Europa: proposición de una nueva escala bioestratigráfica. *Paleontologia i Evolució*, special number 1: 287-295.
- Alberdi M.T., Alcalá L., Azanza B., Cerdeño E., Mazo A.V., Morales J. & Sesé C. (1989). Consideraciones bioestratigráficas sobre la fauna de vertebrados fósiles de la cuenca de Guadix-Baza (Granada España). *Trabajos sobre el Neógeno-Cuaternario*, 11: 347-355.
- Arambourg C. (1979). Vertébrés Villafranchiens d'Afrique du Nord (Artiodactyles, Carnivores, Primates, Reptiles, Oiseaux). 1-141, lám. 25-61. Fondation Singer-Polignac, Paris.
- Azanza B. & Morales J. (1989). Los artiodáctilos de Huélagos, Huéscar-1 y Cullar de Baza-1 (cuenca de Guadix-Baza, Granada). *Trabajos sobre el Neógeno-Cuaternario*, 11: 289-315.
- Bonifay M.F. (1975). "*Hemitragus bonali*" Harlé et Stehlin "Caprinae" de la Grotte de l'Escale (Saint-Estève-Janson, Bouches de Rhône). *Quaternaria*, 18: 215-302.
- Bukhsianidze M. & Vekua A. (2006). *Capra dalii* nov. sp. (Caprinae, Bovidae, Mammalia) at the limit of Plio-Pleistocene from Dmanisi (Georgia). *Courier Forschungs-Institut Senckenberg*, 256: 159-171.
- Carlos Calero J.A., Made J. van der, Mancheño M.A., Montoya P. & Romero G. (2007). *Capra alba* Moyà-Solà, 1987 del Pleistoceno Inferior de la Sierra de Quibas (Albanilla, Murcia, España). *Estudios geológicos*, 62: 571-578.
- Carlos Calero J.A., Mancheño M.A., Montoya P. & Ruiz Bustos A. (2004). El yacimiento pleistoceno de la Sierra de Quibas (Abanilla, Murcia). Nuevas aportaciones. In Calonge A., Gonzalo R., de López Carrillo M. & Pardo M.V. (eds.), Libro de resúmenes de las XX Jornadas de Paleontología, Sociedad Española de Paleontología, Universidad de Alcalá de Henares: 40-41.
- Chen Guanfang (1991). A new genus of Caprini (Bovidae, Artiodactyla) from Upper Pliocene of Yushe, Shansi. *Vertebrata Palasiatica*, 29 (3): 230-239.
- Crégut-Bonnoure E. (1989). Un nouveau caprinae, *Hemitragus cedrensis* nov. sp. (Mammalia, Bovidae) des niveaux Pléistocènes Moyen de la grotte des Cèdres (Le Plan d'Aups, Var). Intérêt Biogéographique. *Geobios*, 22 (5): 653-663.
- Crégut-Bonnoure E. (1992). Les Caprinae (Mammalia, Bovidae) du Pléistocène d'Europe: intérêt biostratigraphique, paléoécologique et archéozoologique. *Mémoires de la Société géologique de France*, n.s., 160: 85-93.
- Crégut-Bonnoure E. (1999). Les petits Bovidae de Venta Micena (Andalousie) et de Cueva Victoria (Murcia). In Gibert J., Sánchez F., Gibert L. & Ribot F. (eds.), The hominids and their environment during the Lower and Middle Pleistocene of Eurasia: 191-228.
- Crégut-Bonnoure E. & Spassov N. (2002). *Hemitragus orientalis* nov. sp. (Mammalia, Bovidae, Caprinae), un nouveau taxon d'Europe orientale. *Revue de Paléobiologie*, 21 (2): 553-573.
- Crégut-Bonnoure E. & Tsoukala E. (2003). The Pleistocene bovids from the Petralona Cave (Macedonia, Greece): new interpretations and biogeographical implications. *Quaternaire*, hors-série 2: 161-178.
- Cuenca-Bescós G., Laplana C. & Canudo J.I. (1999). Biochronological implications of the Arvicolidae (Rodentia, Mammalia) from the Lower Pleistocene hominid-bearing level of Trinchera Dolina 6 (TD6, Atapuerca, Spain). *Journal of Human Evolution*, 37 (3/4): 353-388.
- Daxner G. (1968). Die Wildziegen (Bovidae, Mammalia) aus der altpleistozänen Karstspalte von Hundsheim in Niederösterreich. *Berichte der deutsche Gesellschaft für geologische Wissenschaften. Reihe A. Geologie und Paläontologie*, 13 (3): 305-334.
- Estes R.D. (1974). Social organization of the African Bovidae. Calgary Symposium: 166-205.
- Gibert L., Scott G., Martin R. & Gibert J. (2007). The Early to Middle Pleistocene boundary in the Baza Basin (Spain). *Quaternary Science Reviews*, 26: 2067-2089.

- Hassanin A. & Douzery E.J.P. (1999). The tribal radiation of the family Bovidae (Artiodactyla) and the evolution of the mitochondrial cytochrome b gene. *Molecular Phylogenetics and Evolution*, 13 (2): 227-243.
- Hassanin A., Pasquet E. & Vigne J.D. (1998). Molecular systematics of the subfamily Caprinae (Artiodactyla, Bovidae) as determined from Cytochrome b sequences. *Journal of Mammalian Evolution*, 5 (3): 217-236.
- Jarman P.J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour*, 48: 215-267.
- Kahlke R.D. (1995). Die Abfolge plio-/pleistozäner Säugetierfaunen in Thüringen (Mitteldeutschland). *Cranium*, 12 (1): 5-18.
- Made J. van der (2001). Les ongulés d'Atapuerca. Stratigraphie et biogéographie. *L'Anthropologie*, 105 (1): 95-113.
- Made J. van der (2005). La fauna del Pleistoceno europeo. In Carbonell E. (ed.), *Hominidos: las primeras ocupaciones de los continentes*, Capítulo 4 - Europa; Sección 4.4. Planeta: 394-432.
- Made J. van der, Aguirre E., Bastir M., Fernández Jalvo Y., Huguet R., Laplana C., Márquez B., Martínez C., Martínón M., Rosas A., Rodríguez J., Sánchez A., Sarmiento S. & Bermúdez de Castro J.M. (2003). El registro paleontológico y arqueológico de los yacimientos de la Trincheras del Ferrocarril en la Sierra de Atapuerca. *Coloquios de Paleontología*, spec. vol. 1: 345-372.
- Mazo A.V., Sesé C., Ruiz Bustos A. & Peña J.A. (1985). Geología y paleontología de los yacimientos Plio-Pleistocenos de Huéscar (depresión de Guadix-Baza, Granada). *Estudios geológicos*, 41: 467-493.
- Mead J.I. & Taylor L.H. (2005). New species of *Sinocapra* (Bovidae, Caprinae) from the lower Pliocene Panaca Formation, Nevada, USA. *Palaeontologia Electronica*, 8 (1): 1-20.
- Mol D. & Post K. (2007). Noordzee 2990 Indet? Uitkomsten van een speurtocht. *Cranium*, 24 (1): 5-16.
- Montoya P., Alberdi M.T., Blázquez A.M., Barbadillo L.J., Fumeral M.P., Made J. van der, Marín J.M., Molina A., Morales J., Murelaga X., Peñalver E., Robles F., Ruiz Bustos A., Sánchez A., Sanchiz B., Soria D. & Zsyndlar Z. (1999). La fauna del Pleistoceno Inferior de la Sierra de Quibas (Abanilla, Murcia). *Estudios geológicos*, 55 (3-4): 129-164.
- Montoya P., Alberdi M.T., Barbadillo L.J., Made J. van der, Morales J., Murelaga X., Peñalver E., Robles F., Ruiz Bustos A., Sánchez A., Sanchiz B., Soria D. & Zsyndlar Z. (2001). Une faune très diversifiée du Pléistocène inférieur de la Sierra de Quibas (province de Murcia, Espagne). *Comptes Rendus de l'Académie des Sciences*, 332: 387-393.
- Moullé P.E. (1998). Les grands mammifères de la grotte du Vallonnet (Roquebrune-Cap-Martin, Alpes-Maritimes) Synthèse des études antérieures et nouvelles déterminations. *Bulletin du Musée d'Anthropologie Préhistorique de Monaco*, 39: 29-36.
- Moullé P.E. (2005). *Hemitragus bonali* (Harlé & Stehlin, 1914). *Annales des Amis du musée Crozatier*, 13-14: 116-117.
- Moyà Solà S. (1987). Los bóvidos (Artiodactyla, Mammalia) del yacimiento del Pleistoceno inferior de Venta Micena (Orce, Granada, España). *Paleontologia i evolució*, Mem. Esp., 1: 181-236.
- Ortiz J.E., Torres T., Llamas J.F., Canoira L., García-Alonso P., García de la Morena M.A. & Lucini M. (2000). Datación de yacimientos paleontológicos de la cuenca de Guadix-Baza (sector de Cúllar-Baza, Granada, España) y primera estimación de la edad de la apertura de la cuenca mediante el método de racimización de aminoácidos. *Geogaceta*, 28: 109-112.
- Rodríguez Estrella T., Mancheño M.A., Romero G. & Hernández J.M. (2004). Características geológicas de la Sierra de Quibas (Abanilla, Murcia). Su relación con un yacimiento paleontológico pleistoceno. *Geogaceta*, 35: 115-118.
- Ropiquet A. & Hassanin A. (2004). Molecular phylogeny of caprines (Bovidae, Antilopinae): the question of their origin and diversification during the Miocene. *Journal of Zoological Systematics*, 43 (1): 49-60.
- Sesé C., Alberdi M.T., Mazo A. & Morales J. (2001). Mamíferos del Mioceno, Plioceno y Pleistoceno de la Cuenca de Guadix-Baza (Granada, España): revisión de las asociaciones faunísticas más características. *Paleontologia i Evolució*, 32-33: 31-36.
- Shackleton N. (1995). New data on the evolution of Pliocene climatic variability. In Vrba E.S., Denton G.H., Partridge T.C. & Buckle L.H. (eds.), *Palaeoclimate and evolution with emphasis on human evolution*. Yale University Press, New Haven and London: 242-248.
- Tsoukala E. (1989). Contribution to the study of the Pleistocene fauna of large mammals (Carnivora, Perissodactyla, Artiodactyla) from Petralona Cave Chalkidiki (N. Greece). *Aristotle University of Thessaloniki, School of Geology, Scientific Annals*, 1 (8): 360.
- Vekua A. (1986). The lower Pleistocene Mammalian Fauna of Akhalkalaki (southern Georgia, USSR). *Palaeontographia Italica*, 74: 63-96.
- Wilde B. de (2006). *Caprovis savinii* (Bovidae, Mammalia) rediscovered: horn core finds of an Early Pleistocene antelope from the North Sea floor. *Netherlands Journal of Geosciences - Geologie en Mijnbouw*, 85 (3): 239-243.

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