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Q1 Presence of the Asian origin Bovini, *Hemibos* sp. aff. *Hemibos gracilis* and *Bison* sp.,
at the early Pleistocene site of Venta Micena (Orce, Spain)

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ABSTRACT

The assemblages of large bovids from the European Late Villafranchian are dominated by the presence of the genus *Bison*, a descendant of the Early-Middle Villafranchian forms of *Leptobos*. Chronologically, the oldest record of this genus at the gates of Europe is at Dmanisi, Georgia (1.77 Ma), where it was firstly named *Dmanisibos*. It is recorded until the Holocene. It is the most abundant Quaternary buffalo of the continent and is nearly the only genus recorded in most post-Olduvai Early Pleistocene sites of Europe. The revision of all bone and tooth remains of large bovids from the site of Venta Micena (~1.5 Ma) shows that two species of buffaloes are present at this Early Pleistocene locality. One is clearly a form of *Bison*, while the other corresponds to other different Bovini of small size that may be ascribed to the genus of Indian origin *Hemibos*, thus representing the first record of this genus in the Late Villafranchian of Europe. This paper presents the cranial material of both buffaloes.

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1. Introduction

In recent decades, research at the Early Pleistocene sites of Orce (Guadix-Baza Basin, south-eastern Spain) (Fig. 1), especially the important paleontological locality of Venta Micena, which has produced more than 17,000 specimens of large fossil mammals, has provided key information on the Early Pleistocene fauna of Europe. The comparative study of these bone assemblages (Martínez-Navarro, 1991, 1992a,b; Martínez-Navarro and Palmqvist, 1995; Palmqvist et al., 1999; Martínez-Navarro and Rook, 2003; Martínez-Navarro et al. 2005; Palmqvist et al., 2007;) has helped to detect, among the members of the Late Villafranchian fauna, the presence of species originating in Africa, such as sabre-tooth *Megantereon whitei* and hippo *Hippopotamus antiquus* (Alberdi and Ruiz-Bustos, 1985; Martínez-Navarro and Palmqvist, 1995; Martínez-Navarro et al., 2004; Palmqvist et al., 2007; Martínez-Navarro, 2010). However, it is worth noting that the large mammal assemblages from the Orce sites are basically composed of species with a Holarctic origin, including equids, rhinocerotids, bovids, cervids, and most of the carnivores.

The chronology of Venta Micena has been debated for a long time, but it is possible to estimate its approximate age by combining paleomagnetic data with the biochronological evidence. The site is placed within the *Allophaiomys pliocaenicus* Zone, located below the *Allophaiomys aff. lavocati* Zone (ex. *Allophaiomys bourgondiae* Zone) and above the *Mimomys oswaldoreigi* Zone (Oms et al., 2000a; Agustí and Madurell, 2003). The archaeopaleontological sites of Fuente Nueva-3 and Barranco León-5 are in the *A. aff. lavocati* Zone below the normal Jaramillo subchron, in an approximate age range of 1.3–1.4 Ma (Martínez-Navarro et al., 1997; Oms et al., 2000b; Martínez-Navarro et al. 2003, 2010). The large mammal assemblage from Venta Micena is different in composition and younger than the ones from the Italian sites included within the Tasso faunal unit in the Upper Valdarno, which are dated just above the Olduvai chron (~1.7 Ma) (Torre et al., 1996; Napoleone et al., 2003; Palombo, 2009; Rook and Martínez-Navarro, 2010). However, a comparative study currently in progress between Venta Micena and the Georgian site of Dmanisi, dated around 1.77 Ma (Lordkipanidze et al., 2007), shows important similarities between both assemblages, such the presence of the same species of bovid *Soergelia*, *Soergelia minor*. Given that this species is not recorded in the latest Early Pleistocene assemblages, this suggests an earlier age for the Spanish site. Therefore, it is possible to conclude that Venta Micena is situated above the

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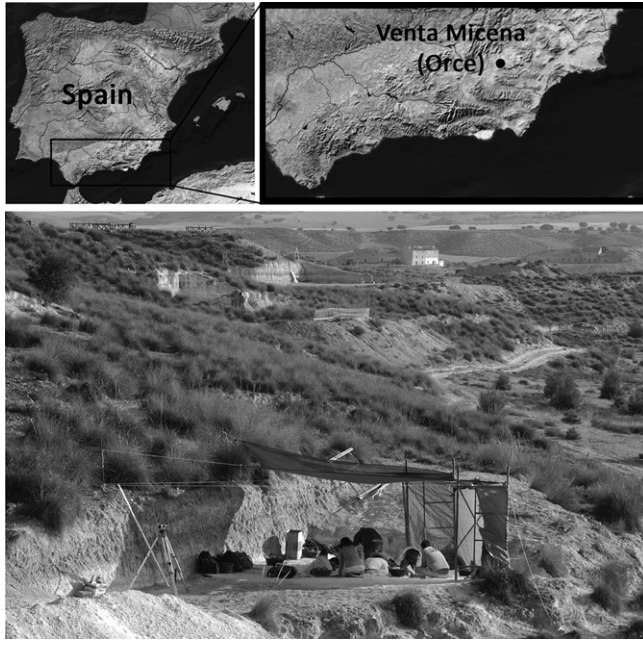


Fig. 1. Top: geographic location of Venta Micena (Orce, Guadix-Baza Basin, south-eastern Spain). Bottom: panoramic of Venta Micena during the field season of 2005.

Olduvai subchron, with an age around 1.5–1.6 Ma, and thus is slightly younger than Dmanisi. This chronology is also supported by new data based on ESR methodology (Duval, in press).

The presence of several human remains at Venta Micena has been proposed, such as cranial fragment VM-0 (Gibert et al., 1983). However, after a long polemic on the supposed human affinities of this fossil, it was concluded that it belonged to a female of a ruminant without cranial appendages, horn cores or pedicels (Martínez-Navarro, 2002).

2. Bovids from Venta Micena

Up to 1990, five species of bovids had been described in Venta Micena (Moyà-Solà, 1987): Caprini indet. (small-sized), *Capra alba*, *S. minor*, *Praeovibos* sp., and *Bison* sp. The assemblage preserved cranial specimens of *C. alba*, *S. minor* and *Praeovibos* sp. However, Caprini indet. was described on only one distal metacarpal, and the presence of *Bison* sp. was based on a very good collection of postcranial elements and teeth, but unfortunately no cranial remains were available. *C. alba* was redescribed as *Hemitragus albus* by Cregut-Bonnoure (1999), but new fossil specimens in the process of study confirm the first classification done by Moyà-Solà.

Moyà-Solà (1987) described only one species of Bovini at the site, ascribed to *Bison* sp., but he noted the presence of significant differences in size and robustness that were attributed to sexual dimorphism. Based on the total excavated collection up to 2005, composed of 938 specimens of cranial and postcranial material (Table 1), the anatomical and metric variability of this fossil Bovini collection is not the exclusive result of sexual dimorphism, but is caused by the presence in the assemblage of two different species of buffaloes.

In 1990, a cranial specimen of a large bovid was unearthed from the site (VM 9000). It was attributed to the same species of the teeth and postcrania initially classified as *Bison* sp. by Moyà-Solà (1987), and ascribed to Bovini gen. et sp. indet. (Martínez-Navarro, 1991). Later, this cranial vault was erroneously ascribed to *Bubalus* sp. (Martínez-Navarro, 1992a). In any case, its anatomy

Table 1
Total elements of Bovini from Venta Micena.

Bovini (<i>Bison</i> + <i>Hemibos</i>) total	
Cranial	
Isolated teeth	389
Palates	3
Mandibles	28
Postcranial	
Atlas	4
Cervical vert.	6
Dorsal vert.	7
Lumbar vert.	18
Indet. vert.	1
Scapulae	4
Pelvis	10
Humerus	47
Radius	21
Ulna	5
Femur	3
Tibia	21
Maleolar bone	11
Pisiform	3
Piramidal	2
Semilunar	5
Scafoides	6
Unciform	9
Magnum	12
Calcaneum	33
Astrágalo	49
Naviculo-cuboid	21
Cuneiform	7
Metacarpal	84
Metatarsal	74
Metapodial indet.	17
Prox. phalanx	19
Medial phalanx	15
Distal phalanx	4
Total	938

was quite different from the crania of *Bison*. The present study ascribes it to the genus *Hemibos*. Fortunately, another cranial specimen of a large bovid from the tribe Bovini showing a cranial structure that differed from VM 9000 was found in 1995. The morphology of this cranial vault (VM 8000) falls clearly within the range of variability of the genus *Bison*.

Unfortunately, although some anatomical and size differences among the teeth and postcranial material of Bovini from Venta Micena are clear, it is not possible to ascribe a significant amount of these specimens to *Hemibos* or *Bison*. Because of this problem, this paper presents the record of both species based on the finding of the two different skull fragments cited above, which allow a clear anatomical identification, and continues the more difficult study of the dentition and postcranial specimens for a monographic volume that will be published elsewhere in the near future.

3. Anatomical description of the cranial specimens of Bovini from Venta Micena

3.1. Specimen VM 9000

This is a cranial vault, unearthed from quarry 3 at grid 3A15, of an unknown medium-to-large-sized bovid found during the 1990 excavation at Venta Micena (Table 2, Fig. 2). This specimen is not well preserved, probably due to the bone-cracking activities of the large hyaenid *Pachycrocuta brevirostris*, the main collecting agency of skeletal elements at this site (Palmqvist et al., 1996; Arribas and Palmqvist, 1998; Martínez-Navarro and Palmqvist, 1999; Palmqvist and Arribas, 2001; Espigares et al., 2010; Palmqvist et al., 2011). The specimen preserves the upper area of the frontal bones, a small part

Table 2Measurements of VM 9000 from Venta Micena and *Hemibos gracilis* from Longdan.

	Venta Micena		Longdan	Longdan
	VM 9000		HMV1247	HMV1248
Thickness of the frontal sinus	>32			
Length of frontal bone at middle			133	~118
Diameter between horn core and orbit			55	
Width of frontal at posterior borders of orbits			190	220
Min. width of frontals (posterior to orbits)			170	
Min. width across lateral surfaces of horn core pedicels	158			
Width across internal surfaces of horn core pedicels	52.5			
Diameter at supraorbital foramina			74	
Interfrontal suture versus coronal suture angle	90°		~90	
Diverging angle of horn cores (at the base)	104°		100°	100°
Antero-posterior diameter of the horn cores (at the base)	r. 52.5	l. 53.5	44	54
Medio-lateral diameter of the horn cores (at the base)	r. 68.5	l. 69.5	69	68
Circumference of the horn cores (at the base)	r. 195	l. 196		

Abbreviations: r.: right; l.: left (measurements in mm).

of the right orbit, the base of the horn cores, the coronal suture, and a small portion of the parietal bone. It possesses a thick frontal sinus, and the parietal has also small sinuses. The horn cores, partially pneumatized and inserted just above the back of the orbital cavities, are antero-posteriorly compressed, show a sub-triangular section, have a flattened posterior face and both posterolateral and anterior keels that are not well marked (Fig. 3).

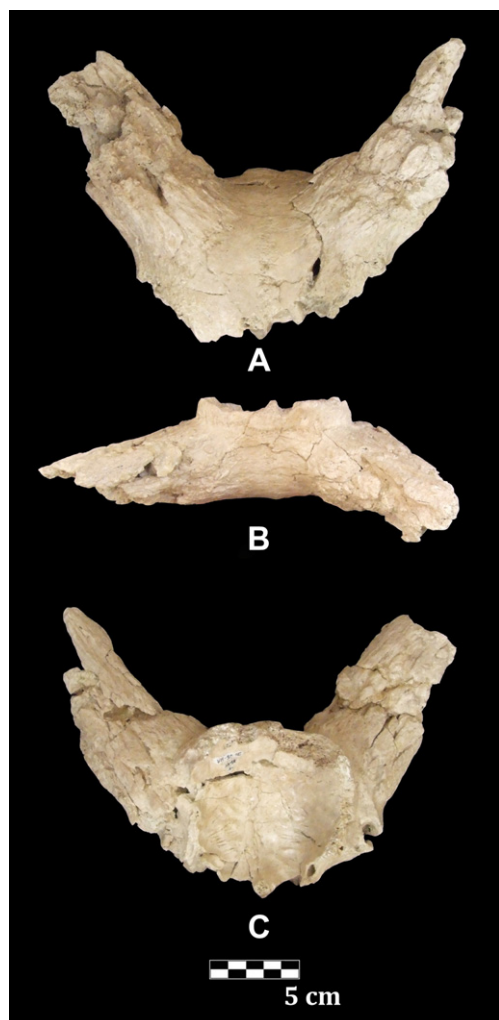


Fig. 2. Cranial vault VM 9000 of *Hemibos* sp. aff. *H. gracilis* from Venta Micena (A: frontal view; B: upper view; C: internal and posterior view). Scale in cm.

Finally, the cranial vault shows a coronal suture parallel to the flat posterior face of the horn cores, describing a T-shaped outline in the intersection with the frontal suture.

Two horn core fragments (VM-2284 a and b), left and right, respectively, that correspond to other individual with similar anatomy and section to VM 9000, were also found. Initially, Moyà-Solà (1987) named these specimens VM-82-C2 and attributed them to *C. alba*.

3.2. Specimen VM 8000

This specimen corresponds to a cranial vault, unearthed from quarry 3 at grids 3E12-13, belonging to an unknown large-sized-bovid found during field excavations in 1995 at Venta Micena (Table 3, Fig. 4). This specimen is not as well preserved as the other described above, probably because of a more intense activity of *P. brevisrostris*. It corresponds to a subadult individual that preserves the upper area of a very pneumatized frontal bone that does not preserve any part of the orbital cavities, with the left side better preserved than the right one. The anterior region of the parietal bone also has sinuses, and shows the coronal suture in contact with the interfrontal one following a V-shaped outline. It also preserves part of the left horn core, which is completely pneumatized and destroyed on the posterior region. It is flattened as a consequence of diagenetic compaction, but still preserves part of the original anatomy, going slightly backward, outward, forward and upward. The right horn core was reconstructed. The preserved anatomy falls within the range of variability of the genus *Bison*.

4. Discussion

4.1. Specimen VM 9000

After a long time without a clear taxonomic adscription available for the specimen VM 9000, and given that it shows some anatomical similarities with the African members of the tribe Tragelaphini, a comparison has now been performed. Tragelaphini is now an endemic tribe in the sub-Saharan region, but during the late Pliocene and Early Pleistocene it is also recorded in North Africa (Arambourg, 1979; Geraads, 1981; Geraads and Amani, 1998).

Following Gentry (1985), the members of Tragelaphini have keeled and spiraled horn cores, a braincase which is little angled on the axis of the face, and teeth which have a fairly simple occlusal surface and are not very high crowned. They are mainly browsers in scrub, woodland and forest. Three extant genera are usually recognized: *Boocercus* (bongo), *Taurotragus* (elands), and *Tragelaphus* (bushbuck, sitatunga, nyala, lesser and greater kudu). Direct

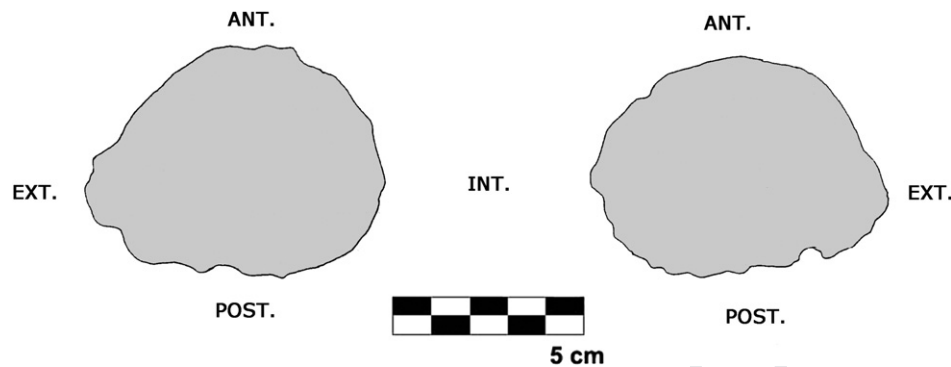


Fig. 3. Basal section of horn cores from specimen VM 9000.

comparisons between Pliocene Tragelaphini *Tragelaphus kyaloae* (Harris, 1991) from Nachukui and Koobi Fora, *Tragelaphus aff. Tragelaphus nakuae* from Hadar (Gentry, 1981), *T. nakuae* (Arambourg, 1941) from Shungura, Nachukui and Koobi Fora (Gentry, 1985; Harris et al., 1988; Harris, 1991), and extant *Tragelaphus (Boocercus) euryceros* from the National Museum of Kenya collections, showed important anatomical similarities to the Spanish specimen VM 9000, but also some differences, based on the presence of a very marked postero-external keel and compact horn cores in the African forms, which are not present in the Venta Micena specimen. It was concluded that VM 9000 is not an African Tragelaphini. Instead, it may be ascribed to the tribe Bovini, and more specifically to the genus *Hemibos*.

Hemibos is represented in the Plio-Pleistocene record by five species. Three, *Hemibos acuticornis*, *Hemibos triquetricornis*, and *Hemibos antelopinus*, are found in the Late Pliocene and Early Pleistocene deposits of the Pinjor Formation (Upper Siwaliks, Indian subcontinent) (Pilgrim, 1939; Nanda, 1979). The fourth species, *Hemibos gracilis*, is located at the site of Longdan, China (Qui et al., 2004) and is the one most similar to the form present in Venta Micena, especially concerning the section of horn cores and their orientation. The fifth species is *Hemibos galerianus*, the youngest of the five: it has been detected at the Early-Middle Pleistocene transition of Ponte Galeria (Italy) (Petronio and Sardella, 1998; Martínez-Navarro and Palombo, 2004) and Ponte Milvio (Martínez-Navarro and Palombo, 2007). Another species, *Hemibos palaestinus*, was described from Israel, in the vicinity of Gadera, and was provisionally dated to the Late Pliocene (Pilgrim, 1941), although this chronology is rather ambiguous (Goren-Inbar, N., personal communication, 2003). A direct anatomical study of this specimen by one of the authors (BMN) suggests that it is not *Hemibos* and corresponds to *Bison*. Fossil specimens of *H. acuticornis*, *H. triquetricornis*, *H. antelopinus*, and *H. palaestinus* are housed in the Natural History Museum, London. Fossils of *H. gracilis* are housed at the Hezheng Paleozoological Museum in Hezheng

Table 3

Measurements of VM 8000 from Venta Micena (*Bison* sp.).

Width of the frontal sinus	25.0	
Width across internal surfaces of horn core pedicels	160.8	
Interfrontal suture versus coronal suture angle	~ 135°–140° (deformed)	
Dorso-ventral diameter of the horn cores (at the base)	r: 59.2	l: 41.4 (deformed)
Antero-posterior diameter of the horn cores (at the base)	r: –	l: –
Circumference of the horn cores (at the base)	r: –	l: –

Abbreviations: r.: right; l.: left (measurements in mm).

(Gansu Province, China) (Qui et al., 2004). Of the two fossils described for *H. galerianus*, one is housed in Suprintendenza Archeologica di Roma (Martínez-Navarro and Palombo, 2004), and the other is a horn core from the Ceselli Collection, housed at the Monastery of Santa Scolastica in Subiaco (near Rome), from the site of Ponte Milvio (Rome) (Martínez-Navarro and Palombo, 2007).

Interestingly, the specimen VM 9000 shows several similarities to the genus *Hemibos*, to *H. antelopinus* but especially to *H. gracilis* (Table 2, Fig. 5) (Qui et al., 2004), species which are both characterized by the presence of elongated and non-prominent frontal bones. Their horn cores have no neck at the base, and the angle between both horn cores is variable, between 85° and 110° in most cases. The orientation of the horn cores is also interspecifically variable in *Hemibos*, but in *H. antelopinus*, and especially in *H. gracilis*, is similar to VM 9000, both upward and outward.

4.2. Specimen VM 8000

VM 8000 corresponds to a subadult individual of a large Bovini that falls within the variability of *Bison*, which is the best recorded buffalo during the European Pleistocene. Based on the cranial anatomy, Bukhsianidze (2005), and other authors previously, considered that *Bison* is a derivation of the earlier Eurasian genus

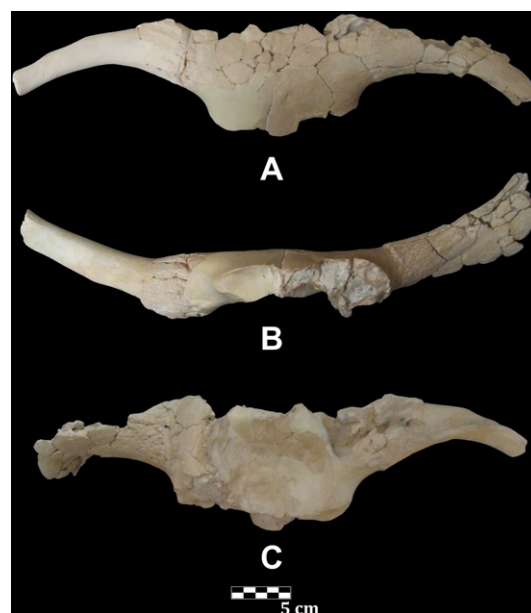


Fig. 4. Cranial vault VM 8000 of *Bison* sp. from Venta Micena (A: upper view; B: frontal view; C: internal and posterior view). Scale in cm.

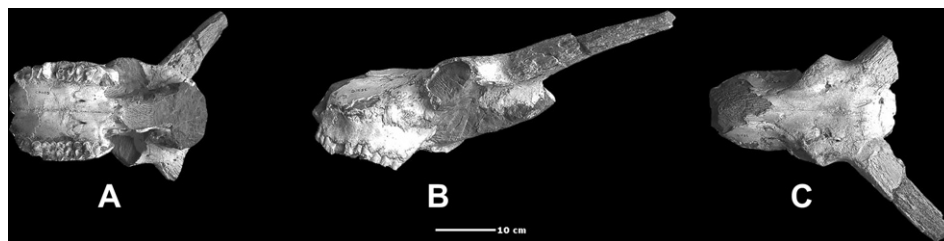


Fig. 5. Cranial specimen HMV 1247, holotype of *Hemibos gracilis* from Longdan (A: basal view; B: left lateral view; C: upper view; figured in Qui et al., 2004, their pl. XXXIV). Scale in cm.



Fig. 6. Geographic record and distribution of the genus *Hemibos* around Eurasia. 1) Venta Micena (Orce); 2) Ponte Galeria and Ponte Milvio; 3) Pinjor (Upper Siwaliks); 4) Longdan.

Leptobos. The same idea, based on morphometric and anatomical data, was also proposed by Martínez-Navarro et al. (2007), who considered that *Bison* originated in an anagenetic evolution from *Leptobos* during the Middle-Late Villafranchian transition (2.0–1.7 Ma). They also differentiated the African origin of the lineage *Pelorovis-Bos*, which separated from the Eurasian lineage of *Leptobos*–*Bison* during the Late Pliocene, or at least in the Early Villafranchian. The oldest record of *Bison* in Europe is the gracile and primitive form *Dmanisibos georgicus* (Vekua, 1995), now named *Bison* (*Eobison*) *georgicus* (Bukhsianidze, 2005), which is dated around 1.77 Ma (Lordkipanidze et al., 2007). The genus is known around the continent at Venta Micena (Moyà-Solà, 1987), as *Bison* (*Eobison*) sp. at Apollonia-1, Greece (Kostopoulos, 1997), *Bison* (*Eobison*) *degiuli* at Pirro Nord, Italy (Masini, 1989), *Bison* *meneri* at Untermassfeld, Germany (Sher, 1997) and *Bison* *schoetensacki* at Vallonnet (Moullé, 1992), but it is also very well recorded during the Middle and Upper Pleistocene and Holocene.

Unfortunately, the anatomical resolution of skull fragment VM 8000 from Venta Micena is not sufficient to ascribe it to one or another species. In addition, the anatomical and metric study of the dentition and postcranial elements should be completed before publication of the final taxonomic determination.

4.3. Paleobiogeography

According to Pilgrim (1939), the evolution of Bovini in the Upper Siwaliks is best described by an evolutionary lineage from *Proamphibos* (Tatrot Formation, Lower and Upper Pliocene) to *Hemibos* (Pinjor Formation, Lower Pleistocene) to *Bubalus* (Middle–Upper Pleistocene–Holocene). The geographical expansion of the *Proamphibos*–*Hemibos*–*Bubalus* lineage is the following: *Proamphibos* is only represented in the Pliocene of the Siwaliks; *Hemibos* is also

recorded during Early Pleistocene times in northern-central China (*H. gracilis* at Longdan; Qui et al., 2004) and Europe at the Early-Middle Pleistocene transition of Italy (*H. galerianus* at Ponte Galeria and Ponte Milvio; Martínez-Navarro and Palombo, 2004, 2007).

In addition, the genus *Bubalus* is well represented in the Middle and Upper Pleistocene fossil record of the Indian subcontinent and Indonesia, and at higher latitudes in China during the interglacial cycles. It dispersed in Central Europe during the late Middle and Late Pleistocene, where it has been described under the specific name of *Bubalus murrensis* (Berckhemer, 1927; Franzen and Koenigswald, 1979; Dam et al., 1997; Schreiber and Munk, 2002), and into the Italian Peninsula, where it is recorded at the Acheulian site of La Polledrara (Rome) (Palombo, 2009).

The finding, with a chronology close to 1.5 Ma, of *Hemibos* sp. aff. *H. gracilis* at Venta Micena, together with the presence of *Bison* sp., which is a typical Eurasian form around the entire continent, changes the age of dispersal of the genus *Hemibos* in Europe, increasing the biogeographical record of this lineage into the westernmost region of the continent (Fig. 6). This dispersal relates to the Late Villafranchian dispersal event in Europe (Martínez-Navarro, 2010; Rook and Martínez-Navarro, 2010; Palombo, 2010), when Asian forms colonized the European subcontinent, and a few taxa of African origin, including the genus *Homo* and sabre-tooth *M. whitei* dispersed in the northern continent around 1.8 Ma (Lordkipanidze et al., 2007; Martínez-Navarro, 2010). Similar species of buffaloes and other large mammals are found in China and in the Iberian Peninsula, suggesting that Spain is not a *cul de sac*.

5. Conclusions

Research at the Early Pleistocene sites of Orce (Guadix-Baza Basin, south-eastern Spain), especially the important paleontological

locality of Venta Micena, has provided new and very important information concerning the European Late Villafranchian fauna. This study reports the first record of *Hemibos* for the European Villafranchian, a genus of Indian origin, which corresponds to a species close to *H. gracilis* found in the early Early Pleistocene Chinese site of Longdan.

Hemibos sp. aff. *H. gracilis* is found at Venta Micena together with the large Bovini *Bison* sp., which is also another Asian immigrant. The faunal composition of the fossil assemblage of Venta Micena is common in the Late Villafranchian of Europe. It is dominated by taxa with an Asian origin, but also records the presence of some species of African origin, which are also recorded in other European assemblages of similar age such as Dmanisi (Georgia), Apollonia-1 (Greece) and Pirro Nord (Italy), which suggests that the Iberian Peninsula was not a *cul de sac* during Early Pleistocene times.

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