New taxonomical, biochronological and palaeoenvironmental data from the Middle Pleistocene site of Cúllar de Baza 1 (Granada, Spain)

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ABSTRACT

The intra-montane Guadix-Baza Basin is one of the few continental basins in Europe that hosts a well-dated set of fossiliferous sites spanning from the latest Miocene to the late Middle Pleistocene. The Cúllar de Baza 1 (CB-1) represents a key site to investigate the effects of the Early-Middle Pleistocene Transition, considered a fundamental transformation in the Earth's climate state. Our review and update of the large mammal assemblage, and particularly equids, is of paramount relevance to understand the systematic affinities and the evolution of the Early and Middle Pleistocene European horses. We confirm the occurrence of two different taxa, the medium sized *Equus altidens* and the larger *E. suessenbornensis*. Moreover, we illustrate that CB-1 is essential for the biochronological studies of the latest Early Pleistocene/Middle Pleistocene transition (Epivillafranchian/Galerian ELMA); in particular with regard to the Last Occurrences of the Etruscan rhino *Stephanorhinus etruscus* and the large deer *Megaloceros savini* and the First Occurrence of the water-rat *Arvicola mosbachensis* in the Iberian peninsula. Finally, a development of a mosaic environment characterised the CB-1 site contrasting with the conditions reported for other Iberian late Early and Middle Pleistocene localities.

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1. Introduction

The time period spanning between ca. 1.4–0.4 Ma ("Early-Middle Pleistocene Transition" or EMPT) was characterised by a series of major events such as a progressive shift from 41 to about 85–125 ka of the orbital rhythm that caused the increase of the amplitude of climate oscillations, the occurrence of longer and more severe glacial periods and the developing of both seasonality and aridity in the Northern Hemisphere. A major climatic shift was the long-term (~80 ka) and severe glaciation, known as the "0.9 Ma event", recorded in correspondence of MIS 24 and MIS 22, that led to substantial increase of global ice volumes and steep decrease of surface sea temperatures (Lisiecki and Raymo, 2005; Maslin and Ridgwell, 2005; Clark et al., 2006; Head and Gibbard, 2015; Maslin and Brierley, 2015). All this climatic instability had important effects on European and especially Mediterranean ecosystems, seasonality and mammal fauna composition (Madurell-Malapeira et al., 2009; Kahlke et al., 2011; Magri and Palombo, 2013; Bertini et al., 2015; Combourieu-Nebout et al., 2015; Fritz et al., 2016; Hosfield, 2016; Palombo, 2014, 2016a, 2016b, 2017; Rodríguez et al., 2016; Suc et al., 2018; Flavia Strani et al., 2019).

The alteration of habitat conditions is well known to deeply influence mammal communities which may develop new community structure and ways to exploit the available plant resources (DeMiguel et al., 2010; DeMiguel, 2016; Lozano et al., 2016; Palombo, 2016a). Herbivorous mammals, for example, are highly susceptible to variation in vegetal communities and, hence, their feeding strategies accurately reflect plant resource availability and
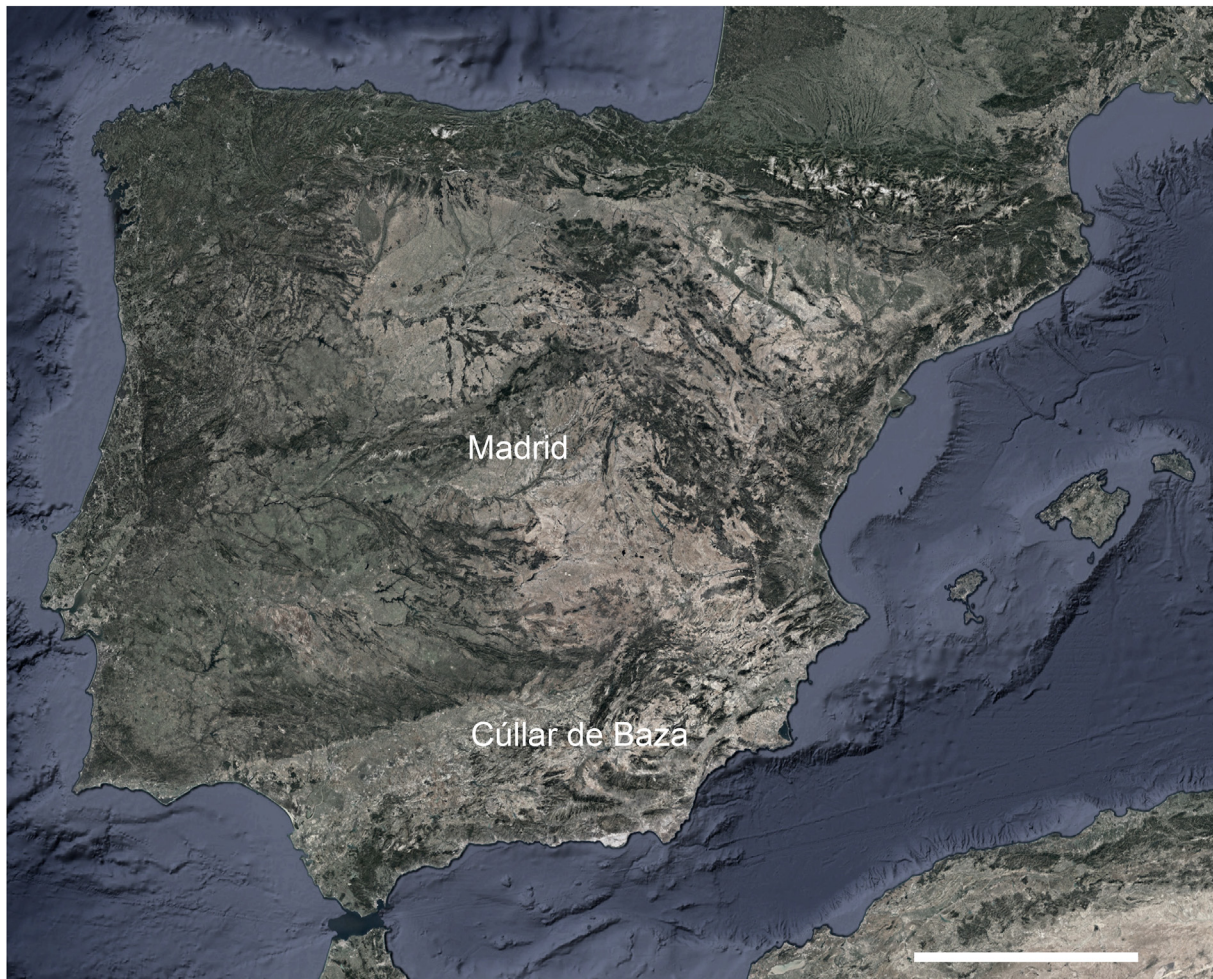
Fig. 1. The CB-1 geographical position within the Iberian Peninsula; scale bar 500 km.

environmental settings. From the study of the feeding behaviours of fossil herbivores pivotal palaeoecological information can be obtained, such as niche occupation and habitat settings (i.e., abundance of open grasslands versus closed canopies, vegetation type availability, degree of aridity, etc.) (Fortelius and Solounias, 2000; Solounias and Semprebon, 2002; Rivals and Athanassiou, 2008; DeMiguel et al., 2010, 2011, 2012; Strani et al., 2015, 2018a,b, 2019).

The intra-montane basin of Guadix-Baza (Province of Granada, southeastern Iberian Peninsula) is one of the few continental basins in Europe hosting an accurately dated set of fossiliferous sites from the latest Miocene to the late Middle Pleistocene (Oms et al., 2000; Arribas and Palmqvist, 2002; Scott et al., 2007; Agustí et al., 2010; Álvarez-Posada et al., 2017) (Fig. 1). The initial palaeontological activities in the Guadix-Baza Basin were performed in the site of Cúllar de Baza-1 (hereinafter CB-1) that was discovered by Rafael Lazo in 1971 during a geological survey and subsequently excavated by Ruiz Bustos from 1973 to 1975 (Fig. 2). The last campaign was carried out in 1987 when a surface of 48 m^2 was excavated and 326 fossils were unearthed (see SD1 for further data). Moreover, the human presence is also testified by scanty lithic artifacts, in particular five chopping tools, two flint flakes and manuports (Vega Toscano, 1989). An early Middle Pleistocene age was assigned to CB-1 using faunal criteria (Ruiz-Bustos and Michaux, 1976; Ruiz-Bustos, 1984). Recently, an estimated age of about 0.75−0.70 Ma was obtained through paleomagnetic data (Scott and Gibert, 2009).

The aim of this work is twofold. Firstly, we aim to provide a detailed systematic revision of the mammal assemblage of CB-1 and, in particular, of the equid remains that represent a key sample to understand the systematics and the evolution of the Early and Middle Pleistocene European horses. Secondly, we provide updated insights for the changes in the terrestrial ecosystems changes after the "0.9 Ma event", in the context of the EMPT, by inspecting for the first time the long-term dental wear patterns (to infer diet) and other ecologically relevant traits (such as molar crown height) of the fossil ungulates of CB-1. Here we compare new data with those from selected southwestern European sites to provide a more global palaeoenvironmental scenario during a time interval of paramount importance for inferring the dynamics.

2. Materials and methods

2.1. Data set

We reviewed 440 large mammal remains discovered in the site of Cúllar Baza-1 during the excavations led by Ruiz Bustos in 1976 and by researchers of the Museo Nacional de Ciencias Naturales-CSIC (MNCN) (Madrid, Spain) in 1987. At the site about 1300 specimens of small mammals and 195 microfauna remains (foraminifers, ostracods, mollusks, fishes and turtles) were discovered in the same years. This material is now housed at MNCN.

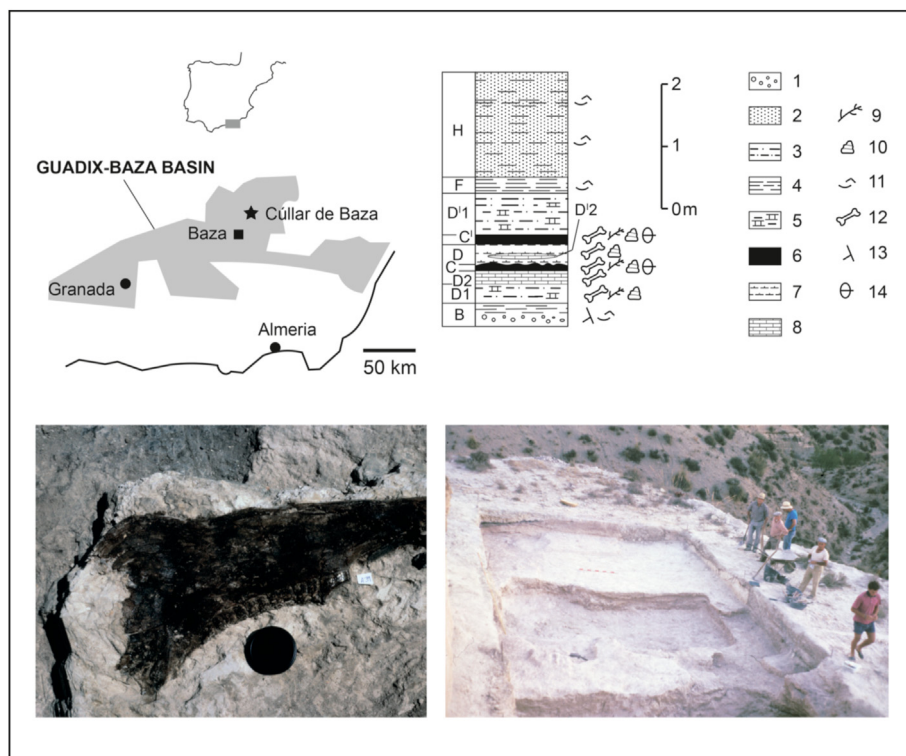The identification of specimens is based on their anatomical

Fig. 2. The CB-1 geographical position within the Guadix-Baza Basin (top left), the CB-1 stratigraphy (top right) modified from Alberdi et al. (2001); discovery of an *Equus* mandible during the excavation in 1987 (bottom left), field activities in 1987 (bottom right). Stratigraphy: 1, Conglomerates and sands; 2, sands; 3, sandy silts; 4, silts; 5, calcareous silt; 6, clays; 7, marls; 8, limestone; 9, vegetal fragments; 10, gastropods; 11, ostracods; 12, preferential levels for the accumulation of bones; 13, root bioturbation; 14, organic matter.

features and morphological and morphometric comparative analyses. All measurements were taken with digital calipers with a precision of 0.1 mm. Morphological and morphometric data used for comparison are from the cited literature. Particular attention was paid to the equid remains representing more than 76% of large mammal specimens. This equid sample was included in the review of European stenonoid horses (Alberdi et al., 1998) and considered in a number of paper dealing with European Equidae (e.g. Alberdi 2010; Alberdi and Palombo, 2013a; 2013b; Alberdi and Piñero, 2015; Piñero and Alberdi, 2015). The CB-1 *Equus* specimens were compared with samples from Iberian (Barranco León 5, Fuente Nueva 3, Huéscar 1, Quibas, Cueva Victoria and Venta Micena) and other European sites (Selvella, Farneta, Pirro Nord, Slivia, Venosa-Loreto, Ponte Galeria in Italy, Süssenborn in Germany and Solilhac in France) (Alberdi and Palombo, 2013a, 2013b; Madurell-Malapeira et al., 2010; Alberdi and Piñero, 2015; Piñero and Alberdi, 2015; Palombo and Alberdi, 2017).

2.2. Long-term patterns of tooth mesowear

Mesowear analyses were performed to infer the terrestrial ecosystem at CB-1. Mesowear is a good dietary indicator in herbivorous mammals as it represents the cumulative effects of ingested items as foods and exogenous particles (although according to some studies the effect of grit and dust is not recorded by dental mesowear but rather by hypsodonty; Kaiser et al., 2013; Kubo and Yamada, 2014) on teeth morphology that are produced in a long period of time (months, years) compared to the lifespan of the animal (Fortelius and Solounias, 2000; DeMiguel et al., 2008; DeMiguel, 2016; De Miguel et al., 2019) (for further information about the method see Text SD2). Here, we examined the occlusal

relief (scored as high or low) and cusps shape (ascored as sharp, rounded or blunt) of the apex of the paracone or metacone of upper molars (M1-M3) and the apex of the metaconid and entoconid of lower molars (m1−m3) of artiodactyl taxa, and the apex of the paracone or metacone of upper teeth (P4-M3) in horses, following Kaiser and Solounias (2003). Obtained data were then compared with that of extant ungulate taxa with well-known feeding behaviours (Fortelius and Solounias, 2000). Occlusal relief and cusp shape scores were then converted to a single mesowear score (MWS) following (Rivals et al., 2009). The score is based on seven cusp types (numbered from 0 to 3), ranging in shape from high and sharp (stage 0) to completely blunt with low relief (stage 3). We do not use the more recent scoring system by Saarinen et al. (2016) because the method by Rivals et al. (2009) has been more customarily used for the analysis of ungulate mesowear, so it enables comparisons among a larger data set of (previously published) fossil taxa. We analysed 28 specimens (*E. suessenbornensis* N = 17; *E. altidens* N = 3; *M. savini* N = 6; and *Capra* sp. N = 2). Hierarchical Clustering Analysis was first performed using Ward method and Euclidean Distance with the percentage of high relief, sharp and blunt cusps. Discriminant analyses were subsequently performed to examine the resolution of mesowear variables applied to the fossil taxa. The percentage of high relief coupled with rounded and blunt cusps were used as independent variables and two dietary (conservative and radical) classifications were used as grouping variables (Fortelius and Solounias, 2000). Descriptive and inferential statistics were conducted using IBM SPSS Statistics 24. Further information about material (e.g. specimen list) and methods are provided in SD. See also DeMiguel et al. (2008, 2010, 2011, 2016 and 2019) for specific information about statistics.

3. Systematic palaeontology

Class Mammalia LINNAEUS 1758
Order Proboscidea ILLIGER, 1811
Family Elephantidae GRAY, 1821
Genus *Mammuthus* BROOKES, 1828

3.1. Description

Specimen MNCN-13035 - a small fragment of tusk (about 88 mm in length). The Schreger lines are locally detectable on the natural cross-section of the tusk, but the pattern is not sufficiently clear and informative for the genus/species identification. It is well known that the Schreger pattern, a unique characteristic of proboscidean ivory visible in cross-sections of tusks (Obermayer, 1881), consists of two intersecting sets of spiral lines that radiate clockwise and counterclockwise, whose intersection forms two types of Schreger angles, named "concave angles" and "convex angles", which respectively open towards the medial/inner and lateral/outer area of the tusk. The angle width increases from the tusk nerve/pulp cavity (inner angles) towards the dentine-cementum junction (outer angles), but at a different pace in *Mammuthus* with respect to *Palaeoloxodon* and extant elephants (Espinoza and Mann, 1993; Fisher et al., 1998; Palombo and Villa, 2001, 2007; Trapani and Fisher, 2003). The values of the convex outer Schreger angles of *Mammuthus*, measured at the dentine-cementum, is on average less than those of the other elephants, although few exceptions have been recorded (Ábelová, 2008), but, moving to the pulp cavity, the variability ranges overlap especially as regards to the inner convex angles (Palombo and Villa, 2007). Accordingly, although the width of the convex Schreger angles (including a few close to the dentin-cementum junction) measurable in the CB-1 tusk, is hardly greater than $90-95°$, the value cannot be considered conclusive enough for identifying the specimens as belonging to *Mammuthus*.

Specimen MNCN-13035 - a right hemimandible fragment where only a small portion of the horizontal branch with m2 (dp3/dm3) and m3 (dp4/dm4) is preserved (Fig. 3, Table S1). The m2 (dp3/dm3), rather plump and low-crowned, in moderately advanced wear, is almost complete and shows its original count of x5x plates (assuming that the last loop belong to a platelet slightly warped by the pressure exerted by the erupting m3). The number of plates falls in the range of both *M. meridionalis* specimens from Valdarno and *M. trogontherii* from Süssenborn (Table S1). According to Maglio (1973), in *Palaeoloxodon namadicus* (including *P. antiquus* as younger synonym) the number of plates ranges from 6 to 7, while Guenther (1977) and Aguirre (1968−1969) respectively indicated for *P. antiquus* a normal range x6x-x8x and 8−9, and Pohlig (1888) stated that x5x may also occurs, though rarely. Although the enamel pattern of the CB-1 m2 is poorly diagnostic, as it frequently occurs in this tooth, the enamel figure of the third lamina shows, however, some features consistent with *Mammuthus*. The loop has a tripartite structure with a central oval expansion, flanked on each side by elongated rings as it is commonly found in *Mammuthus*. The same pattern is present, even though less evident, in the fourth lamina. The enamel in averagely thin, weakly folded in the lateral parts of loops, showing fine wrinkles that became more evident and stronger in the middle parts, especially on the mesial side of occlusal figure of the fourth lamina. The loop of the fifth lamina is moderately buccally inclined, and an isolated ring is present on this side, where the effect of the pressure exerted by m3 is particularly evident. On balance, an identification of the tooth as a m2 of *M. meridionalis* or *M. trogontherii* remains open. The fragment of m3 is badly preserved. The first four plates, in very initial wear, are fairly deformed with an unclear wear pattern. Few isolated rings

Fig. 3. Fragment of a right hemimandible of *Mammuthus* sp. MNCN 13035 with m2 and m3 in occlusal view, scale bar 50 mm.

are still present, the enamel, basically unfolded due to the initial wear, is moderately thicker than in m2, ranging from about 1.6 to 2.2 mm, with an average value of 1.63 mm.

Specimen MNCN 13196 - fragment of molariform tooth with three incomplete plates in an advance wear. The occlusal enamel figures consist of two separate loops, as it sometimes occurs in very worn molariform teeth. Based on the maximum width of the fragment (≈ 70 mm), it is possible hypothesize that the tooth is a fourth molar.

MNCN-13230, MNCN-13231, two caput femoris do not showing any trace of fusion, even initial, to the femur. Their dimensions (medial-lateral x antero-posterior breadth $= 159,5 \times 156,3$ in MNCN-13230, and $= 155,2 \times 151,0$ in MNCN-13231) suggest both belong to the same young individual.

MNCN-13227, a right cuboid fragment whose preservation status prevents any identification of taxonomically diagnostic features.

Order Carnivora BOWDICH, 1821
Family Hyaenidae GRAY, 1821
Genus *Crocuta* KAUP, 1828
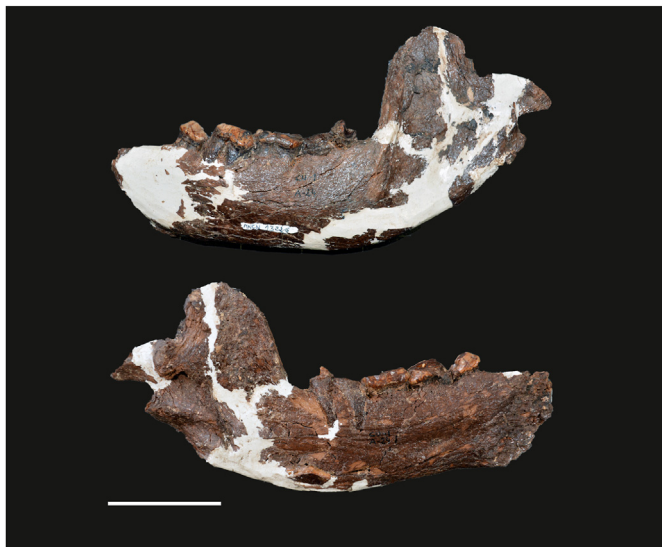*Crocuta crocuta* ERXLEBEN, 1777 (Fig. 4).

Fig. 4. Left heminadible of *Crocuta crocuta* (MNCN-13226): buccal (up) and lingual (down) views. Scale bar 50 mm.

3.2. Description

MNCN-13226 - Left heminadible. The mental region of the hemimandible is very damaged and lacks in the incisors and the canine. The tooth wear is particularly marked in the crown tips of p3 and p4. The p2 is reduced in size compared both to p3 and p4. The horizontal branch is deeper in correspondence with m1, the vertical branch is slightly damaged, but a wide masseteric fossa can be observed. The glenoid articulation is damaged but moderately developed. The great development of the p3 in relation to the other premolars and the low development of the talonid of the m1 confirm the attribution to *Crocuta crocuta* (Alcalá and Morales, 1989). The length/width ratio of the lower p4 has been compared with that of *Crocuta* ssp. specimens from selected Middle and Late Pleistocene European localities (Sardella and Petrucci, 2012) (Bonifay, 1971; Ballesio, 1979; Argant, 1991; Testu, 2006), but it is not possible to establish a clear relations due to the scarcity of our sample and the overlapping ranges of the selected *Crocuta* ssp. (Fig. SD1). Furthermore, there is no consensus among authors in considering the different Pleistocene European spotted hyena fossil remains as subspecies of the African spotted hyena such as *Crocuta crocuta praespelaea* (Schütt, 1971), *C. c. intermedia*, *C. c. petralonae* (Kurtén and Poulianos, 1977) and *C. c. spelaea* (Kurtén, 1957; Werdelin and Solounias, 1991) or, instead, as different species (*C. spelaea*; Soergel, 1937) or subspecies such as *Crocuta spelaea intermedia* (Bonifay, 1971). Recently, according to Rohland et al. (2005), the living spotted hyena from Africa and cave hyenas from Eurasia are intermingled in phylogenetic analyses thus questioning the taxonomic delineation of the Pleistocene spotted hyenas as a subspecies or even species distinct from extant spotted hyenas. For these reasons, we ascribed the specimen from CB-1 to *Crocuta crocuta*.

Family Canidae FISCHER, 1817
Genus *Vulpes* FRISCH, 1775
Vulpes sp.

3.3. Description

MNCN-13128 - fragment of left hemimandible, no teeth are preserved. We ascribe this remain to *Vulpes* for the morphology of

the masseteric fossa and for the outline of the mandibular body.

(MNCN-13129) – Incomplete radius. The diaphysis is rectilinear and anteroposteriorly flattened. The distal epiphysis is elliptical with a lateral extension (styloid apophysis). This morphology is consistent with *Vulpes*.

Genus *Canis* LINNAEUS, 1758
Canis mosbachensis SOERGEL, 1925

3.4. Description

MNCN-13197 - right hemimandible. In the toothrow, showing a moderate curvature, the p3 is placed below the level of the alveolar plane of p2 and p4. The hypoconid of the m1 is large and the crest between the hypoconid and the entoconid is strong and sinuous. The protoconid of the m2 is large and prominent. The lower m1 has been morphometrically compared with specimens belonging to different *Canis* species as *C. mosbachensis* from European and Chinese Early and Middle Pleistocene sites, *C. etruscus* from Italian Early Pleistocene sites, *C. lupus* ssp. from Middle Pleistocene to Recent sites and *Lycaon lycanoides* from the Middle Pleistocene Germany site of Untermassfeld (Fig. SD2). The remains from CB-1 are set in the *C. mosbachensis* variability, any further consideration (as its small size) could be rather speculative since the few samples. Following (Bartolini Lucenti et al., 2017) and based on both morphological and morphometric features we therefore ascribe these remains to the medium-sized wolf-like *Canis mosbachensis*.

Order Perissodactyla OWEN, 1848
Family Rhinocerotidae GRAY, 1821
Genus *Stephanorhinus* KRETZOI, 1942
Stephanorhinus aff. *S. etruscus* (FALCONER, 1868).

3.5. Description

The remains (Text SD3) belong to the same individual and were already described in detail by Cerdeño (1989). According to this author, the three carpal and the metacarpal bones have similar morphology and dimensions of the *S. etruscus* from the French locality of Senéze. Moreover, the ratio diagrams, in particular the semilunar and the pyramidal ones (Fig. SD3), show a major affinity of the CB-1specimens with *S. etruscus*. For these reasons we agree with Cerdeño (1989) even if new findings could better clarify the systematic position of the CB-1 rhino.

Family Equidae GRAY, 1821
Genus *Equus* LINNAEUS, 1758
Equus altidens von REICHENAU, 1915 (Fig. 5).

3.6. Description

Equus altidens remains (Text SD3) are the most abundant in the Cúllar de Baza 1 site. The cheek teeth display the typical stenonoid protocone and the double knot shape but are smaller than in *E. stenonis*. No complete skull was discovered. The upper cheek teeth (P2-M3) are medium in size. The protocone is small and oval-triangular in shape, the mesial part is short while the distal is moderately elongate, flattened or lingually indented. The pli caballin is generally present and the plis of the fossettes are moderate. The hypocone is mainly open and more or less oval in shape with a marked distal groove and slightly marked mesial grooves; in some M3 the hypocone is isolated inside the loph. The hypsodonty index (H/L ratios, where H is the maximal height of the tooth and L is the maximal length at 10 mm the base of the crown, following Eisenmann et al., 1988) is 3.09 in the P3-4 and 3.27 in the M1-2. The lower premolars show a double knot shape, the metaconids and metastylids display short, rounded and sometimes clearly pointed metastylids and a "V-shaped" linguaflexid. The ectoflexid is shallow

Fig. 5. Remains of *Equus altidens altidens* from Cúllar de Baza 1 (Granada, Spain). MNCN-13170: left hemimandible in internal (1) and occlusal (2) views; MNCN-15731: right p2-m3 in occlusal view (3); MNCN-13086: a left P2 (4); MNCN-13139: a right astragalus in anterior (5) and posterior (6) views; MNCN-13094: right P3-4 (7); MNCN-13083: left P3-4 (8); MNCN-13169: a left MCIII (9); MNCN-13223: a distal portion of MCIII (10); MNCN-13146: a 1PHIII in anterior (11) and posterior (12) views; MNCN-13147: a 2PHIII in anterior (13) and posterior (14) views; MNCN-13089: right M1-2 (15); MNCN-13145: a distal portion of MCIII (16); MNCN-13104: left M3 (17); MNCN-13091: right M1-2 (18). Scale bar 10 mm.

and does not enter in the isthmus of the premolars, but it is deep and penetrates the isthmus touching the linguaflexid in the molars. The lower cheek teeth (p2-m3) are also medium in size. The limb bones are slender, in particular the metapodials and the phalanges, more than in the other stenonoid species, including the most related taxa *E. senezensis* (sensu Alberdi et al., 1998) and *E. a. granatensis*. The body mass of *E. altidens altidens* averages out at 297 kg whereas *E. altidens granatensis* at 359 kg following the specific study of the Equini tribe (Alberdi et al., 1995; Alberdi and Palombo 2013a).

Multivariate analyses were performed to estimate variation and differences in size and proportions. Discriminate analysis (DA) for MCIII, MTIII, AST and 1PHIII in the aim to maximizing the separation between the groups already recognized in previous papers (Fig. SD4). These analyses (DA) indicate their similarities with other equid forms identified as *E. altidens* and *E. suessenbornensis* from different European localities (Süssenborn, Pirro Nord, Slivia, Selvella-Gioiella, Venosa-Loreto, Cueva Victoria, Quibas, Huéscar 1, Barranco León 5, Fuente Nueva 3, Venta Micena) and their differences with others stenonoid species as *E. senezensis senezenses* and

E. senezensis stehlini (Valdarno, Casa Frata, Senèze) (Alberdi and Palombo, 2013a, 2013b; Alberdi, 2010; Alberdi et al., 1998; Alberdi and Piñero, 2015; Piñero and Alberdi, 2015, among others) (Fig. 5 and Fig. SD4; Tables SD2; SD3 and SD4).

 Family Equidae GRAY, 1821
 Genus *Equus* LINNAEUS, 1758
 Equus suessenbornensis WUST, 1900 (Fig. 6).

3.7. Description

The remains fom CB-1 (Text SD3) fall in the morphological and dimensional range of *Equus suessenbornensis*, a large and robust horse, but smaller than *E. major* (*sensu* Alberdi et al., 1998). The dental morphology is similar to that of *E. altidens,* but the enamel shows a more plicated pattern in the upper cheek teeth. The upper cheek teeth (P2-M3) are larger in size and the crowns are tall and robust. Some morphological convergences with the teeth of the caballine type are recognizable, such as the long protocones with concave lingual borders and the larger mesostyles and grooves on the premolars. The styles are simple or weakly grooved on the molars. Most of the teeth are very worn and the plis are not therefore visible; the only dentary row is very worn, and its size is comparable to that of *E. suessenbornensis*. The body mass of this species is around 565 kg (see Alberdi et al., 1998).

The lower cheek teeth show cingular structures as the protostylids that are similar in shape to the caballoid equids, but some other dental characteristics as the stenonian shape of the double-knot, although more derived than in *E. stenonis*, clearly indicate an advanced taxon within the basic stenonoid type. The preflexid and postflexid are slightly folder. The ectoflexid is shallow and does not enter the isthmus in the premolars, but it is deep and penetrates the isthmus touching sometime the linguaflexid in the molars. No lower cheek teeth are recorded in the CB-1 site. Finally, *E. suessenbornensis* is characterized by a very robust and large

Fig. 6. Remains of *Equus sussenbornensis* from Cúllar de Baza 1 (Granada, Spain). MNCN-13195: distal portion of a right tibia; 2: MNCN-13194, distal articulation of a right tibia; 3: MNCN-13193, a right MTIII; 4: MNCN-13182, a right astragalus in anterior view; 5: MNCN-13182, a right astragalus in posterior view; 6: MNCN-13184, a right astragalus in anterior view; 7: MNCN-13184, a right astragalus in posterior view; 8: MNCN-13194, a distal portion of a left MCIII; 9: MNCN-13186, a 2PHIII in anterior view; 10: MNCN-13186, a 2PHIII in posterior view; 11: MNCN-13189, a right in proximal view; 12: MNCN-13190, a right triquetum in anterior view; 13: MNCN-13192, a 1PHIII in anterior view; 14: MNCN-13192, a 1PHIII in posterior view; 15: MNCN-13191, a 1PHIII in anterior view; 16: MNCN-13191, a 1PHIII in posterior view. Scale bar 10mm.

appendicular skeleton (Fig. 6 and Fig. SD4; Tables SD2; SD3 and SD4).

Order Cetartiodactyla MONTGELARD & DOUZERY, 1997
Family Suidae GRAY, 1821
Genus *Sus* LINNAEUS, 1758
Sus sp.

3.8. Description

The morphology and dimension of the upper canine (MNCN-13123) do not allow to ascribe this remain to any *Sus* species, in particular to the Pleistocene one *S. scrofa*.

Family Cervidae GOLDFUSS, 1820
Genus *Megaloceros* BROOKES, 1828
Megaloceros savini (DAWKINS, 1887) (Fig. 7).

3.9. Description

In the cranial remains of large deer (Text SD3) from CB-1, the frontal bones are partially visible only in MNCN-19797 but, due to its poor preservation, it is not possible to establish whether they are concave or convex. The pedicles are short and sub-circular, diverging in relationship to the sagittal plane. The coronet is slightly marked. The beam shows a transversal compression that becomes distally stronger. In lateral view, the beam is dorsally inclined, curving in the first two portions. A slight inflection is observed between the portions of the beam. The beam abruptly changes its direction from the third tine, going upward and forming an angle of about 135°. In frontal view, the beams diverging themselves and describe a sinuous shape until the third tine. The three tines are set in the same cranio-caudal plane, the first two tines are anteriorly separated from the beam, the third one posteriorly. The first tine is placed very close to the coronet, and it has a large size and is flat. The second and the third tines are reduced in size and are transversally compressed.

Upper teeth are very damaged and it is therefore not possible to describe the morphological features. For the lower teeth it is important to observe that the p4 is not molarised and, as stated by Azanza and Morales (1989), the occurrence of an enamel islet has an intraspecific variation and it is not diagnostic.

We here confirm the attribution given by Azzaroli (1979) of these remains to the giant deer *Megaloceros savini* due the presence of the palmated brow tine close to the burr. Moreover, in our material, the first three tines are set in the same longitudinal plane, differing from the *Praemegaceros* antler. According to Azzaroli (1979) this giant deer species is related with *Megaloceros giganteus* and *Megaloceros antecedens* constituting the "*Megaloceros giganteus* group". This taxonomical attribution is however debated (cf. e.g. Kahlke, 1956, 1965; Azanza and Morales, 1989; van der Made and Tong, 2008; Vislobokova, 2013; Croitor, 2018 and references in those papers).

Family Bovidae GRAY, 1821
Genus *Bison* GRAY, 1821
Bison sp. (Fig. 8)

3.10. Description

In the right metatarsal, the 2nd/3rd tarsal and cubonavicular facets are demarcated in proximal view by a small ridge and are characterized by the occurrence of small medial tubercle on the posterior/medial corner of the facet for the fused 2nd/3rd tarsal. According to (Gee, 1993) these features are peculiar of the genus *Bison*. This specimen has been also morphometrically compared with other metatarsal bones belonging to different Pleistocene *Bison* samples (Fig. SD5). However, this analysys does not clarify its specific attribution, also considering that the actual phylogenetic relationships between Western European early Middle Pleistocene *Bison* are still debated (see Palombo, 2017 and references therein).

Genus *Capra* LINNAEUS, 1758
Capra sp. (Fig. 8)

3.11. Description

The right hemimandibles (MNCN-13165, MNCN-13166) belong to two adult individuals, based on the wear degree of the teeth, which have morphology similar to *Capra* and different from *Hemitragus*. In particular, with respect to *H. bonali* from the French site of la Grotte de l'Escale, the molar lobules are more separated from each other and the posterior lobule of the lower m3 is less developed, as already stated by Azanza and Morales (1989). Conversely, the ratio diagram of the lower p4 − m3 series (Fig. SD6) seems to support the hypothesis of a major affinity of the CB-1 specimen with *H. bonali*. Since there is no consensus about the taxonomy and systematic of thar/goat remains found in the post-Olduvai LFAs
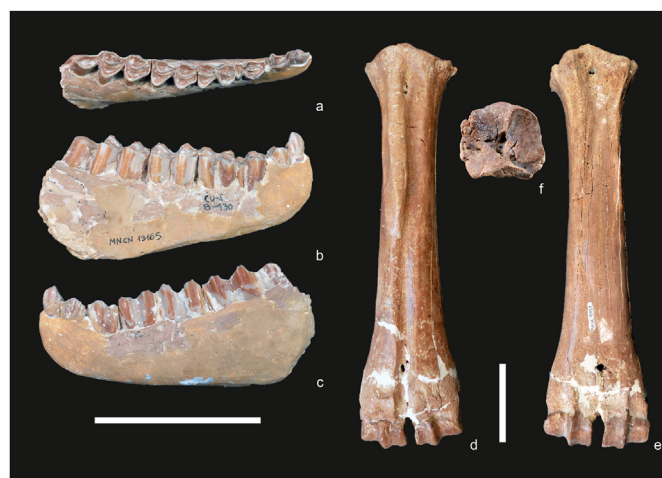

Fig. 7. Left antler MNCN-19796 of *Megaloceros savini*: external view. Scale bar 50 mm.

Fig. 8. Right hemimandible MNCN 13165 of *Capra* sp.: occlusal (a), labial (b) and lingual views (c). Right metatarsal bone of MNCN-13132 *Bison* sp.: dorsal (d), ventral (e) and proximal views (f). Scale bar 50 mm.

from SW Europe and, after Crégut-Bonnoure (2007 and references therein), all the Spanish caprine remains from Venta Micena, Barranco Léon, Fuente Nueva, Quibas and Huéscar 1 (1.5–0.9 Ma) have to be referred to *H. albus* instead of "*Capra*" *alba* (Palombo, 2017 and references therein). We therefore retain the attribution given by Azanza and Morales (1989) pending new discoveries that could shed light on this taxonomic question.

3.12. Notes on the small vertebrate fauna

The small mammal assemblage from the CB-1 consists of the following taxa (Sesé et al., 2001): *Sorex* sp., *Neomys* sp., *Crocidura* sp., *Cricetulus* (*Allocricetus*) *bursae*, *Eliomys quercinus*, *Apodemus* aff. *A. sylvaticus*, *Microtus* (*Microtus*) *brecciensis*, *Arvicola mosbachensis* and *Lepus* cf. *L. granatensis*.

According to Sesé (1989), it is possible to ascribe the glirid material from CB-1 to *Eliomys quercinus* due to the absence of the accessory crests in the lower molars. In the *Arvicola* sample the molars are rooted, hypsodonts and the enamel is thicker in the posterior borders of the lower molars triangles and in the anterior borders of the upper ones. The *Mimomys* fold is not observed.

Besides this small mammal association, the following squamate reptiles occur in the CB-1 site: *Blanus cinereus*, *Chalcides* cf. *Ch. bedriagai*, *Acanthodactylus* cf. *A. erythrurus*, *Timon* cf. *T. lepidus*, *Podarcis* sp., cf. *Natrix* sp. and *Rh. scalaris* (Barbadillo, 1989; Blain, 2005; Blain and Bailon, 2006). The absence of amphibians may be because of either the small size of the sample or taphonomic biases (Agustí et al., 2010).

4. Dietary behaviour of CB-1 herbivores: inference from the mesowear analysis

Perissodactyls. The equid *E. suessenbornensis* displays similar distributions of sharp and rounded cusps (55.6% and 44.4%, respectively) and high and low relief (50%) resulting in a high MWS of 1.36 (Table 1). No incidence of blunt cusps is recorded. This mesowear pattern points to medium levels of abrasion in the diet of this fossil horse, as typical of mixed feeders. The other equid *E. altidens* has 100% sharp apices and high relief, and a score of 0, which is indicative of lower levels of abrasion, which contrasts with the medium-to-high abrasive diets of extant *Equus*. According to the low sample size available for *E. altidens*, we can consider such a dietary inference as tentative. Artiodactyls. The cervid *M. savini* exhibits mesowear comprised of a predominance of high (83.3%) occlusal relief (recorded in all but one the examined individuals) and either sharp (66.6%) and rounded (33.3%) cusps and a score of 0.75 (Table 1), a signal that reveals that diet was minimally abrasive. Finally, *Capra* sp. has mesowear comprised of high occlusal relief (100%) and combination of sharp (50%) and rounded (50%) cusps, and a score of 0.5, suggesting a somewhat intermediate level of abrasion.

Hierarchical Clustering Analysis produced good resolution in distributing extant ungulates and fossil populations according to

Table 1
Summary of dental mesowear and microwear analysis.

SPECIES	N	%Sharp	%Rounded	%High	%Low	MWS
Equus suessenbornensis	18	56	44	50	50	1.36
Equus altidens	2	100	0	100	0	0
Megaloceros savini	6	67	33	83	17	0.75
Capra sp.	2	50	50	100	0	0.5

Abbreviations:number of specimens measured (N); percentage of specimens with high (%High) and low (%Low) occlusal relief; percentage of specimens with sharp (%Sharp) and rounded (%Rounded) cusps; mesowear score (MWS).

their dental mesowear (Fig. 9A). Two main clusters are recognized, and the dendogram separates clearly taxa with a preference for soft and intermediate abrasive foods (cluster A) from those that enjoyed more abrasive foods (cluster B). All taxa from CB-1 are groupes in cluster A, except for *E. suessenbornensis*, placed in cluster B with most of the grazing ungulates.

Discriminant analyses performed with mesowear variables provided a satisfactory dietary discrimination with 74.1% of extant taxa correctly classified according to the conservative and radical classifications (68.5% and 74.1%, respectively, in cross-validation). Bivariate diagrams based on the discriminant analyses (Fig. 9B and C) show different classification for the equids, with *E. suessenbornensis* being a mixed feeder and *E. altidens* a browser in both types of classification (Fig. 9B and C). This apparent browse specialisation for the latter may be a consequence of the small sample size, so we can conclude that *E. altidens* might have been exhibited a mixed diet as well, and that the few individuals considered here browsed in the last period before death. With regard to the artiodactyls, *Capra* sp. is considered to be a mixed feeder (Fig. 9B, C) and *M. savini* a browser according to both classifications (Fig. 9B and C). Results for these must be also tentatively taken due to restricted samples available for analysis.

5. Discussion

5.1. Biochronological considerations

Fossil remains discovered at the CB-1 site are crucial to explore the systematic and the evolution of Early and Middle Pleistocene European equids. As described above two species are recorded, the medium sized *Equus altidens* and the large sized *Equus suessenbornensis*, thus confirming the hypothesis of the previous works where two different forms were detected (Ruiz-Bustos 1976; Alberdi and Ruiz Bustos, 1989).

A number of authors agree in considering that *E. altidens* had to evolve from a large stenonoid horse leading to a smaller and more slender species, while *E. suessenbornensis*, due to its size, was hypothetically related to *E. major* in spite of the wide temporal gate separating these two species (Palombo and Alberdi, 2017). Other authors (Guerrero-Alba and Palmqvist, 1997) stated that *E. altidens* was a new Early Pleistocene outlander coming from an African species, *E. numidicus*, or to be part of a "non-stenonoid" widely disseminated group, which includes Early to Middle Pleistocene slender horses sharing some traits such as short protocones, a long metaconide, a not very deep lingual groove and developed styles (Eisenmann, 2004). All these considerations support the hypothesis that *E. altidens* originated in Europe through an anagenetic evolutionary process within the stenonian lineage as a response to the climate and environmental changes occurred during the Early-Middle Pleistocene (Sánchez Chillón et al., 1994; Azanza et al., 1999).

The compound of stenonoid and caballoid features shown by *E. suessenbornensis* led some authors to suggest that this taxon could be an evolutionary intermediate between stenonoids and caballoids, or to consider it as a stenonoid horse showing some traits converging towards those of caballine horses. In particular, some authors hypothesize that *E. suessenbornensis* is a descendant of *E. major* (Grossouvre and Stehlin, 1912; Forsten, 1999; Alberdi et al., 1998), which is last recorded in Europe about 1.7 Ma (Musil, 1992), while others propose *E. suessenbornensis* close to (or a direct descendant of) *E. stenonis* (Nobis, 1971; Samson, 1975; Azzaroli, 1990). Some others, instead, reject any affinity between *E. suessenbornensis* and *E. stenonis* (Musil, 1969, 1992), considering this form as an archaic caballoid or a true caballine (Gromova, 1949a, 1949b). There are some features of *E. suessenbornensis*
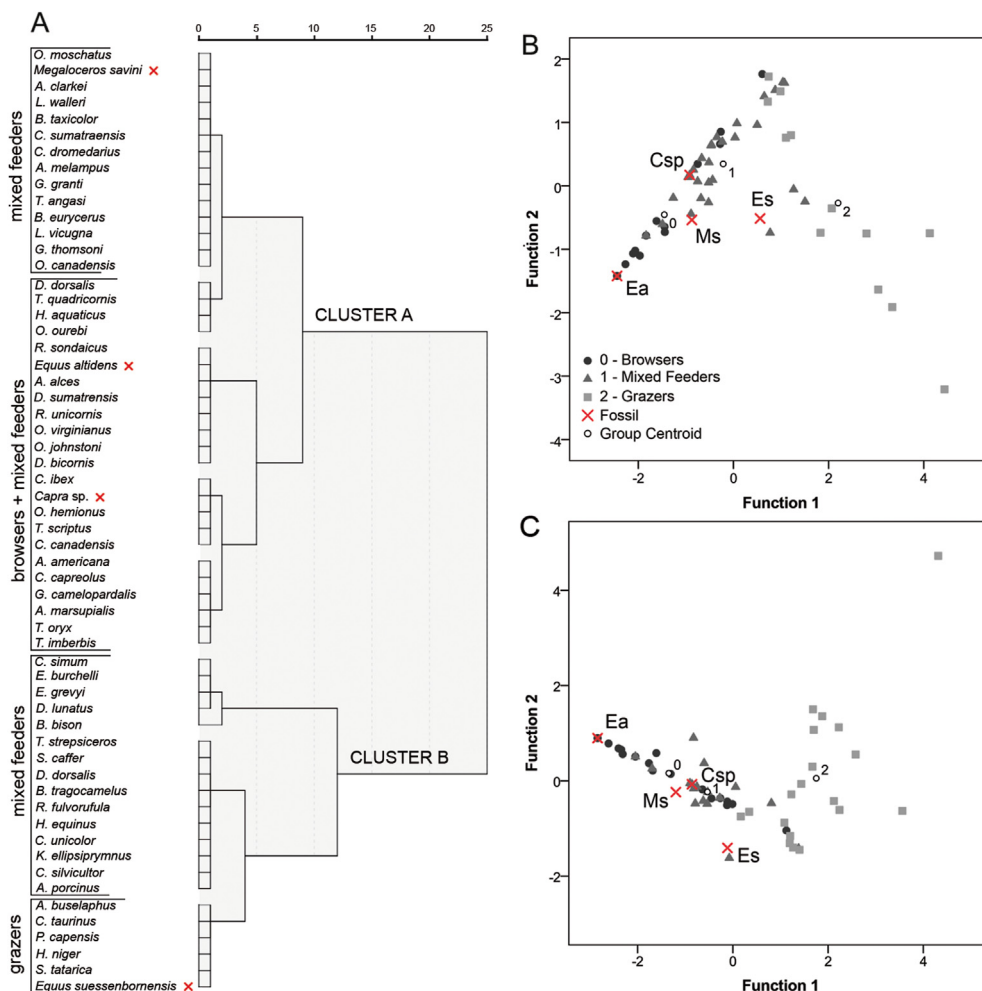
Fig. 9. Hierarchical Clustering Analysis (A) and bivariate diagrams based on discriminant analysis using conservative (B) and radical (C) classifications. Fossil taxa abbreviations: Es, *Equus suessenbornensis*; Ea, *Equus altidens*; Csp, *Capra* sp.; Ms, *Megaloceros savini*. Extant data from Fortelius and Solounias (2000).

(e.g., complicated enamel pattern, upper cheek teeth with rather long protocones having concave lingual borders, lower cheek teeth with marked protostylids) that are similar to those of caballoid equids (Gromova and Dubrovo, 1975), but some other dental characteristics (e.g., the stenonian shape of the double-knot, although more derived than in *E. stenonis*) clearly indicate an advanced taxon within the basic stenonoid type.

The biochronological relevance of *E. altidens* and *E. suessenbornensis* is remarkable because they are present from the latest Early to the Middle Pleistocene (Epivillafranchian to Galerian ELMA) in various European sites. It is worth noting that, among the *E. altidens* subspecies/ecomorphotypes, *E. a. altidens* is associated with *E. suessenbornensis* in sites from Germany, Italy, France, Romania, Hungary and Russia, while in others Spanish localities (Fuente Nueva-3, Barranco León-5, Venta Micena) *E. suessenbornensis* is associated with *E. a. granatensis*.

E. altidens and *E. suessenbornensis* constitute two monophyletic lines of the Plio-Pleistocene equids: *E. altidens* is at the end of the stenonoid line *livenzovensis-stenonis-senezensis-altidens* whereas *E. suessenbornensis* is placed in the *major-suessenbornensis* line, mingling stenonoid and caballine traits (Alberdi et al., 1998) even if there is no consensus about this hypothesis (e.g., Guerrero-Alba and Palmqvist, 1997).

At CB-1 site, the odd-toed ungulates are also represented by few remains tentatively ascribed to *S. etruscus*, which might represent

one of the last occurrences of this taxon in the Iberian Peninsula (Cerdeño, 1993). The disappearance of *S. etruscus* is in fact diachronic in Europe: in central Europe is reported in the late Early Pleistocene (Villafranchian biochron) whereas it survived in the Italian and the Iberian peninsulas until the Early–Middle Pleistocene transition (Epivillafranchian - Galerian biochrons) (Pandolfi et al., 2017).

The even-toed ungulates are represented by a few remains of a suid (*Sus* sp.), a large deer (*Megaloceros savini*) and two bovids (*Bison* sp. and *Capra* sp.). Only the large deer has some biochronological relevance, since its diffusion may characterise the beginning of the Epivillafranchian biochronologial unit (see e.g. Palombo, 2016b; 2018 and reference therein; Bellucci et al., 2015; Palombo, 2018). In the Iberian Peninsula, remains showing some affinities with *M. savini* are first reported in Northern Spain at Sima del Elefante (level TE9; ca. 1.2 Ma) (Atapuerca) (Rosas et al., 2006). Since then, the species has been identified at Cal Guardiola Layer CGRD2 (Terrassa, Catalonia) (Madurell-Malapeira et al., 2010), in the Vallparadís Section, EVT12 (ca. 1.0 Ma) (Strani et al., 2019), and specimens identifiable as or closely relate to *M. savini* are reported from Cueva Victoria (Cartagena, Murcia) (= *Megaloceros novocarthaginiensis*) (Van der Made, 2015). Recently, van der Made (2019) has described a new species of *Megaloceros*, *M. matritensis*, on the basis of material from different localities from a terrace of the Manzanares River (Madrid area, Spain). According to this author,

M. novocarthaginiensis, *M. savini* and *M. matritensis* constitute a temporal sequence showing a gradual change, with a clear lowering of the bifurcation of the brow tine and main beam, an increase in the premolars, and increase in enamel thickness, and a reduction in size. *M. savini* from CB-1 may thus represent one of the last occurrences of the species in the Iberian Peninsula and, consequently, can be considered as an important local biochronological marker.

Due to scarce remains found in the CB-1 site, it is not possible to provide a specific attribution for the bovids *Bison* sp. and *Capra* sp. Before the Jaramillo subchron, *Bison* with differences in size are recorded in Europe. As stated by (Palombo, 2017), it is unclear whether the two lineages existed in Eurasia and dispersed independently into southern western Europe between 1.5 and 1.2 Ma (i.e. subgenus *Eobison* and *Bison*) (Sher, 1997; van der Made, 2013) or the differences in size and a few morphological traits as the robustness of metapodial bones in Southwestern European specimens could depend on phenotypic plasticity and intra-specific variation. The earliest record of a large-sized bison, *Bison schoetensacki*, corresponds to the French site of Le Vallonet (Jaramillo subchron; (Moullé et al., 2006), while a bison with slenderer metapodials, *Bison menneri*, is present in the coeval site of Untermassfeld (Germany; Kahlke et al., 2011). The few fossils of *Bison* from CB-1 do not allow any attribution to *B. schoetensacki* or *B. menneri*. The early record of the genus *Capra* in southwestern Europe is reported from the late Gelasian site of Fonelas 1 (Spain) (*Capra betica*; Arribas and Garrido, 2008). As discussed by (Palombo, 2017), the Spanish remains show some similarities with those of *Capra dalii* from Dmanisi (Bukhsianidze and Vekua, 2006) that are regarded as the ancestor of "*Capra alba*", a caprine only recorded in the Early Pleistocene sites of Venta Micena, Barranco Léon 5, Fuente Nueva 3, Quibas, Huéscar 1 (Spain) ranging from about 1.5 to 0.9 Ma. However, it is worth noting that (Cregut-Bonnoure, 2007) and references therein) considers all the Spanish remains as belonging to the genus *Hemitragus* (*H. albus*). Further findings in the CB-1 site will allow resolving this taxonomical issue.

The elephant remains found at CB-1 site have been already briefly described by Ruiz Bustos (1976) (limited to a fragment of mandible with the second and third incomplete molariform tooth in the dental eruption sequence), Mazo (1989) and Ros-Montoya (2010). Ruiz Bustos (1976) tentatively identified these remains as *M. meridionalis*, though acknowledging the modest taxonomical value of juvenile molariform teeth. Mazo (1989) and Ros-Montoya (2010), conversely, considered them as belonging to *M. trogontherii*.

The observation of compelling morphological and dimensional differences in the second molariform tooth of *M. meridionalis* and *M. trogontherii* is a challenging task because the wide variability shown by the three first moloriform teeth. Particularly, the morphology of the enamel figure of worn laminae on the occlusal surface is quite similar in the second tooth of the two species, and range of dental parameters partially overlaps. Moreover, although *Mammuthus primigenius* second teeth are quite well known and represented in the fossil record (see Maschenko et al., 2005; 2013; Baigusheva et al., 2016; Rufí et al., 2018) it is not the same as regards to *M. meridionalis* and particularly *M. trogontherii* (see e.g. Maglio, 1973; Mazo et al., 1990; van Essen, 2011; Albayrak and Lister, 2012; Pawłowska et al., 2014; Tong, 2012; Tong and Chen, 2016; Baigusheva et al., 2018). The poor documentation increases the difficulty to achieve a correct species attribution.

In view of the puzzling scenario (Fig. 10) of the replacement of *M. meridionalis* by *M. trogontheri* in Western Europe at the Early to Middle Pleistocene transition, the taxonomical assessment of various specimens becomes problematic especially in the case of teeth having limited identifiable features because they are incomplete, belong to very young individual, or due to their

preservation status, the wear degree, the lack of firm data about hypsodonty, the doubtful geological age, the poor or not statistically valid consistency of the sample (Lister et al., 2005; Palombo and Ferretti, 2005; Virág, 2009) (see inter alios Ferretti, 1999; Lister, 2004; Lister et al., 2005; van Essen, 2003, 2011; Palombo and Ferretti 2005, Virág, 2009; Virág and Pazonyi, 2014; Ros-Montoya, 2010; Palombo and Alberdi, 2015). In Spain, the presence of *M. meridionalis* at Huéscar-1, and the apparent lack in the fossil record of *Mammuthus* molariform teeth with mix/intermediate features, support the hypothesis of the exclusive presence of *M. meridionalis* during the late Early Pleistocene (Ros-Montoya et al., 2018), suggesting a later dispersal of the steppe mammoth in the Iberian Peninsula. The available data, however, do not allow to ascertain the time of the replaced by *M. trogontherii*, due the uncertainties about the species to which the elephant remains from Cueva Victoria (latest Early Pleistocene, Gibert and Scott, 2015; Palombo and Alberdi, 2015) and Cúllar de Baza (earliest Middle Pleistocene) belong.

The spotted hyaena *Crocuta crocuta*, the wolf-like canid *Canis mosbachensis* and *Vulpes* sp. constitute the carnivoran assemblage of CB-1. The oldest known stratigraphical occurrence (LlSDk/HlSDk = local Lowest/Highest known Stratigraphical Datum *sensu* Palombo, 2009) of the spotted hyaena *Crocuta crocuta* in Europe is reported in Atapuerca (Northern Spain), in the TD4W level of Trinchera de Ferrocarril (Garcia and Arsuaga, 2001; Cuenca-Bescós and García, 2007), dated to about 0.9 Ma (Berger et al., 2008). At that time, *Pachycrocuta brevirostris* was still present in northeastern Spain (c. 0.83 Ma in Vallparadis EVT7 LFA, Terrassa, Catalonia, (Madurell-Malapeira et al., 2010, 2009). Palombo (2017) underlines that the ecological traits of Pleistocene *Crocuta* cannot be successful in any competition with the short-faced hyaena, the nearly contemporaneous presence of *C. crocuta* in northern and *P. brevirostris* in southern Spain may thus indicate that *Pachycrocuta* had already disappeared from the Cantabrian territory by the latest Early Pleistocene. If confirmed, the occurrence of the spotted hyaena in the CB-1 site provides a strong evidence of the complete replacement of the giant hyena also in the southern Iberian Peninsula around 0.75 Ma.

On the other hand, there is an important faunal turnover that affected much earlier the canids. Around 1.4 Ma a decrease in the diversity has been recorded (Palombo et al., 2008) coinciding with the appearance and dispersal of two new species of medium-to large-sized canids (Sotnikova and Rook, 2010): *C. mosbachensis* and *Lycaon lycaonoides*. These species are documented in the sites of Venta Micena, Barranco León 5 and Fuente Nueva 3, in the Guadix-Baza Basin, spanning approximately 1.4–1.2 Ma (Duval et al., 2012; Toro-Moyano et al., 2013). According to the recent revision provided by (Bartolini Lucenti et al., 2017), the latest Early Pleistocene wolf-like canids from the Iberian Peninsula can be ascribed to the same species that has also been reported in the roughly coeval German site of Untermassfeld (Sotnikova, 2001), i.e., *C. mosbachensis* even if, according Boudadi-Maligne (2012), the occurrence of *C. arnensis* in the late Early Pleistocene site of Cueva Victoria can not be ruled out. The material from CB-1 fully confirms the attribution to this wolf-like canid characterised by a long stratigraphic record, spanning from 1.5 Ma (Venta Micena, Iberian Peninsula) to 0.4 Ma (Vértesszőlős, Hungary) (Sardella et al., 2014).

Finally, the small mammal assemblage also testifies an important faunal renewal in southwestern Iberian Peninsula, recorded in particular in the sites of Huéscar 1 (ca. 0.9 Ma) and CB-1 (ca. 0.75 Ma). The phyletic evolution (e.g., development of ever-growing molars) from the advanced *Mimomys savini* (Huéscar 1) to the first representatives of the water-rat *Arvicola mosbachensis* (CB-1) is documented (Sesé et al., 2001).
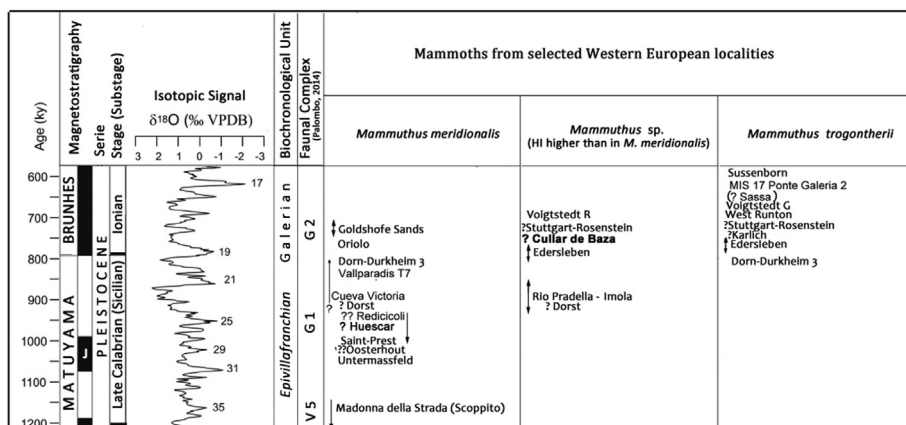
Fig. 10. Biochronological assessment of selected late Early and early Middle Pleistocene Western European sites yielding *Mammuthus* dental remains.

5.2. Palaeoenvironment considerations

Mesowear analyses resulted in two different feeding regimes for the fossil species here investigated, with the equids *E. suessenbornensis* and *E. altidens* equalling patterns of extant mixed feeders and being thus specialised on both soft dicots and grass plants and external abrasives, the bovid *Capra* sp. being probably a mixed feeder, and the deer exhibiting a browsing behaviour.

The presence of *E. altidens* in southwestern Europe could confirm a spread of open landscapes thus having a significant influence on the ecological structure of the large mammal palaeocommunities that probably favoured the dispersal of this taxon. Moreover, the finding of two equids taxa, *E. altidens* and *E. suessenbornensis*, could represent a case of sympatry in which the strong difference in weight would have eluded strong competition (Forsten, 1988; Alberdi et al., 1995, 1998; DeMiguel et al., 2012). The average of body mass for *E. altidens* is 297 kg (in CB-1 218 kg, reconstructed from only one specimen) whereas for *E. suessenbornensis* is 515.53 kg (in CB-1 487 kg) (Palombo and Alberdi, 2017). The decrease in body weight in stenonoid equids may be concomitant to the climatic and vegetational changes occurred from the Early Pleistocene onwards. According to (Sánchez Chillón et al., 1994), the climatic context in the Iberian Peninsula where *E. altidens* inhabited should be warm or warm-temperate and the predominant climate in Western Europe during this period was warm and humid with a prevalence of forest or forest-savanna vegetation (Alberdi et al., 1998; and references therein). During the final part of the *E. altidens* biochron (early middle Galerian), the vegetation changes coexist with the global climatic changes that took place around 1 Ma, called "Glacial Pleistocene" (Alberdi et al., 1998; and references therein). Most of the small-sized equids inhabited open and dry environments (e.g., steppes) generally exhibiting an abrasion-dominated diet whereas large-sized taxa lived in more closed and humid areas like savanna-mosaic and woodlands showing a more diverse feeding behaviour with also the inclusion of dicotyledons in diet (Marín-Leyva et al., 2016; Saarinen et al., 2016, 2021; Boulbes and van Asperen, 2019), thus suggesting different ecological niche occupation. Finally, *E. altidens* represents a terminal form of the stenonoid equids whereas *E. suessenbornensis* is a stenonoid equid with a certain convergence with the caballin horses. As a consequence of the climatic change occurred around 1.0−0.8 Ma, European biota underwent a faunal and floristic turnover that was characterized, among equids, by the substitution of stenonoid horses with the caballoid ones (Alberdi et al., 1998; and references therein).

It is worth noting the low presence of specialised browsers among the taxa examined (though we do not discard possible browsing for the rhino *Stephanorhinus etruscus* on the basis of previous findings from other sites in the Guadix-Baza Basin; Palmqvist et al., 2008a, b) which presumably discard a strong development of forests and wooded areas under highly wet conditions. The presence of patchy ecosytems (including open areas and tree patches) in CB-1 is compatible with the reconstruction of other sites from the basin (Mendoza et al., 2005) and with the taphonomy of the mammal assemblage of CB1 which is consistent with a climatic deterioration (attested by the low diversity of rodent species) (Alberdi et al., 2001). However, the well-attested occurrence of articulated bones suggests a lacustrine-mud flat depositional context for the CB1 deposit, where bones remained dispersed in a muddy surface and buried during flooding stages (Alberdi et al., 2001). In contrast, more humid conditions and the presence of habitats characterised by both open grasslands and closed canopies are reported in other late Early Pleistocene/Middle Pleistocene localities of the Iberian Peninsula, such as at Gran Dolina (TD6 level; ca. 0.8 Ma) (Burjachs, 2001; Cuenca-Bescós et al., 2017; Blain et al., 2018) and at Vallparadìs Estació (layer EVT7; ca. 0.86 Ma) (Strani et al., 2019). At Vallparadìs Estació ungulates display all three main dietary adaptations (browsing, mixed feeding, grazing) with an abundance of individuals showing a seasonal short-term mixed diet which point to an increase of seasonality after the "0.9 Ma event" glacial period (Strani et al., 2019). Mesowear signal for the Vallparadìs Estació *E. altidens* population also points to a clear grazing behaviour in contrast to the Cúllar de Baza-1 population. This discrepancy is probably attributable to a low sample size of the latter species, so it is not possible to discard that more abrasive diets (either as mixed feeding or grazing) were exhibited by this equid in CB-1. Hence, *E. altidens* could have displayed a higher degree of dietary plasticity than the one usually observed for this species (Boulbes and van Asperen, 2019). Finally, the role of the thermal water contribution to lacustrine systems in the Baza basin deserves some attention because it may have contributed to enhance the environmental productivity and have some indirect impact on the large mammal structure (e.g., García-Aguilar et al., 2014).

6. Conclusive remarks

The results of our research illustrate that Cúllar de Baza 1 is a key site for the studies of the latest Early Pleistocene/Middle Pleistocene transition (Epivillafranchian/Galerian ELMA) providing some biochronological insights useful for better characterising the latest

Early Pleistocene/Middle Pleistocene transition (Epivillafranchian/ Galerian ELMA) in the Iberian Peninsula. In the CB-1 site the Last Occurrences of the Etruscan rhino *Stephanorhinus etruscus* and the large deer *Megaloceros savini*, and the First Occurrence of the water-rat *Arvicola mosbachensis* are in fact recorded.

Finally, according to our new palaeoenvironmental findings, it seems that there was development of a mosaic environment (relatively dry, with somewhat open clearing and probably also with important seasonal fluctuation) in the CB-1 site contrasting with the conditions reported for other Iberian late Early and Middle Pleistocene localities. This is consistent with the last great floristic change in the Iberian Peninsula that took place in the Early Pleistocene and culminated in the EMPT with the increase of the continental aridity. A notable fall in temperature along with marked dryness would have been decisive in the total disappearance of many floristic species (Postigo Mijarra et al., 2009). This habitat heterogeneity in Cúllar de Baza-1 might have allowed the local evolution of a variety of ungulate taxa.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2021.106932.

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