

THE QUIBAS SITE (MURCIA, SPAIN): NEW HERBIVORES FROM THE EARLY-MIDDLE PLEISTOCENE TRANSITION

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Abstract. The Early Pleistocene site of Quibas, in Sierra de Quibas (Murcia, Spain) was discovered in 1994 and has since then provided abundant material of typical Epivillafranchian taxa. This biochron belongs to the Early-Middle Pleistocene transition (1.2 – 0.78 Ma), characterised by a change in orbital cyclicity from a 41 kyr cycle to 100 kyr that intensified the climate and culminated in the most important faunal turnover of the Pleistocene regarding large mammals. The Group of Palaeoanthropology of the National Museum of Natural Sciences (CSIC, Spain) and the Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA, Spain) carried out four field seasons from 2015 to 2018. Here we present the large herbivorous mammals recovered from the field, including the first citation of two taxa new to the locality: *Stephanorhinus* cf. *etruscus* and *Bison* cf. *voigtstedtensis*. We also provide the first description of previously mentioned taxa: *Dama* cf. *vallonnetensis* and *Sus* sp. Together with the remaining herbivores, the faunal community shows a strong European affinity with some regionalism. Compared with other Iberian localities, the site of Quibas stands out for the lack of hominin fossils or any evidence supporting their presence in the area, a peculiar scenario given that the Early-Middle Pleistocene transition broadly speaking sees the arrival of humans into Europe.

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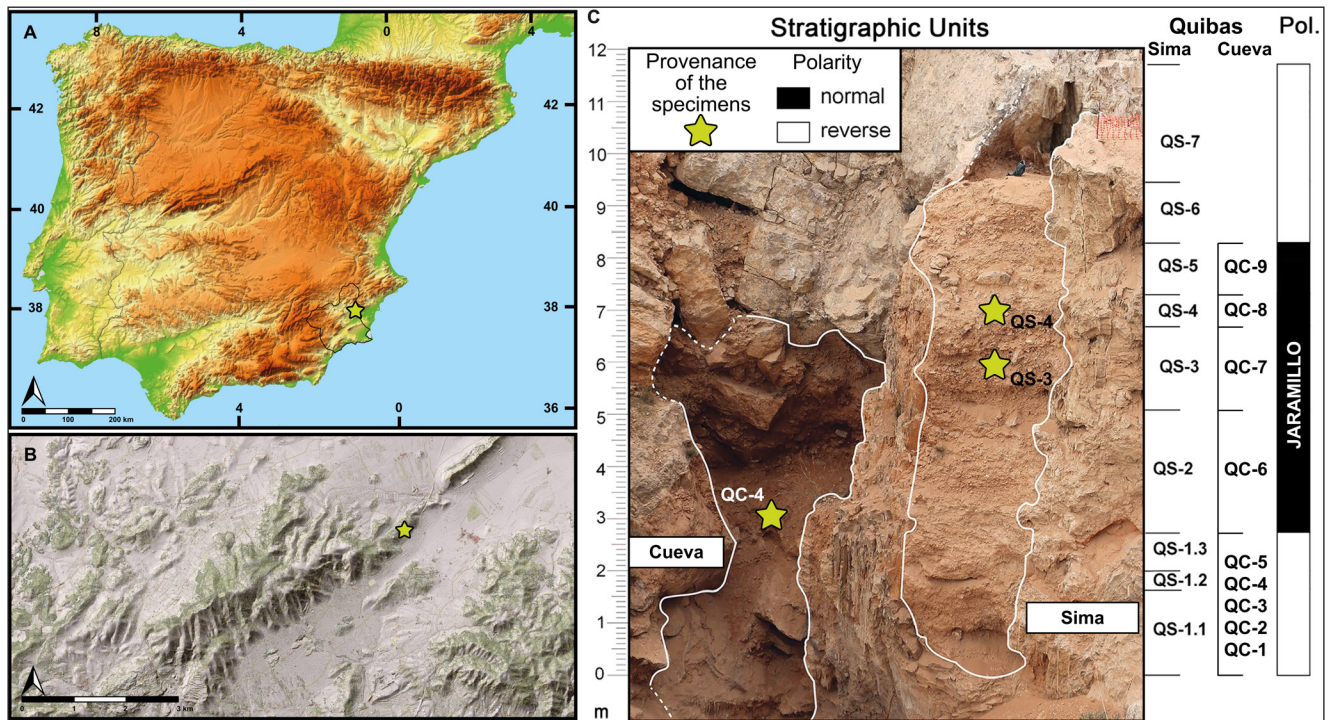


Fig. 1 - Geographic location of the fossiliferous site of Quibas and stratigraphic framework. A) Map of the Iberian Peninsula and geographic position of Murcia. B) Location of Quibas within the Sierra de Quibas. C) Structural and stratigraphic context of the Quibas site (picture modified from Piñero et al. 2020). The yellow stars stand for the Quibas site and the provenance of the studied specimens.

INTRODUCTION

Since its discovery in 1994, multiple research projects have been carried out at the Quibas site, resulting in the identification of more than 70 species of vertebrates and invertebrates (Montoya et al. 1999, 2001; Carlos-Calero et al. 2006c, b; Alba et al. 2011, Blain et al. 2014; Pérez-García et al. 2015; Piñero & Alberdi 2015; Piñero et al. 2015, 2020). Made et al. (2008) published the most recent faunal list of the site, including five herbivorous macromammals: *Equus altidens* von Reichenau, 1915, *Sus* sp., Cervidae indet. cf. *Dama nestii vallonnetensis* (Lumley, Kahlke, Moigne & Moullé 1988), Ovibovini indet. cf. *Praeovibos* sp. and *Capra alba* Moyà-Solà, 1987. Later, Piñero & Alberdi (2015) identified *E. suessenbornensis* Wüst, 1901. These species belong to the Epivillafranchian biochron (1.2 - 0.78 million years ago [Ma]), characterized by the replacement of the Villafranchian fauna by the Galerian fauna throughout the Early-Middle Pleistocene transition (EMPT; Kahlke 2004). This transition responds to a progressive change from obliquity dominated cycles to excentricity dominated cycles, which imply the intensification of climatic fluctuations. Consequently, terrestrial biomes reconfigured, affecting faunal communities (Kahlke 2000;

Madurell-Malapeira et al. 2014). This was the most relevant dispersal event of the Pleistocene in terms of the evolution and reorganization of large terrestrial mammal communities (Rook & Martínez-Navarro 2010; Bellucci et al. 2015; Palombo 2018). Ungulate mammals are particularly sensitive to changes in climatic cyclicity and the environment (Azzaroli et al. 1988; Koufos et al. 2005; Strani et al. 2019).

Piñero et al. (2020) dated the stratigraphic succession of Quibas to the 1.2-0.78 Ma interval, which places the site in the biochronological framework mentioned above, corresponding to the Early Pleistocene. The importance of Quibas relies on the continuous record from pre-Jaramillo to post-Jaramillo intervals, related to the first arrival of *Homo* in Europe (Toro-Moyano et al. 2013).

Our objective is to update the faunal fossil record of the site and provide the results of work carried out by the Group of Palaeoanthropology of the National Museum of Natural Sciences (CSIC, Spain) and the Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA). The joint team carried out four-season fields from 2015 to 2018. Here we present the results regarding the fossil record of macromammal herbivores, the most abundant in the assemblage of large mammals.

GEOLOGICAL SETTING

The palaeontological site of Quibas (38°18'51" N, 1°4'42"W) is on the southeast slope of the Sierra de Quibas (Abanilla locality, Murcia) in the southeast of the Iberian Peninsula (Fig. 1). This carbonate massif is 6 km long and 2.5 km wide with a north-east – south-west orientation. It lies in the Middle Subbaetic region (Baetic Mountains) at the intersection of three faults with N110E, N160E and N175E orientation (Durán et al. 2004; Rodríguez-Estrella et al. 2004).

The Sierra de Quibas mountain is composed of allochthonous subbaetic sediments with a carbonate series dominated by Lower Jurassic units (marl, clay and gypsum) (Rodríguez-Estrella et al. 2004). The great karstic activity at the Pliocene-Pleistocene transition resulted in a complex karstic system within the Lower Jurassic limestone and dolostone of the mountain range. The palaeontological site is within this karstic complex, specifically in an endokarstic structure that involves galleries infilled with Pleistocene detrital deposits (clay, sand and breccia) (Durán et al. 2004).

The site is organised into three main sections of which two have more palaeontological relevancy (Rosas et al. inedit [2017]): Quibas-Cueva (QC), a 9 m long and 5 m wide horizontal gallery; and Quibas-Sima (QS), a 12 m deep and 2 m wide vertical chasm. The two areas are separated by calcitic speleothems (Carlos-Calero et al. 2006c). Recent work carried out by Piñero et al. (2020) dates the stratigraphic succession of the Quibas section to between approximately 1.08 – 0.98 Ma. In the palaeontological analysis, specimens from levels QC4, QS3 and QS4 have been accurately determined. Levels QS3 and QS4 have been dated to the Jaramillo subchron by biochronological analysis of micromammals and magnetostratigraphy (Piñero et al. 2020, 2022). Following the correlation hypothesis proposed during the fieldwork, level QC4 correlates with part of the QS1, just prior to the Jaramillo subchron (ca. 1.072 Ma). This hypothesis is plausible considering the dating of the Quibas-Cueva Base at around ca. 1.08 Ma (Piñero et al. 2020).

MATERIAL AND METHODS

The studied fossil material was collected during the 2015-2018 field seasons, and comes from the Quibas-Cueva (QC) and Quibas-Sima (QS) sectors of the Quibas palaeontological site (Murcia, Spain). The material belongs to three levels of Quibas-Cueva (QC4, QC5,

L	Maximum length
l	Medial length
DAP	Antero-posterior diameter
DT	Transverse diameter
o	On the occlusal surface
b	On the base of the crown
p	On the proximal epiphysis
d	On the distal epiphysis
BP	Maximum transverse diameter of the proximal epiphysis
BD/Bd	Maximum transverse diameter of the distal epiphysis
MC	Metacarpus
MT	Metatarsus

Tab. 1 - Abbreviations for measurements used in the present work.

QC6) and two of Quibas-Sima (QS3, QS4), with only specimens from QC4, QS3 and QS4 being suitable for detailed systematic analysis. The fossil labels describe the following information: site/year/level-sublevel/square/number. As an example, Q'18/QS3-1/N21/11 refers to Quibas, year 2018, level QS3, sublevel 1, N21 square, fossil number 11. The fossil material is stored in the Department of Palaeobiology (Group of Palaeoanthropology) of the National Museum of Natural Sciences (CSIC, Madrid, Spain), pending its final deposit at the Museo Arqueológico de Murcia. The material relevant for taxonomic purposes was scanned into 3D models. The studied sample consists of 278 macromammal fossils.

For taxonomic determinations we consulted the reference collections of the National Museum of Natural Sciences and the Museum of Comparative Anatomy of Vertebrates. The nomenclature for the fossils descriptions and measurements for equids follows Eisenmann et al. (1988), and for rhinoceroses we followed Guérin (1980) for the nomenclature and Mazza (1988) for measurements. In the case of the artiodactyls, the nomenclature of the dentition follows Bärmann & Rössner (2011) and Made (1996); the latter is also applied to the nomenclature and measurement of suids. For cervids and bovids the measures were taken according to specifications by Made & Tong (2008) and Made (1989, 2012), except for Ld for the distal phalanx when pertinent (Von Den Driesch 1976). Apart from the specified nomenclature in Table 1, equid phalanges are as 2FIII, with the Arabic number indicating the number of the phalanx and the roman numeral indicating the digit (also for metapodials). Premolars and molars are given as P and M, respectively, preceded by a d in the case of deciduous teeth. The dentition is identified with a superscript for the upper elements and a subscript for the lower elements. The present article only describes the most taxonomically relevant fossils. All measurements are in millimetres (mm) unless specified. We took the measurements with electronic sliding calipers with 0.1 mm resolution and ± 0.2 mm error.

Once the fossil material was determined, we carried out the statistical analyses. Bivariate analyses are for the P² and MC III of equids, MC IV of rhinoceroses, M³ of cervids and the first phalanx of bovids. The MC III of the rhinoceros was analysed through a violin diagram with a box plot. In the case of the MC III of the horse, we calculated the robusticity index as the product of Bd and l (Bd/l). For the statistical analyses we used PAST v.4.04 software (Hammer et al. 2001). The data considered for each analysis is mentioned in each case throughout the manuscript. We also calculated the minimum number of individuals (MNI) when the high fragmentation of the material made it possible.

SYSTEMATIC PALAEOLOGY

We determined that 127 fossils out of a sample of 278 macromammals remains are from herbivores. Herein we describe the 33 most relevant fossils.

P ²	Side	DAPo	DTo	DAPb	DTb	DAP	DT								
Q'18/QS3/N21/11	L	41.4	27.1	44.4	27.5	42.4	28.2								
MC III		1	2	3	4	5	6	7	8	9	10	11	12	13	16
Q'18/QS3/N23/1	L	-	239.95	-	-	50.7	34.4	-	-	3.9	45.8	-	35.4	29.4	9.1
Humerus															
Q'18/QS3-2/M21/2	R	297.71	271.31	36	44.3	97.55	11.2	75.2	85.9	44.4	38.6	42.7	-	-	-
Q'18/QS3/N20/5	R	-	-	-	-	-	-	74.7	85.4	-	-	-	-	-	-
Radius															
Q'18/QS3/N22/3	R	336.29	325.55	41.5	28.2	74.7	35.9	82.9	61.8	38.2	74.7	26.9	14.6	-	-
Ulna															
Q'17/QS3/O22/16	L	-	84.2	47.1	54.1	73	-	-	-	-	-	-	-	-	-
Q'18/QS3/N21/5	L	-	-	51.8	51	-	-	-	-	-	-	-	-	-	-
2FIII															
Q'17/QS3/Q22/1	-	49.2	36.9	40.8	49.3	33.6	46.3	-	-	-	-	-	-	-	-
3FIII															
Q'17/QS3/Q23/2	-	-	-	-	c.44.2	c.27	-	-	-	-	-	-	-	-	-

Tab. 2 - Measurements of *Equus altidens* specimens from Quibas. Dimensions in millimetres (mm).

Order **Perissodactyla** Owen, 1848

Family **Equidae** Gray, 1821

Genus *Equus* Linnaeus, 1758

Equus altidens von Reichenau, 1915

Pl. 1, figs. A-D; Fig. 2

Referred material. Left P² (Q'18/QS3-1/N21/11), two right humeri (Q'18/QS3-2/M21/2, Q'18/QS3-1/N20/5), left (Q'17/QS3/O22/12) and right radius (Q'18/QS3/N22/3), left (Q'17/QS3/O22/16) and right ulna (Q'18/QS3/N21/5), left MC III (Q'18/QS3-1/N23/1), 2F III (Q'17/QS3/Q22/1), 3F III (Q'17/QS3/Q23/2).

Measurements. See Table 2.

Description. The P² has the lower half fragmented and sediment deposition on most of the occlusal surface, preventing us from observing the fold pattern of the enamel, but allowing us to see that it is unworn. The mesostyle is well developed, unlike the parastyle. The protocone is reduced and has a subtriangular shape with a deep postprotoconal groove. (Pl. 1, fig. A)

The postcranial elements show the characteristics of the genus: the **humeri** have three main tubercles on the proximal epiphysis of equal height from a cranial and dorsal perspective, and a prominent deltoid tuberosity. The **ulnas** lack the distal third portion of the bone with the remaining end reduced. The **MC III** has two incisions on the proximal epiphysis for the rudimentary metacarpals and only one sagittal ridge on the distal epiphysis. The **2F III** is wider than it is long and the proximal articular surfaces are concave and equal in size. The condyles of the distal epiphysis have the same height. The **3F III** is 'U' shaped from the dorsal view and has two ungual apophyses.

Remarks. The MNI indicates two individuals, both at a subadult or young adult stage of

maturity. According to Silver (1963), the fusion stage of the proximal epiphysis of the humerus (Q'18/QS3-2/M21/2) indicates an age of approximately three and a half years. This matches with the fusion stage of both ulnas, which allows us to postulate that these three elements belong to the same individual.

Following the most up-to-date taxonomic and biogeographic reviews of the equids that inhabited Europe during the last 2 Ma it seems necessary to consider at least the systematic features proposed for *Equus steblini* Azzaroli, 1964, *E. stenonis* Cocchi, 1867, *E. altidens*, *E. suessenbornensis* Wüst, 1901 and *E. apolloniensis* Koufos, Kostopoulos and Sylvestrou, 1997 (Cirilli et al. 2021; Cirilli 2022). *Equus steblini* and *E. stenonis* have been recorded in Western and Central Europe until about 1.8-1.3 Ma. In order to rule out the possible attribution of the Quibas specimens to all species of the genus *Equus* present in Western Europe in the Early Pleistocene, data from *E. livenzovensis* have been included, although its last occurrence seems to be at ca. 2 Ma ago at Fonelas-1 (Alberdi et al. 1997). The presence of specimens assigned to both *E. altidens* and *E. suessenbornensis* has been previously determined at Quibas, agreeing with the chronology proposed for the levels (Piñero & Alberdi 2015). Biometric comparison with the synchronic taxon *E. apolloniensis* has not been considered, as its distribution seems to be restricted to Eastern Europe (Gkeme et al. 2021; Cirilli 2022).

The P² shows the typical derived characteristics of stenonoid horses present in *E. altidens* (Alberdi et al. 1998): a subtriangular protocone and a deep postprotoconal groove. Piñero & Alberdi (2015) already mentioned these characteristics in previous studies of the equids from Quibas. On

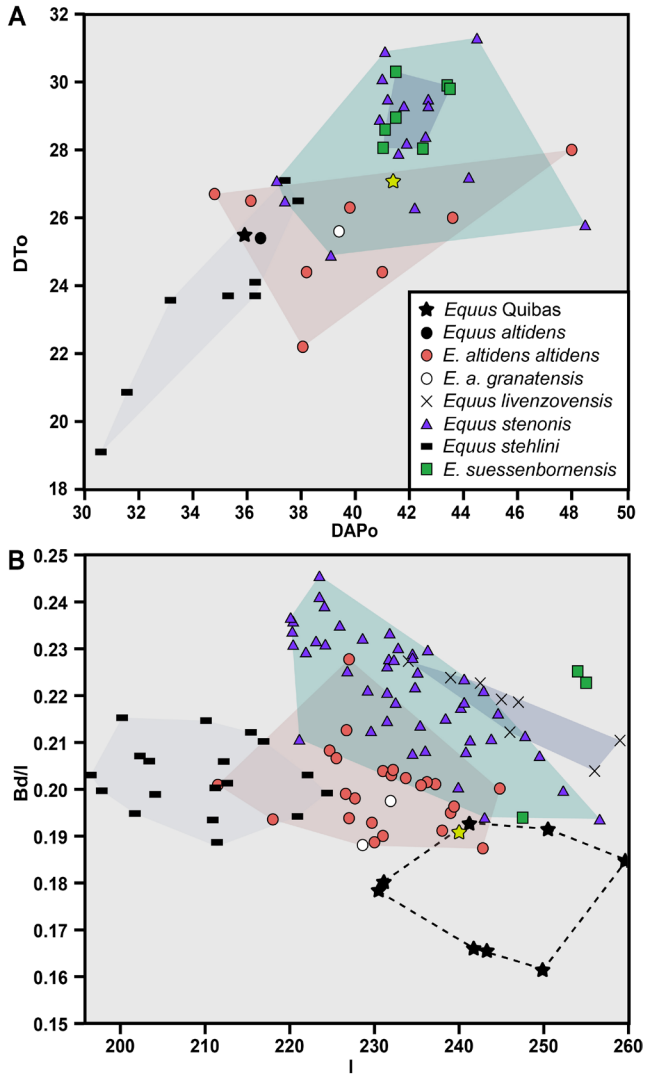


Fig. 2 - *Equus altidens*. A) bivariate analysis of the upper premolar with both occlusal transverse diameter and anteroposterior diameter. B) bivariate analysis of the left third metacarpal with medial length and robusticity index. S-G: Selvella-Gioiella. Data extracted from Alberdi & Ruiz Bustos (1985), Alberdi et al. (1997), Montoya et al. (1999), Sarrion Montañana (2010), Alberdi & Piñero (2012, 2014), Alberdi y Palombo (2013), Piñero y Alberdi (2015), Made et al. (2017), Cirilli et al. (2021) and Cirilli (2022) .

the other hand, the other equid species previously identified from Quibas, *E. suessenbornensis*, has a long protocone, concave lingual borders, developed mesostyles and vestibular valleys (Alberdi et al. 1998). The bivariate analysis of the occlusal surface of the P² with DAPo - DTo (Fig. 2A) shows in a morphological range of small dimensions in all specimens assigned to *E. stehlini*, separating them from the Quibas specimen. *E. stenorini* has a wider range of variability in its proportions, with values that overlap with *E. suessenbornensis* and *E. altidens* and include the morphometry of the Quibas spe-

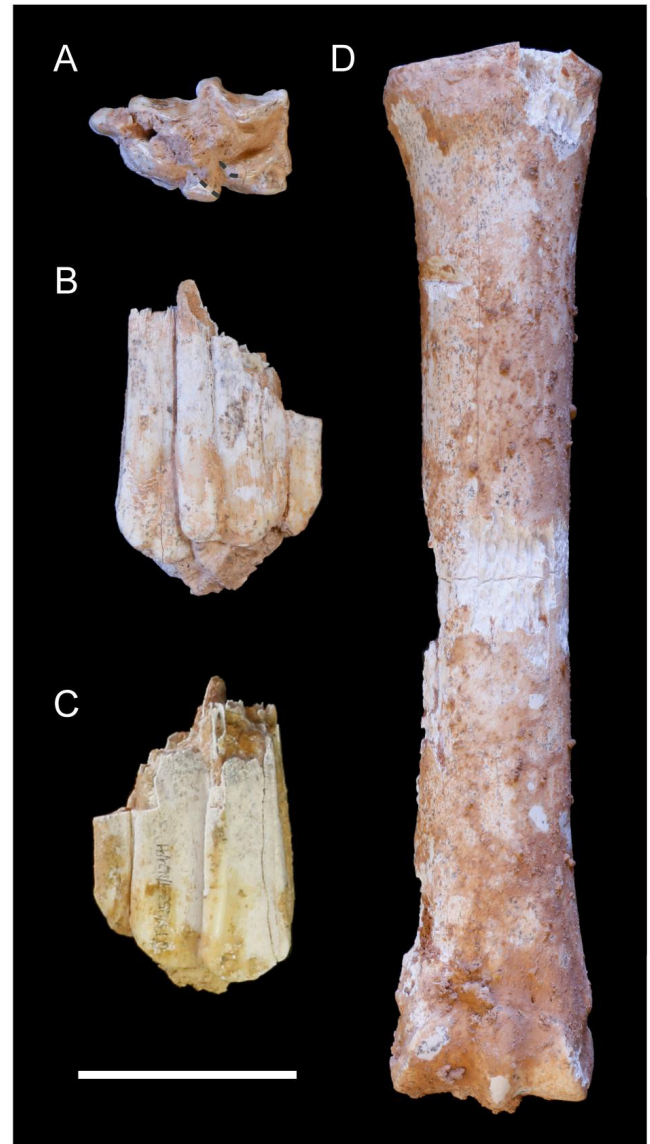


PLATE 1

Equus altidens.
 A-C - upper second premolar, Q'18/QS3-1/N21/1: A, occlusal view indicating the protocone; B, vestibular view; C, lingual view.
 D - left third metacarpal, Q'18/QS3-1/N23/1: cranial view.
 Scale bar: 50 mm.

cimen. This analysis clearly differentiates both species previously identified from Quibas, with more rectangular and slender morphologies in *E. altidens* and quadratic and more robust morphologies in *E. suessenbornensis*. The specimen here described falls within the variability of *E. altidens*. Although it is not similar to any sample in particular, it is closer to those of Cueva Victoria (*E. altidens*) or Saint Vallier (*E. stenorini*) than to the P2 from Quibas previously studied by Montoya et al. (1999). This difference in the material from the same site and

species may be due to attrition, since our premolar does not show any wear whilst the premolar studied by Montoya et al. (1999) shows an advanced dental wear stage.

The results of the **MC III** analysis (bivariate analysis 1 – Bd/l; Fig. 2B) separate the morphologies of *E. livezovensis*, *E. stenonis* and *E. stehlini* with good resolution. The first species shows a long metacarpal relative to its robusticity, which contrasts with the minimal length values found in *E. stehlini*. *E. stenonis* has higher mean values and higher variability, but still no overlap with *E. stehlini*. Of the species previously reported from Quibas, *E. suessenbornensis* has the greatest length and robustness (with the exception of the questionably identified specimen from Cueva Victoria; Alberdi & Piñero 2012), while *E. altidens* is characterized by high variability in length and robustness (both with lower values). Among the species considered in this analysis, the specimen described here falls better within the variability of *E. altidens*, as do the rest of the Quibas specimens for which data are available. It is not possible to observe a clear differentiation between the subspecies of the latter (*E. altidens altidens* and *E. altidens granatensis*). As previously indicated by Piñero & Alberdi (2015), the Quibas specimens are particularly slender compared to *E. altidens* specimens from other sites, so they are grouped together in showing different proportions (Fig. 2B). Piñero & Alberdi (2015) also observed a similarity between specimens from Quibas and Venta Micena, although our metacarpal falls within the general variability of *E. altidens*. This similarity could be explained by the older chronology of the palaeontological levels from which these authors collected the fossils at Quibas, closer in age to Venta Micena. Unfortunately, it was not possible to access the Venta Micena material. The MC III studied here is within the variability of *E. altidens*, although at its limits and close to the other Quibas specimens.

The assignment of the specimens to the species *E. altidens* agrees with the latest biochronological and biogeographical proposals for equids in Europe set out in Cirilli et al. (2021) and Cirilli (2022). The scarcity of measurements on specimens of *E. a. granatensis* hampers our ability to cover the variability of this subspecies and therefore prevents us from determining fossil material at the subspecific level.

Family Rhinocerotidae Gray, 1821
Genus *Stephanorhinus* Kretzoi, 1942

Stephanorhinus cf. *etruscus* (Falconer, 1868)

Pl. 2, figs. A-F; Fig. 3

Referred material. Left MC III (Q'17/QS3/O20/1) and MC IV (Q'17/QS3/P20/1). We largely assign a dentition fragment to this taxon (Q'17/QS3/P21/9).

Measurements. See Table 3.

Description. The **MC III** preserves the proximalmost 10 centimetres of the dorsal side. The articular facets for the unciform and the MC II are complete. The articular facet for the magnum is fragmented at the palmar limit of the two facets mentioned above (unciform and MC II) (Pl. 2, fig. A). The articular facets for the MC IV are absent.

The articular facet for the unciform is slightly concave with a subtriangular shape and a right anterior angle. The maximum length is 27.7 mm. The articular facet for the MC II is flat and weakly developed, with its distal point slightly lower than the distal point of the facet for the unciform. Lastly, the articular facet for the magnum is notably concave. The great fragmentation of the diaphysis prevents us from observing other taxonomically relevant characteristics.

The left **MC IV** is almost complete, lacking only the lateral half of the articular facet for the unciform and a fragment of the proximal palmar region of the diaphysis. The articular facet for the unciform is notably concave along the medio-lateral axis and slightly convex along the dorso-palmar axis. The articular facets for the MC III are round and enclose an angle close to 90°. These facets are extremely close to each other but do not make contact (Pl. 2, fig. C). The diaphysis curves immediately after the distal end of the palmar facet for the MC III, which is in contact with the unciform facet.

MC III	Side	L	BP	BS	DS	BD	DD	Bda
Q'17/QS3/O20/1	L	-	52.6	-	-	-	-	-
MC IV								
Q'17/QS3/P20/1	L	161.7	36.7	30	19.6	41.8	36.8	33

Tab.3 - Measurements of *Stephanorhinus* cf. *etruscus* specimens from Quibas. Dimensions in millimetres (mm).

PLATE 2

Stephanorhinus cf. *etruscus*.

A-B - third left metacarpal, Q'17/QS3/O20/1: A, dorsal view of the proximal epiphysis with the reconstruction of the missing fragments based on the *S. etruscus* specimen from Senèze (210959, Guérin 1980); B, cranial view indicating the curvature of the diaphysis with the unciform facet.

C-F - left fourth metacarpal, Q'17/QS3/P20/1: C, axial view indicating the articular facets; D, dorsal view of the proximal epiphysis; E, palmar view; F, transverse section of the middle diaphysis.

Scale bar: 50 mm.



Remarks. The estimated MNI indicates one individual. The material determined as *Stephanorhinus* shows poorly developed relief with a smooth and even shape. The general morphology is elongated and slender.

Concerning the **MC III**, the articular facets for the MC II and the unciform are not dorsally extended as in the morphology shown by Guérin (1980) for *S. etruscus* from Senèze (Pl. 2, fig. A). In dorsal view the curvature between the unciform facet and the diaphysis is more similar to that of *S. etruscus* from Figline than the morphology of *S. hundsheimensis* (Toula 1902) from Mosbach, both illustrated by Fortelius et al. (1993) (Pl. 2, fig. B). The average size of the BP of the MC III is similar in both species recorded in Europe during the Early-Middle Pleistocene transition and differs from the measurements reported for *S. kirchbergensis* (Jäger, 1839) and *S. hemitoechus* (Falconer, 1868). The specimen from Quibas is close in size to the means of both *S. etruscus* and *S. hundsheimensis* (Fig. 3A).

The **MC IV** has the palmar facet for the MC II and the unciform facet connected, in agreement with the description of Ballatore & Breda (2019). The perimeter of the palmar facet for the MC III is continuous, similar to the specimen of *S. etruscus*

from Senèze. The morphology of the medial section of the diaphysis shows a shape intermediate between those of *S. hundsheimensis* from Vallonet and *S. etruscus* from Senèze, both illustrated by Lacomat (2005) (Pl. 2, fig. F). Fortelius et al. (1993) reported that the MC IV of *S. etruscus* are flatter dorso-palmarly than in *S. hundsheimensis*. Analysing the proportions of the metapodials with $L - BD$ we can see some distance between the two species, with the Quibas specimen near the majority of *S. etruscus* and particularly close to some specimens from Upper Valdarno (Fig. 3B). However, some specimens of *S. etruscus* from Upper Valdarno show great variability in measurements (Fortelius et al. 1993; Mazza 1988; Pandolfi et al. 2017) and overlap with the values of specimens attributed to *S. hundsheimensis* from sites such as Soleihac (Lacomat 2005) or Isernia (Fortelius et al. 1993).

The morphology and measurements described for the Quibas specimens are more similar to those of *S. etruscus*, reinforced by the distribution of *S. etruscus* and *S. hundsheimensis* in the Iberian Peninsula in the Pleistocene (Made 2010). Despite these similarities, the scarce and fragmentary fossil material from the Quibas site leads us to propose *Stephanorhinus* cf. *etruscus* as a provisional taxonomic assignment.

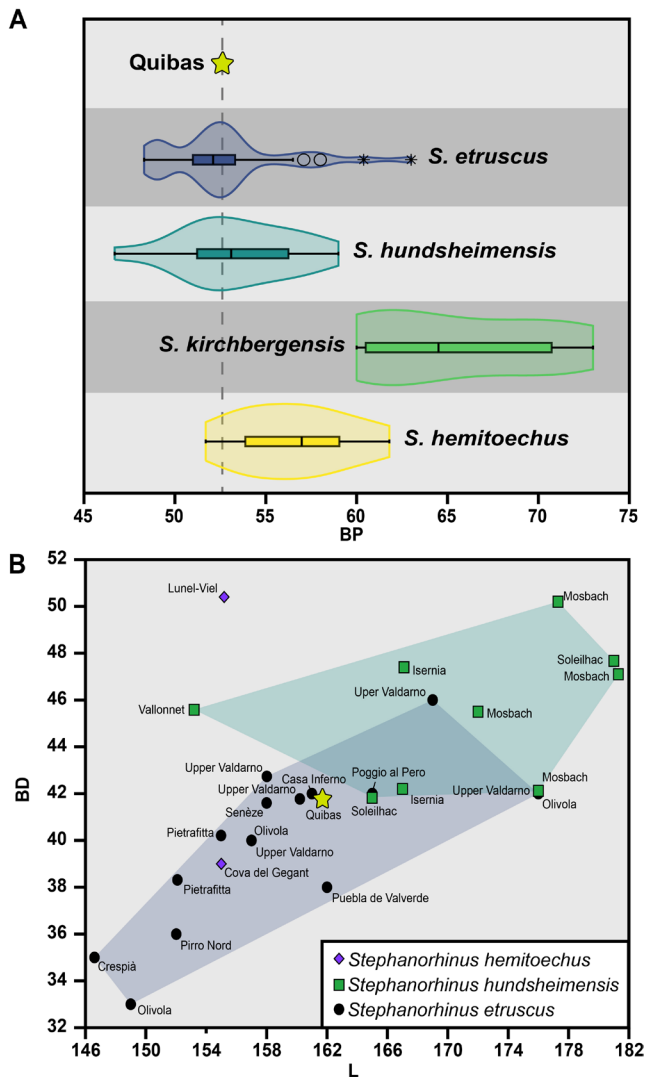


Fig. 3 - *Stephanorhinus* cf. *etruscus*. A) violin diagram with boxplot of the left third metacarpal; B) bivariate analysis of the left fourth metacarpal with the length and maximum transverse diameter of the distal epiphysis. Data extracted from Guerin & Heintz (1971), Bonifay (1973), Dubar et al. (1978), Mazza (1988), Cerdeño (1990), Fortelius et al. (1993), Mazza et al. (1993), Alberdi et al. (1997), García-Fernández et al. (2003), Lacombe (2005) and Pandolfi et al. (2017).

Order Artiodactyla Owen, 1848
Family Suidae Gray, 1821
Genus *Sus* Linnaeus, 1758

Sus sp.

Pl. 3, figs. A-F

Referred material. Right MT IV (Q'18/QS3/P19/17), left intermediate phalanx (Q'18/QS3-2/M22/1).

Measurements. See Table 4.

Description. The right **MT IV** is elongated and slender and with proximal and distal ends damaged. The diaphysis is quadratic and flat on the cranial

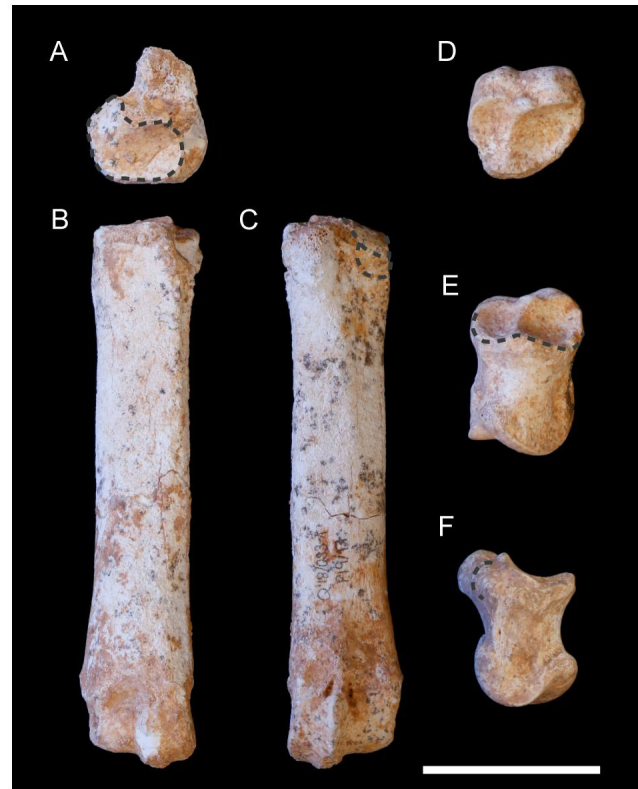


PLATE 3

Sus sp.

A-C - right fourth metatarsal, Q'18/QS3/P19/17: A, dorsal view of the proximal epiphysis indicating the anterior region of the articular facet for the cuboid; B, cranial view; C, plantar view indicating the lateral half of the posterior extension.

D-F - left intermediate phalanx, Q'18/QS3-2/M22/1: D, dorsal view of the proximal epiphysis; E, cranial view indicating the anterior margin; F, palmar/plantar view indicating the posterior tuberosities.

Scale bar: 30 mm.

side. The proximal end only preserves the anterior region of the articular facet for the cuboid and the articular facet for the MT V. This anterior region also has a pronounced concavity (Pl. 3, fig. A). The sagittal ridge of the distal end is incomplete on both cranial and plantar sides.

The **intermediate left phalanx** is complete and excellently preservation. The articular facet for the proximal phalanx takes up most of the proximal surface, with the lateral half considerably bigger than the medial one (Pl. 3, fig. D). The posterior edge of this articular facet bears a little tubercle at the medial groove. The palmar side has a posterior tuberosity in which the lateral projection is larger than the medial one (Pl. 3, fig. F). The articular facet for the distal phalanx orientates strongly to the axial axis of the limb on the maximum cranialmost point of the anterior side, which is also discernible in the anterior aspect of the proximal end (Pl. 3, fig. E).

Tab. 4 - Measurements of *Sus* sp. specimens from Quibas. Dimensions in millimetres (mm).

Metapod	Side	I	DAPp	DAPps	DAPpf	DTp	DAPd	DTd
Q'17/QS3/P20/3	-	-	-	-	-	-	-	19.3
MT IV								
Q'18/QS3/P19/17	R	94.9	-	-	-	-	-	19
Intermediate phalange								
		L						
Q'18/QS3-2/M22/1	L	26.3	20.3	18.9	13.5	19.2	17.5	17.3

Remarks. We attribute two fossils to an indeterminate species of this genus. The MNI estimated is one.

The **MT IV** is remarkably similar to contemporary specimens of *S. scrofa* Linnaeus 1758 except for a more elongated, robust and wide diaphysis. The Quibas specimen has a more rectangular proximal articular facet and the articular facet for the cuboid is wider in the anterior region, with a deeper concavity. The lateral half of the posterior extension is more strongly inclined towards the plantar side (Pl. 3, fig. C).

The **intermediate phalanx** has the more cranial aspect of the distal articular facet more angled towards the axial axis than specimens in the reference collection (contemporary *Sus scrofa*). This also applies to the anterior edge of the proximal epiphysis. The articular facet of contemporary *S. scrofa* is smaller and less extended on the proximal surface than the fossil specimen, with both halves similar in size and shape. The tubercle at the medial groove is smoother in the reference collection specimens.

All characteristics agree with the description of *Sus* (Schmidt 1972; Hillson 2016). The following reasons prevented us from identifying the material to the species level: chronological overlap of the fossil record of *S. scrofa* and *S. strozzii* Forsyth Major, 1881, both present at the Early-Middle Pleistocene transition; poorly developed taxonomic studies and diagnostic features on postcranial elements of both species; lack of studies on the intraspecific variability of the postcranial elements, with chronologic and geographic characterization of *S. scrofa* and *S. strozzii* in Europe pending further review (Cherin et al. 2020).

Family Cervidae Goldfuss, 1820
Genus *Dama* Frisch, 1775

Dama cf. *vallonnetensis* (Lumley, Kahlke, Moigne & Moullé, 1988)

Fig. 4

Referred material. Left M³ (Q'16/QC4/K20/1), fragmented left radius (Q'16/QC4/Re/16).

Measurements. See Table 5.

Description. The M³ is a brachydont tooth that only preserves the crown. On the vestibular side, the metastyle and the metacone style are weaker than the other styles. The mesostyle is oriented mesially on the occlusal surface and has a strong development of the cingulum at the base of the crown, which continues to the paracone style (Fig. 4B). This cingulum also connects the paracone style to the parastyle. Regarding the occlusal surface, we see the metaconule fold on the distal wall of the posterior infundibulum. On the lingual side, the lobes show a strong projection that is greater on the anterior lobe. We can also see a moderate development of the cingulum that continues to the mesial side of the anterior lobe and the distal side of the posterior lobe. This cingulum involves the entostyle, although it only preserves the base.

The proximal epiphysis of the **radius** is small and shows some damage. The anterolateral region is absent and the line of fusion visible. On the dorsal side, the articular surface for the humerus is medio-laterally oval with the medial groove not very deep and the lateral facet flat and inclined to the cranial side. On the medial facet we see a fovea. The caudal edge is higher than the cranial edge and bears a V-shaped incision for the ulna (Fig. 4C).

Remarks. The development and wear of the M³ indicates a young adult individual, as does the radius. We estimate one MNI.

Following the trait descriptions of Lister (1996) for *Dama* and *Cervus*, the M³ matches characters 1 –

M ³	Side	DAP	DAPb	DTa	DTp	Ha (Hbu)
Q'16/QC4/K20/1	L	19.6	17.6	20.6	19.0	15.6
Radius						
	Lado	DAPp				
Q'16/QC4/Re/16	L	20	-	-	-	-

Tab. 5 - Measurements of *Dama* cf. *vallonnetensis* specimens from Quibas. Dimensions in millimetres (mm).

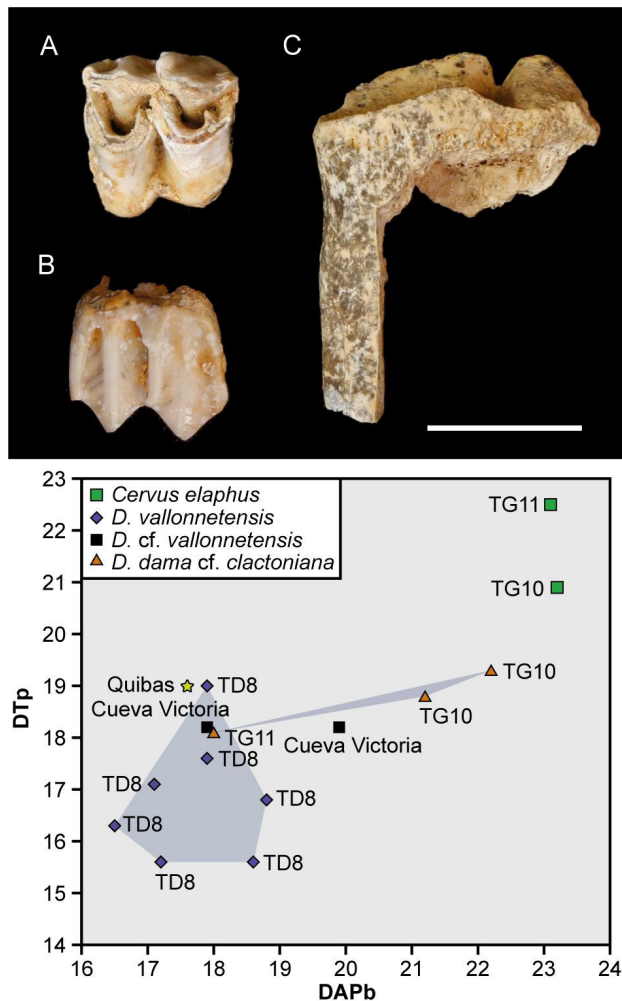


Fig. 4 - *Dama cf. vallonnetensis*. Plate with fossil material and graphic representation with bivariate analysis. Plate: A-B left upper third molar, Q'16/QC4/K20/1: A) occlusal view; B) vestibular view. C) fragmented left radius, Q'16/QC4/Re/16: anterior view. Scale bar: 20 mm.

Graphic: Bivariate analysis with both posterior transverse diameter and antero-posterior diameter on the base of the crown of the left upper third molar. Data extracted from Made (1999, 2012), Breda & Lister (2013) and Made et al. (2017).

4 for the first genus mentioned, although the metaconule fold is on the posterior infundibulum. One of the diagnostic characteristics of the M^3 mentioned by Di Stefano (1996) and illustrated by Lister (1996) to distinguish the two genera is the presence of a lingual cingulum that includes the entostyle and continues to the distal side of the metaconule. This trait is found in *Cervus* but not in *Dama*. According Di Stefano (1996) and Lister (1996), the molar illustrated in Fig. 4 matches most of the characteristics of *Dama* except for the presence of a metaconule fold in the posterior infundibulum of the M^3 and a moderate development of the cingulum that comprises, although weakly, the interlobular entostyle. In

addition, *Cervus* is characterized by having evolved forms, whilst *Dama* and *Axis* illustrate more archaic features (an entostyle and metaconule fold) that get weaker as species evolve and even disappear in some cases (Di Stefano & Petronio 1998, 2002).

Axis is another genus recorded in the Early Pleistocene whose differential diagnosis relative to red deer and fallow deer may be challenging. Most characteristics of *Axis* are present in the antler morphology, like in the majority of cervids (Croitor 2014, 2018). Regarding the teeth, and specifically the M^3 , we find that this genus usually has the metaconule fold reduced or absent (Di Stefano & Petronio 2002; Petronio et al. 2013). Contrary to this statement, other authors identify the M^3 of *Axis* as a tooth with a well-developed interlobular style and cingulum (Made et al. 2017), which highlights the difficulty to determine cervid specimens in the fossil record. Nevertheless, these features are present in other fossil specimens like *Dama roberti* Breda & Lister, 2013, which shows a well-developed entostyle and a vestibular cingulum that extends mesially and distally. Pfeiffer (2002) stated that along the *Dama* lineage more than one state for a particular character can be present in the same species.

The bivariate analysis of the DAPb – DTp for the M^3 (Fig. 4) shows a clear difference between the genera *Dama* and *Cervus*, the latter being larger. *Dama* has greater variability in DAPb than in DTp, which is better reflected in the subspecies *D. dama clactoniana* (Falconer, 1868). *D. vallonnetensis* is better defined in both variables. The M^3 from Quibas is near the specimens of Atapuerca TD8, determined as *D. vallonnetensis*. It is important to consider that the amount of data for each taxon on this analysis varies, and therefore the results should be considered with caution. Previous studies from the locality reported the presence of a *Dama*-like cervid and even cited the presence of Cervidae indet. cf. *Dama nestii vallonnetensis* on the site, the latter lacking description of the material (Montoya et al. 1999; Made et al. 2008).

Regarding the radius, the relationship between the coronoid processes of the caudal and cranial edges and the sagittal relief are more similar to *Dama* than *Cervus* (Lister 1996; Breda 2015). The anterior margin of the proximal epiphysis is straight, without the characteristic relief of *Cervus*, whilst the lateral edge shows no thickening (Fig. 4). This matches the third character of Lister (1996) for the radius, which indicates the absence of relief on

the medial half of the proximal articular surface of *Dama*. On the other hand, the anterior margin of *Cervus* is more sinuous, especially on the medial half. Species of *Dama* have a notable slope on this anterior margin, as does our specimen from Quibas. The V-shaped incision of the caudal edge agrees with the description for *Dama*; the incision in *Cervus* is U-shaped and deeper. On the caudal side, the facets of the caudal margin also match the descriptions for *Dama* (Breda 2015).

Other possible species for our specimens would *D. nestii* (Azzaroli, 1947) and *D. eurygonos* (Azzaroli, 1947), both described mainly on cranial characters and antlers (Di Stefano & Petronio 1998, 2002) and even postcranial elements (Petronio 1979). Neither of these publications mentions specific characteristics on the M³ for comparison. Croitor (2006) provides some description of *D. eurygonos* upper molars, but the only comparable result “[...] weak interrupted *cingulum* borders lingual sides of all molars [...]” does not negate the remaining arguments for *D. vallonnetensis*. On the other hand, the fallow deer identified in Atapuerca TD8 by Made et al. (2017) matches the moderate styles and entostyle shown in our specimen.

We focus on the M³ for our determination since locomotor strategies and ecological preferences can overshadow taxonomically relevant morphology on postcranial elements (Croitor 2006, 2014, 2018), although the characteristics of the radius support the assignment to *Dama*. The characters of the M³ and radius plus the bivariate analysis performed support the presence of *D. cf. vallonnetensis*. Most importantly, the upper molar matches in both description and dimensions the fallow deer from Atapuerca TD8 (Made et al. 2017), coincident in age with Quibas. We use this nomenclature following the proposal of Croitor & Bonifay (2001), which states that fallow deer from Late Villafranchian should use *vallonnetensis* as the specific epithet.

Our determination should be considered with caution since most cervids are described mainly on cranium and antlers, and postcranial elements in some cases. The fossil record of Quibas did not provide us with these elements, and therefore we propose the preliminary determination of *Dama cf. vallonnetensis*.

Family Bovidae Gray, 1821
Genus *Bison* Hamilton Smith, 1827

***Bison cf. voigtstedtensis* Fischer, 1965**

Pl. 4, figs. A-I; Fig. 5

Referred material. Left hemimandible with M₁, M₂ and dP₃ associated (Q’17/QS3/O22/2), right M₂ (Q’17/QS3/Q20/1), proximal phalanx (Q’18/QS4/O20/1) and distal phalanx (Q’18/QS3-1/O20/5, Q’18/QS3-1/O20/15).

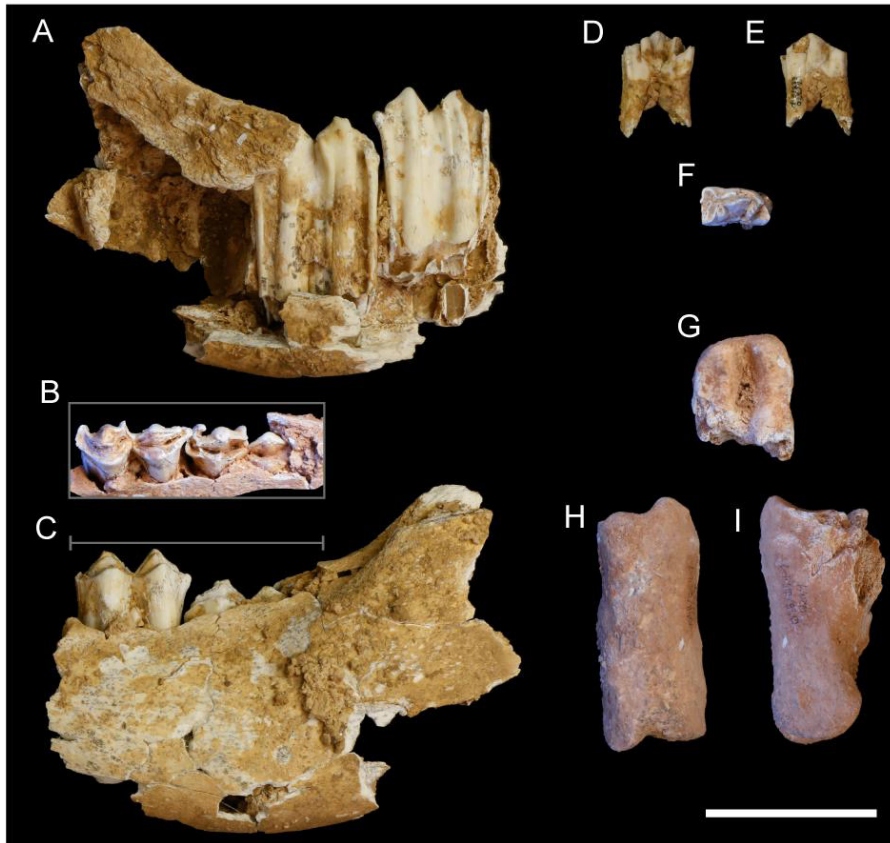
Measurements. See Table 6.

Description. The **hemimandible** preserves the lingual side of the mandibular body and the beginning of the mandibular ramus. The M₁ and the M₂ are on their respective dental alveoli whilst the dP₃ is off its alveolus, although it was found together with the hemimandible. Both molars show strong hypsodonty with slight wear on the occlusal surface and an entostylid that is well developed (Pl. 4, fig. B). The M₁ emerges from the bone and shows wear on both lobes that is more pronounced on the anterior one. On the vestibular side the ectostylid is low. The preprotocristid and internal postmetacristid are wide. The mesostylid is stronger than the metastylid and entostylid. These three stylids have a distal orientation on the occlusal surface and the entostylid has little distal extension. The M₂ is emerging and shows the same characters of the mesostylid and metastylid, with slight wear on the anterior lobe and no wear on the posterior lobe. The preprotocristid shows a small fossa from the enamel fold on the occlusal surface (Pl. 4, fig. B). Both molars from the hemimandible have U-shaped valleys between the metaconid and entoconid on the lingual side. The right isolated M₂ (Q’17/QS3/Q20/1) shows identical and symmetric anatomical characteristics

dP ₃	Side	DAPO	DT	DTa	DTp		
Q’17/QS3/O22/2	L	20.2	10.9	-	-		
dP₄							
Q’18/QS3-1/N20/2	R	34.9	13	13.4	12.6		
M₁							
Q’17/QS3/O22/2	L	31.1	13.4	13.5	14.2		
M₂							
Q’17/QS3/Q20/1	R	36.7	15.8	14.5	15.4		
Radius		BFd	BFdm	BFdl			
Q’18/QS3-1/M22/3	L	72.44	37.49	33.76			
MC III-IV		DTd					
Q’17/QS3/O22/5	R	60.00					
Proximal phalange		L	DAPp	DAPpf	DTp	DAPd	DTd
Q’18/QS4/O20/1	L	71.1	-	-	-	25.3	30.3
Q’18/QS3-1/O20/3	R	-	39.9	36.5	31.9	-	-
Intermediate phalange		DAPd					
Q’18/QS3-1/O20/7	L	31.9					
Distal phalange		DTp	Ld				
Q’18/QS3-1/O20/5	L	23.6	53.5				

Tab. 6 - Measurements of *Bison cf. voigtstedtensis* specimens from Quibas. Dimensions in millimetres (mm).

PLATE 4

*Bison cf. voigtstedtensis.*

A-C - left fragment of hemimandible with the first and second lower molars, Q'17/QS3/O22/2: A, lingual view; B, occlusal view of the lower molars; C, vestibular view.

D-F - left deciduous third lower premolar, Q'17/QS3/O22/2: D, lingual view; E, vestibular view; F, occlusal view.

G-I - proximal phalange, Q'18/QS4/O20/1: G, dorsal view of the proximal epiphysis; H, cranial view; I, palmar/plantar view.

Scale bar: 50 mm.

to the M_2 of Q'17/QS3/O22/2, including the wear stage. This suggests that the hemimandible and the isolated M_2 belong to the same individual. The molars show approximately the same DAP through their height (more evident on the M_1). The associated dp_3 has the anterior stylid fragmented on the lingual side and the occlusal surface shows slight wear (Pl. 4, fig. D, F).

The **proximal phalanx** is robust and elongated. The proximal articular surface has a deep U-shaped groove, and the caudal edge is continuous with a smooth pit (Pl. 4, fig. H). The axial side is straight, and the plantar side fragmented on the dorsal half, comprising the proximal epiphysis. The slenderness suggests that it is a posterior phalange.

Both **distal phalanges** lack the posterior tuberosity for the flexor, Q'18/QS3-1/O20/5 with the posterior half on the axial side missing. The dorsal edge is straight and relatively short, with a poorly developed apophysis for the extensor. The general morphology is robust.

Remarks. We estimate an NMI of one individual. The emergence of the molars and the dental wear suggest an approximate age of 18 months (Hillson 2005).

The hypsodonty and robusticity of the **molars** indicate that this material belongs to a bovid, and the presence of ectostylids determines it as a Bovinae (Made 1998). Within this subfamily we find populations assigned to several species of bovid genera in the Pleistocene of the geographic region where the Quibas specimens were found: *Leptobos*, *Bison* (*Eobison* and *Bison*), and *Bos*.

The lower molars of *Leptobos* show strong buttresses with dental cement between them, a low ectostylid, faint stylids, and the absence of a metaconule fold (Azanza & Morales 1989; Duvernois 1990). Our specimen only shares with species of this genus the presence of strong buttresses and the absence of a metaconule fold, lacking the cement between lobes. Kostopoulos et al. (2018) also mentioned the lack of the preprotocristid fossa in *Leptobos* when lower molars are unworn, whereas this fossa is clearly visible in our specimen. Regarding the other two genera, the infundibula and enamel folds agree with species of the genera *Bos/Bison* (Hillson 2005). We followed Slott-Moler (1990) in separating this pair, and according to his criteria, our specimen shows the characteristics of species of *Bison*: its ectostylid is shorter and wider than in species

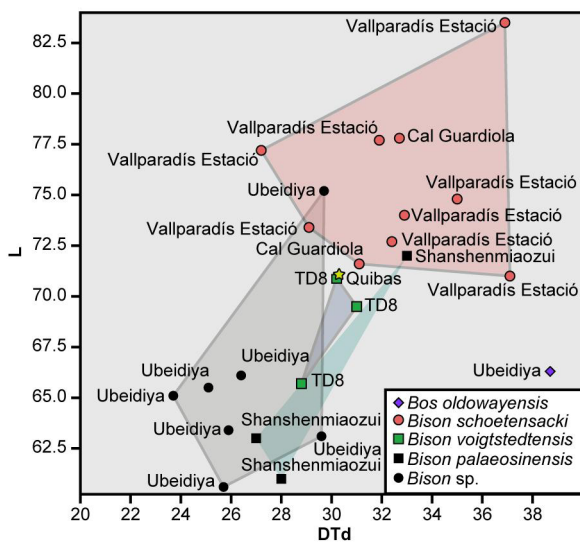


Fig. 5 - *Bison* cf. *voigtstedtensis*. Bivariate analysis of the proximal phalanx with distal transverse diameter and length. Data extracted from Breda et al. (2010), Martínez-Navarro et al. (2012), Made et al. (2017), Tong et al. (2017) and Sorbelli et al. (2021).

of *Bos*, the lingual groove is shallow with a rounded, horizontal base and the entostylid is distally oriented. Comparison of our molars with those figured by Bona & Sala (2016), Tong et al. (2017), and Kostopoulos et al. (2018) also support the attribution to species of *Bison* (triangular and narrow shape, enamel fold on the preprotocristid, and strong development of the mesostylid and entostylid).

Within *Bison*, we find proposals that distinguish two subgenera: *Eobison* for primitive specimens and *Bison* for derived specimens. According to Kostopoulos (1997), the former has lower molars that are prismatic and narrow in shape with weak mesostylid and entostylid, a considerable presence of cement, an ectostylid connected to the anterior lobe and lacking the goat fold, internal basal pillars, and an anterior constriction on the lobes. Our specimen differs in the development of the stylids (since both mesostylid and entostylid are well developed), the significant presence of cement (which might be relative given its wear stage), and the presence of an anterior constriction on the lobes (it forms the preprotocristid fossa). Given these dissimilarities, the minor relevance of some coincident attributes (shape of molars and lack of goat fold), and the greater agreement of criteria with the previously mentioned characteristics, we believe the species under exam shows derived features and therefore does not belong to *Eobison*.

Regarding our **first phalanx**, we find some descriptions in the literature that allow for determination of the genus. When considering the criteria of McCuaig Balkwill & Cumbaa (1992) our specimen matches some of the characteristics for species of *Bos* (anterior margin with a single concavity coinciding with the medial groove of the proximal articular surface, and a concave abaxial margin in dorsal view) and some of species of *Bison* (smooth pit on the caudal edge with a U-shaped medial groove on the proximal articular surface). Considering further criteria for discrimination (Brugal 1995; Made et al. 2017; Tong et al. 2017; Sorbelli et al. 2021), the assignment of the first phalanx of Quibas to a species of *Bison* is supported: proximal articular surface wide with an axial margin that is mostly straight with a slight concavity and a convex abaxial margin, with a rectangular shape of the articular surface; it also shows a similar width throughout its length.

Within *Bison* species, the determination of our material becomes complicated. The description of species is mostly based on cranial characters, horn cores, or metapodials (Made 2013; Masini et al. 2013; Mead et al. 2014; Kostopoulos et al. 2018), all absent in our sample. For this reason, we will focus on the analysis of the proximal phalanx to identify the species present in Quibas. The early wear stage of the molars and the low discriminating ability between species of *Bos* and *Bison* of M1 and M2 (López González et al. 1999) prevent us from performing analyses on these elements.

We carried out a bivariate analysis on the proximal phalanx (L – DTd, Fig. 5) that shows that species *Bison* has more slender phalanges than *Bos*. We can see that the ‘Ubeidiya specimens are the most slender in our sample, whereas *Bison schoetensacki* Freudenberg, 1910 is the most robust (Sorbelli et al. 2021). Our specimen falls in the middle of the graphic and between these two data sets, showing intermediate slenderness together with *Bison voigtstedtensis*. The specimen from Quibas groups best with the fossils of *B. voigtstedtensis* from Atapuerca TD8 (Ata06, TD8b, G-04, 119), but close to specimen IPS14977 of *B. schoetensacki* from Cal Guardiola (Sorbelli et al. 2021).

The **distal phalanges** show the characteristics of *Bison*, whereas *Bos* has more sinuous dorsal, solar and medial margins and a more developed apophysis for the extensor.

Following the statement in the fallow deer section, our identification should be considered with caution, as the taxonomy of most large bovids is based on cranial and horn core characters, or metapodials (Sher 1997; Breda et al. 2010). In consequence, based on the systematic description of our material and the analysis performed on the first phalanx, we propose *Bison* cf. *voigtstedtensis* as a preliminary identification of the large bovid present in Quibas.

Genus *Capra* Linnaeus, 1758

Capra alba Moyà-Solà, 1987

Pl. 5, figs. A-E

Referred material. Right maxilla fragment with P², P³, P⁴, M¹ (Q'16/QC4/Re/20), P³, P⁴, M¹, M² (Q'17/QS3/Q23/6), M¹, M², M³ (Q'18/QS4/O19/3), right hemimandible with P₂, P₃, dP₄, M₁, M₂ (Q'18/QS3-1/N22/1), P₂, P₃, P₄, M₁ (Q'17/QS3/O21/5), M₂, M₃ (Q'16/QC4/J20/1), left hemimandible with M₃ (Q'16/QC4/J20/1). Isolated teeth: left M³ (Q'15/QC4-QC5/Re/16), left M₁ (Q'15/QC4-QC5/M20/3), left M₂ (Q'16/QC4/Re/7), right (Q'18/QS3-1/O19/6, Q'18/QS3-1/O19/9, Q'18/QS3-1/O19/14) and left MC III (Q'18/QS4-1/P19/25), right (Q'15/QC4-QC5/Re/13, Q'16/QC4/L20/7, Q'18/QS3-1/O19/3) and left MT III (Q'18/QS3-1/O19/17).

Description. All the dentition is hypsodont, with prismatic and angular lobes (triangular in molars).

The dP₄ has three lobes, with the anterior and intermediate lobes mesially inclined, and the posterior one with a vertical orientation relative to the mandible. We find an ectostylid between the intermediate and posterior lobes on the vestibular side.

The P₃ is rectangular and mesio-distally wide. We see a slight concavity on the distal end of the vestibular side, preceded by an anterior convexity that extends mesially to the lingual side. On the lingual side a V-shaped valley is visible on the mesial end. The P₄ is also rectangular, with its wide section on the distal end a posterior enlargement, separated from the principal lobe of the tooth by a lingual-vestibular constriction. In the M₁ the mesostylid and the goat-fold on the anterior lobe are marked and project to the lingual and vestibular sides, respectively. The metastylid also stands out and projects towards the lingual side. In an older individual (Q'17/QS3/O21/5) we only observe the triangular shape of the lobes, and only in the posterior lobe

we can see an infundibulum. The M₂ narrows from the root to the coronal end on the mesial side. In the M₃ the anterior and intermediate lobes project distally, whilst the third lobe is oriented to the vestibular side. This third lobe is round without being convex. The ectostylids are poorly developed.

Both **upper premolars** (P³ and P⁴) have a quadratic morphology typical of Caprinae. Regarding the **upper molars**, Q'15/QC4-QC5/Re/16 and Q'17/QS3/Q23/6 have some traits that are not shared with the remaining specimens: an irregular outline of the infundibula, an interlobular enamel fold on the lingual side and vestibular styles oriented towards the central axis of the tooth. On the other hand, most teeth have the parastyle and metastyle diverging from the central tooth axis while the mesostyle is oriented mesially. The M³ of an immature individual shows a poorly developed metastyle except for a little opening on the occlusal surface (Pl. 5, figs. A, B); an older individual (Q'15/QC4-QC5/Re/16) presents a highly developed metastyle (Pl. 5, figs. C-E).

The **metacarpals** are slender compared to the **metatarsals**, although their length is similar. Most of the metapodials have the distal epiphysis unfused, which makes a biometric study of the robusticity difficult.

Remarks. The estimated MNI indicates the presence of four individuals: two adults and two juveniles, all of different ages according to their dental wear.

The characteristics mentioned for each element of the **dentition** indicate that the material belongs to the subfamily Caprinae, specifically to species of the genus *Capra*, and rule out the genera *Ovis*, *Praeovibos* and *Hemitragus* (Rivals & Blasco 2008; Zeder & Pilaar 2010).

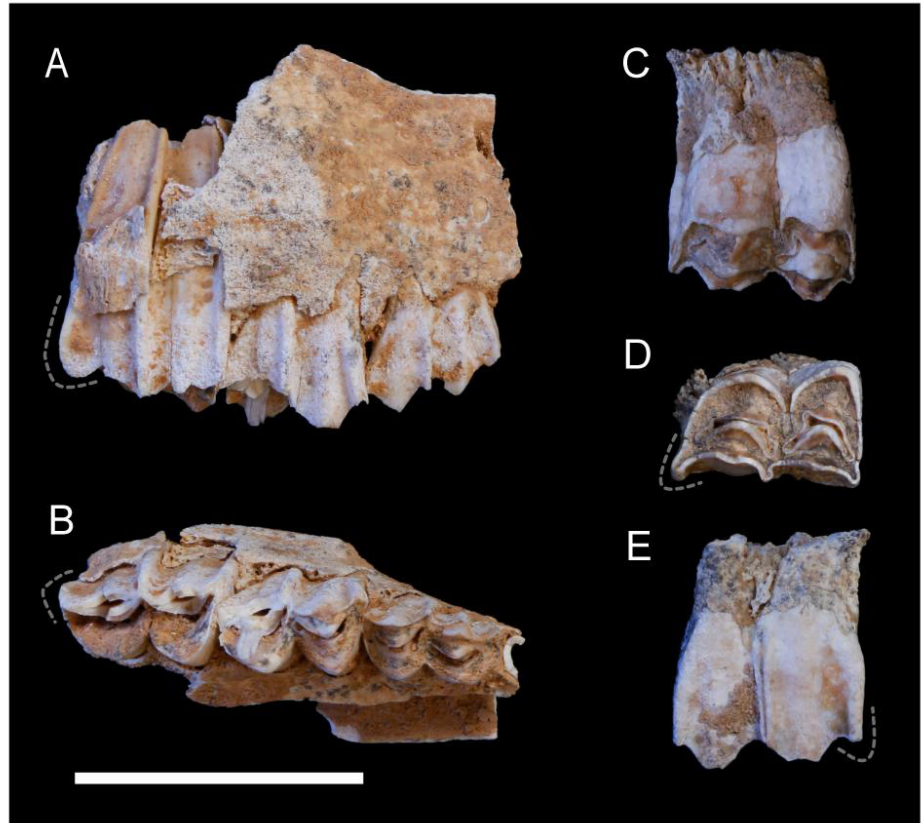
The determination of this species is based on two main characteristics: the robusticity of the metapodials and the development of the metastyle in the M³. Carlos-Calero et al. (2006b) mention this last characteristic, as well as its variability, as weighty arguments to identify *C. alba*. It is present on the Quibas specimens here studied (Pl. 5). This variability and the size disparity observed in our sample present the possibility of a marked sexual dimorphism in the dentition and metapodials of *C. alba*, previously observed on scapulas and horn cores of other specimens from Quibas (Carlos-Calero et al. 2006b; Made et al. 2008).

PLATE 5

Capra alba.

A-B - right maxilla with upper first, second and third molars, Q'18/QS4/O19/3: A, vestibular view; B, occlusal view.
C-E - left upper third molar, Q'15/QC4-QC5/Re/16: C - lingual view; D - occlusal view; E - vestibular view. The discontinuous line indicates the metastyle.

Scale bar: 30 mm.



The **metacarpals** studied are slenderer and more similar to the **metatarsals** than in a modern *Capra pyrenaica* Schinz 1838 specimen. This agrees with the previous statements of Montoya et al. (1999) and Carlos-Calero et al. (2006b). A biometrical analysis of the metapodials is not possible due to the immaturity of the specimens and the fragmentation of the material, although the characteristics match those described by Montoya et al. (1999); Carlos-Calero et al. (2006b) and Vicente Gabarda et al. (2016) for *C. alba*.

Regarding *Praeovibos*, this genus has a developed cingulum at the base of both upper and lower molars, as well as an interlobular fossette on the occlusal surface of the upper molars, both absent in the specimens from Quibas and the fossilis of the species of *Capra* we consulted (Crégut & Guérin 1979). These characteristics of *Praeovibos* are visible in other specimens: one from Maasvlakte (Netherlands) described by Van Kolfshoten & Vervoort-Kerkhoff (1999), in which we can clearly see a notable cingulum at the base accompanied by poorly developed ectostylids, and another from Fonelas P-1 (Spain), in which the fossettes of the upper molars are easy to identify (Garrido 2008b). The M_3 from Quibas share the weakly developed ectostylids but

lack a cingulum at the base, being smooth on every face. Since the description of *Praeovibos* is mostly based on the skull and horn cores, we did not find detailed descriptions concerning the postcranial elements, and the metacarpus figured by Montoya et al. (1999) lacks such detail.

Another Caprinae from the Villafranchian period is *Gallogoral* (Rook & Martínez-Navarro 2010). This genus is infrequent at most sites (except for Senèze) and is usually underrepresented in the fossil record (Andrés Rodrigo 2011). The only record of species of *Gallogoral* in the Iberian Peninsula is in the north-east, at the site of Puebla de Valverde (2.14 – 1.95 My, Sinusía et al. 2005). We find two main aspects that let us dismiss the villafranchian *Gallogoral* based on the dentition (Guérin 1965): the presence of a fossette on the occlusal surface between the two lobes of the upper molars (absent in our specimens) and the absence of the goat-fold in the M_1 (present in our specimens). Although we observe an interlobular enamel fold on the lingual side of some upper molars, these do not form a fossette, which would not appear in older stages, since the molars are markedly worn, whereas specimens of the species of *Gallogoral* present such fossetta in early stages of wear. From the postcranial remains

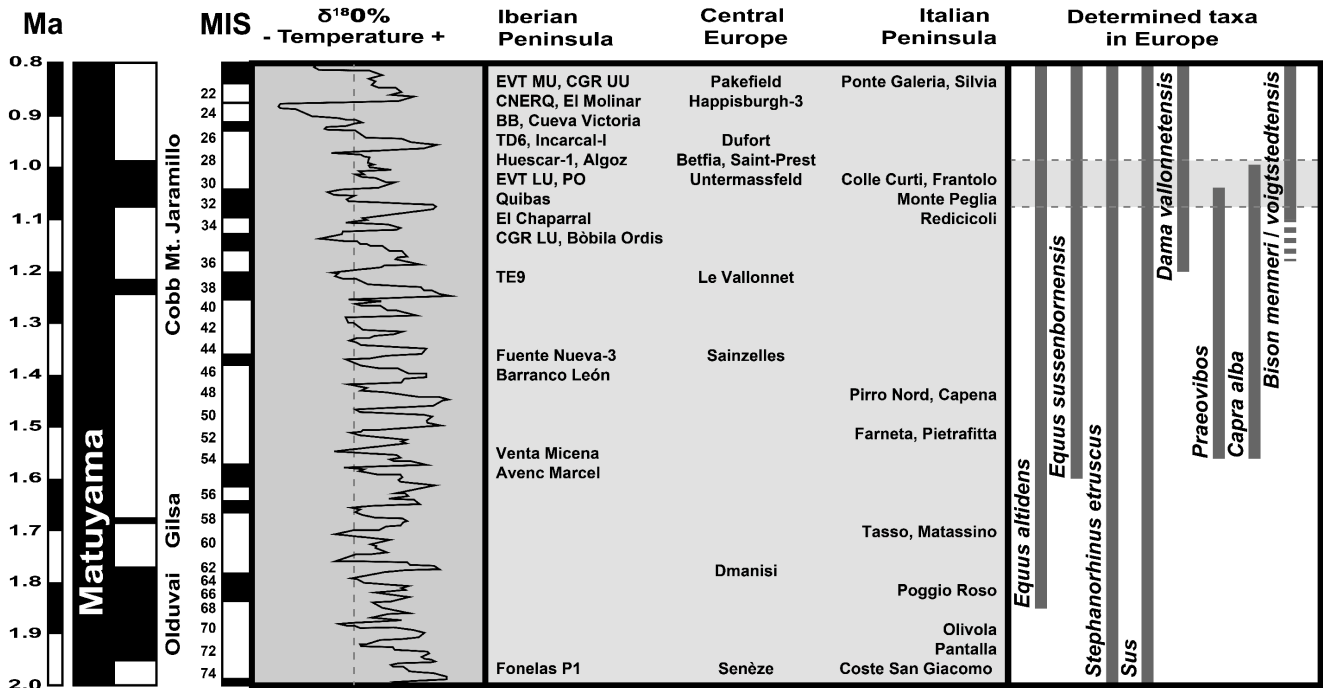


Fig. 6 - Chronological range of Late Villafranchian and Epivillafranchian herbivores species recorded in Quibas and estimated chronology of the main archaeo-palaeontological sites in Europe. EVT: Estació Vallparadis Terrassa; MU: Middle Unit; CGR: Cal Guardiola; UU: Upper Unit; CNERQ: Cueva Negra del Estrecho del Río Quipar; BB: Barranc de la Boella; TD6: Trinchera Dolina-6; LU: Lower Unit; PO: Ponton de la Oliva; TE9: Trinchera Elefante-9.

we found that metapodials are shorter and more robust in *Gallogoral* compared to our specimens, which are longer, slenderer and have clearly marked characteristics, unlike the specimens shown by Andrés Rodrigo (2011).

The herbivorous macromammals of the Quibas site identified in the present work are *Equus altidens*, *Stephanorhinus* cf. *etruscus*, *Sus* sp., *Dama* cf. *vallonnetensis*, *Bison* cf. *voigtstedtensis* and *Capra alba*. These taxa join the previously identified herbivores *Equus suessenbornensis* and *Praeovibos* sp. (Fig. 6).

DISCUSSION

The two sectors considered in this work, Quibas-Cueva (QC) and Quibas-Sima (QS) are chronologically close according to Piñero et al. (2020) and represent the pre-Jaramillo and Jaramillo periods, respectively. The base level of Quibas-Cueva is dated between 1.2 – 1.07 Ma, just prior to the beginning of the Jaramillo subchron represented in Quibas-Sima (1.07 – 0.99 Ma). At the same time, Rosas et al. (2017, unpubl.) realized that the infilling process of both sectors belongs to the same depo-

sitional stage, and therefore can be regarded as one single site despite the material distribution within the endokarstic structure. From this information and the chronological proximity of the sampled levels (QC4, QC5, QC6, QS3 and QS4) we studied the material of both sectors together. Specifically, in the palaeontological analysis presented in this work, specimens from levels QC4, QS3 and QS4 have been precisely identified. Levels QS3 and QS4 have been clearly dated to the Jaramillo subchron and level QC4 can be dated near the limit of the Jaramillo subchron (ca. 1.072 Ma) taking into account the stratigraphic correlations (Piñero et al. 2020, 2022; Fig. 1).

Among the herbivores presented here there is a noteworthy absence of *Praeovibos* material, since Carlos-Calero et al. (2006c) recovered from Quibas-Cueva more material with clear affinities to this genus. Similarly, no element of our sample could be attributed to the species *Equus suessenbornensis*, previously reported in Quibas by Piñero & Alberdi (2015). Since it has not been possible to review all the specimens found in excavation campaigns prior to 2015, the presence of *Praeovibos* and *E. suessenbornensis* in the association cannot be ruled out and these taxa will also be taken into account in the dis-

Tab. 7 - Faunal assemblage of Quibas including the new material.

Mollusca	<i>Bythinella</i> sp., <i>Chondrina farinesii farinesii</i> , <i>Iberus gualtieranus</i> , <i>Jaminia (Jaminia) quadridens</i> , <i>Oxychilus (Ortizius) mercadali</i> , <i>Palaeoglandina montenati</i> , <i>Pomatias sulcatus</i> , <i>Pseudotachea splendida</i> , <i>Rumina decollate</i> , <i>Sphincterochila (Albea) candidissima</i> , <i>Testacella</i> sp. aff. <i>Testacella (Testacella) haliotidea</i> , <i>Trochoidea (Xerocrassa) murcica</i>
Arthropoda	cf. <i>Armadillium</i> sp., Coleoptera indet., Diplopoda indet
Amphibia	<i>Bufo</i> sp., <i>Bufo viridis</i> , <i>Pelodytes</i> sp.
Reptilia	Agamidae indet., <i>Blanus</i> gr. <i>B. cinereus</i> , <i>Coronella girondica</i> , <i>Dopasia</i> sp., <i>Elaphe</i> cf. <i>E. scalaris</i> , <i>Lacerta lepida</i> , Lacertidae indet., <i>Malpolon monspessulanus</i> , <i>Natrix</i> sp., <i>Ophisaurus manchenioi</i> , <i>Psammodromus algerus</i> , Serpentes indet., <i>Tarentola mauritanica</i> , <i>Testudo hermanni</i> or <i>Chersine hermanni</i> , <i>Vipera latastei</i> , <i>Zamenis scalaris</i>
Aves	<i>Anthus pratensis</i> , <i>Athene noctua</i> , <i>Carduelis</i> , <i>Carduelis chloris</i> , <i>Carduelis spinus</i> , <i>Columba livia</i> , <i>Coturnix</i> , <i>Cuculus canorus</i> , <i>Delichon urbica</i> , <i>Geronticus eremita</i> , <i>Gypaetus barbatus</i> , <i>Oenanthe hispanica</i> , <i>Otus scops</i> , <i>Parus major</i> , <i>Phoenicurus ochruros</i> , <i>Prunella modularis</i> , <i>Saxicola rubetra</i> , <i>Saxicola torquata</i> , <i>Serinus serinus</i> , <i>Strix aluco</i>
Mammalia	<i>Allophaiomys</i> sp., <i>Apodemus sylvaticus</i> , <i>Castillomys rivas rivas</i> , <i>Crociodura kornfeldi</i> , <i>Elyomis quercinus</i> , <i>Erinaceus</i> sp., <i>Hystrix refossa</i> , <i>Miniopterus</i> cf. <i>horaceki</i> , <i>Myotis myotis</i> , <i>Myotis nattereri</i> , <i>Neomys</i> sp., <i>Oryctolagus</i> cf. <i>giberti</i> , <i>Prolagus calpensis</i> , <i>Rhinolophus euryale</i> , <i>Rhinolophus ferrumequinum</i> , <i>Rhinolophus hipposideros</i> , <i>Sciurus</i> aff. <i>magistri</i> , <i>Sciurus</i> aff. <i>vulgaris</i> , Felidae indet. cf. <i>Megantereon</i> , <i>Lynx pardinus</i> , <i>Meles meles meles</i> , <i>Vulpes alopecoides</i> , <i>Canis</i> sp., <i>Macaca sylvanus florentina</i> , <i>Equus altidens</i> , <i>Equus suessenbornensis</i> , <i>Stephanorhinus</i> cf. <i>etruscus</i> , <i>Sus</i> sp., <i>Dama</i> cf. <i>vallonmetensis</i> , <i>Bison</i> cf. <i>voigtstedtensis</i> , <i>Ovibovini</i> indet. cf. <i>Praeovibos</i> sp., <i>Capra alba</i>

cussion of the herbivore assemblage. Regarding the carnivores, work on the fossil material from Quibas is underway at present. The updated faunal list of Quibas is in Table 7.

Origin of the macromammal herbivore assemblage from Quibas

We present four new taxa from the Quibas site, as well as descriptions of the previously identified fallow deer and suid (Made et al. 2008). All the herbivorous macromammals recorded at the site have controversial phylogenetic relationships and/or their origin is unresolved.

The fossil record of both *Equus altidens* and *E. suessenbornensis* encompasses the Early-Middle Pleistocene transition (EMPT) in Europe, especially in the southwest (Palombo & Alberdi 2017; Cirilli 2022). Both species have controversial phylogenetic relationships (Boulbes & van Asperen 2019; Cirilli et al. 2021). In the case of *E. altidens*, we find three different hypotheses (see Palombo & Alberdi 2017 and references therein): a European origin as descendant of *E. stenonis* through anagenetic processes, an African origin as descendant of *E. tabeti* Arambourg, 1970/*E. numidicus* Pomel, 1897 (reflected in morphological analysis; Guerrero-Alba & Palmqvist 1997; Cirilli et al. 2021), and a possible Asian origin as descendant of *E. qinyangensis* Deng & Xue, 1999. For *E. suessenbornensis*, a European origin as descendant of *E. major* Delafond & Deperet, 1893 is the most parsimonious hypothesis based on biometrical and morphological analyses (Palombo & Alberdi 2017). Following the European origin hy-

pothesis, Palombo & Alberdi (2017) suggested that the coexistence of both species in Quibas (similar to other fossiliferous sites across Europe) most probably reflects sympatric speciation from ecological differences. The European origin of *E. altidens* and *E. suessenbornensis* is supported by the recent re-assessment of equids from Greece (Gkeme et al. 2021).

Stephanorhinus etruscus, on the other hand, shows a clearer fossil record than the equids. The earliest record of this species is in the Pliocene of Spain (Las Higerelas, 3.3 Ma), where it persisted until ca. 0.9 Ma (Pandolfi et al. 2017). From here, the record roughly agrees with a coherent expansion towards the east: chronologically the arrival of the species is recorded through France and Italy to Germany, extending to Greece, the Balkans and Turkey (Pandolfi et al. 2017). However, the last appearance is in the Iberian and Italian peninsulas, both acting as refugees. The fossil record of *S. etruscus* in the Iberian Peninsula synchronous with Quibas is at Atapuerca TD4-8, Cueva Victoria, Huéscar 1, El Chaparral, Venta Micena, and tentatively at Atapuerca TE7-14 and Barranco León 5 (Made et al. 2017). As mentioned above (Systematic Palaeontology, Rhinocerotidae) two species are present in the Iberian Peninsula and Europe during the EMPT: *S. etruscus* and *S. bundhseimensis*, the latter recorded starting at 1.5 Ma. The morphology of these species is extremely similar and therefore their identification is difficult (Ballatore & Breda 2013). The enamel proteome analysis recently carried out by Cappellini et al. (2019) supports the

European origin reflected by the fossil record for species of this genus, the subsequent dispersal towards eastern Eurasia and the relationship between *S. etruscus* and *S. hundsheimensis* as descendants of a primitive lineage. Nevertheless, this analysis also showed the paraphyletic traits of *Stephanorhinus*. We will not delve into this matter as it invalidates the previous systematic relationships of the genus based on ecological preferences and morphology.

The fossil record of *Sus* is extensive and widespread. In the Early Pleistocene two species are present in Europe: *S. strozzi* and *S. scrofa*. The former survived as an element of the Villafranchian fauna and the second appeared in the Galerian, surviving until today. A previous review of the suids fossil record in Europe identified a gap between 1.8 – 1.2 Ma (Martínez-Navarro et al. 2015) but recently Made et al. (2017) demonstrated the existence of fossils determined as *Sus* sp. within that time, thus completing the continuity of the fossil record. In Europe *S. strozzi* is abundant until 1.8 Ma and persisting until 0.9 Ma (Martínez-Navarro et al. 2015; Bona & Sala 2016). The latest record of the species is at Vallparadís Composite Section (Cherin et al. 2019, 2020) at ca. 1.1 Ma, close to that of La Boella (ca. 1 Ma, Vallverdú et al. 2014), both in the north of the Iberian Peninsula and with similar chronologies to Quibas. Simultaneously, the first record of *S. scrofa* in Europe is in the Iberian Peninsula at ca. 0.9 Ma in Atapuerca TD6 (Made 1999), which suggests the coeval existence of both species in the Iberian Peninsula and Europe. The phylogenetic relationships within species of this genus remain unresolved, with some hypotheses suggesting *S. strozzi* as a descendant of *S. arvensis* and *S. scrofa* descending *S. lydekkeri* Zdansky, 1928. However, recent work by Cherin et al. (2018) does not support these hypotheses but relates *S. strozzi* to verrucosic pigs from Island South East Asia and *S. scrofa* to the intermediate form *S. lydekkeri*, thus also connecting it with verrucosic pigs. Cherin et al. (2018) reviewed *S. strozzi* and limited its record to Europe and west-Asia, whilst Groenen et al. (2012) were able to establish the origin of *S. scrofa* in Southeast Asia.

According to Made et al. (2017), we find three species of *Dama* during the 1.1 – 0.9 Ma period in southwest Europe: *D. vallonnetensis*, *D. nestii* and *D. robertorum* Breda & Lister, 2013. Within this timespan, *D. vallonnetensis* fossils have been recovered in

the Iberian Peninsula in Atapuerca TD4-8, Cueva Victoria and El Chaparral, and tentatively recorded in Atapuerca TE7-14, Fuente Nueva 3 and Barranco León 5 (Made et al. 2017). Even so, the review of the cervids from the sites of Fuente Nueva 3 and Barranco León 5 by Abbazzi (2010) only accepts the presence of *Praemegaceros* cf. *verticornis* Dawkins, 1872 and *Metacervoceros rhenanus* Dubois, 1904 at these localities. As we have already stated above, Made et al. (2008) lists the presence of cf. *Dama nestii vallonnetensis* in Quibas. There is controversy surrounding this species, as some specimens determined as *D. vallonnetensis* have been reassigned to other genera (*Cervus*, *Axis*, *Euraxis*, *Pseudodama*) or species and subspecies (*nestii*, *euygonos*) (Kahlke 1997; Di Stefano & Petronio 1998, 2002; Pfeiffer 2002; Breda & Lister 2013; Petronio et al. 2013; Croitor 2014). Croitor (2006, 2014, 2018) explains that several reassignments are most likely due to similar locomotor strategies and ecological preferences when studies focus on postcranial morphology, especially those concerning *Pseudodama* and *Euraxis*. Croitor & Bonifay (2001) clarify that *D. vallonnetensis* is an archaic fallow deer that is more abundant in southern Europe. Concerning the origin of this fallow deer, morphological and molecular analyses confirm this genus as a close relative of Megacerini (Mennecart et al. 2017 and references therein; Heckeberg 2020), although its origin is controversial. Its fossil record is restricted to the European continent, suggesting a local radiation (Croitor 2014), whilst other authors suggest an Asian immigration reflected in mitochondrial and nuclear phylogenies (Gilbert et al. 2006). Like the genus *Dama*, the fossil record of *D. vallonnetensis* is restricted to Europe (Croitor 2014).

Regarding *Bison* cf. *voigtstedtensis* our material is close to that of Atapuerca TD8, although the taxonomic status of this species is somewhat debated and it is considered by several authors to be a subspecies of *B. schoetensacki* (for more information see Sorbelli et al. 2021). In a similar time range, we find four species in the Iberian Peninsula: *B. degiulii* Masini, 1989, *B. menneri* Sher, 1997, *B. voigtstedtensis*, and *B. schoetensacki*. The earliest presence of species of *Bison* (*Eobison*) in this region is at Venta Micena ca. 1.5 Ma (Martínez-Navarro et al. 2011; Sorbelli et al. 2021), and tentatively at Fuente Nueva 3 and Barranco León 5 as *B. degiulii* (Made et al. 2017). *B.* cf. *menneri* was identified at Sima del

Elefante TE9c (ca. 1.2 Ma, Huguet et al. 2017) and *B. voigtstedtensis* is present at Atapuerca (TD4-6) and Cueva Negra del Estrecho del Río Quípar (Made et al. 2017; Álvarez-Posada et al. 2018; López Jiménez et al. 2020). Lastly, *B. schoetensacki* is present in Vallparadís Estació, Cal Guardiola and tentatively recorded at El Chaparral, Pontón de la Oliva and Cueva Victoria (Made et al. 2017; Sorbelli et al. 2021). Little information exists about the skeleton of *B. voigtstedtensis* and about its phylogenetic relationships. The hypodigm of *B. voigtstedtensis* is restricted to Europe, mainly in the Central-Western area. The controversy and rarity of this species complicates the interpretation of its geographic distribution and origin. However, the oldest record is in Atapuerca TE 4-7 (Spain) at ca. 1.1 Ma (Made et al. 2017), indicating a possible European nature of the species. Looking at the *B. schoetensacki* record (as the species with which *B. voigtstedtensis* shares its highly debated taxonomy) the first record is in Western Europe during the EMPT in Le Vallonnet and Cal Guardiola at ca. 1.2 – 1.1 Ma (Brugal 1995; Sorbelli et al. 2021). This species spreads rapidly throughout Europe, from Spain and Italy to the British Isles and reaching central Asia at the end of the Middle Pleistocene (Breda et al. 2010; Sorbelli et al. 2019). This rapid dispersion and the broad, European distribution prevent us from knowing the precise origin of the taxon, leading us to the same conclusion as for *B. voigtstedtensis*: a European nature of the species that might also imply a European origin.

The genus *Praeovibos* appears for the first time in Europe in Fonelas P-1 (Garrido 2008; ca. 2 Ma Arribas et al. 2009) and ranges from southwestern Europe to the Yukon in Alaska, surviving until the Middle Pleistocene (McDonald et al. 1991). In contrast to our sample, Carlos-Calero et al. (2006a) found material attributable to cf. *Praeovibos*; Crégut-Bonnoure in Garrido (2008) identified the material from Quibas as *P. mediterraneus* Crégut-Bonnoure 2002, which is the only attempt to reach a specific determination, mainly due to the scarcity of comparative material. Morphological comparisons of this caprine led some authors to identify the genus as monophyletic (*P. priscus*) and as an ancestor of *Ovibos* (Garrido 2008; Arribas et al. 2009; Stefaniak et al. 2021). A mitochondrial DNA phylogenetic analysis places *Praeovibos* within the diversity of *Ovibos*, suggesting that the former might

be an earlier morphotype of the latter (Campos et al. 2010). *Praeovibos* immigrated into Europe from Asia, where the origin of the genus is placed (Arribas et al. 2009).

Capra alba is a species from the Early Pleistocene of the Iberian Peninsula present at Venta Micena, Quibas, Huéscar-1 and tentatively at Barranco León 5 (Made et al. 2017). On the other hand, studies on the Quibas site suggest the taxonomic consideration of the species *C. alba* as *Hemitragus albus* (Crégut-Bonnoure 1999; Montoya et al. 1999). Arribas & Garrido (2008) suggest that *C. alba* is a descendant of *C. baetica* Arribas & Garrido, 2008, also identified only in the Iberian Peninsula, while Made et al. (2008) state the uncertainty of the phylogenetic position of *C. alba* with three hypotheses: it may suggest a primitive species, a form more closely related to *Hemitragus*, or be more closely related to *Pseudois* or *Ammotragus*. This caprine has an extremely restricted record and shows a possible endemism event in the southeastern Iberian Peninsula.

Even though the phylogenetic relationships and the origins of the identified taxa are not completely clear, the fossil record of *E. altidens*, *S. etruscus*, *D. vallonnetensis*, *B. voigtstedtensis* and *C. alba* shows a strong European affinity or restricts their presence to Europe. This indicates a dominance of European taxa at the Quibas site, except for *Sus* sp. and cf. *Praeovibos* sp., both of Asian origin but not fully comparable since we could not determine the species in either case.

The Quibas site in a biochronostratigraphic context

The herbivorous macromammals studied here (Fig. 6) and the remaining large mammals identified in previous studies (Table 7) are placed within the Epivillafranchian framework. However, many taxa typical of this period (1.2 – 0.78 Ma) are not present in the site, which raises some questions. Some of these taxa are (Madurell-Malapeira et al. 2019): *Homotherium latidens* (Owen, 1846), *Megantereon whitei* (Broom, 1937), *Panthera gombaszoegensis* Kretzoi, 1938, *Puma pardoides* (Owen, 1846), *Panthera* sp., *Pachycrocuta brevirostris* (Gervais, 1850), *Crocuta crocuta* (Erxleben, 1777), *Lycan lycaonoides* (Kretzoi, 1938), *Ursus deningeri* von Reichenau, 1904, *Mammuthus meridionalis* (Nesti, 1825), *Hippopotamus antiquus* Desmarest, 1822, *Megaloceros savini*

(Dawkins, 1887), *Cervus elaphus* Linnaeus, 1758, *Capreolus* sp., *Bison schoetensacki*, *Ammotragus europaeus* Moullé, Echassoux & Martínez-Navarro, 2004, *Sus strozzi* and *Stephanorhinus hundsheimensis*. *A. europaeus* and *C. elaphus* appear in the lower and upper limit of the biochron, respectively. The most remarkable characteristic of Quibas is the minimal presence of large carnivores (some material was determined as cf. *Megantereon* but there is no mention of it since Carlos-Calero et al. 2004) and the absence of mammoths, hippos and humans. The present paper mentions the large mammals *Stephanorhinus* and *Bison* for the first time, which suggests that the lack of these taxa may be due to their stratigraphic position or taphonomic biases and not an actual absence in the faunal community.

According to Magri & Palombo (2013), the Jaramillo interval registers low values of diversity, origination and extinction of taxa for the Iberian Peninsula but shows a high turnover index (i.e., a change in faunal taxonomic composition). Spain was the first area reflecting this turnover compared to France and Italy, which also implies a regionalism within the already diverse southwestern Europe. This local event is apparent in the presence of endemic species such as *Capra alba* or the slenderness of *Equus altidens* in the specimens from Quibas (Fig. 2).

The fossil sites that harbour typical Epivillafranchian taxa and have similar chronologies to Quibas in the Iberian Peninsula are the Vallparadís Composite Section (VCS), Barranc de La Boella, Atapuerca (TD4-7, TE7-14), El Molinar, Pontón de la Oliva, El Chaparral, Cueva Victoria and Cueva Negra del Estrecho del Río Quípar (CNERQ). In other regions of Europe similar sites are Algoz, Le Vallonnet, Durfort, Saint-Prest, Untermassfeld, Colle Curti, Betfia and Happisburgh-3. In the Iberian Peninsula, we find that Cueva Victoria, CNERQ, El Chaparral, Sima del Elefante and Gran Dolina have similar environmental conditions, somewhat wetter than Quibas, and except for El Chaparral and Cueva Victoria, those sites show evidence of human presence. Both Cueva Victoria and CNERQ share some characteristics with our site, such as the geographic location, macro- and micromammal taxa, chronological age, and the karstic character of the site. On the other hand, CNERQ differs in palaeoenvironment, depositional environment and presence of hominin fossils or

artefacts, the latter being absent from the site under exam (the most remarkable aspect). This raises some questions as to why Quibas shows no sign of hominins, as El Chaparral and Cueva Victoria. The palaeoenvironmental reconstruction of the Quibas site, for both Quibas-Cueva and Quibas-Sima (Montoya et al. 1999; Piñero et al. 2020) indicates an open and relatively dry environment, especially for QS3 and QS4, dominated by rocky areas and patches of more humid and arboreal areas. This is consistent with the new mention and description of *Stephanorhinus*, possibly *Sus*, *Dama* and *Bison* testifying to a diversity of environments. Compared with Cueva Victoria and CNERQ, Quibas was drier, had a rocky area and was far from relatively large water bodies (Gibert et al. 2016; López Jiménez et al. 2020). This could suggest some obstacles to accessibility and survival. However, Quibas had some cavities open and accessible slightly earlier than 1 Ma, which were later infilled with sediments and fossil remains swept along by rain (Romero et al. 2009).

Considering the sites of El Chaparral (Cádiz, Spain) and Cueva Victoria (Cartagena, Murcia) we see an extremely similar situation: both sites are on the slope of a mountain range, with fossils embedded within the sediment infilling of a karstic structure, a patchy environment with a dry open landscape with remaining forested and humid areas, and a restricted record of Epivillafranchian mammals without evidence of *Homo* (Fernández-Sánchez et al. 2017). If the lack of human presence is confirmed in the future, the environmental characteristics mentioned above might explain this absence. Later, at ca. 0.75 Ma, Cúllar Baza-1 shows similar conditions to Quibas, El Chaparral and Cueva Victoria although in this case there is evidence of human presence (Bellucci et al. 2021), which raises some questions as to whether the human absence relates to taphonomic biases or eco-physiographic human preferences. It is important to mention that the chronology of Cúllar Baza-1 is still disputed due to the contradictory biochronological estimates (0.73–0.9 Ma; Alberdi et al. 1989) with the estimate of 441 ± 27 ka by applying techniques of amino acid racemization analysis in gastropods by Ortiz et al. (2000).

Figure 6 shows graphically the correlation between the main European sites of the 2–0.8 Ma chronological span and the presence of the taxa identified at Quibas.

CONCLUSIONS

Here we present the herbivorous large mammal fossil material gathered during four field seasons (2015-2018) at Quibas. Typical taxa from the site are *Equus altidens*, *E. suessenbornensis*, *Praeovibos* sp. and *Capra alba*. New material has been identified for the first time at the site: *Stephanorhinus* cf. *etruscus* and *Bison* cf. *voigtstedtensis*, along with the first description of *Dama* cf. *vallonnetensis* and *Sus* sp. Most of the taxa show a strong European affinity, and some regionalism, concordant with the faunal dynamics of the Early-Middle Pleistocene transition that characterizes the southwestern region of Europe. *Sus* sp. and *Praeovibos* sp. are the only taxa of Asian origin, although the identification of the species (*S. scrofa* and *P. prisus* as Asian, and *S. stroggzi* and *P. mediterraneus* as European) may change this last statement.

The Quibas site (Murcia, Spain) shows a particular scenario in the southeast Iberian landscape:

- A transitional faunal association with signs of possible endemism events. The European affinity of the herbivorous macromammals at the site is notable.

- Lack of most typical Epivillafranchian fauna and hominins, both widely recorded in the Iberian Peninsula during this time. Possible explanations for these absences remain unclear and require a deeper study of the whole fossiliferous site.

- The absence of anthropic influence provides the opportunity to study a wild fauna community in a generally hominin-influenced landscape.

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