New record of cold-adapted fauna on the Castilian Plateau: Woolly rhinoceros – *Coelodonta antiquitatis* (Blumenbach, 1799) – at La Mina (Burgos, Spain)

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ABSTRACT: La Mina is one of three sites, along with Cueva Millán and La Ermita, located in the middle course of the Arlanza river. La Mina was excavated for the first time in 2006 and three test pits were carried out. In one of them, evidence of two Palaeolithic occupations was identified and several remains of woolly rhinoceros were recovered. Amino acid racemisation dating yielded an age of 52.5 ka BP, the earliest Upper Pleistocene date for *Coelodonta antiquitatis* on the Iberian Peninsula. This new record may have several implications for understanding the access routes to the Castilian Plateau, together with the definition of a new migratory wave of this species at the end of the Pleistocene. The location of La Mina on the Castilian Plateau may help researchers to complete the movements of this species through the Middle and Upper Palaeolithic on the Iberian Peninsula.

KEY WORDS: Iberian Peninsula, Middle Palaeolithic, migration, teeth, Upper Pleistocene.

The Iberian Peninsula was one of the main refuges of the last glacial period, along with the Italian and Balkan peninsulas (Gómez & Lunt 2007; Gómez *et al.* 2014; Real *et al.* 2022). Comprehension of the environmental conditions of this period can help us to understand the living conditions of the last Neanderthals in Europe and the ecosystem of Europe's southernmost cold-adapted faunas. During this period, the protagonists of the *Mammuthus–Coelodonta* faunal complex (see Kahlke & Lacombat, 2008) included the woolly rhinoceros (*Coelodonta antiquitatis*), the mammoth (*Mammuthus primigenius*) and the reindeer (*Rangifer tarandus*), while the arctic fox (*Vulpes lagopus*), the wolverine (*Gulo gulo*), the musk ox (*Ovibos mochatus*) and the saiga (*Saiga tatarica*) appeared in smaller proportions (Álvarez Lao & García 2011).

The Castilian Plateau, considered inhospitable for human settlement in the Middle Palaeolithic, has received less attention by researchers. However, in recent decades, several studies have shown that human groups traversed this territory parallel to the fauna and the flora with which they coexisted in the most climatically adverse periods of the Upper Pleistocene (Mateos *et al.* 2014). In addition to the well-known Valdegoba deposit (Quam *et al.* 2001; Diez *et al.* 2008; Arceredillo 2016) there are numerous sites on the Castilian Plateau, and its mountain ranges such as Prado Vargas, San Quirce, Guantes and Cueva Corazón in the Cantabrian mountains (Navazo *et al.* 2005; Mateos *et al.* 2014; Martín Sanz 2018; Terradillos-Bernal *et al.* 2022); Millán, la Ermita, Hundidero, Estatuas and Peña Miel on the Iberian mountains (Diez *et al.* 2008; Navazo *et al.* 2011; Ríos-Garaizar & Eixea 2019); and finally the deposits of Cueva del Búho, Cueva de la Zarzamora, Portalon del Tejadilla and Abrigo del Molino in the Central range (Sala *et al.* 2010, 2011; Álvarez-Alonso *et al.* 2018).

The glacial landscape during the Upper Pleistocene on the Iberian Peninsula has been reconstructed thanks to the pollen and microfaunal record, cave sediments and geographical features associated with glacial environments (Cascalheira *et al.* 2021; Hughes 2021). During the isotope stage 3 (OIS3), there were strong thermal alternations that have been well studied in marine sediments and glacial environments by several researchers, whose equivalences in continental environments have been discussed on several occasions (Burjach & Julià 1994; d'Errico & Sánchez Goñi 2003; Jiménez-Espejo *et al.* 2007). Botanical and faunal records on the Iberian Peninsula reflect, during OIS 3, an alternation between forest environments and open spaces with oscillating cold and warm periods (Daura *et al.* 2017). Studies of this period are scarcer on the Castilian Plateau, where a variety of vegetation representing these alternations has also been identified (Moure & García Soto 1983). Microfaunal records indicate an open or semi-open environment with humid areas near the La Mina site (Moure & García Soto 1983; Diez *et al.* 2008).

Until recently, evidence of cold-adapted species has been restricted to the Cantabrian region and the north-east with occasional deposits in central and southern Iberia (Balbin & Alcolea

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1994; Álvarez Lao & García 2011). However, recent analyses have made it possible to complete the distribution of the cold fauna on the Castilian Plateau with sites such as Portalón del Tejadilla (Segovia) (Sala *et al.* 2020) or Mudá (Palencia) (Álvarez-Lao 2007; Arceredillo 2016).

The main goals of this study are to present the woolly rhinoceros records from La Mina and to place them within the chronological framework of the Upper Pleistocene of the Iberian Peninsula.

Coelodonta antiquitatis

The earliest representative of the genus *Coelodonta*, *Coelodonta thibetana*, was found in the Zanda Basin in south-western Tibet in the Pliocene (ca. 3.7 Myr BP) (Deng *et al.* 2011). The presence of *Coelodonta nihowanensis* between 2.55 and 1.0 Myr BP has been recorded at several Chinese localities such as Longdan, Shitougu, Zhoukoudian, Lingy and several deposits in the Nihewan Basin (Kahlke & Lacombat 2008). The arrival of *Coelodonta* in Europe seems to have been at the beginning of the Middle Pleistocene, around OIS 13/12 (500–400 ka). The earliest record is from Bad Frankenhausen with *Coelodonta tologoijensis* (Kahlke & Lacombat 2008) although this species was also present in the same period in most of Russia (Foronova 1999). The *C. tologoijensis* from Bad Frankenhausen has been considered by Guérin (2010) and Uzunidis *et al.* (2022) as a *C. antiquitatis praecursor*. The last representatives of European *C. antiquitatis* have been recorded in Gönnersdorf at around 13,600 ± 80 years in Switzerland (Kuzmin 2010) and in Asia at around 13 and 10 ka in several deposits in Siberia (Orlova *et al.* 2004).

Coelodonta antiquitatis was present, on the Iberian Peninsula in the Middle Pleistocene in La Parte (Asturias), >150 ka, although its maximum expansion was reached in the Upper Pleistocene (Álvarez-Lao & García 2011; Gómez-Olivencia *et al.* 2014; Sala *et al.* 2020) with remains found from Siberia across to the Iberian Peninsula, Scotland and Greece (Guérin 2010; Pandolfi & Tagliacozzo 2013). During the Upper Pleistocene, the arrival of cold fauna is recorded at two different times. On the one hand, between 41 and 36 ka, these species have been identified in the Cantabrian region, eastern Catalonia, Andalusia and Portugal, with two specific records – both *Mammuthus primigenius* – in Padul and Figueira Brava (Antunes & Santinho 1992; Altuna & Mariezkurrena 2000; Álvarez-Lao & García 2011). Another wave took place around 32 and 20 ka, as suggested by remains from Lezexiki and Cueva del Cuco (Castaños & Castaños 2007; Álvarez-Lao & García 2011).

The Iberian record of *C. antiquitatis* is from 34 deposits located in four main areas: north-eastern Catalonia (6); central Iberia (3); the Cantabrian region (23); and the Castilian plateau (2) (Álvarez-Lao & García 2011; Álvarez-Lao 2014; Sala *et al.* 2020). Some of these remains have been known since the beginning of the 20th century, but there has been an increase in the number of individuals and deposits discovered since the early years of the present century.

La Mina

La Mina (42°5′15″N/3°25′9″W) is one of the three sites, together with La Ermita and Cueva Millán, located 970 m above sea level in a transversal valley of the Arlanza river in the Hortigüela municipality (Burgos) (Figs 1, 2) (Diez *et al.* 2008). The first three test pits in the cave were dug in 2006 (Diez *et al.* 2008).

The cave is halfway up the slope in Bathonian limestone (Domeño Formation, Middle Jurassic), on the northern slope

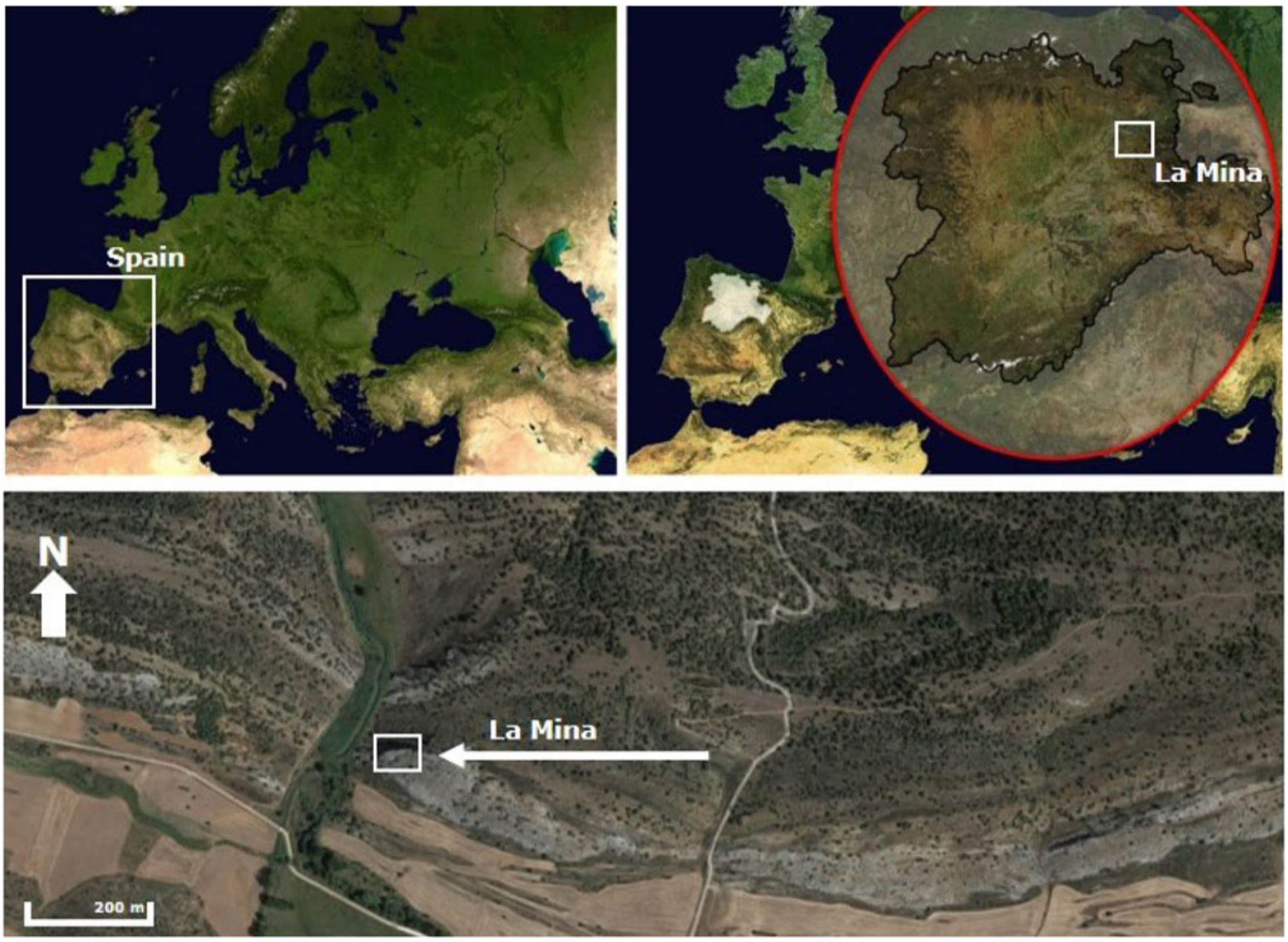

Figure 1. Geographical location of La Mina site on the Castilian Plateau.

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Figure 2. Location of La Mina site in the Valparaiso valley.

of the southern flank of an anticline cut by the Valparaíso River, which forms a rocky outcrop in a N80°E direction. Its geomorphological and landscape context is made up of open spaces, valleys and very steep slopes with many cliffs and vertical walls with rocky surfaces in the higher areas. The stratification of the cliff limestones has a direction of N120°E and a dip of 34°SW. The cave is in one of the most karstifiable layers on the anticline flank, in the Oricedo sector, which has a strong diaclastic fault line in favour of which the cave galleries have an east–west (dominant) and north-west–south-east (secondary) direction, together with a north-east–south-west conjugate. The cave is 105 m long, ending in a 2-m sinkhole. It is a pressure tube with an elliptical section and a diameter of about 2 m, running along a series of perpendicular fractures to the stratification surface on a 40° slope in a N40°W direction and is characterised by two phases of karstification. On reaching the rocky outcrop, the tube ends in an opening with an elliptical section at its northern end. The surfaces of the cave walls are characterised by the predominance of corrosion, mainly on the sides of the tube walls, and the absence of formations, with only some carbonate matting associated with the stratification planes.

Eleven rhinoceros dental remains were found in the third test pit, which contained the highest sedimentary and stratigraphic sequence. For this reason, it is employed here to describe the stratigraphic sequence. It has a maximum depth of 1.50 m. The stratigraphy in section E (Fig. 3) is, from bottom to top:

- CM.C3.4: Up to 60 cm visible of slightly fine gravelly very fine sandy mud, red, plastic, humid, with small rounded autochthonous limestone clasts. The matrix (<2 mm) comprises sandy clays and silts, mineralogically composed of quartz (53.40%), illite (23.70%), microcline (12.70%), clinochlore (7.90%) and calcite (2.30%). The top has slopes of 40°S towards the cave interior, which is more or less parallel to the floor of the cave. It is sterile. Sedimentologically, it can be interpreted as a mud flow deposit.
- CM.C3.3: 13 to 14 cm of greyish-brown muddy very coarse gravel. There is a predominance of native autochthonous clasts, rounded, centile 14 cm and mean 2 cm. The matrix is sandy silt and clay (sandy mud) and its composition is quartz (42.70%), calcite (27.90%), illite (16.20%), microcline (8.50%) and clinochlore (7.90%). Its contact is powerfully erosive on the underlying level. It contains archaeological material, including the woolly rhinoceros teeth studied here, numerous carnivore' remains, bones, flint flakes and ceramic fragments. It appears to be a solifluxion or debris flow deposit.
- CM.C3.2: It is organised in two sub-levels:
  - o CM.C3.2b: 10 to 15 cm of clays and silts with coarse gravelly mud, reddish to brown in colour. The matrix is sandy clay and silt (sandy mud) and consists of quartz (48.10%), illite (24.10%), calcite (12.60%), microcline (8.10%) and clinochlore (7.10%). It is erosive over the underlying rock. Towards the cave interior there is a greater abundance of small pebbles.
  - o CM.C3.2a: 15 cm of brown clays and silts with coarse gravels and cobbles (very coarse gravelly mud), in diffuse contact with the previous level. The clasts are autochthonous limestone, rounded and altered. The matrix is sandy silt and clay (sandy mud), mostly quartz (70.60%), accompanied by microcline (10.80%), calcite (8.60%), illite (7.50%) and clinoclore (2.50%). The appearance is very chaotic and gives the impression of being jumbled. It contains archaeological

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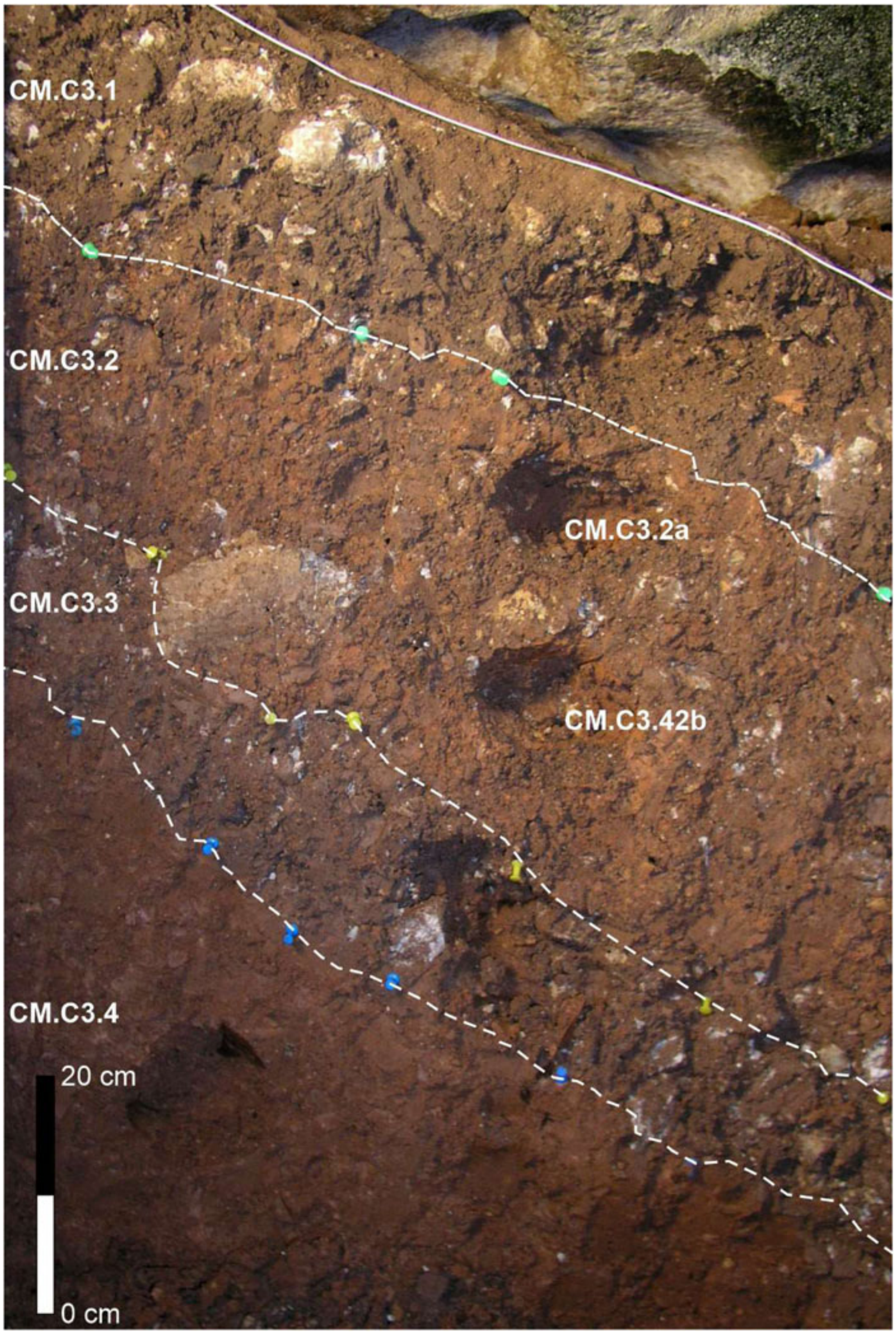

Figure 3. Stratigraphic profile of the third test pit where the rhinoceros dental remains are located.

material: hyena teeth; flint flakes; and ceramics. The bones are arranged vertically.

Both sub-levels can be interpreted as debris flow deposits.

- CM.C3.1: 25 cm of muddy very coarse gravels, dark brown in colour. The clasts are autochthonous limestone, rounded and little altered; centile 10 cm and mean 2 cm. The matrix, sandy silt and clay (sandy mud) is abundant and the general aspect is heavily mixed. It is made up of quartz (43.90%) and calcite (38.80%), accompanied by illite (14.20%) and clinochlore (3.19%). It is erosive over the underlying level. It seems to correspond to a debris flow deposit with subsequent remobilisations.

The deposit is dismantled at the top. There is a 30 cm of autochthonous limestone breccia adhered to the wall 30 cm above the current ground level.

Two possible faunal assemblages (CM.C3.3 and CM.C3.2a) have been identified in this sequence which offer an idea of the possible occupations of the cavity. The first assemblage includes 55 rolled bone remains with carnivore bite marks. This group has not yielded any archaeological remains. Most of the fossils correspond to fragmented diaphyses of medium to large herbivores. The second aggregate includes 493 fossils and 13 lithic items. Carnivore coprolites and digested bones were also recovered.

The identified remains of large and small birds and mammals include 21 taxa (Diez *et al*. 2008): *Grus grus*; *Erinaceus europaeus*; *Eurotestudo* sp.; *Oryctolagus cuniculus*; *Lepus* sp.; *Hystrix* sp.; *Ursus arctos*; *Canis* sp.; *Vulpes vulpes*; *Panthera* sp.; *Lynx pardina*; *Felis sylvestris*; *Crocuta crocuta spelaea*; *Meles meles*; *Coelodonta antiquitatis*; *Equus ferus*; *Equus hydruntinus*; *Sus scrofa*; *Cervus elaphus*; *Rupicapra pyrenaica*; and *Bos*/*Bison* sp.

The presence of lithic industry and cut marks on some bones, as well as the identification of *Crocuta*, hyena coprolites and gnawed bones in La Mina, do not allow us to know whether the rhinocerotids were brought to the cavity by Neanderthals or carnivores.

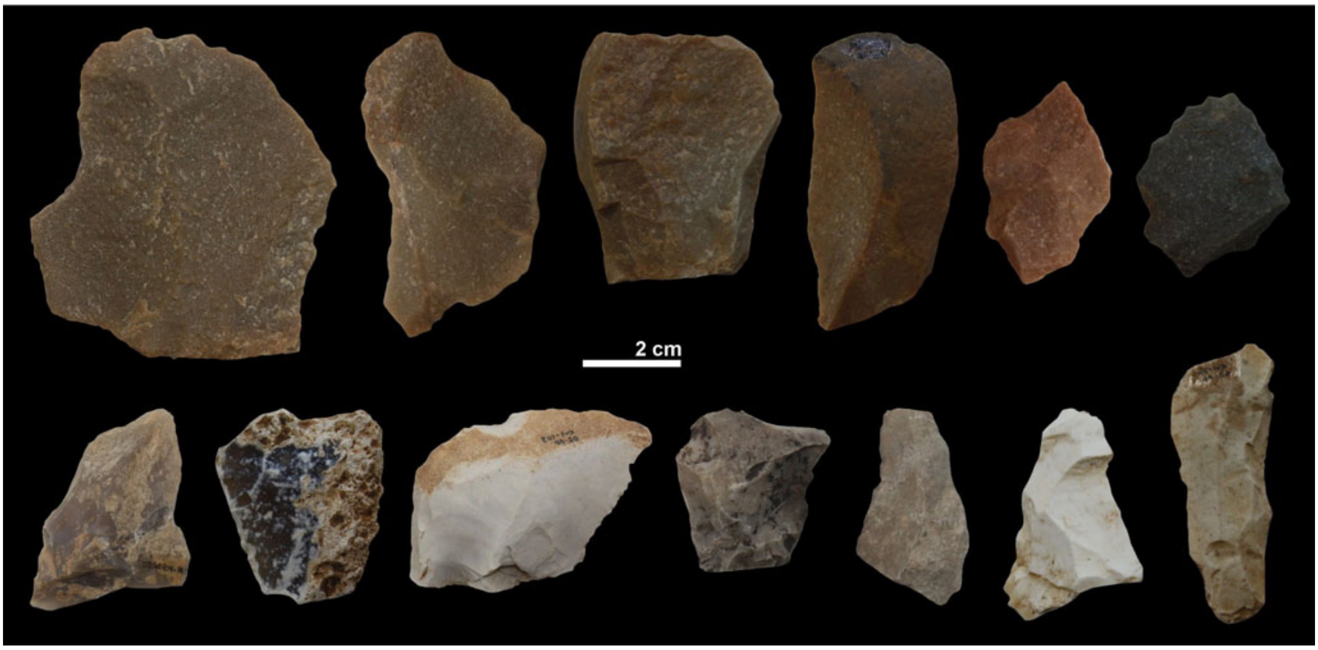

Figure 4. Lithic remains from La Mina.

The raw materials mainly consist of flint and quartzite. The flint has macroscopic characteristics similar to those found at the Mousterian La Ermita and Millán sites, except for one lamellar flake made from allochthonous material. Exhausted cores have been recovered with orthogonal exploitation. A number of naturally-backed blades, Levallois flakes, several denticulates, a quartzite retouched point and a straight lateral scraper on natural backing have been identified. Although the tools were found in disturbed sediment, their technological features and their shape types are typical of the Upper Pleistocene Mousterian repertoires (Diez *et al*. 2008) (Fig. 4).

The deposit was dated using amino acid racemisation on a rhinoceros tooth. Results revealed an approximate age of 52.5 ka BP (Diez *et al*. 2008). This date places the site at the beginning of oxygen isotope stage 3 (OIS 3) (60–24 ka BP).

1. Material and methods

Eleven fossil remains were identified as belonging to rhinoceros. Eight of them are dental fragments, difficult to identify and measure, and the other three correspond to a D4 (upper fourth decidual) (05.LM.E3.M5), a p3 (lower third premolar) (05.40.LM.738) and a m1 (lower first molar) (05.40.LM.759).

The nomenclature used in the description of the material follows the model of Guérin (1980) and Made (2010), and measurements follow Made (2010) (Figs 5, 6): DAP = maximum anteroposterior diameter; DAPb = basal anteroposterior diameter taken in the zone of contact between the root and the crown; DT = maximum transverse diameter; H = maximum crown height; Hci =shortest distance between the cingulum and the lower border of the crown; and Hli = the distance between the point where the bases of the lingual cusps meet and the lower border of the crown.

There are few studies of age at death for the family Rhinocerotidae. These analyses mainly focus on species such as the woolly rhinoceros (Borsuk-Bialynika 1973; Álvarez-Lao 2007; Kirillova & Shidlovskiy 2010; Dirks *et al*. 2016) and *Stephanorhinus hundheimensis* (Fortelius & Solounias 2000; Kahlke & Kaiser 2011). Garutt (1994) conducted an exhaustive study of this species using a large collection of woolly rhinoceros mandibles and maxillae, considering morphological elements that had not been used in previous studies, as well as the replacement of teeth.

Álvarez-Lao (2007) used teeth, the most frequent elements, from a large reference collection to determine age from the degree of wear of the occlusal surfaces and the attrition observed in the enamel on the anterior and posterior faces of the

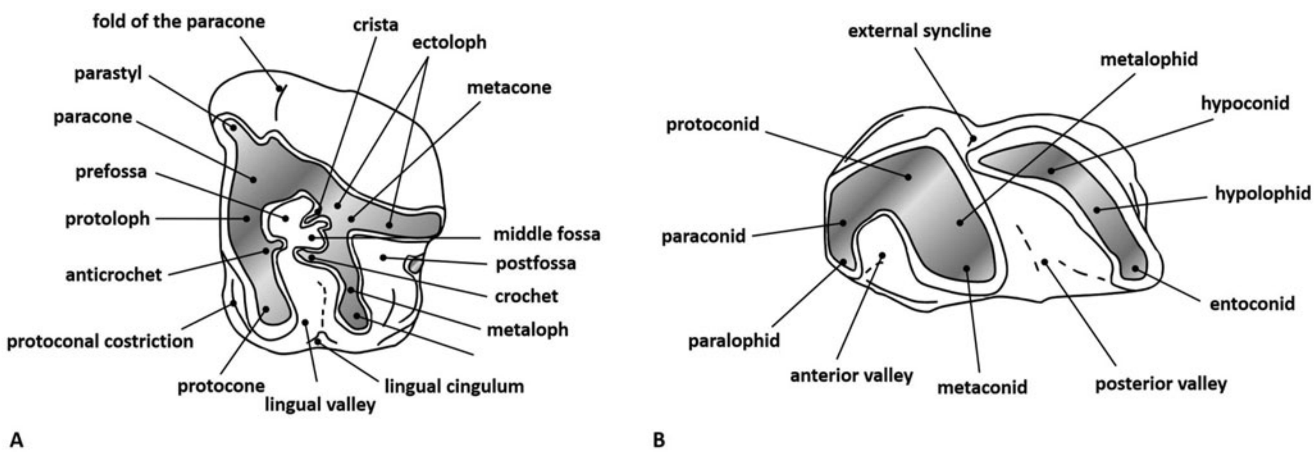

Figure 5. Dental nomenclature. (a) Upper teeth. (b) Lower teeth (Made 2010).

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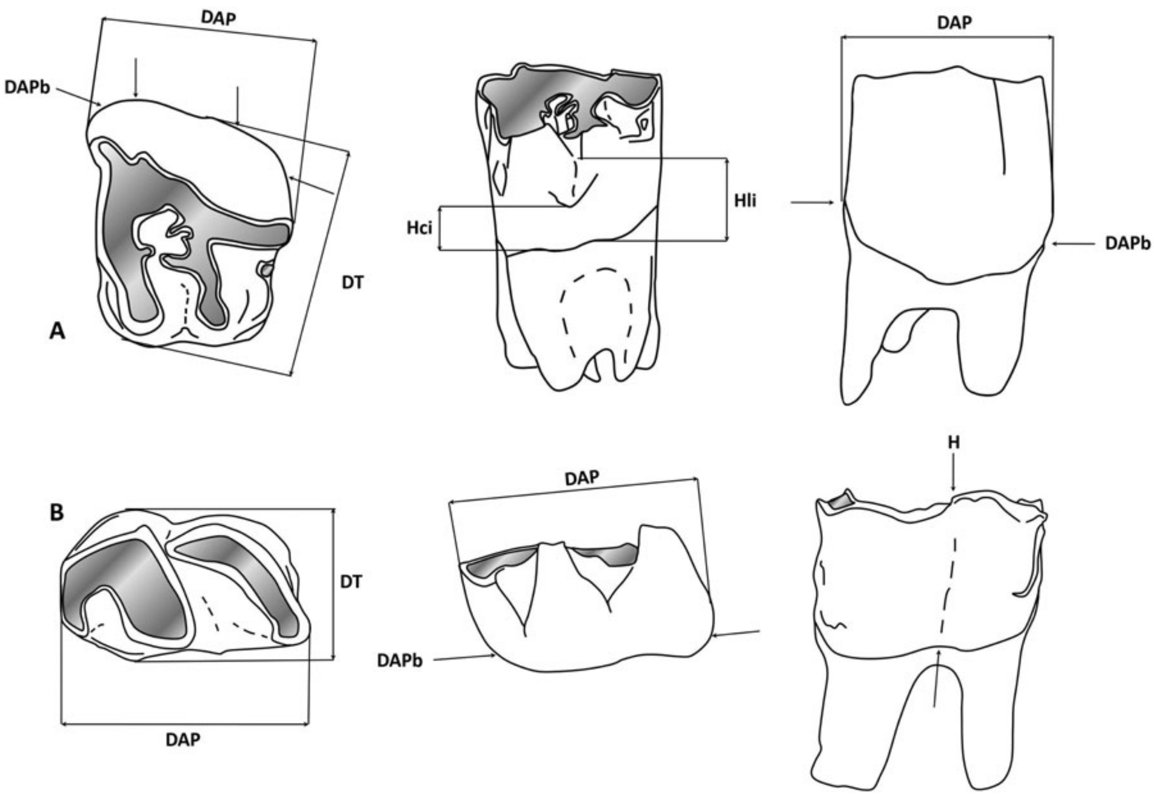

Figure 6. The way of measuring the teeth. (a) Upper molar (b) Lower molar.

premolar–molar line. Finally, he correlated his data with the age groups defined by Borsuk-Bialynika (1973). Kirillova & Shidlovskiy (2010) designed a methodology that contributes the study of the cementum layers of the upper first molar and the observable growth lines in the nasal and frontal horns. These authors established the white rhinoceros as a comparison group, and concluded that the results of both methods and the tooth wear analysis are similar. Cement growth lines was also the methodology chosen by Dirks et al. (2016). Álvarez-Lao (2014) also used white rhinoceros' data to determine the age of the specimens identified at Jou Puerta using the age of eruption and wear given in Hillman-Smith *et al.* (1986). In the present study, we employed age at eruption as well as dental wear defined by Hillman-Smith *et al.* (1986) to facilitate comparison with other Iberian records.

2. Results

The rhinoceros records recovered at La Mina consist of 11 items: a D4; a p3; an m1; and eight enamel remains (Fig. 7).

D4 has rough, narrow enamel. The ectoloph shows an anteroposterior orientation, marked metacone column, elongated ridges and a crochet almost closing the central fossa, a rare feature according to Guérin (1980, 2010). The protocone is very constricted as, in some cases, in *S. hemitoechus* (Guérin 1980). It has narrow lingual valleys. Both prefossa and postfossa are anteroposteriorly oriented. This item presents a developed lingual cingulum. This character is normally absent in *Coelodonta* according to Guérin (2010).

The lower premolar has a deep and open syncline, a short, narrow metaconid and a broad metalophid. The entoconid is more or less at the same level as the metaconid. The metaconid has an anterior position while the metalophid is oriented anteriorly. The anterior valley is wide and has a V-shape, like the posterior one, the latter is similar to *S. hemitoechus* (Made 2010). The posterior valley is narrower than the anterior one and has a posterior orientation. This tooth does not present any cingula. Measurements are similar to those of other European *Coelodonta*. P3 measurements are close to those of specimens from Asturias such as La Parte and Jou Puerta (Table 1) and slightly lower than those from Basque sites such as Labeko Koba.

The lower first molar shows a high degree of wear that hinders observation of the morphological features of the occlusal surface. However, the enamel is thick and rough and there are no cingula. This tooth is larger than those from Jou Puerta and similar to those from Labeko Koba (Table 1). In all cases, values are within the ranges analysed by other authors for this species in Europe (Guérin 1980; Álvarez-Lao 2007; Sala *et al.* 2020).

Several analyses of age of eruption in white rhinoceros conducted by Bigalke *et al.* (1950) and Wallach (1962) (in Hillman-Smith *et al.* 1986) suggest that the fourth upper decidual appears around 140 days, the third lower premolar from the fourth year (unspecified date) and the first lower molar at around three years. Considering the wear of D4 and m1, we conclude that these items cannot be from the same specimen, and we thus estimate the presence of two individuals. The first one is represented by the fourth upper decidual and the second by the third premolar and the first lower molar due to the similarity with Labeko Koba's mandible.

The first specimen, represented by D4, is between 140 days and eight years old, the eruption age of the fourth upper premolar. Following the criteria developed by Hillman-Smith *et al.* (1986) for the white rhinoceros due to their phylogenetic and ecological similarities (Antoine 2012), also used by Álvarez-Lao (2014), Tong & Wang (2014) and Fourvel *et al.* (2015) for the *Coelodonta* remains recovered at Jou Puerta, Fouvent-Saint-Andoche and Shanshenmiaozui, the wear of this item corresponds to phase V, with an age between 1.5 and 3 years. This age coincides with Garutt's (1994) observation in his study on the ontogenetic development of the woolly rhinoceros. This author places a similar attrition of D4 in the CII phase with an age between 2 and 3 years. Something

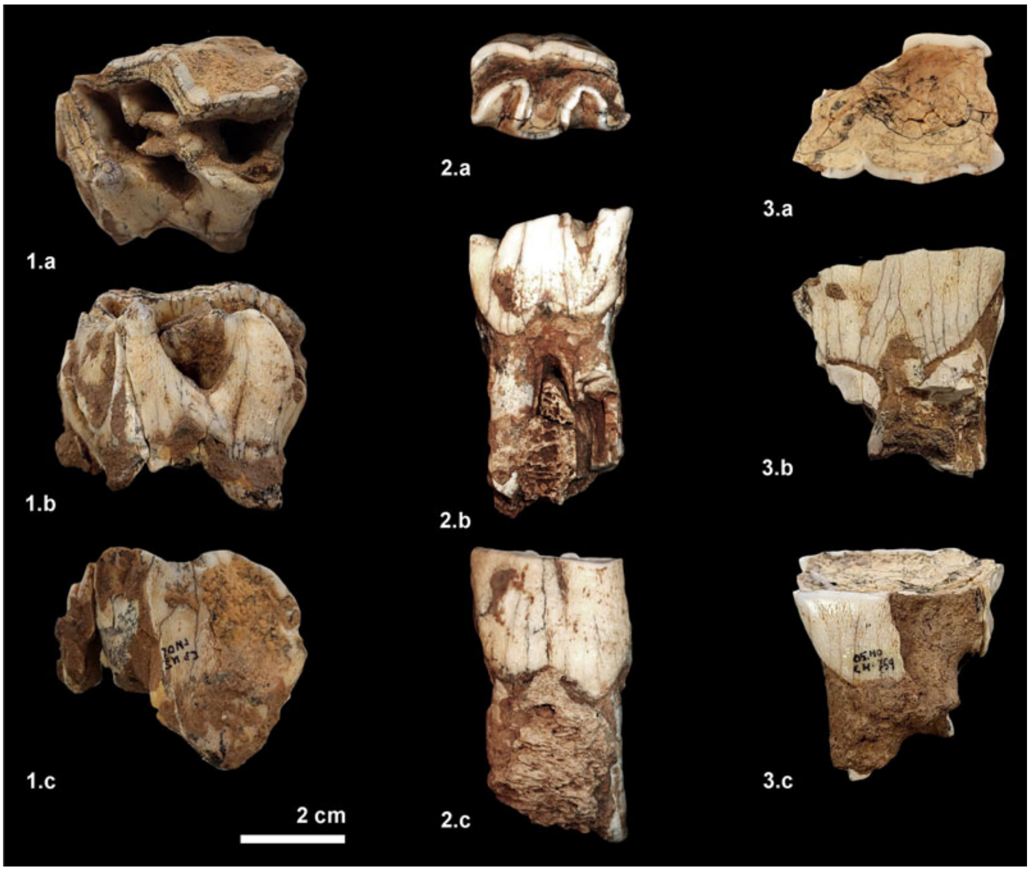

Figure 7. *Coelodonta antiquitatis* dental remains identified at La Mina (LM): (1) 05.LM.E3.M5 – upper right fourth decidual (D4): (1.a) occlusal view; (1.b.) lingual view; (1.c) buccal view. (2) 05.40.LM.738 – lower left third premolar (p3): (2.a) occlusal view; (2.b) lingual view; (2.c) buccal view. (3) 05.40.LM.759 – lower left first molar (m1): (3.a) occlusal view; (3.b) lingual view; (3.c) buccal view.

different occurs with the second individual, represented by p3 and m1. This last item shows maximum wear with complete loss of enamel on the occlusal surface. According to the Hillman-Smith classification, this would occur in white rhinoceroses from the age of 30 years, phase XV, although the wear of the third premolar would not coincide in any of its phases with those of the first molar. However, if we take as a reference the mandible recovered at Labeko Koba, where a similar wear is observed for both items, p3 and m1, this degree of erosion would be complementary. Álvarez-Lao (2007) assigns an adult–elderly age range for this mandible, including it in his group 3. Due to the similarity with the items from La Mina, its wear is assigned to the same group and therefore the same relative age, an adult–elderly following the phases defined by Borsuk-Bialynicka (1973). According to the mortality curves modified by Bacon *et al*. (2008) from the data of Hillman-Smith *et al*. (1986), the specimen represented by D4 is a juvenile while the one represented by p3 and m1 is an old adult in the last stage of life.

3. Discussion

The presence of several species from the family Rhinocerotidae is common throughout the European Pleistocene. Several frameworks have been proposed for the distribution of the two main rhinocerotid genera in this period. Fortelius *et al*. (1993) relies on the presence/absence of species at different sites, but without defining their distribution. Sardella *et al*. (1998) presents data specifically for Italy and Von Koenigswald & Heinrich (1999) provide a large amount of data base on the distribution of a large number of species, mainly from central Europe, but without providing specific data on changes between species.

Coelodonta antiquitatis has received various names since the first descriptions of its remains by Pallas (1773). Despite this variety in nomenclature, the morphological characteristics are well established. The lower jugal teeth are small but have high crowns, rough and thick enamel, and paralophids, metalophids and hypolophids separated by valleys (Guérin 1980; Made 2010). The lower premolars have closed V-shaped valleys with a large difference in level and lack lateral cingula. In the first molar, the valleys are V-shaped in the first molar with a marked difference in height. There are no cingulae, unlike *S. hemitoechus* in which these are frequent (Guérin 1980, 2010; Made 2010). The morphological characters observed in the dentition from La Mina, together with the measurements taken, suggest its assignment to the species *C. antiquitatis.* The upper dentition is generally smaller than *Stephanorhinus* teeth, with rougher enamel, higher crowns, quadrangular ectolophs, posteriorly directed protocones, shorter hypocones, narrower lingual valleys, deep prefossae and ridges and hooks that tend to isolate the central fossa (Guérin 1980; Made 2010). The upper fourth decidual from La Mina has closed the middle fossa although the crochet is not well developed. The protoloph and metaloph are oriented anterioposteriorly and there is no lingual cingulum as described by Guérin (1980).

The arrival of *Coelodonta* to the Iberian Peninsula seems to have occurred in several waves since the Middle Pleistocene (Álvarez-Lao & García 2011; Álvarez-Lao 2014). The presence of *Coelodonta* on the Castilian Plateau is an interesting phenomenon, recorded previously at the Peña de Mudá (Palencia) and Portalón del Tejadilla sites (Álvarez-Lao 2007; Arceredillo 2016; Sala *et al*. 2020). Peña de Mudá was mentioned by Casiano del Prado (1864), who described several rhinoceros' teeth without assigning them to a specific taxon. This was done by

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Table 1 Measurements of the items recovered at La Mina and their comparison with similar *Coelodonta* specimens.

		D4s						P3i				M1i			
Site		DAP	DAPb	DT	H	Hci	Hli	DAP	DAPb	DT	H	DAP	DAPb	DT	H
La Mina[1]		48.5	45.7	34.8		21.6	33.1	30.8	29.1	23.3	20.7	40.8	28.4	30.6	22.2
Lezika		44	36	39.3	38.5										
Labeko Koba		44.5						32		24		42.5		32.5	
Labeko Koba		46		38.5				38		24		54		31	
Labeko Koba		46		38				37		24				31	
Labeko Koba		52		45				34		27				31	
Labeko Koba								35.5		26.5	57				
Arrikrutz												49		54	
La Parte								33		25					
Jou Puerta		46.24		40.6								44.01		26.07	
Jou Puerta												45.1		26.3	
Jou Puerta												51.41		28.85	
Jou Puerta												50.64		28.97	
Cueva del Nando												41.9		27.8	25
Cueva del Nando												40.2		27.3	27
Arenys de Mar												41.8		60.5	
Arenys de Mar												48.5		59	
Arroyo Culebro								37		34.5		52		31	
Arroyo Culebro								38.5		26		51.5		30.5	
Portalón del Tejadilla		45.3		38.7											
Aven de Coulon												34		31	
Starunia												48		21	
Kesslerloch												50.7		33.6	
Ordos												53		30	
Wieringermeer								27.6		18.5		35.5		29.5	
Romain la Roche		50		47											
Romain la Roche		47		47											
Neumark Nord									30.2	23.6					
Neumark Nord									30.9	23.5					
Arago										26.28					
Cavillon Cave										23.73					
Mars Cave										25.04					
Europa	n	20		23				27		30		31		43	
	Mean	48.6		43.3				34.2		24		47.7		29.3	
	Min.	44		39				29		18		38		23	
	Max.	57		55				39.5		29		56		33	

[1]Own data. (Guérin 1980; Álvarez-Lao 2007; Castaños *et al.* 2009; Álvarez-Lao 2014; Sala *et al.* 2020)

Calderón (1876), who assigned them to *Rhinoceros mercki*. Álvarez-Lao (2007) assigned one of the four remains at the Geo-mining Museum (Madrid) to *Coelodonta*. The lack of data on the deposit, location and dating prevents its designation to a specific context.

The remains from La Mina, initially classified as *S. hemitoechus* (Diez *et al.* 2008), have provided the only dating of the deposit, 52.5 ka. This date places the woolly rhinoceros of La Mina as the oldest of the Iberian Upper Pleistocene, only surpassed by the Middle Pleistocene La Parte site (Álvarez-Lao &

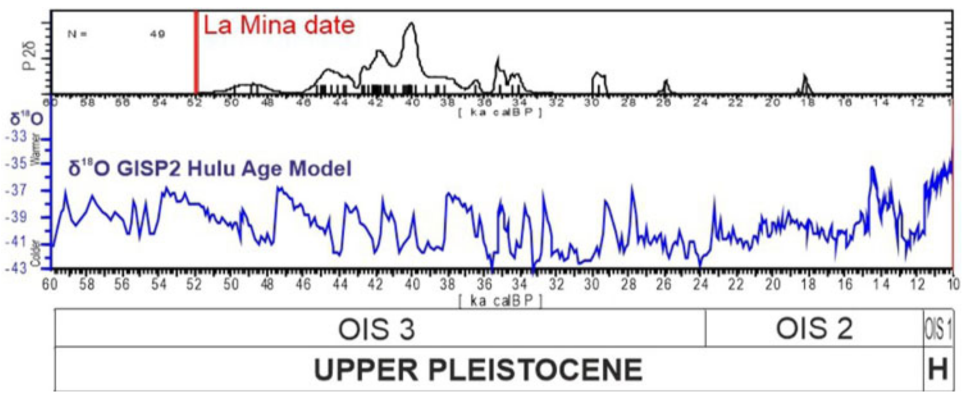

Figure 8. Curve of cumulative probability of radiocarbon dates (AMS) obtained from Iberian deposits with remains of *Coelodonta antiquitatis* (Blumenbach, 1799), showing amino acid racemisation dating from a molar of the species recovered at Level CM.C3.3 of the La Mina cave. Calibration was done by the IntCal 2020 curve (Reimer et al. 2020) using CalPal software (version 2020) (Weniger & Jöris 2004). It is compared with the δ18O GISP2 Hulu Age Model curve (Grootes et al. 1993; Meese et al. 1994; Wang et al. 2001).

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Table 2 Sites where *Coelodonta antiquitatis* remains have been found on the Iberian Peninsula, location and chronological dates.

Site	Province	Level	General chronology	Lab. Code	Date BP	SD	cal BP age (INTCAL2020)	Material	Method	References
La Parte	Asturies	c	OIS6 Middle Pleistocene	GEO3BCN-CSIC	188,500	11,000		Speleothems with several bone fragments	U-Th series	Álvarez-Lao & García-García (2006)
La Parte	Asturies	c	OIS6 Middle Pleistocene	GEO3BCN-CSIC	141,114	8500		Speleothems with several bone fragments	U-Th series	Álvarez-Lao & García-García (2006)
Jou Puerta	Asturies		OIS3 Late Pleistocene	Beta- 313518	25,340	110	30,070–29,110		AMS 14C	Álvarez-Lao (2014)
Jou Puerta	Asturies		OIS3 Late Pleistocene	Beta-313520	29,500	150	34,410–33,730		AMS 14C	Álvarez-Lao (2014)
Jou Puerta	Asturies		OIS3 Late Pleistocene	Beta-313519	32,150	200	36,970–36,050		AMS 14C	Álvarez-Lao (2014)
Rexidora	Asturies		OIS3 Late Pleistocene	Beta-366977	37,640	860	42,870–40,990		AMS 14C	Álvarez-Lao *et al.* (2015)
Cobrante	Cantabria	6	Late Pleistocene	OxA-32505	35,150	650	41,480–39,000	Phalanx 2, *Cervus elaphus*	AMS 14C	Castaños Ugarte (2009), Marín-Arroyo *et al.* (2018), Rasines del Río (2005, 2008, 2009)
Cobrante	Cantabria	6	Late Pleistocene	GrA-32436	30,020	160	34,710–34,230	Bone fragment	AMS 14C	Muñoz Fernández & Santamaría Santamaría (2009), Tejero Cáceres (2009)
Cobrante	Cantabria	6	Late Pleistocene	GrA-22442	33,320	310	39,360–36,920	Bone fragment	AMS 14C	Rasines del Río (2005), Muñoz Fernández & Santamaría Santamaría (2009), Tejero Cáceres (2009)
Covacho Arenillas	Cantabria	II	OIS3 Late Pleistocene	GrN-19597	33,870	1700	42,090–34,770	Bone fragment	AMS 14C	Castaños (1996)
Covacho Arenillas	Cantabria	IIO	OIS3 Late Pleistocene	GrN-19599	34,660	1600	42,580–35,780	Bone fragment	AMS 14C	Castaños (1996)
El Cuco	Cantabria	X	OIS3 Late Pleistocene	OxA-27196	42,350	700	46,050–44,050	Shell, *Patella vulgata*	AMS 14C	Castaños & Castaños (2007), Rasines del Río *et al.* (2011), Gutiérrez-Zugasti *et al.* (2018)
El Cuco	Cantabria	X	OIS3 Late Pleistocene	OxA-27115	46,200	650	50,220–47,020	Shell, *P. vulgata*	AMS 14C	Castaños & Castaños (2007), Rasines del Río *et al.* (2011), Gutiérrez-Zugasti *et al.* (2018)
El Cuco	Cantabria	XIII	OIS3 Late Pleistocene	OxA-30851	46,400	800	50,760–46,960	Shell, *P. vulgata*	AMS 14C	Castaños & Castaños (2007), Rasines del Río *et al.* (2011), Gutiérrez-Zugasti *et al.* (2018)
Labeko Koba	Gipuzkoa	VII	OIS3 Late Pleistocene	OxA-21793	35,400	650	41,650–39,250	Diaphyseal fragment, indeterminate	AMS 14C	Altuna & Mariezkurrena (2000), Arrizabalaga (2000), Wood *et al.* (2014)
Labeko Koba	Gipuzkoa	VII	OIS3 Late Pleistocene	OxA-21840	35,250	650	41,550–39,110	Diaphyseal fragment, indeterminate	AMS 14C	Altuna & Mariezkurrena (2000), Arrizabalaga (2000), Wood *et al.* (2014)
Labeko Koba	Gipuzkoa	VII	OIS3 Late Pleistocene	OxA-X-2314-43	36,500	750	42,410–40,210	Diaphyseal fragment, large taxon	AMS 14C	Altuna & Mariezkurrena (2000), Arrizabalaga (2000), Wood *et al.* (2014)
Labeko Koba	Gipuzkoa	VII	OIS3 Late Pleistocene	OxA-21766	36,850	800	42,550–40,470	Tibia diaphyseal fragment, *Capra pyrenaica*	AMS 14C	Altuna & Mariezkurrena (2000), Arrizabalaga (2000), Wood *et al.* (2014)
Labeko Koba	Gipuzkoa	IX upper	OIS3 Late Pleistocene	OxA-23199	38,400	900	43,250–41,570	Antler base, *Megaloceros giganteus*	AMS 14C	Altuna & Mariezkurrena (2000), Arrizabalaga (2000), Wood *et al.* (2014)
Labeko Koba	Gipuzkoa	IX upper	OIS3 Late Pleistocene	OxA-22559	36,000	700	42,190–39,710	Tibia diaphyseal fragment, *Bos* sp.	AMS 14C	Altuna & Mariezkurrena (2000), Arrizabalaga (2000), Wood *et al.* (2014)
Labeko Koba	Gipuzkoa	IX upper	OIS3 Late Pleistocene	OxA-22653	36,850	800	42,550–40,470	Tibia diaphyseal fragment, *Bos* sp.	AMS 14C	Wood *et al.* (2014)

(*Continued*)

Table 2 Continued.

Site	Province	Level	General chronology	Lab. Code	Date BP	SD	cal BP age (INTCAL2020)	Material	Method	References
Labeko Koba	Gipuzkoa	IX upper	OIS3 Late Pleistocene	OxA-21792	36,550	750	42,420–40,260	Diaphyseal fragment, medium sized artiodactyl, possibly *C. elaphus*	AMS 14C	Wood *et al.* (2014)
Labeko Koba	Gipuzkoa	IX lower	OIS3 Late Pleistocene	OxA-21777	37,700	900	42,930–40,970	Right tibia, *Equus* sp.	AMS 14C	Wood *et al.* (2014)
Labeko Koba	Gipuzkoa	IX lower	OIS3 Late Pleistocene	OxA-22563	37,800	900	42,970–41,050	Metatarsal, *C. elaphus*	AMS 14C	Wood *et al.* (2014)
Labeko Koba	Gipuzkoa	IX lower	OIS3 Late Pleistocene	OxA-22562	38,100	900	43,120–41,280	Humerus, *C. elaphus* (juvenile)	AMS 14C	Wood *et al.* (2014)
Labeko Koba	Gipuzkoa	IX lower	OIS3 Late Pleistocene	OxA-22561	38,000	900	43,070–41,190	Distal humerus, *C. elaphus*	AMS 14C	Wood *et al.* (2014)
Labeko Koba	Gipuzkoa	IX lower	OIS3 Late Pleistocene	OxA-22560	37,400	800	42,720–40,920	Radius, *C. elaphus*	AMS 14C	Wood *et al.* (2014)
Labeko Koba	Gipuzkoa	IX lower	OIS3 Late Pleistocene	OxA-22564	37,900	900	43,030–41,110	Metatarsal, *Bos* sp.	AMS 14C	Wood *et al.* (2014)
Urtiagako Leizea	Gipuzkoa		OIS3 Late Pleistocene	Ua-37426	29,755	710	35,670–32,470	Bone fragment		Altuna & Mariezkurrena (2010)
Abauntz	Navarre	f	Late Pleistocene	GrN-21011	21,600	200	26,250–25,570	Bone, unidentified unidentified		Altuna *et al.* (2001–2002), Utrilla *et al.* (2015)
Mainea	Navarre		OIS3 Late Pleistocene	Beta-522535	42,740	600	46,210–44,370	P2 right, *Coelodonta antiquitatis*	AMS 14C	Rodríguez-Almagro *et al.* (2021)
Leguintxiki	Navarre	IIIb	Late Pleistocene	Ua-3397	14,865	140	18,430–17,830		AMS 14C	Nuin (1995–1996), Castaños (1996)
Teixoneres	Barcelona	II	Late Pleistocene	MAMS-17600	36,850	211	42,100–41,300	Metapodial, *C. elaphus* (human marks)	AMS 14C	Talamo *et al.* (2016), Álvarez-Lao *et al.* (2017)
Teixoneres	Barcelona	II	Late Pleistocene	MAMS-17607	34,940	173	40,630–39,590	Long bone, large taxon	AMS 14C	Talamo *et al.* (2016), Álvarez-Lao *et al.* (2017)
Teixoneres	Barcelona	II	Late Pleistocene	MAMS-18668	39,000	260	42,890–42,370	Long bone, small taxon (human marks)	AMS 14C	Talamo *et al.* (2016), Álvarez-Lao *et al.* (2017)
Teixoneres	Barcelona	II	Late Pleistocene	MAMS-18669	40,800	320	44,570–43,010	Humerus, *C. elaphus* (human marks)	AMS 14C	Talamo *et al.* (2016), Álvarez-Lao *et al.* (2017)
Teixoneres	Barcelona	II	Late Pleistocene	MAMS-18670	30,780	110	35,490–34,690	Radius indeterminate, medium taxon	AMS 14C	Talamo *et al.* (2016), Álvarez-Lao *et al.* (2017)
Teixoneres	Barcelona	II	Late Pleistocene	MAMS-17601	39,320	263	43,020–42,500	Long bone, medium taxon	AMS 14C	Talamo *et al.* (2016), Álvarez-Lao *et al.* (2017)
Teixoneres	Barcelona	II	Late Pleistocene	MAMS-17608	34,900	175	40,590–39,550	Long bone, medium taxon	AMS 14C	Talamo *et al.* (2016), Álvarez-Lao *et al.* (2017)
Teixoneres	Barcelona	III	Late Pleistocene	MAMS-18671	47,200	670	51,900–47,820	Tibia, *C. elaphus* (human marks)	AMS 14C	Talamo *et al.* (2016), Álvarez-Lao *et al.* (2017)
Teixoneres	Barcelona	III	Late Pleistocene	MAMS-18672	42,020	370	45,300–44,260	Long bone, medium taxon	AMS 14C	Talamo *et al.* (2016), Álvarez-Lao *et al.* (2017)
Teixoneres	Barcelona	III	Late Pleistocene	MAMS-18673	40,610	340	44,440–42,920	Femur, *C. elaphus* (human marks)	AMS 14C	Talamo *et al.* (2016), Álvarez-Lao *et al.* (2017)
Teixoneres	Barcelona	III	Late Pleistocene	MAMS-17609	42,250	359	45,490–44,370	Bone, unidentified unidentified	AMS 14C	Talamo *et al.* (2016), Álvarez-Lao *et al.* (2017)
Teixoneres	Barcelona	III	Late Pleistocene	MAMS-17603	41,270	327	44,810–43,490	Long bone, medium taxon	AMS 14C	Talamo *et al.* (2016), Álvarez-Lao *et al.* (2017)
Teixoneres	Barcelona	III	Late Pleistocene	MAMS-17604	41,560	337	44,900–43,980	Long bone, medium taxon	AMS 14C	Talamo *et al.* (2016), Álvarez-Lao *et al.* (2017)
Riera dels Canyars	Barcelona	Layer 1	H4 Late Pleistocene	Beta 273965	33,800	350	39,840–37,360	Charcoal, *Pinus sylvestris* type	AMS 14C	Daura *et al.* (2013)
Riera dels Canyars	Barcelona	Layer 1	H4 Late Pleistocene	OxA-23643	34,540	350	40,510–38,990	Charcoal, *P. sylvestris* type	AMS 14C	Daura *et al.* (2013)
Riera dels Canyars	Barcelona	Layer 1	H4 Late Pleistocene	OxA-2416-44	34,980	350	40,900–39,380	Charcoal, *P. sylvestris* type	AMS 14C	Daura *et al.* (2013)

Riera dels Canyars	Barcelona	Layer 1	H4 Late Pleistocene	OxA-23644	34,810	360	40,780–39,220	Charcoal, *P. sylvestris* type	AMS 14C	Daura *et al.* (2013)
Riera dels Canyars	Barcelona	Layer 1	H4 Late Pleistocene	OxA-24057	34,900	340	40,810–39,330	Charcoal, *P. sylvestris* type	AMS 14C	Daura *et al.* (2013)
Portalón de Tejadilla	Segovia	CAM-1	OIS3 Late Pleistocene	Beta-488205	30,780	150	35,530–34,650	Tooth (canine), *Crocuta crocuta*	AMS 14C	Sala *et al.* (2020)
La Mina	Burgos	CM.C3.3	OIS3 Late Pleistocene		52,500			Tooth, *C. antiquitatis*	RA	Diez *et al.* (2008)

Radiocarbon dates provided with their calibration using the InteCal 2020 curve (Reimer *et al.* 2020) and using CalPal software (v. 2021) (Weniger & Jöris 2004).

García 2006). Sesé & Soto (2002) suggest that the Los Rosales site could also belong to the Middle Pleistocene and Álvarez-Lao & García (2010, 2011) include the remains of Arroyo Culebro in the early Upper Pleistocene. However, neither Los Rosales nor Arroyo Culebro have yielded numerical dates, making the La Mina remains the oldest from the Iberian Upper Pleistocene at present and suggest an earlier arrival in this period.

This new date indicates that *Coelodonta* entered the Castilian Plateau earlier than traditionally thought. Its presence seems constant throughout OIS 3, with a slight increase between 42 and 39 ka (Fig. 8).

The earliest presence of cold-adapted faunas on the Iberian Peninsula is still not well defined. Evidence of *Rangifer tarandus* seems to date back to approximately 200 ka at the Mollet site (Álvarez-Lao 2007) and >150 ka at La Parte, where the oldest remains of *Coelodonta antiquitatis* on the Iberian Peninsula have also been found. *Mammuthus* appeared on the Iberian Peninsula in the Middle Pleistocene, although its greatest expansion occurred around 14 ka. Mammoths only appeared consistently in the record (13 sites between chronologies 14–38 ka) in the 38 ka period, coinciding with the presence of *Gulo gulo* (Lezetxiki, 21–25 ka), *Alopex lagopus* (Aitbitarte III, 18–20 ka), *Ovibos mochatus* (L'Arbreda, 17–18 ka), *Saiga tatarica* (Abauntz, 13.5 ka) and *Rangifer tarandus*, whose records are the most abundant of cold fauna with a more or less continuous presence from 80 to 9 ka (Santa Catalina) (Álvarez-Lao 2007; Rufi *et al.* 2018; Rodríguez-Almagro, 2021) (Table 2).

La Mina adds a new site with *Coelodonta* to the 34 presented by Álvarez-Lao (2014) and Rodríguez-Almagro *et al.* (2021) and a new dating to the 14 previously dated sites (53 dates). This discovery raises two new aspects, not only regarding the distribution of this genus but also the possible access routes to the Castilian Plateau during the Palaeolithic. Álvarez-Lao & García (2011) discuss three detected entries for this species to the Iberian Peninsula, one in the Middle Pleistocene and two in the Upper Pleistocene (three including Arroyo Culebro). The first of the Upper Pleistocene took place between 41 and 36 ka at sites such as Labeko Koba and Covacho Arenillas; and the second between 32 and 20 ka with deposits such as Leguintxiki, Abauntz, Cueva del Cuco, Lezetxiki and Jou Puerta (Álvarez-Lao & García 2010; Álvarez-Lao 2014). The new record and dates push back the arrival of this taxon to the Iberian Peninsula by at least 10 ka. The possible absence of material between 53 and 100 ka could be due to either an absence of this species on the Iberian Peninsula or the fact that the period is outside the carbon-14 limit, which restricts dating in some cases.

The discovery of frozen individuals in the Siberian permafrost has provided further insight into their anatomy, suggesting poor adaptation to extremely snowy environments due to their short legs and lack of hooves or pads (Kingdon 2008). The remains recovered in their soft tissues show high contents of Asteraceae and other shrubby plants (Boeskorov *et al.* 2011). These data were confirmed by Tiunov & Kirillova's (2010) studies of carbon (13C/12C) and nitrogen (15N and 14N) isotopes in Siberian specimens. The analysis of these isotopes has also reflected possible changes in the seasonal composition of the diet. A closer isotopic study was carried out by Rodríguez-Almagro *et al.* (2021) on the remains recovered at Mainea (OIS 3). The woolly rhinoceros' representatives from this site lived in environments dominated by the mammoth steppe. No other species associated with cold climates have been located at La Mina, in contrast to other Cantabria deposits at low altitudes. Analyses of pollen remains from sites where woolly rhinoceros remains have been recovered on the Iberian Peninsula, with the caution of chronological difference, reveal a great variety of landscapes, large forests and open environments (Iriarte 2000; Álvarez-Lao *et al.* 2015; Rivals &

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Álvarez-Lao 2018; Rodríguez-Almagro *et al.*, 2021). It would therefore be interesting in the future to design studies to better understand the ecological capabilities of *Coelodonta* from the more forested ecosystems near the coast from those at higher altitudes and with more steppe-like potential ecosystems (Rodríguez-Almagro *et al.*, 2021). Two nearby sites in the same region, La Ermita and Cueva Millán, which are also located in the same OIS 3 (59–27 ka), contained ecosystems dominated by temperate forest landscapes with deciduous forests with small patches of conifers and open spaces with herbaceous plants (Moure & García Soto 1983). In Millán, pine, oak and birch have been identified, as well as different aquatic species and eight herbaceous taxa (Moure & García Soto 1983). The presence of *Eliomys quercinus*, *Microtus duodecimcostatus*, *Microtus agrestris* and *Microtus nivalis* in Millán and La Ermita confirm the presence of these open or semi-open environments (Moure & García Soto 1983; López García 2007). The faunal records and taphonomic evidence recorded in these two deposits suggest an occupation in temperate phases (Diez *et al*. 2008).

Currently, 32 of the 34 sites with woolly rhinoceros remains of the Iberian Peninsula have been located in the north: 23 in the Cantabrian region; six in Catalonia; and three on the Castilian Plateau. The other two are in the centre, in Madrid. According to Delpech (1983), populations of woolly rhinoceros entered the Iberian Peninsula by crossing the Pyrenees at the western and eastern extremities, and occupied the Cantabrian and Catalan regions, respectively. These access routes have also been taken into account by Arrizabalaga & Ríos-Garaizar (2012), who added that after crossing these areas, fauna roamed freely and occupied other territories, but always followed the same geographical axes. These authors propose several mountains passes between the Cantabrian coast, the plains of Alava and the Ebro valley, which were later connected to the Castilian Plateau. These passes were widely used by human groups and were also probably favourable for fauna passage, as many of these groups followed herds and established their settlements in passing places. We can therefore infer two possible access routes to the Castilian Plateau from both extremes of the Pyrenees: from the west, through the upper Ebro valley; and from the east, through the Egea and Arga valleys.

These two possibilities could explain the presence of woolly rhinoceros on the Castilian Plateau and also the remains found in the centre of the Peninsula. An additional possibility may have been through the Cantabrian mountains range via passes such as Palombera, San Glorio, Piedrasluengas, El Escudo, Estacas de Trueba, La Lunada or La Sía. All of these passes are close to the Prado Vargas and Peña de Mudá deposits. Díez Fernández-Lomana & Navazo (2005, Fig. 7) suggest several passes through this mountain range, which were maintained during the Upper Palaeolithic (La Palomera, Ojo Guareña,

Figure 9. Possible access routes from the Pyrenees to the Iberian Peninsula, and proposed access routes to the Castilian Plateau. (a) Cantabrian coast. (b) Access to the Ebro Valley. (c) Mediterranean coast. Red numbers indicate possible access passes from the Cantabrian region to the Castilian Plateau: (1) La Sía, (2) Lunada, (3) Estacas de Trueba, (4) Escudo, (5) Palombera, (6) Piedrasluengas and (7) San Glorio. Green numbers indicate Upper Palaeolithic sites closed to La Mina and sites with *Coelodonta antiquitatis* in the Castilian Plateau. (1) La Mina. (2) La Palomera. (3) Ojo Guareña. (4) Penches. (5) Peña de Mudá. (6) Portalón del Tejadilla.

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Penches, La Blanca, etc.) and in historical times. This could explain the presence of remains at the Peña de Mudá and Portalón del Tejadilla sites, opening up further possibilities for the population of the Castilian Plateau as also suggested by Rodríguez-Almagro *et al*. (2021) (Fig. 9).

4. Conclusions

In this paper we present a new deposit containing cold-adapted fauna in the Spanish Castilian Plateau. New evidence describes, illustrates and characterises both taxonomically and metrically the new records of *C. antiquitatis.* On the Iberian Peninsula, the woolly rhinoceros has been found in 34 deposits, most of them located in the Cantabrian region. The rest of the deposits are located in the Levant and central Iberia, with two deposits to date on the Castilian Plateau.

Dating obtained from one of the rhinoceros' teeth from the site permits the addition of another access point to the two previously recorded for this species during the Upper Pleistocene. This date pushes back the arrival of *Coelodonta* to Iberia during this period by 10 ka, placing it in a region in which remains from Mudá and Portalón del Tejadilla were its only representatives. This location on the Castilian Plateau, together with the dating obtained, may help us to understand the possible access routes of cold-adapted fauna to this area. Further analysis will be necessary to fully comprehend these arrivals and to complete the map of cold-adapted fauna in a region where deposits from this period, corresponding to OIS 3, are not very abundant.

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7. Competing interests

None.

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