



General palaeontology, systematics and evolution (Vertebrate palaeontology)

First occurrence of the extinct deer *Haploiodoceros* in the Iberian Peninsula in the Upper Pleistocene of the Cova del Rinoceront (Castelldefels, Barcelona)



Première découverte du cerf fossile Haploiodoceros en péninsule Ibérique dans la séquence Pléistocène supérieur de la grotte des Rhinocéros (Castelldefels, Barcelona)

Montserrat Sanz ^{a,*}, Joan Daura ^a, Jean-Philip Brugal ^b

^a Grup de Recerca del Quaternari (GRQ) del Seminari Estudis i Recerques Prehistòriques (SERP), Departament Prehistòria, H. Antiga i Arqueologia, Facultat de Geografia i Història, Universitat de Barcelona, C/Montalegre, 6-8, 08001 Barcelona, Spain

^b Aix-Marseille université, CNRS, UMR 7269, Maison méditerranéenne des sciences de l'homme, BP 647, 5, rue du Château-de-l'Horloge, 13094 Aix-en-Provence, France

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ABSTRACT

The Cova del Rinoceront is the first site in the Iberian Peninsula where the genus *Haploiodoceros* has been documented. This discovery of abundant remains is also its first recorded occurrence in Europe during the Upper Pleistocene. The new fossil record strengthens claims that this genus was widely distributed during the Pleistocene, occupying a longer time span at least until MIS 5. Cranial and post-cranial skeletal remains ascribed to this species were recovered from the uppermost layers of the Cova del Rinoceront. The diagnostic features that allow these remains to be unequivocally assigned to *H. mediterraneus*, include their cranial morphology and antler shape, comprising two sickle-shaped beams, curving backwards and laterally, and a long frontal basal tine. This paper highlights the problems of deer systematics and identification given the high degree of fragmentation of the genus, their relatively homogeneous morphology, a virtual absence of reliable characters and the overlap of measurements between species.

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RÉSUMÉ

La grotte du Rhinocéros est le premier site ibérique livrant des restes abondants du genre *Haploiodoceros*. Il s'agit également de la première mention de ce genre dans le Pléistocène supérieur européen. Cette nouvelle découverte démontre que ce genre était largement distribué au Pléistocène, avec une survie jusqu'au MIS 5. Plusieurs crânes et éléments post-crâniens proviennent des niveaux supérieurs de la séquence de la grotte des Rhinocéros, et l'attribution est bien confirmée par la morphologie crânienne et des bois en fourche simple, dirigés vers l'arrière et sur le côté, et un andouiller frontal très long. De plus, des questions sur la systématique des cervidés et le problème de leur identification

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* Corresponding author.

E-mail addresses: grq@ub.edu, sanzborras@hotmail.com (M. Sanz), jdaura_lujan@ub.edu (J. Daura), brugal@mms.h.univ-aix.fr (J.-P. Brugal).

sont soulevées, en rapport avec le fort degré de fragmentation dans la documentation fossile, la morphologie relativement homogène de cette famille ou l'absence de caractères diagnostiques bien définis, ainsi que le chevauchement des mesures entre différents genres et espèces.

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1. Introduction

Remains of medium-sized deer from two Late Middle Pleistocene sites in the South of France have been attributed to a new genus with a single species, *Haploiodoceros mediterraneus* (Croitor et al., 2008). The two sites are, respectively, Lunel-Viel (Hérault), where the taxon was initially identified as *Euctenoceros mediterraneus* (Bonifay, 1967), and Igue-des-Rameaux (Tarn-et-Garonne), situated 190 km to the west, where the species was identified for a second time (Brugal in Rouzaud et al., 1990). The key element permitting the diagnosis of the genus is the shape of the deer's antlers, which present a simple, primitive morphology comprising two branches: a sickle-shaped antler beam that curves backwards and laterally, and a long frontal tine, indicative of a degree of specialization that differs from that of all other known genera of deer. Indeed, the antlers of *H. mediterraneus* are proportionally larger than those of other similar-sized deer. Other features that allow this deer to be distinguished from *Cervus elaphus* include its dental and post-cranial bones (Croitor et al., 2008; Noury, 1997). Additionally, the proportions of its fore- and hind limbs are indicative of the locomotion of a saltatorial runner, similar in this respect to *Dama clactoniana* (Croitor et al., 2008).

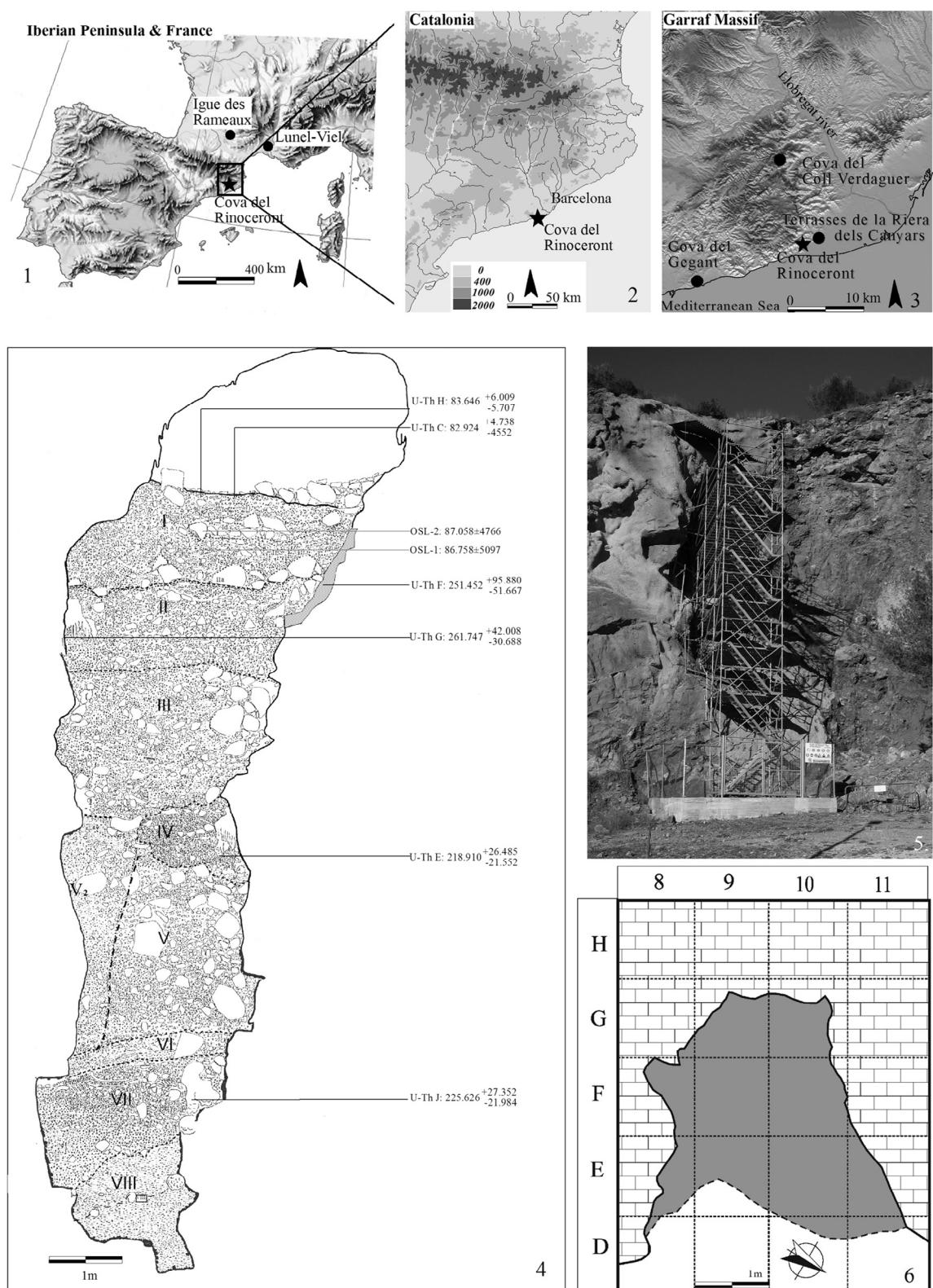
According to Croitor et al. (2008) and following the chronology proposed by Bonifay (1981), the medium-sized deer found at these two sites in France date from the Middle Pleistocene (estimated at ~300–350 ka BP by biochronology). Both sites yielded species, such as *Hyaena prisca* and the small wolf *C. lupus lunellensis* (Brugal and Boudadi-Maligne, 2011). Although *Haploiodoceros* remains have hitherto been unidentified in the Iberian Peninsula, an earlier origin in the Lower Pleistocene has been proposed. The deer materials recovered from various Iberian sites, including Venta Micena-2 and Atapuerca (TD6), could be good candidates for ancestors; however, the remains are poor and often too fragmented to confirm their taxonomic status and verify this hypothesis (Croitor et al., 2008). It should be noted that the first paleontological studies undertaken by Bonifay (1967) suggested a Villafranchian origin for the remains, providing a preliminary identification as *Euctenoceros* (=*Eucladoceros*) *mediterraneus*. However, as it is apparent in the taxonomic names used by this author, there was some uncertainty regarding the genus name. The presence of distinct, infrequent remains of the cervid genus *Haploiodoceros* in the South of France in the Middle Pleistocene, as well as the absence of any evidence of this deer in other geographical areas, suggest its endemic distribution.

Cervids remains are relatively common taxa in Pleistocene archaeological and paleontological sites; yet, because they are usually fragmentary, and because their

morphology is relatively homogeneous with few diagnostic characters at lower taxonomic levels, deer systematics remains somewhat imprecise, especially for the small- to medium-sized deer record (Lister, 1990). The taxonomy is based largely on antler morphology, which generally provides the most reliable characters for identifying genera and species, while correlations with post-cranial elements are often uncertain.

In the Iberian Peninsula, where *H. mediterraneus* has hitherto remained unrecorded, the presence of various small- to medium-sized deer during the Upper Pleistocene has been recorded at several sites, although in many cases, taxonomic attribution is controversial. At Las Majolicas (southern Iberian Peninsula), a small *Cervus elaphus* has been identified, its size being attributed to the climatic differences faced by northern and southern populations, while the size of the smallest specimens in this set has been attributed to sexual dimorphism (Domingo and Alberdi, 2004). In the centre of the Iberian Peninsula, various medium-sized deer have been documented in Cueva del Camino (Pinilla del Valle). The most frequent is the fallow deer, *Dama dama* cf. *geiselana* (Álvarez-Lao et al., 2013; Arsuaga et al., 2012; Van der Made, 2001), although previous studies classified the species as *D. clactoniana* (Buitrago-Villaplana, 1992), with well-documented post-cranial and cranial remains (e.g., antlers), followed by the red deer, *Cervus elaphus*, and a few remains of the roe deer, *Capreolus capreolus*. In other areas of the Iberian Peninsula, such as the central Mediterranean coast, *Dama dama* and *Cervus elaphus* have been identified, for example, at Bolomor, dated from MIS 5 (Martínez del Valle, 2001). However, in Cova Negra, Martínez del Valle (1996) discussed the difficulties of assigning fallow deer to a species level, revising the paleontological identification to *Dama* sp. and proposing an intermediate form between the Middle Pleistocene and the modern fallow deer for this site. A similar discussion followed at the Middle Pleistocene site of Solana del Zamborino (Martín-Penela, 1987). In Portugal, fallow deer remains are scarce and fragmentary (Cardoso, 1993). The situation is similar at various Middle and Late Pleistocene sites in southern Europe, where potential confusion has been noted between different genera, including *Cervus*, *Dama* (Brugal and Yravedra, 2005–2006) and, now presumably, also *Haploiodoceros*.

The discovery of a large sample of *Haploiodoceros mediterraneus* and the completeness of these skeletal remains (cranial and post-cranial) from the Upper Pleistocene layers of the Cova del Rinoceront (Northeast of the Iberian Peninsula) provide new information about the morphology and systematics of this species and enable us to propose, extending its geographical and chronological distribution. The occurrence highlights the persistence of this small- to medium-sized deer until the beginning of the



Upper Pleistocene and raises concerns about valid deer identification.

2. Cova del Rinoceront

The Cova del Rinoceront ($41^{\circ}16'24.92''N$, $1^{\circ}57'39.18''E$) lies in the Garraf Massif, in the municipality of Castelldefels, 20 km southwest of Barcelona (Fig. 1). The massif forms part of the *Serralades Costaneres Catalanes* (Catalan Coastal Range), a low-relief mountain chain (<600 m high), composed of Jurassic and Cretaceous limestone and dolomite (Esteban and Julià, 1973) overlying Triassic deposits. The massif represents one of the most important karstic systems in NE Iberia, occupying an area of $\sim 500 \text{ km}^2$ (Salas, 1987; Solé, 1964).

The Garraf Massif contains several Middle and Upper Pleistocene sites, including the Cova del Gegant (Daura et al., 2010a) and the Cova del Coll Verdaguer dated to MIS 3 (Daura et al., 2010b) and the Terrasses de la Riera dels Canyars attributed to Heinrich Stadial 4 (Daura et al., 2013) (Fig. 1).

The site is located in an abandoned quarry known as *ca n'Aymerich*. The entrance and the original morphology of the cave were completely destroyed by mining during the 1960s. The Cova del Rinoceront was discovered in 2002 (Daura et al., 2005; Daura et al., 2010c) by two of the authors (MS and JD), and has been excavated since 2003. Prior to its excavation, rehabilitation work was undertaken at the site to guarantee the preservation of the deposit and the safety of fieldwork conditions (Sanz et al., 2011).

The site lies at an altitude of 25 m amsl and is located just 1 km inland from the extant coastline. The cave has formed in a fracture zone known as la Ginesta fault, with a NE-SW orientation observable over a 2-km distance. The ten excavation and rehabilitation campaigns conducted at the site between 2002 and 2012, have established that the stratigraphic sequence has a thickness of 11 m and a width of between 1.5 and 3 m. The sequence is contained within three main units, comprising eight layers recognized from top to bottom (Fig. 1). The Cova del Rinoceront assemblage comprises mainly natural faunal remains, although a few stone tools have also been recovered.

The uppermost unit (Unit 1) is formed primarily by layers I to III, three alternating phases of detrital accumulation that define each layer (I, II, III), respectively. The deposits are composed of sub-rounded gravels and boulders, sands and clays (Daura, 2008). Layers I and II were completely excavated between 2003 and 2010 so that today fieldwork is focused on layer III. The concentration of the bone assemblage in level I and II is high and several of the skeletal elements are articulated (i.e. humerus-ulna-radius). Significantly, the species that have been identified are represented by both cranial elements and parts of the correlative post-cranial skeleton; ribs and vertebrae are less

common and isolated teeth are infrequent, except incisors. Although taphonomic studies are in progress, carnivore activity is the main agent of bone modification, while the association between the stone artefacts and animal bones is doubtful.

To date, *Haploiodoceros mediterraneus* remains have been documented in layers I and II, where they constitute the bulk of the ungulates identified in the first level and represent the predominant species in terms of the number of individuals (MNI = 12); *Capra* sp. remains are the second most abundant of the ungulates in level I (MNI = 5), followed by those of a red deer (*Cervus elaphus*, MNI = 1) and a large young bovid (*Bos/Bison*, MNI = 1). In this layer, carnivores are only represented by several lynx (*Lynx pardinus*, MNI = 4) and a bear (*Ursus arctos*, MNI = 1) represented by a deciduous tooth. The faunal remains recovered from layer II are still in the process of restoration and counts are not yet available, but a wolf (*Canis* sp.) and several lynx have been identified. Finally, tortoises (*Testudo hermanni*) are present in both levels (NISP ≥ 71).

U-Th dating results, based on the average date of two samples taken from the flowstone capping the top layer (layer I), show that the minimum age of the Cova del Rinoceront is $83.8 \pm 5.9 \text{ ka BP}$. OSL dating of sediment from the upper layers was processed using the additive dose method and while it cannot be considered to provide a true age assessment, the resulting ages are consistent with the overall sequence and with the U-Th dates for the capping speleothem and so, support this minimum age, giving layer I a chronology of around $87.1 \pm 4.8 \text{ ka BP}$. In addition, four U-Th dates were obtained from the rockwall speleothem, giving a chronological range between 218 and 261 ka BP. The average age estimated is 234 ka BP and this can be used as the maximum age. These results show that the Cova del Rinoceront sequence spans > 200 to 85 ka BP, covering isotopic stages 7 to 5.

3. Methodology

The *Haploiodoceros* remains described here were recovered from layers I and II of the Cova del Rinoceront during the fieldwork undertaken by GRQ-SERP (University of Barcelona) between 2003 and 2010. Most of the materials discussed herein are from level I where 87% of the large mammals have been restored. The materials from level II are still undergoing restoration because the specimens are covered by a breccia matrix. Restoration is being carried out in the GRQ-SERP archaeological laboratory (la Guixera) maintained by the Castelldefels Town Council. A *Haploiodoceros* skull, shown in Fig. 2, was prepared for exhibition at the main conservation centre in Valldoreix (Catalonia), the Centre de Restauració de Béns Mobles de Catalunya (CRBMC-Generalitat de Catalunya).

Fig. 1. 1. Location of the sites where *Haploiodoceros* remains were identified. 2. Cova del Rinoceront in the northeast of Iberian Peninsula. 3. Regional location of Cova del Rinoceront, Terrasses de la Riera dels Canyars, Cova del Coll Verdaguer and Cova del Gegant. 4: Stratigraphic profile of the site with dates. U-Th (U-Series dating speleothems). OSL (Optical Stimulated Luminescence). 5. Cova del Rinoceront site. 6. Site plan showing the surface of layers I and II.
Fig. 1. 1. Sites avec présence d'*Haploiodoceros*. 2. Grotte du Rhinocéros dans le Nord-Est de la péninsule Ibérique. 3. Situation de la grotte du Rhinocéros, Terrasses de la Riera dels Canyars, et grottes de Coll Verdaguer et Gegant. 4. Profil stratigraphique avec datations (U-Th = uranium-thorium sur spéléothèmes, OSL). 5. Site de la grotte du Rhinocéros. 6. Plan montrant la surface des niveaux I et II.

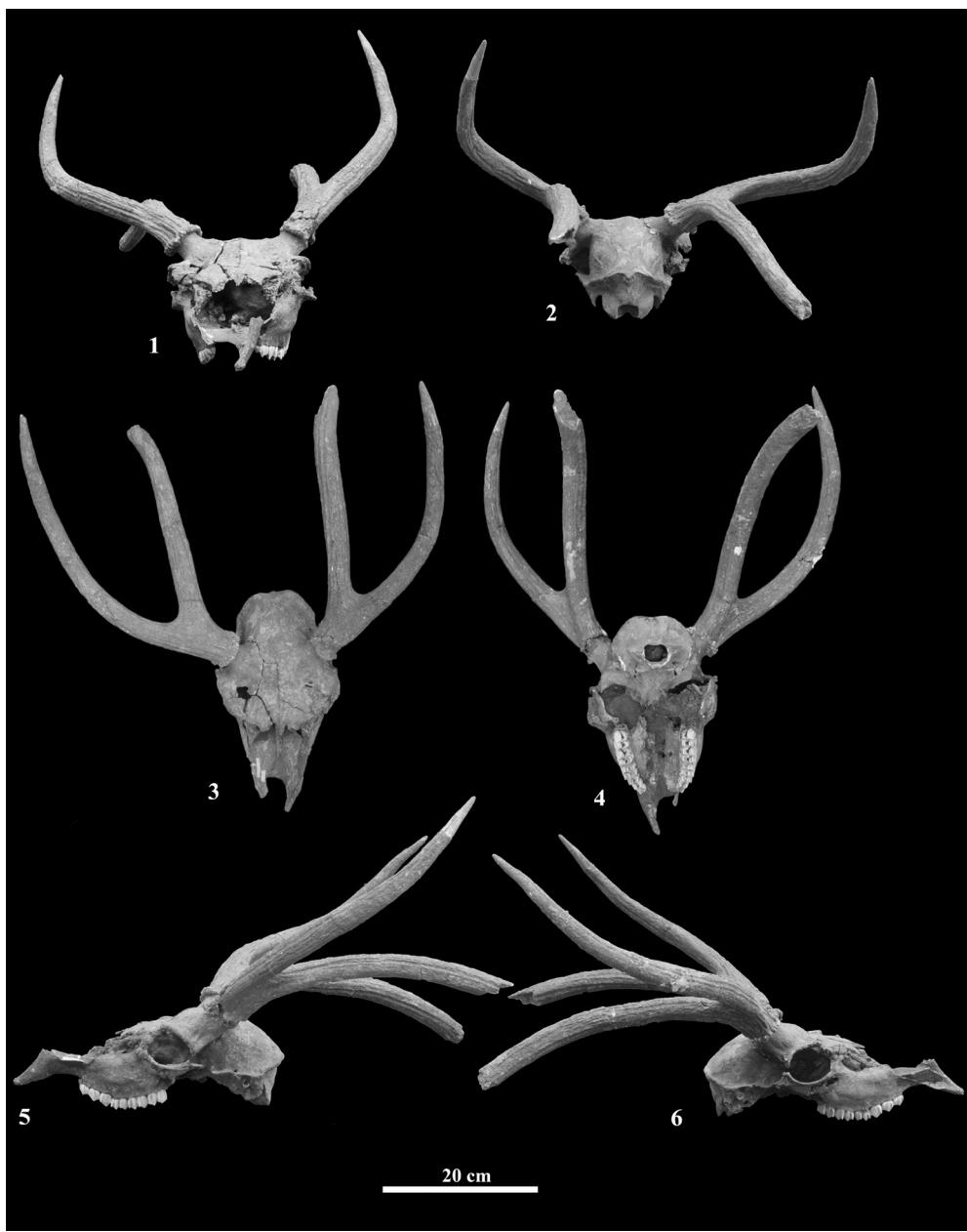


Fig. 2. *Haploiodoceros mediterraneus* complete skull from Cova del Rinoceront (CR-I-2022). 1. Anterior view. 2. Posterior view. 3. Dorsal view. 4. Inferior view. 5. Right lateral view. 6. Left lateral view.

Fig. 2. Crâne complet d'*Haploiodoceros* de la grotte du Rhinocéros (CR-I-2022). 1. Vue antérieure. 2. Vue postérieure. 3. Vue dorsale. 4. Vue inférieure. 5. Vue latérale droite. 6. Vue latérale gauche.

The fieldwork at the Cova del Rinoceront was carried out using standard archaeological methods with three-dimensional plotting of finds and features (position, slope, etc.). Large mammal bones were mapped *in situ* prior to removal. Sediments were dry-sieved using superimposed 5- and 1-mm mesh screens. The surface excavated is ~6 m² with a thickness that ranges between 1 and 1.5 m for each layer.

Deer bones were first identified taxonomically. The distinction between *Dama* and *Cervus* was verified with the

help of the literature (Di Stefano, 1995; Di Stefano and Petronio, 1997; Lister, 1996) and the Paleontological Collections of the Natural History Museum of Barcelona (MGB), the Institut Català de Paleontologia Miquel Crusafont (ICP) and the Arxiu Històric de Sitges (AHSI), and the Chordate Collection (MCNB-Cord) at the Natural History Museum of Barcelona. The features of the *Haploiodoceros* remains were examined with reference to Bonifay (1967), Noury (1997) and Croitor et al. (2008), particular attention being given to antler shape, skull and dentition morphology and

post-cranial characters. In addition, a direct comparison was undertaken with Igue-des-Rameaux specimens housed in the Maison méditerranéenne des sciences de l'homme (UMR 7269, Aix-en-Provence, France).

Various biometric data were used to compare the *Haploiodoceros* remains from the Cova del Rinoceront with other fossil remains and modern deer, including *Dama dama geisalana* (Pfeiffer, 1998), *D. dama clactoniana* (Leonardi and Petronio, 1976), *Cervus elaphus* (Altuna and Marriezkurrena, 2000), modern *Dama dama* (Leonardi and Petronio, 1976) and *Haploiodoceros mediterraneus* (Croitor et al., 2008).

Finally, in this study, we examine the deer remains from neighbouring sites in the Garraf Massif, including the Cova del Gegant, the Cova del Coll Verdaguer and the Terrasses de la Riera dels Canyars so as to establish the presence/absence of *Haploiodoceros* in younger deposits in the same area. The fieldwork at these sites is largely being undertaken by GRQ-SERP (University of Barcelona); however, the collections from earlier work were also reviewed (MGB, AHSI, ICP).

4. Systematic palaeontology

Family CERVIDAE Goldfuss, 1820
 Subfamily CERVINAE Goldfuss, 1820
 Genus *Haploiodoceros* Croitor et al., 2008
Haploiodoceros mediterraneus Bonifay, 1967

4.1. Referred specimens

Skulls (references CR-I-2022, 3998, 3999, 4021; CR-II-6189), hemimandibles (references CR-I-3292, 945, 1380, 2089, 1364, 944, 3317, 2470, 4614), humeri (CR-I-3244), radii (references CR-I-1490, 636, 2075, 4554, 3246, 3075), femur (CR-I-3207), tibiae (references CR-I-3204, 3320, 3255, 2067), metacarpi (references CR-I-4635, 3178, 2147, 3248, 4555, 2119, 2521, 2065, 923) and metatarsi (CR-I-3073, 1321, 4562, 2082, 1488, 4291).

4.2. Description

Several cranial specimens ($NISP \geq 8$) were recovered from layers I and II of the Cova del Rinoceront. The most significant aspect of the finds is the optimum conservation of the mandibles, maxillae and skulls, especially that of the neurocranium with unshed antlers. According to Croitor et al. (2008), the key characters permitting the diagnosis of the genus *Haploiodoceros* are its skull and antler shape. The morphology of antlers, even if deciduous, constitutes a key feature in Cervid taxonomy.

Antlers: The main characteristic of all the antlers recovered from the Cova del Rinoceront is their typical two-tined morphology (Figs. 2 and 3), expressed in all ontogenetic stages in the large sample. The almost complete antlers are characterised by the circular cross-section of the antler beam, the long, cylindrical basal tine and the sickle-shaped

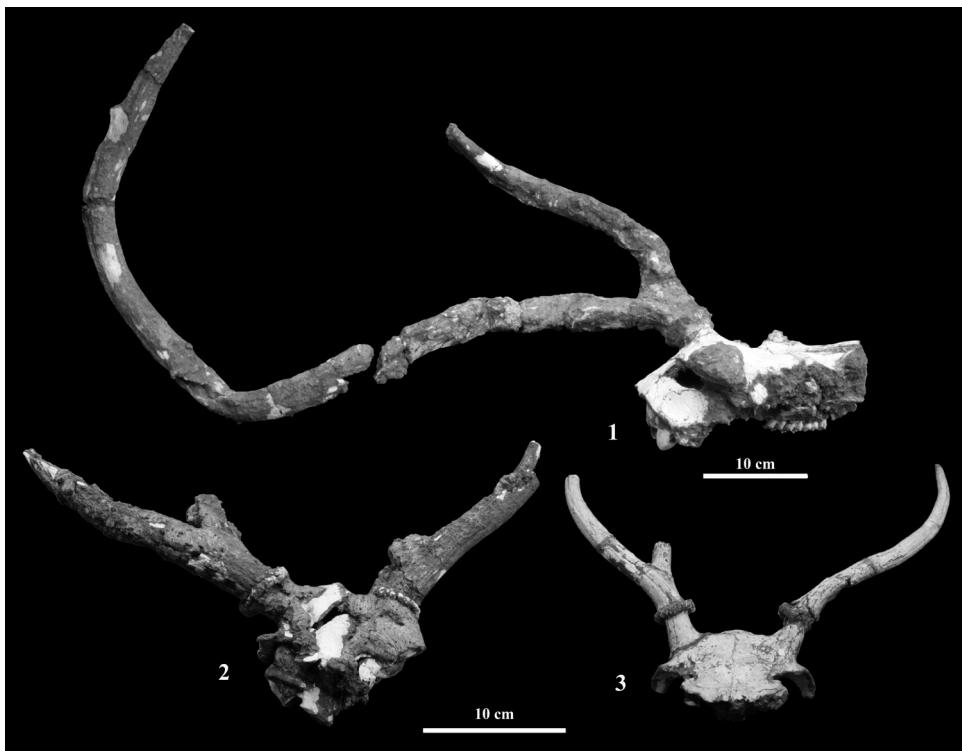


Fig. 3. *Haploiodoceros mediterraneus* remains from Cova del Rinoceront. 1. Lateral view of a complete skull with the left antler (CR-II-6189). 2,3. Frontal view of two individual skulls (CR-I-3999 and CR-I-4021).

Fig. 3. *Haploiodoceros mediterraneus* de la grotte du Rhinocéros. 1. Vue latérale d'un crâne complet avec le bois gauche (CR-II-6189). 2 et 3. Vue frontale de deux crânes (CR-I-3999 et CR-I-4021).

Table 1

Measurements (in mm) of antlers of *Haploiodoceros mediterraneus* from Cova del Rinoceront.

Tableau 1

Mesures (en mm) des bois de *Haploiodoceros mediterraneus* de la grotte du Rhinocéros. DLM : Diamètre latéral-médial ; DAP : Diamètre antéro-postérieur ; H : hauteur.

	CR-I-2022	CR-I-4021	CR-I-3999	CR-I-2022	CR-I-3998
DLM pedicle	29.4	20.8		22.6	
DAP pedicle	30.3	22.4		26.1	
DLM burr	45.6	35.9	48.1		55.6
DAP burr	44.2	38.5	49.3		58.1
DLM above burr	34.7	23.7		16.9	37.1
DAP above burr	39.1	28.8	36.5		
H ramification	85.3	66.6	76.3	52.5	78.6

DLM: latero-medial diameter; DAP: antero-posterior diameter; H: height.

beam. The angle between the basal tine and the beam above the ramification is around 55–70°, similar to that described in the specimen from Lunel-Viel (60–80°). The ramification height is greater than the diameter of the antler base (**Table 1**) and this lower placement of the bifurcation is closely related to the straighter angle. The antler surfaces are ornamented with ribs and longitudinal furrows. No shed antlers were recovered from either layer.

Skull: The length of the skull (CR-I-2022) is around 300 mm, comprising a long braincase and a broad frontal bone (ca. 117 mm in the Cova del Rinoceront specimens) with respect to the shorter breadth of the braincase (ca. 80 mm). This feature is related to the sideward and backward orientation of the pedicles, the latter being relatively short and robust, which is a distinctive character of this deer as described by Croitor et al. (2008).

Upper dentition: The upper premolar dentition is characterised by a fairly well developed lingual split that separates the hypocon and the protocon. This is clear in p2, less pronounced in p3 while p4 remains unsplit. For the upper molars, the angle between the lingual side of the protocon and that of the metaconid is around 35–37°. In general, the columns of lingual cones and styles are less pronounced than those in red deer.

Lower dentition: In the lower dentition, the p2 present a rounded shape in lingual profile, the p3 have a pronounced paraconid, metaconid and entoconid and the p4 present advanced molarization. The central lingual columns of the molars are short. The m1 and m2 usually show an anterior lingual fold. The m3 present a clear step between the entoconid and the hypoconid. The shape of the mandible is more similar to that of fallow deer than that of red deer, based on

the features described by Di Stefano (1995), i.e. *Haploiodoceros* mandibles are characterised by a shorter diastema than that found in red deer, a right mandibular angle and a rectilinear ramus with a curving outward aspect below the dentition (**Table 2** and **Fig. 4**).

Post-cranial skeleton: As for the post-cranial bones, the morphology of the metapodials differs in their proximal facet. The metacarpi ascribed to *Haploiodoceros* present a more marked indentation of the insertion than do those of the *Cervus elaphus*. The metatarsi present a crest between the anterior facet of the naviculo-cuboid and the grand cuneiform, and the posterior naviculo-cuboid facet is more backward sloping (**Fig. 5**). As pointed by Croitor et al. (2008) for Lunel-Viel specimens, the metacarpal bones from Cova del Rinoceront have a similar length range than the radius.

4.3. Biometry

Haploiodoceros mediterraneus from the Cova del Rinoceront constitutes a biometrically homogeneous group, differing greatly from the red deer found both at nearby sites (the Cova del Gegant and the Terrasses de la Riera dels Canyars) and in northern Iberia (Altuna and Mariezkurrena, 2000), as well as from modern Italian fallow deer (Leonardi and Petronio, 1976) and from modern *Axis axis* from outside the overlapping area (**Table 3**, **Figs. 6–8**).

Based strictly on biometric measurements, similarities are noted with other Pleistocene fallow deer, i.e. *D. clactoniana* and *D. dama geisalana*. As shown in **Fig. 6**, the *H. mediterraneus* metacarpus measurements overlap with those of *D. clactoniana*, as well as with the mean values for

Table 2

Measurements (in mm) of lower tooth series of *Haploiodoceros mediterraneus* from Cova del Rinoceront, measured at the tooth crown base.

Tableau 2

Mesures (en mm) des séries dentaires inférieures de *Haploiodoceros mediterraneus* de la grotte du Rhinocéros, prises à la base des couronnes. L : longueur.

Reference	L p2–m3	L p2–p4	L m1–m3	L p2–p4/L m1–m3 × 100
CR-I-3292	105.3	38.6	63.3	61.0
CR-I-945	101.9	40.6	64.6	62.8
CR-I-1380	104.3	39.3	65.1	60.4
CR-I-2089	103.7	40.6	63.2	64.2
CR-I-1364	104.4	39.5	65.5	60.3
CR-I-944	102.0	39.9	63.0	63.3
CR-I-3317	101.7	37.5	63.8	58.8
CR-I-2470	107.9	53.2	65.2	81.6

L: length.

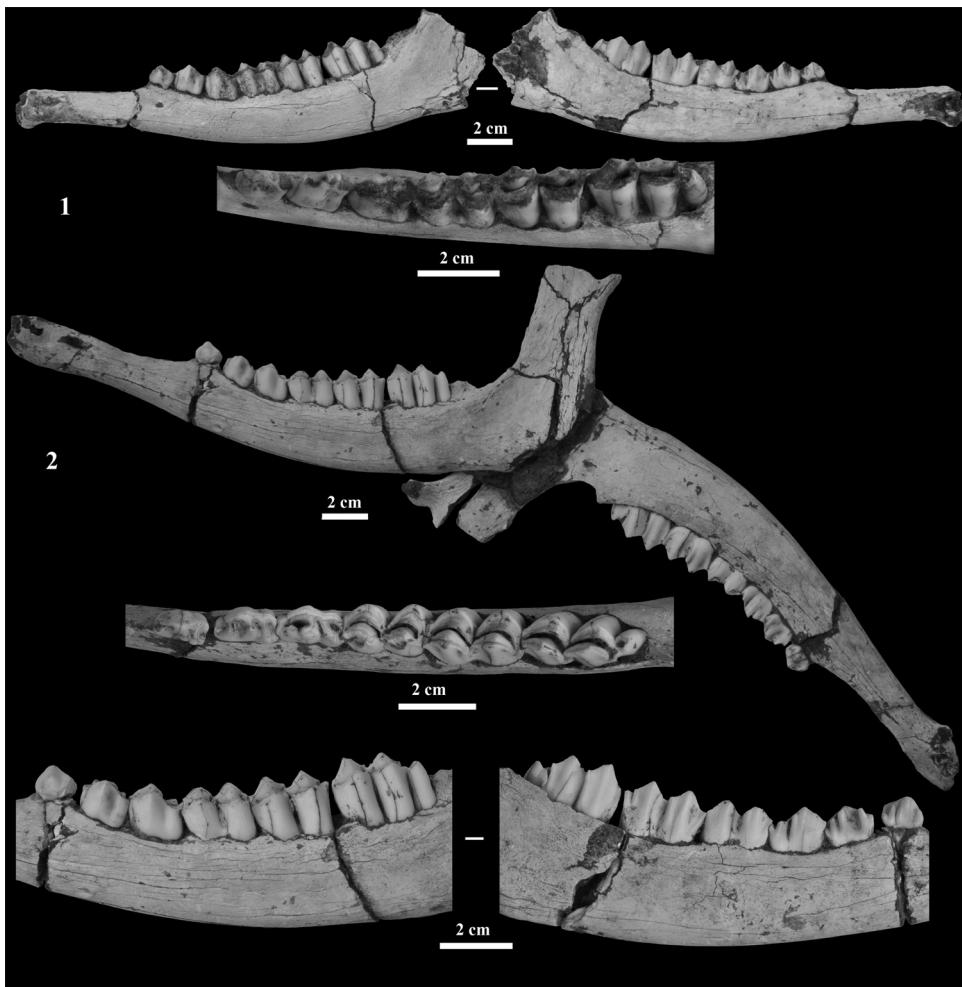


Fig. 4. *Haplodoceros mediterraneus* from Cova del Rinoceront. 1. Left hemimandible, labial, lingual and occlusal views (CR-I-4614). 2. Left and right hemimandibles, labial and lingual, occlusal, and labial and lingual views (CR-I-2470).

Fig. 4. *Haplodoceros mediterraneus* de la grotte du Rhinocéros. 1. Hémimandibule gauche, vues vestibulaire, linguale et occlusale (CR-I-4614). 2. Hémimandibules gauche et droite, vues vestibulaire, linguale et occlusale et vues vestibulaire et linguale (CR-I-2470).

female and the smallest male *D. dama geisleriana*. However, as far as the data related to the metatarsi are concerned, the Cova del Rinoceront specimens present more slender and longer bones than those of the other Pleistocene fallow deer, so any overlap is restricted solely to the *D. dama geisleriana* females and the *D. clactoniana* species. On the basis of these biometric measurements, the data for the Pleistocene fallow deer lie mainly between those reported for the *H. mediterraneus* specimens from the Cova del Rinoceront and Lunel-Viel. Moreover, as regards the data for the radii, there is some slight overlap between the females of *D. dama geisleriana* and the smaller specimens of *D. dama clactoniana* and the larger, recent specimens of *Dama dama* (Fig. 8).

Finally, a comparison with the same genus from Lunel-Viel shows the Cova del Rinoceront specimens to have more slender and slightly longer metatarsi. Moreover, the transverse diameters of the proximal and distal epiphyses of their metapodials are significantly narrower (Figs. 6 and 7). The Cova del Rinoceront specimens also have slightly

longer radii but they present similar distal measurements (Fig. 8).

Although not the specific focus of this paper, it is noticeable that data for the red deer from the Cova del Rinoceront are quite distinct from those of the other deer specimens, presenting significantly smaller distal transverse diameters than the range presented by other *Cervus elaphus* populations. The species is, however, represented by the cranial and post-cranial bones of just one female in layer I of the Cova del Rinoceront.

4.4. Deer remains in nearby sites

A review of deer remains from the neighbouring sites of the Garraf Massif area (the Cova del Gegant, the Cova del Coll Verdaguer and the Terrasses de la Riera dels Canyars) rules out the presence of *Haplodoceros mediterraneus*. Only red deer are present at each of these sites, together with *Capreolus capreolus* at the Cova del Coll Verdaguer.



Fig. 5. *Haploiodoceros mediterraneus* limb bones from Cova del Rinoceront. 1. Humerus (CR-I-3244). 2. Radius (CR-I-2075). 3. Femur (CR-I-3207). 4. Tibia (CR-I-3320). 5. Metacarpus (CR-I-2521). 6. Metatarsus (CR-I-4562).

Fig. 5. *Haploiodoceros mediterraneus* de la grotte du Rhinocéros, os longs. 1. Humérus (CR-I-3244). 2. Radius (CR-I-2075). 3. Fémur (CR-I-3207). 4. Tibia (CR-I-3320). 5. Métacarpien (CR-I-2521). 6. Métatarsien (CR-I-4562).

Table 3Measurements (in mm) of limb bones of *Haploiodoceros mediterraneus* from Cova del Rinoceront.**Tableau 3**Mesures (en mm) des os longs de *Haploiodoceros mediterraneus* de la Grotte du Rhinocéros. DT: Diamètre transversal distal; DAP: diamètre antéro-postérieur; L: longueur max.; N: nombre de spécimens; Min: valeur minimale; Max: valeur maximale; δ : déviation standard (un sigma).

	Reference	L	DT prox	DAP prox	DT dist	DAP dist
Radii	CR-I-1490	215	40	22	35	24
	CR-I-636	235	44	23	38	26
	CR-I-2075	239	42	24	39	26
	CR-I-4554	226	43	23	38	26
	CR-I-3246	236	46	24	40	
	CR-I-3075		43	24		
	N	5	6	6	5	4
	Min	215	40	22	35	24
	Max	239	46	24	40	26
	Mean	230.2	43.2	23.3	38.2	25.6
Tibiae	δ	9.8	1.9	0.8	2.0	0.9
	CR-I-3204	291			36	29
	CR-I-3320	298	56	56	37	29
	CR-I-3255	301	63		38	29
	CR-I-2067		59	61	36	31
	N	3	3	2	4	4
	Min	291	56	56	36	29
	Max	301	63	61	38	31
Metacarpi	Mean	296.7	59.3	58.8	36.9	29.4
	δ	5.1	3.1	3.6	0.9	0.9
	CR-I-4635	219	31	22	31	21
	CR-I-3178	231	34	23	32	23
	CR-I-2147	232	32	23	32	21
	CR-I-3248	226	34	22	34	23
	CR-I-4555	221	31	23	28	21
	CR-I-2119	237	32	23	30	21
	CR-I-2521	222	32	22	31	21
	CR-I-2065	221	30	22		
Metatarsi	CR-I-923		32	23	32	21
	N	8	9	9	8	8
	Min	219	30	22	28	21
	Max	237	34	23	34	23
	Mean	226.1	31.9	22.5	31.2	21.4
	δ	6.5	1.3	0.5	1.6	0.9
	CR-I-3073	248	29	32	35	22
	CR-I-1321	241	29	31	32	22
	CR-I-4562	250	28	31	34	23
	CR-I-2082	252	27	32	32	21
	CR-I-1488	251	29	32	32	22
	CR-I-4291		31	31	34	22
	N	5	6	6	6	6
	Min	241	27	31	32	21
	Max	252	31	32	35	23
	Mean	248.4	28.9	31.5	33	22
	δ	4.4	1.4	0.6	1.2	0.6

DT: distal transverse diameter; DAP: antero-posterior diameter; L: maximum length; N: number of specimens; Min: minimum value; Max: maximum value; δ : standard deviation (one sigma).

Taxonomic assignments to their corresponding deer species are based on the diagnostic features of antlers, dentition and post-cranial skeletal elements.

Although red deer are well represented in the assemblages of the Cova del Gegant and the Terrasses de la Riera dels Canyars, both are dominated by horse specimens, *Equus ferus* and the less frequently documented *E. hydruntinus*, as well as by other open-landscape taxa, e.g. large bovids (Daura et al., 2013). No counts are yet available from the Cova del Coll Verdaguer; however, red deer and horse remains are fairly dominant in the faunal record, in association with other ungulates, including goat, roe deer and wild boar.

5. Discussion

The anatomical characters recorded for *H. mediterraneus* are important because they enable us to rule out the presence of *Dama dama* in the uppermost levels of the Cova del Rinoceront, as had previously been inferred when no diagnostic elements were available (Daura, 2008; Daura et al., 2010c). However, the reliability of these taxonomic assignments has been called into question (Sanz, 2006).

This new record of *H. mediterraneus* provides evidence of a longer chronological distribution of the genus dating to MIS 5. The presence of this deer in the South of France in the late Middle Pleistocene (~MIS 7–9) could be related

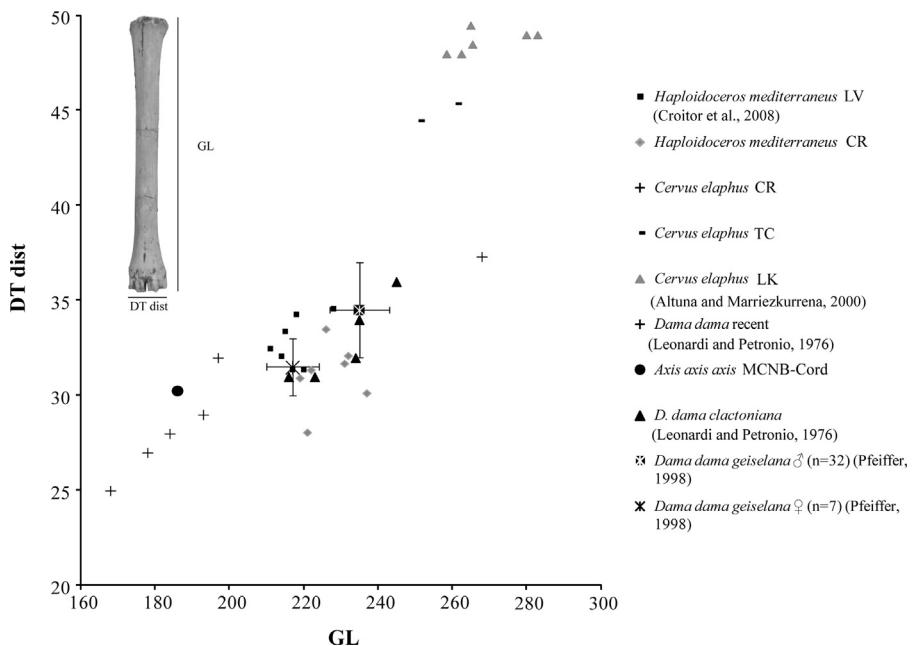


Fig. 6. Greatest length (GL) × distal transverse diameter (DT dist) of metacarpi (in mm) of different Pleistocene and modern deer. LV: Lunel-Viel; CR: Cova del Rinoceront; TC: Terrasses de la Riera dels Canyars; LK: Labeko Koba; MCNB-Cord: the Chordate Collection from the Natural History Museum of Barcelona. Minimum and maximum range and mean are plotted for *D. dama geiselana* (data from Pfeiffer, 1998).

Fig. 6. Longueur maximale (GL) et diamètre transversal distal (DT dist) de métacarpiens de cervidés pléistocènes et actuels (en mm). LV : Lunel-Viel ; CR : grotte des Rhinocéros ; TC : terrasse de la Riera dels Canyars ; LK : Labeko Koba ; MCNB-Cord : Musée d'histoire naturelle de Barcelone, coll. Chordate. *D. dama geiselana* avec moyenne, minimum et maximum (données de Pfeiffer, 1998).

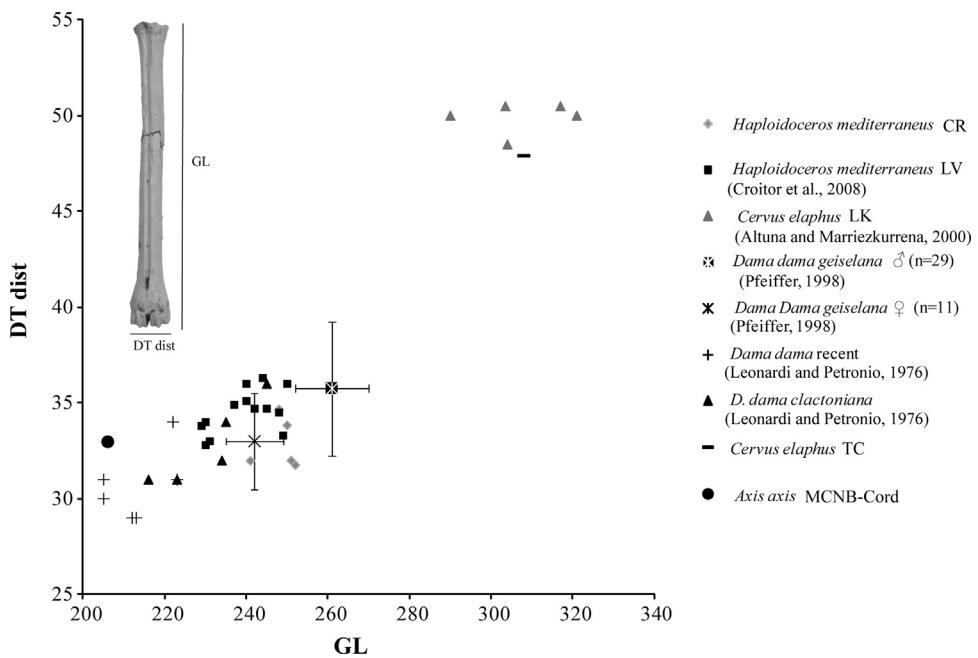


Fig. 7. Greatest length (GL) × distal transverse diameter (DT dist) of metatarsi (in mm) of different Pleistocene and modern deer. LV: Lunel-Viel; CR: Cova del Rinoceront; TC: Terrasses de la Riera dels Canyars; LK: Labeko Koba; MCNB-Cord: the Chordate Collection from the Natural History Museum of Barcelona. Minimum and maximum range and mean are plotted for *D. dama geiselana* (data from Pfeiffer, 1998).

Fig. 7. Longueur maximale (GL) et diamètre transversal distal (DT dist) de métatarsiens de cervidés pléistocènes et actuels (en mm). LV : Lunel-Viel ; CR : grotte du Rhinocéros ; TC : terrasse de la Riera dels Canyars ; LK : Labeko Koba ; MCNB-Cord : Musée d'histoire naturelle de Barcelone, coll. Chordate. *D. dama geiselana* avec moyenne, minimum et maximum (données de Pfeiffer, 1998).

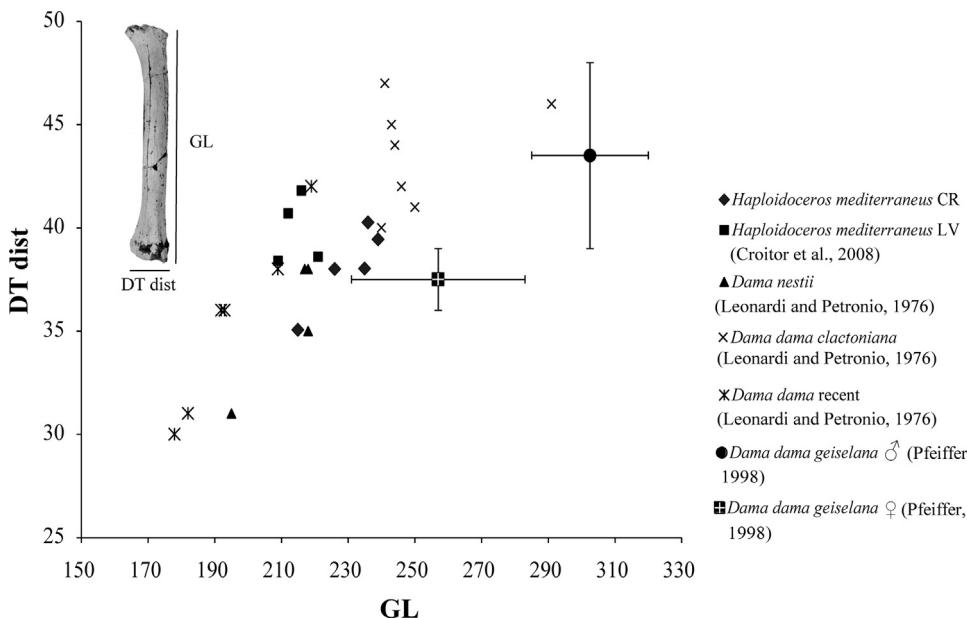


Fig. 8. Greatest length (GL) × distal transverse diameter (DT dist) of radii (in mm) of different Pleistocene and modern deer. LV: Lunel-Viel; CR: Cova del Rinoceront. Minimum and maximum range and mean are plotted for *D. dama geiselana* (data from Pfeiffer, 1998).

Fig. 8. Longueur maximale (GL) × diamètre transversal distal (DT dist) de radius (en mm) de différents cervidés pléistocènes et actuels. LV : Lunel-Viel ; CR : Grotte du Rhinocéros. Variations (min–max) et moyenne pour *D. dama geiselana* (données de Pfeiffer, 1998).

to the northward spread of the Iberian populations and, consequently, the species might have achieved its widest distribution during the Pleistocene, thus, strengthening the importance of the well-established populations in the Iberian Peninsula. An endemic distribution in the south of France may also have been derived from this dispersal, as suggested by Croitor et al. (2008). Finally, it should be noted that this genus has never previously been identified in the Upper Pleistocene, despite the frequent and abundant deer remains at many sites, from which it might be inferred that the genus was restricted to the Iberian Peninsula.

The total absence of *H. mediterraneus* at younger sites in the surrounding area, including MIS 3 at the Cova del Gegant and at the Cova del Coll Verdaguer as well as at the Heinrich Stadial 4 in the Terrasses de la Riera dels Canyars, suggests that its extinction occurred at the beginning of the Last Glacial period, at least in the Iberian region.

Moreover, the presence of this genus in the Upper Pleistocene of the Iberian Peninsula might be attributed to a climatic factor, i.e. the existence and late persistence of this genus in this area could be related to the refugial peninsular conditions, as has been observed for other species (Brugal and Valente, 2007; Cardoso, 1996; Stuart, 2005). However, the absence (or non-recognition) of this poorly known deer in the fossil record in the Iberian Peninsula should be stressed, as that in other classic European refugia, including the Italian Peninsula. However, given the importance of this ungulate in the Cova del Rinoceront record, with 12 individuals in layer I, it seems that this genus may well have been more widespread than previously believed (Croitor et al., 2008).

A further point needs to be made concerning chronology, given that the age of the deposits at Lunel-Viel and Igue-des-Rameaux are based on biochronology and not on

direct dating. Indeed, the Cova del Rinoceront record, without the results of direct dating, might have been related with traditional “Mindel-Riss interglacial” (i.e., Middle Pleistocene) fauna. However, as discussed above, the dating framework available for this site provides a chronological attribution to MIS 5. This seems to suggest the need for older works to be revised so that the fossil record can be reconsidered chronologically.

Finally, the absence of this genus in the fossil record (as mentioned above) could point to a problem of taxonomic identification because remains are usually fragmentary and often lack diagnostic elements (e.g. antlers). Moreover, the similar osteological and dental characters of *Haploiodoceros* and other deer species (especially Pleistocene fallow deer) could lead to confusion, e.g. the molarized premolars, the less pronounced columns of lingual cones and styles in the molars, the mandible shape and/or the similar morphology of the limb bones. As might be the case that similar-sized deer have widely overlapping measurements, as shown in Figs. 6–8. As such, there are various grounds for questioning taxonomic identifications based solely on the biometric data or the anatomical features of fragmentary material. Clearly, more information is required in order to define this genus anatomically; however, more criteria are now available to define and discriminate it from other Pleistocene deer as a result of this new material from the Cova del Rinoceront. In addition, more detailed anatomical and taxonomic studies could lead to the identification of new taxa within the genus *Haploiodoceros*.

Preliminary studies of the faunal composition of the Cova del Rinoceront assemblage indicate global temperate conditions with a notable presence of the Mediterranean tortoise, *Testudo hermanni*, a climatic indicator (García and Arsuaga, 2003) present in other sites, including the Cova

Negra during MIS 5a–MIS 3 (Morales and Sanchís, 2009), the Cueva del Camino during MIS 5a (Arsuaga et al., 2012; Álvarez-Lao et al., 2013) and the Cova del Gegant (Fèlix et al., 2006) during MIS 3 (Daura et al., 2010a). The absence of species adapted to open environments, such as the horse, and the presence of *Capra* might be indicative of a wooded and relief environment for the Cova del Rinoceront. Note that the red deer, *Cervus elaphus* is scant in the record but is a ubiquitous generalist species present in a wide range of habitats (García et al., 2009; Rivals et al., 2009). Nevertheless, the Cova del Rinoceront should enable us to reconstruct the environmental conditions of this poorly known genus. The high number of *Haploiodoceros* individuals combined with the ecofactual evidence (fauna, pollen, charcoal and phytoliths) and the results of other analyses (i.e. microwear and isotopes) warrant a better understanding of their ecology, ethology and palaeoenvironmental conditions.

6. Conclusion

The recovery of several almost complete crania, together with two sickle-shaped beams curving backwards and laterally and a long frontal basal tine with the anatomical features described herein provides the first known evidence of the genus *Haploiodoceros mediterraneus* in the Iberian Peninsula. The Cova del Rinoceront is the first site in the Iberian Peninsula in which the genus *Haploiodoceros* has been documented and, moreover, this is also the first occurrence of this taxon in the early Upper Pleistocene in Europe, occupying a longer time span at least until MIS 5.

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