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Paleoecology of an extinct Cervidae (*Haploidoceros mediterraneus*) of the Middle-late Pleistocene in Southern Europe

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A B S T R A C T

Haploidoceros mediterraneus is one of the recently described cervid taxa endemic to the Iberian Peninsula (three sites) and southern France (two sites). Compared to the other endemic cervids from Iberia that have emerged, as well, during the mid-Middle Pleistocene, its chronological and geographical range are more expanded, indicative of a relative adaptative success. However, very little is known about *H. mediterraneus* ecology. From site contexts and faunal associations, its habitat during the Middle and Late Pleistocene corresponded to open forest under a mildly-humid temperate Mediterranean or semi-continental climate. First, its diet was reconstructed using dental meso- and microwear and second, its relationships with other cervids over time was analysed using Multiple Component Analysis (MCA). Diet reconstruction indicates that it was mostly a browse-dominated mixed-feeder during the Middle Pleistocene. Such a relatively flexible diet has allowed it to coexist, often with some cervid taxa (*Cervus* and *Capreolus*) and exceptionally with others (*Praedama/Megaloceros* and *Dama* sp.) by resource partitioning. During the Late Pleistocene, *H. mediterraneus* shifted toward a more browse-specialized diet. At this period, co-occurrence analyses show that the presence of *H. mediterraneus* seems to exclude that of *C. capreolus* and *D. dama*. The evolution of *H. mediterraneus* dietary habits from the Middle to the Late Pleistocene may have led to direct competition with other browsing-specialist cervids, which may be one of the causes of its extinction.

1. Introduction

The specific diversity of cervids between the mid-Middle Pleistocene and the Late Pleistocene in Western Europe was viewed as relatively reduced until recently when new research has described several new taxa. Several of them have emerged in the Mediterranean region, especially in the Iberian Peninsula, notably *Megaloceros matritensis* (Van der Made, 2019), *Dama celia* (Van der Made et al., 2023) and *Haploidoceros mediterraneus* (Bonifay, 1967; Croitor et al., 2008; Van der Made and Mazo, 2014). The emergence of cervid taxa during the mid-Middle Pleistocene in the Iberian peninsula may be related to specific environmental conditions (Van der Made et al., 2023), the impoverishment of the large herbivore guild in this area in comparison with others (Croitor, 2018), and the low diversity of bovid species in

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comparison with Asian or African arid ecosystems (Croitor et al., 2019). From this three newly described cervid taxa, only one is currently documented to have spread toward the south of France: *Haploidoceros mediterraneus*.

This species was first reported as *Euctenoceros* (= *Eucladoceros*) *mediterraneus* from the Middle Pleistocene of Lunel-Viel (Southern France) and considered as a Villafranchian relict (Bonifay, 1967). New remains were discovered twenty years later in the Igue des Rameaux (Southwestern France) (Rouzaud et al., 1990). Then the fossils from these two sites were studied and discussed in detail (Croitor et al., 2008). More recently, more specimens of different chronological dates were discovered in the Iberian Peninsula at Cova del Rinoceront (North-eastern Spain), PRERESA (centre of Spain) and Gruta da Aroeira (Portugal) (Croitor et al., 2019, Croitor et al., 2018; Daura et al., 2015; Sanz et al., 2014; Van der Made and Mazo, 2014–2015). Current data have expanded the chronological range of *H. mediterraneus* from MIS 12/11 (Gruta da Aroeira) to MIS 5 (Cova del Rinoceront) and the geographical range from Portugal (Gruta da Aroeira) to Southern France (MIS 7, Lunel-Viel). Thus, compared to the other endemic cervid taxa from the Iberian Peninsula, *H. mediterraneus* was relatively successful and survived to the Middle-Late Pleistocene transition.

The ecological niche occupied by *H. mediterraneus* is still not fully understood. The cranio-dental morphology combines a mixture of adaptations toward grazing and browsing in low-productive environments (Croitor et al., 2019; Croitor et al., 2018; Croitor et al., 2008) and, until now, only the diets of the population from Cova del Rinoceront and Gruta da Aroeira have been investigated (Rivals et al., 2016; Sanz et al., 2024). They characterized *H. mediterraneus* as a browse-dominated mixed feeder with a diet similar to that of *D. dama*. From the Cova del Rinoceront study, it is suggested that these two species excluded each other because of their ecological proximity (Croitor et al., 2018; Rivals et al., 2016). *Dama* cf. *vallonnetensis* and *H. mediterraneus*, however, co-occurred in the Middle Pleistocene site of Gruta da Aroira (Croitor et al., 2019). Moreover, in Lunel-Viel and PRERESA, both from the Middle Pleistocene, *H. mediterraneus* co-existed with *C. capreolus*, another cervid browser-specialist (Rivals and Lister, 2016; Saarinen et al., 2016; Tixier and Duncan, 1996). Thus, Middle Pleistocene *H. mediterraneus* populations appear to be more tolerant to the presence of potential competitors.

This study aims to better understand the inter-specific relationship *H. mediterraneus* experienced with the other cervid taxa by reconstructing the ecological niches they occupied through time. It provides inferences on the ecology and dietary habits of *H. mediterraneus* and the other coexisting cervids analysed in their geo-chronological range.

2. Sites description

2.1. Gruta da Aroeira

The Gruta da Aroeira (also known as Galeria Pesada) is an archaeological site forming part of the Almonda karst system and located in Torres Novas, Portugal (Fig. 1). The site was discovered in 1991 by STEA *(Socieda de Torrejana de Espeleologia e Arqueologia)*. It was first excavated between 1997 and 2002 by A. Marks and colleagues (Marks et al., 2002a, 2002b) with first human remains found (Trinkaus et al., 2003). In 2013, new excavations were undertaken at the back of the cave with the aim of reaching bedrock (Daura et al., 2018). The Aroeira stratigraphy spans a thickness of about 4 m and comprises three major stratigraphic units (Daura et al., 2017). The uppermost unit, Unit 1, is a brecciated infill capped by flowstone and the basal unit, Unit 3, is an endokarst fluvial deposit, archaeologically sterile. Unit 2 is a 2.2 m thick mud-supported breccia corresponding to the Acheulean layer X. The U-series results for the speleothems suggest a maximum age for layer X, whose deposition can therefore be located within the 389–436 ka interval corresponding to late MIS 12/beginning of MIS 11 (Daura et al., 2017; Hoffmann et al., 2013; Sanz et al., 2024; Zilhão, 2023).

Layer X has yielded a human cranium (Aroeira −3) associated with Acheulean tools and burnt bones (Daura et al., 2018; Daura et al., 2017; Sanz et al., 2020; Sanz et al., 2018). Most of the raw materials used are quartz and quartzite cobbles available in the vicinity of the site that were knapped on-site and used to process hard material, mainly wood (Daura et al., 2018). In association with the human and lithic remains, 333 plotted-animal bones and teeth were also recovered during the 2013–2015 fieldworks (Sanz et al., 2024). From this collection, the main represented species correspond to cervids (22 % of the Number of Identified Specimens) so, unsurprisingly, the non-identifiable bones assigned to medium-sized animals are also the most abundant, followed by equids (14 % NISP). Other taxa are less frequent: for example, rhinoceros (1.5 % NISP), large bovid (*Bos* sp.), *Macaca* and suid (<1 % NISP). Fragmentation complicates species assignment; however, some palaeontological features suggest that the rhinoceros remains correspond to *Stephanorhinus etruscus*. The presence of carnivores in the assemblage is scarce (2.4 % NISP). The most abundant is that of the bear (NR = 6), which presents the palaeontological features of *Ursus*

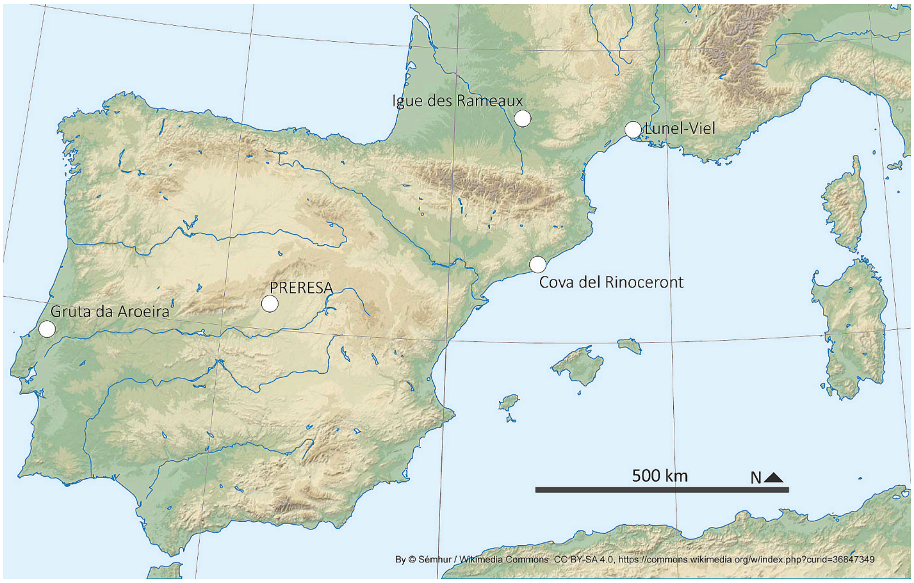

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Fig. 1. Geographical position of Gruta da Aroeira, Igue des Rameaux, Lunel-Viel, PRERESA and Cova del Rinoceront.

deningeri. The lynx is identified by one dental remain. Other taxa are also present (0.9 % NISP), including beaver and tortoise (Sanz et al., 2024). These animal populations appear to have been sustained by ecosystems constituted by the woodland and open landscapes that surrounded the site. The faunal assemblage derives primarily from anthropogenic activities conducted at the cave, which was probably used as a residential campsite. Human subsistence analyses suggest a preference for the targeting of large mammals, such as medium-sized deer and equids that were transported to the site for subsequent processing.

Among the cervids, four species have been described: *Cervus elaphus* (Minimum Number of Individuals = 1), *Praedama* cf. *savini* (MNI = 2), *Haploidoceros mediterraneus* (MNI = 2), and *Dama* cf. *vallonnetensis* (MNI = 1) which resulted in Gruta da Aroeira being the most ancient documented occurrence of the genus *Haploidoceros* (Croitor et al., 2019).

Along with large mammals, 20 taxa of herpetofauna and small mammals were recorded: Salamandridae indet., *Pelodytes* sp., *Bufo spinosus*, Anura indet., Lacertidae indet., cf. *Coronella girondica*, *Natrix* cf. *maura*, Ophidia indet., *Sorex* sp., *Crocidura* sp., *Rhinolophus ferrumequinum*, *Rhinolophus* sp. (small size), *Myotis myotis*, *Myotis* sp. (middle size), cf. *Miniopterus schreibersii*, *Iberomys brecciensis*, *Pliomys episcopalis*, *Apodemus* cf. *A. flavicollis*, *Allocricetus bursae* and *Eliomys quercinus* (López-García et al., 2018). The microfauna association indicates an environment and a climate related to an open-woodland landscape (ca. 60 % of forested cover), under relatively mild and humid conditions with a more pronounced continentality compared to the current period (López-García et al., 2018).

2.2. Igue des Rameaux

The Igue des Rameaux cave (Saint-Antonin-Noble-Val, Tarn-et-Garonne, France) was discovered in 1971 and the palaeontological site itself in 1985 by the S.S.A.C. (*Société Spéléo-Archéologique de Caussade*) (Fig. 1). Excavations were then undertaken between 1985 and 1991. It is a deep-karstic cave with a vertical entrance (aven/trap-fall) followed by a gallery cut in two by a large carbonate concretion. Two fossiliferous zones were found on both sides of the concretion: Aval and Amont that are very similar in term of represented species (Coumont, 2006; Rouzaud et al., 1990). Studies on microfauna and horse remains indicate that the Aval deposit is probably slightly older than the Amont (Jeannet, 2005; Uzunidis, 2021; Uzunidis-Boutillier, 2017). No direct dating was possible at Igue des Rameaux and the chronological attribution relies on biochronological analysis. The temperate faunal association would suggest an interglacial or interstadial stage (Rouzaud et al., 1990) and the evolutionary stages of wolves, lions and horses would be bracketed from MIS11 and MIS 7, and most probably consistent with MIS 9 (Argant and Brugal, 2017; Boudadi-Maligne, 2010; Uzunidis-Boutillier, 2017) for both zones.

Several factors may have been involved in the accumulation of the Igue des Rameaux deposits. In the Amont zone, the Pleistocene entrance was a vertical opening which indicates that the animals may have been trapped into the cave. Seventy-six lithic artefacts have been found in this part of the cave which indicate that humans may have come to take opportunistic advantage of the presence of carcasses of animals that have died accidentally (Brugal and Jaubert, 1991). In the Aval zone, a Pleistocene horizontal entrance seems plausible which could have allowed the carnivores' access to the cave. The great number of their remains could, therefore, be indicative of lairs, more precisely by lions and wolves (Argant and Brugal, 2017; Boudadi-Maligne, 2010).

The fauna association found in the Igue des Rameaux is diversified both in herbivore and carnivore species with: *'Palaeoloxodon' antiquus*, *Coelodonta antiquitatis*, *Equus mosbachensis*, *Equus hydruntinus*, *Haploidoceros mediterraneus*, *Cervus elaphus*, *Hemitragus* sp., *Bos primigenius*, *Sus scrofa*, *Canis lupus lunellensis*, *Vulpes* sp., *Ursus arctos*, *Crocuta spelaea*, *Hyena prisca*, *Panthera spelaea*, *Lynx* sp., Mustelidae, Lagomorpha and *Marmota* sp. (Argant and Brugal, 2017; Boudadi-Maligne, 2010; Coumont, 2006; Croitor et al., 2008; Brugal *in* Rouzaud et al., 1990; Uzunidis, 2021; Uzunidis et al., 2022a; Uzunidis-Boutillier, 2017). *Equus mosbachensis* is the main represented species in the Amont zone with at least 25 individuals. Cervids, on the contrary, are scarce with only two individuals of *H. mediterraneus* and three individuals of *Cervus elaphus*.

Sixty-one taxa of herpetofauna and small mammals were also recorded in association with the large mammals. Their study indicates that the climate during the accumulation of the Amont zone was semi-continental, colder and dryer compared to current-day climate. The forest cover (trees and bushes) corresponded to about 34.8 % of the vegetal composition while the grasslands were well-developed (46.2 % of the vegetal composition of the environment) (Jeannet, 2005; Jeannet and Mein, 2016).

2.3. Lunel-Viel I

The Mas des Caves site is an archaeo-palaeontological site located in Lunel-Viel (Hérault, France) (Fig. 1). It is a complex of several caves: Lunel-Viel I, II and III first discovered in 1800 and excavated in the beginning of the 19th century (de Serres et al., 1828) and during the 20th century, between 1962 and 1982 (Bonifay, 1968) with the discovery of Lunel-Viel IV in 1971, which is an extension of the Lunel-Viel I gallery. Since 2019, new excavations have been undertaken in the main cave, Lunel-Viel I, in order to better understand the site formation and dating (Brugal et al., 2022; Brugal et al., 2021). Lunel-Viel I is the main fossiliferous deposit that has yielded the majority of the material. The excavation area is of about 240 m^2 and the infilling is of about 6 m thick with 14 layers identified (Bonifay, 1968). Across the layers, much refitting of both lithic and faunal remains has been carried out that distinguishes two homogeneous sets ("ensembles") in the accumulation: the superior (layers 1 to 5) and the inferior (layers 6 to 14) parts (Fosse, 1996; Fosse, 1994; Le Grand, 1994). Biochronological and paleoecological analysis based on the high diversity of species found in Lunel-Viel I suggests that the accumulations took place within the same temperate period in the second half of the Middle Pleistocene (Bonifay, 1971; Bonifay, 1967; Bonifay and Bonifay, 1965; Brugal et al., 2021). Dating by ESR/U-series and pIR-IR290 indicates that the deposit occurred between 300 and 200 ka, contemporaneous with MIS 7 (Falguères et al., 2024).

During the Middle Pleistocene, the roof of the cave collapsed forming a large sink-hole allowing an easy access Lunel-Viel I for both humans and carnivores (Brugal et al., 2021; Falguères et al., 2024). The presence of over 500 lithic artefacts (Matthias, pers. com.) indicates short occupations by hominids and strong involvement of hyenas in the ungulate's accumulation (Fosse, 1996).

At least 75 taxa from large to small vertebrates were recorded in Lunel-Viel I (Argant and Mallye, 2005; Bonifay, 1991; Bonifay, 1980; Bonifay, 1971; Boudadi-Maligne, 2010; Brugal, 1985; Brugal et al., 2022; Brugal et al., 2021; Croitor et al., 2008; Falguères et al., 2024; Fosse, 1994; Fosse et al., 2021; Uzunidis, 2021; Uzunidis-Boutillier, 2017). The herbivores correspond to 11 species representing 62 % of the large mammal identified remains. The most abundant group is the cervids (36 %) with *Cervus elaphus*, *Haploidoceros mediterraneus*, and few *Capreolus* sp., *Megaloceros* sp., followed by large bovids (*Bos primigenius*, 15 %) and the equids (11 %) with *Equus mosbachensis palustris* and *Equus hydruntinus minor*. Other groups represent each less than 1 % of the identified remains of large mammals: *Stephanorhinus hemitoechus*, *S. kirchbergensis, Sus scrofa* and Proboscidea. The *H. mediterraneus* from Lunel-Viel represents the most abundant population documented to date with a combined MNI of 83 individuals. The carnivores correspond to 14 species and represent 21 % of the identified remains; they are dominated by the hyaenids (14 %), *Hyaena prisca* and mainly *Crocuta spelaea intermedia*, the canids (less than 5 %) with *Canis lupus lunellensis*, *Cuon priscus* and *Vulpes vulpes*, the felids (less than 2 %) with *Panthera spelaea*, *Lynx pardinus spelaeus*, *Felis monspessulana*, and *Panthera pardus*. Also, few remains of *Ursus* cf. *deningeri*, *Meles thorali spelaeus*, *Mustela palerminea*, *Lutra* sp. and Pinnipedia are recorded.

Meso- and micro-mammals are also represented by nine species (Brugal et al., 2021; Donard, 1982; Jeannet, 1976; Pelletier, 2018): *Talpa* sp., *Sorex* sp., *Microtus brecciensis*, *Apodemus sylvaticus*, *Eliomys quercinus*, *Pliomys lenki*, *Pitymys duodecimcostatus*, *Microtus agrestis* and *Oryctolagus cuniculus*. Other taxa such as birds (33 taxa, Mourer-Chauvire, 1975), reptiles, amphibians, fish and malacofauna (Brugal et al., 2021) are also documented.

Paleoenvironmental information about the Lunel-Viel I accumulation is still scarce. Faunal associations of both large and small species suggest a temperate humid Mediterranean climate (Bonifay, 1980; Brugal et al., 2021; Fosse, 1994). Dental wear analysis on equids and bovids are consistent with a rich mosaic habitat with herbaceous open areas and riverside woodland (Uzunidis, 2020).

2.4. PRERESA

PRERESA (Getafe, Madrid, Spain) is an archaeological open-air site located on the Complex Terrace of Butarque on the right bank of the Manzanares river valley at 18 km south east of Madrid in Spain (Fig. 1). A single clay-level, 30 cm of average thickness, rich in lithic and faunal remains was investigated in an area of 255 m^2 (Panera et al., 2014; Rubio-Jara et al., 2016; Yravedra et al., 2012). First, the accumulation was dated according to OSL analysis to MIS 5 (Yravedra et al., 2012); however, a new date was obtained through ESR which associated the deposit with the beginning of MIS 6 (Moreno et al., 2019).

The level from PRERESA was deposited during a flood episode. It represents a collection of 754 lithic artefacts associated with large mammals and microfauna remains (Rubio-Jara and Panera, 2019). The history of the site is complex and taphonomic study indicates that the accumulation resulted from human activities, especially focused on proboscideans, while punctual carnivore actions and accidental deaths occur, especially concerning two carcasses in connexion with *Bos primigenius* and *Haploidoceros mediterraneus* (Yravedra et al., 2019).

One or two individuals of relatively diverse species have been found, both of herbivores and carnivores (Yravedra et al., 2019). The represented herbivore species are: Proboscidea (MNI = 1), *B. primigenius* (MNI = 2), *Equus ferus* (NMI = 1), *Haploidoceros mediterraneus* (NMI = 2) and *Capreolus capreolus* (MNI = 1). Few carnivores are also represented: *Panthera leo* (MNI = 1), *Vulpes vulpes* (MNI = 1) and *Meles meles* (MNI = 1).

Meso- and micro-vertebrates are well represented: *Erinaceus europaeus*, *Crocidura russula*, *Rhinolophus ferrumequinum*, Rodentia, *Eliomys quercinus*, *Apodemus* sp., *Cricetulus* (*Allocricetus*) *bursae*, *Arvicola* aff. *sapidus*, *Microtus cabrerae*, *Microtus duodecimcostatus* and *Oryctolagus cuniculus*, *Pelobate cultripes*, *Pelodytes* sp., *Bufo bufo*, *Bufo calamita*, *Hylas* sp., *Pelophylas perezi*, *Timon lepidus*, *Psammodromus* cf. *algirus*, *Blanus* sp., *Natrix maura*, *Coronella* sp. and *Vipera latastei* (Sesé et al., 2011). A micro-vertebrate study is indicative of mild humid conditions within a mosaic landscape of herbaceous plants, bushes and riverside woodlands (Blain et al., 2019; Blain et al., 2013; Sesé et al., 2011). The pollen spectrum from PRERESA is characterized by the fluctuations of xeric plants and Cupressaceae with the presence of *Pinus* in moderate quantity, very few graminoid herbs, and the absence of aquatic taxa. The geological substrate, composed of marl-gypsum, may explain the abundance of gypsophile taxa. The landscape may have then been dominated by herbaceous dicots with limited presence of trees (Gil-García et al., 2019).

2.5. Cova del Rinoceront

Cova del Rinoceront is a palaeontological cavity located near Barcelona (Castelldefels, Spain) (Fig. 1). The site was discovered in 2002 and excavated since (Daura et al., 2015). The cavity was partially destroyed during quarrying activities in the 1960s that have exposed the fossiliferous vertical sedimentary fill, 11 m thick and 1.5 to 3 m wide. The sequence has been divided into three units (units 1, 2 and 3). The *H. mediterraneus* remains are mainly documented in unit 1 that was excavated between 2003 and 2010 (Rivals et al., 2016; Sanz et al., 2014) and which is correlated to MIS 5 (Daura et al., 2015).

Evidence of human presence is quite scarce in Cova del Rinoceront since only 22 artefacts were recovered in total; twelve from Unit 1 (Daura et al., 2015). While the bottom of the sequence (Units 2 and 3) resulted most probably from the accidental falling of the animals, an access into the cave was conceivable during the accumulation of Unit 1. Taphonomic study also indicates carnivore activities with a possible use of the site as a lair (Sanz et al., 2018).

In Unit I, the main represented large species are *Haploidoceros mediterraneus* (MNI = 18), followed by *Capra* cf. *ibex* (MNI = 7). The other ungulates are scarce with large bovids (MNI = 1) and *Cervus elaphus* (MNI = 1). Carnivores are represented by *Canis lupus* (MNI = 1), *Lynx pardinus* (MNI = 4) and *Ursus arctos* (MNI = 1) (Croitor et al., 2018; Daura et al., 2015).

The meso- and micro-vertebrates are very diverse with 29 taxa (López-García et al., 2016). Along with botanical studies, they are indicative of a temperate Mediterranean climate, slightly more humid than nowadays. The environment corresponded to a mix of wooded and open areas dominated by grasses and other dicotyledonous herbaceous plants (Daura et al., 2015; López-García et al., 2016).

3. Materials and methods

The ecological niche of *Haploidoceros mediterraneus* and its relationship with the other contemporaneous cervids were investigated through dental wear and co-occurrence analysis. We performed all the statistical analyses with R version 4.3–RStudio version 4.3.3 using the package FactoMineR (Lê et al., 2008).

3.1. Dental wear analysis

Within the six accumulations where *H. mediterraneus* is documented (Aroeira, Rameaux-Amont, Lunel-Viel I inferior and superior, PRERESA and Rinoceront), all the available teeth of cervid species were sampled for dental wear analysis. The analyses were conducted by two experienced researchers (FR and AU) and the data are given in Table 2.

The two applied methods: dental mesowear and microwear aim to classify the herbivore among three major categories: browser, mixed-feeder and grazer. Browsers focus on dicots corresponding to woody plants and herbs, grazers feed mostly on graminoid plants, and mixed-feeders alternate between the two types of plants.

3.1.1. Dental mesowear

Dental mesowear is an analytic tool that records dietary wear on herbivore teeth based on the physical properties of the food that impact the teeth during mastication (Fortelius and Solounias, 2000). Sharp buccal cusps correspond to low abrasion diets and are driven by attrition processes (tooth-on-tooth), while rounded and blunted cusps corresponding to abrasive diet is related to abrasion processes (tooth-on-food). Dust and grit ingested during the feeding process can have an effect on the mesowear signature (Kaiser et al., 2009) but high levels of abrasion are more likely due to the phytoliths contained in grasses and, therefore, related to the diet (Kaiser et al., 2013; Saarinen and Lister, 2016). Mesowear is cumulative tooth wear but the time span covered by dental mesowear within the individual's life is unclear. It could correspond to a lifetime signal (Ackermans et al., 2020) or to several years before the animal's death (Louys et al., 2012; Ulbricht et al., 2015; Uzunidis et al., 2023a).

In this study, we have selected the paracone of the second molars of well-preserved teeth as recommended by Fortelius and Solounias (2000). When not available, first or third molars were selected. Broken, unworn, partially worn and extremely worn teeth were excluded from the analysis following Fortelius and Solounias (2000) and Rivals et al. (2007a, 2007b).

The morphology of the cusps was analysed macroscopically using the "ruler method" proposed by Mihlbachler et al. (2011) and modified by Rivals et al. (2013). The cusp shape and relief are categorized within seven groups: 0 = high and sharp cusp; 1 = high, narrow angle and slightly rounded cusp; 2 = high, large angle and rounded cusp; 3 = medium high and very rounded cusp; 4 = low and round cusp; 5 = almost flat cups; 6 = blunt with no relief. The average value of mesowear from a single sample is represented by a "mesowear score" (MWS). Current browsers score between 0 and 2, mixed-feeders from 1 to 2.5 and grazers from 2 to 5.5. A total of 214 teeth were analysed: 156 teeth of *H. mediterraneus*, 54 teeth of *C. elaphus*, three teeth of *P.* cf. *savini* and one of *Megaloceros* sp.

3.1.2. *Dental microwear*

Dental microwear refers to the analysis of the microscopic traces left on the enamel during the masticatory process (Walker et al., 1978). Micro-traces can be generated by multiple factors: primarily, the presence of phytoliths within the plants that reflect the dietary choices of the animal (Rivals et al., 2015; Walker et al., 1978), but external particles such as dust and grit can also produce micro-traces (Gallego-Valle et al., 2020; Rivals and Semprebon, 2017; Schulz-Kornas et al., 2020). In contrast to dental mesowear, microwear is indicative of a short-time window diet in the individual's life corresponding to the last days to a month (Hoffman et al., 2015; Teaford and Oyen, 1989; Winkler et al., 2020).

Here, the microwear analysis follows the protocol and classification established by Solounias and Semprebon (2002) and Semprebon et al. (2004). The occlusal surface of each tooth was cleaned using acetone and then 96 % ethanol. Then, the surface was moulded with high-resolution silicone (vinylpolysiloxane) and casts were made using clear epoxy resin. The transparent casts were analysed with a stereomicroscope at magnification of x35. Observations were restricted to a standard surface of 0.16 mm^2 using an ocular reticule. The micro-traces were identified following the classification that divide the traces into pits (small and large), scratches (fine, coarse and hypercoarse), and gouges. Pits are circular or sub-circular scars, while scratches are elongated microfeatures with straight and parallel sides. Small pits are shallow and appear bright while large pits and gouges are deeper and appear dark due to less light refraction. Large pits are about twice the diameter of small pits and are less regular and gouges are much larger (about three time the size of a small pit) and have very irregular edges. The scratch texture was assessed as being either fine (i.e., narrow scratches that appear relatively shallow and have low refractivity), coarse (i.e., wide scratches that are also relatively deep but have high refractivity, relatively shiny), or a mixture per tooth surface. Each tooth was assigned a univariate scratch width score (SWS) as a qualitative score of the observed scratch texture based on Solounias and Semprebon (2002) and Semprebon et al. (2004) and modified by Rivals et al. (2007b, 2010). Teeth with predominantly fine scratches scored '0', teeth with mixed fine and coarse scratches scored '1', and teeth with predominantly coarse scratches were assigned a score of '2'.

The second premolars were discarded from the analysis since they do not record the same signal as the other teeth (Kaiser and Solounias, 2003; Xafis et al., 2017) and specimens with badly preserved enamel or taphonomic defects were also discarded following the description from previous works (King et al., 1999; Micó et al., 2023; Uzunidis et al., 2021).

In Gruta da Aroeira, two teeth of *H. mediterraneus*, two of *C. elaphus* and four of *P.* cf. *savini* were suitable for the analysis. In Rameaux-Amont, six teeth of *H. mediterraneus* were analysed and 3 of *C. elaphus* (60 % of the initial selected teeth). In Lunel-Viel I-inferior, 40 *H. mediterraneus* teeth were suitable for the analysis (86.9 % of the selected teeth), 17 of *C. elaphus* (58.6 % of the initial sampling) and one of *Megaloceros* sp. In Lunel-Viel I-superior, 23 teeth of *H. mediterraneus* were studied (85.1 % of the initial sampling) and four teeth of *C. elaphus* (66.6 % of the initial sampling). In PRERESA, one tooth of *H. mediterraneus*, corresponding to the individual found, was studied. Finally, in Cova del Rinoceront: 19 teeth of *H. mediterraneus* and two of *C. elaphus* were analysed.

3.2. *Cervid species co-occurrence analysis*

In order to analyse the co-occurrence of *H. mediterraneus* with other cervid species, we compared fossil assemblages within the temporal and geographical ranges of *H. mediterraneus*. We compiled 24 associations from the Middle Pleistocene (MIS 11, 9, 7 and 6) and 16 from the Late Pleistocene (MIS 5) from Iberia and the South of France (Table 1).

We employed Multiple Correspondence Analysis (MCA), which is a statistical tool that analyses the relationship pattern between more than two categorical dependant variables (Abdi and Valentin, 2007) and gives a two-dimensional Euclidian space representation (Arruda Silva et al., 2020). In our case, the variables correspond to the cervid species that may be either absent or present depending on the individual, here represented by the fossil sites. The position of the variables relative to each other on the graph represents the relationships between them (species A absent when species B is present, species A present when species B is absent, species A and species B often present at the same sites, species A and species B often absent from the same sites). The analysis is based on the presence/absence of the cervid species which have allowed us to 1) include deposits for which the number of specimens were not known, 2) minimize the impact of the distinct accumulator agent that may have played a role in the quantitative representation of each species in each assemblage. *Haploidoceros mediterraneus* was plotted as an illustrative variable while other cervids' presence/absence are an active variable. It means that *H. mediterraneus* presence/absence is not included in the analysis but added to the result to check their association with the active variables. This choice was made to avoid disrupting the structure of relationships between the active variables with a species that is exceptionally present in the sites. For this analysis, *Praedama* cf. *savini* and *Megaloceros* sp. which follow one another chronologically in Iberia, which are poorly represented and which both belong to the Megalocerotini tribe (Vislobokova, 2013) have been grouped together.

4. Results

4.1. *Haploidoceros mediterraneus and contemporaneous cervids' diets*

The lowest Mesowear score (MWS) of *H. mediterraneus* is displayed in PRERESA where the unique individual has a value of 1 and the highest corresponds to Rameaux-Amont specimens with a value of 2.33. The other populations are in-between: Aroeira (MWS = 2), Lunel-Viel I-Inferior (MWS = 1.65), Lunel-Viel I-superior (MWS = 1.59) and Rinoceront (MWS = 1.29) (Table 2). The MWS are, therefore, quite low in all the populations and correspond to the range values of extant browsers and mixed-feeders. Only the population from Rameaux-Amont overlaps slightly with the grazers MWS ranges (Fig. 2).

Red deer mesowear scores range between 1 in Aroeira to 3.5 in Rinoceront. The MWS from the Rameaux-Amont population equals 2.25, 2.11 at Lunel-Viel I-inferior and 2.83 at Lunel-Viel I-superior (Table 2). No red deer remains were encountered in PRERESA. Red deer MWS are indicative of a more diverse diet than *H. mediterraneus* since they plot with browsers to mixed-feeders in Aroeira, grazers in Rinoceront, and mixed-feeders to grazers in Rameaux-Amont, Lunel-Viel I-Inferior and Lunel-Viel I-superior (Fig. 2).

Other cervids' species are represented with *H. mediterraneus*, for example, *Dama* cf. *vallonnetensis* at Aroeira and *C. capreolus* at Lunel-Viel I inferior and superior and PRERESA. Unfortunately, no dental material was available for dental wear analysis. Three teeth of *P.* cf. *savini* were, however, suitable for dental mesowear analysis in Aroeira. Their mean mesowear score equals 1.67 which is consistent with a mixed-feeding diet. In Lunel-Viel I-inferior, a *Megaloceros* sp. maxillary (Brugal et al.,

Table 1
Summary of the archaeological/paleontological sites used in this work with their geographical positions, date, presence (1) or absence (0) of *C. elaphus*, *D. dama*, *C. capreolus*, *R. tarandus*, *Praedama* sp./*Megaloceros* sp. and *H. mediterraneus* and the references of the original works.

Site	Location	Age	*C. elaphus*	*Dama* sp.	*C. capreolus*	*R. tarandus*	*P.* cf. *savini*/ *Megaloceros* sp.	*H. mediterraneus*	References
Aroeira	Portugal	MIS 12/11	1	1	0	0	1	1	This study; Croitor et al., 2019
Rameaux-Amont	France	MIS 9	1	0	0	1	0	1	This study; Coumont, 2006; Croitor et al., 2008; Rouzaud et al., 1990
Lunel-Viel I-inferior	France	MIS 7	1	0	1	0	1	1	This study; Brugal et al., 2021; Croitor et al., 2008
Lunel-Viel I-superior	France	MIS 7	1	0	1	0	0	1	This study; Brugal et al., 2021; Croitor et al., 2008
PRERESA	Spain	MIS 6	0	0	1	0	0	1	This study; van der Made and Mazo, 2014; Yravedra et al., 2019
Rinoceront	Spain	MIS 5	1	0	0	0	0	1	This study; Croitor et al., 2018; Daura et al., 2015; Rivals et al., 2016
Arago l. B	France	MIS 9	0	1	0	0	0	0	Moigne et al., 2006
Arago l. C	France	MIS 11	1	1	0	1	0	0	Moigne et al., 2006
Terra Amata l. C1b	France	MIS 11	1	1	0	0	0	0	El Guennouni, 2001
Torralba	Spain	MIS 9	1	1	0	0	0	0	Santonja and Pérez-González, 2002
Ambrona	Spain	MIS 9	1	1	1	0	0	0	Soto et al., 2001; Villa et al., 2005
Gran Dolina TD10–1	Spain	MIS 9	1	1	1	0	0	0	Blasco et al., 2013
Bolomor l. XVIIc	Spain	MIS 9	1	1	0	0	1	0	Blasco et al., 2013
Bolomor l. XIII-XIV	Spain	MIS 7	1	1	0	0	1	0	Blasco, 2011
Bolomor l. XI	Spain	MIS 6	1	1	0	0	1	0	Blasco et al., 2013
Bolomor l. XII	Spain	MIS 6	1	1	0	0	1	0	Blasco et al., 2010
Payre l.G	France	MIS 7	1	1	1	1	1	0	Moncel, 2008
Payre l.F	France	MIS 7	1	1	1	0	0	0	Moncel, 2008
Mollet l.5	Spain	MIS 7	1	1	1	0	0	0	Maroto et al., 2012
Galeria Peseda	Portugal	MIS 7	1	1	0	0	0	0	Trinkaus et al., 2003
Peyrards l.inf	France	MIS 6	1	0	1	0	0	0	Daujeard, 2008
Rigabe	France	MIS 6	1	0	0	0	0	0	Dessart, 2001; Uzunidis-Boutillier, 2017
Coudoulous II l.9	France	MIS 6	1	0	0	1	0	0	Uzunidis and Brugal, 2018; Uzunidis-Boutillier, 2017
Cuesta de la Bajada	Spain	MIS 6	1	0	0	0	0	0	Santonja et al., 2014
Arlanpe l. SQ2	Spain	MIS 6	1	0	1	1	0	0	Rios-Garaizar et al., 2015
Aubesier l.V	France	MIS 5	1	1	1	1	1	0	Fernandez, 2006
Aubresier l.H	France	MIS 5	1	1	1	0	1	0	Fernandez, 2006
Moula-Guercy l. XV	France	MIS 5	1	1	1	1	1	0	Valensi et al., 2012
Payre l.D	France	MIS 5	1	1	1	0	0	0	Moncel, 2008
Bolomor l.IV	Spain	MIS 5	1	1	0	0	0	0	Blasco et al., 2013
Peyrards l.b	France	MIS 5	1	0	1	0	0	0	Daujeard, 2008
Peyrards l.a	France	MIS 5	1	0	1	0	0	0	Daujeard, 2008
Peyre I&II	France	MIS 5	1	0	1	0	1	0	Fourvel, 2012
Artenac l.10	France	MIS 5	1	0	1	1	1	0	Fourvel, 2012
Camino	Spain	MIS 5	1	1	1	0	0	0	Álvarez-Lao et al., 2013
Antón l. III-b/d/i/j	Spain	MIS 5	1	0	1	0	0	0	Sanz et al., 2019
Valdavara 3	Spain	MIS 5	1	0	1	0	0	0	Vaquero et al., 2018
Artazu l.VI	Spain	MIS 5	1	0	0	0	0	0	Castaños et al., 2019
Arlanpe l. SQ3	Spain	MIS 5	1	0	1	0	0	0	Rios-Garaizar et al., 2015

2021: Fig. 4) was available with a MWS of 3 that could also be consistent with a mixed-feeding diet (Table 2; Fig. 2).

At the microwear scale, the *H. mediterraneus* specimens from Rameaux-Amont and Rinoceront are characterized by an intermediate number of pits and scratches (Table 2). The populations fall in between the extant leaf browsers and the extant grazers and indicate mixed feeding traits (Fig. 2). The microwear patterns show a moderate to relatively high percentage of specimens with large pits (from 16.67 % at Rameaux-Amont to 52.63 % at Rinoceront), and few specimens with gouges in only one case (Rinoceront = 5.26 %). Both fine and coarse scratches are present, and hypercoarse scratches are absent. Consequently, browsing on hard fruits and seeds can be excluded because of the absence of hypercoarse scratches (Semprebon et al., 2004, 2011), but without totally excluding the possible consumption of soft fleshy fruits. *Haploidoceros mediterraneus* from Aroeira, Lunel-Viel I-inferior and Lunel-Viel I-superior display a lower quantity of scratches compared to the previous populations, and therefore are classified among the extant browsers (Fig. 2). The two individuals from Aroeira are also characterized by the presence of large pits, a mixed scratch width score (SWS = 1) and no gouges or hypercoarse scratches (Table 2). The presence of large pits and the higher number of scratches compared to the other browsing *H. mediterraneus* populations indicate that they must have included higher amounts of abrasive components into their diet (Semprebon et al., 2011). In Lunel-Viel I-superior, a moderate presence of large pits with no gouges or hypercoarse scratches and a majority of fine scratches (SWS = 0.65) are observed (Table 2), which are indicative of a very soft diet. However, they are also characterized by a high number of pits that can be related to the ingestion of dust within their

Table 2

Summary of dental meso- and microwear data for cervids from Gruta da Aroeira, Igue des Rameaux-Amont, Lunel-Viel I – inferior, Lunel-Viel I – superior, PRERESA and Cova del Rinoceront. Abbreviations: # = identifier of the teeth; n = Number of specimens; MWS = Mesowear score; NP = Mean number of pits; NS = Mean number of scratches; %LP = Percentage of specimens with large pits; %G = Percentage of specimens with gouges; SWS = scratch width score; %HC = Percentage of specimens with hypercoarse scratches; %XS = Percentage of specimens with cross scratches; m = Mean; s = Standard deviation. The authors of the analysis are also given.

Site/Species		Mesowear		Microwear								Author of the analysis
		n	MWS	n	NP	NS	%LP	%G	SWS	%HC	%XS	
Aroeira												FR
H. mediterraneus	m	1	2	2	16	14.75	100	0	1	0	0	
	s				0.7	0.35						
C. elaphus	m	2	1	2	29.5	9.75	100	50	1.5	50	0	
	s				2.83	2.48						
P. cf. *savini*	m	3	1.67	4	18.37	13	100	0	1.25	0	0	
	s		1.52		1.1	1.08						
Rameaux-Amont												AU
H. mediterraneus	m	6	2.33	6	19	17.42	16.67	0	1	0	0	
	s		0.5		4.28	2.35						
C. elaphus	m	4	2.25	3	19.67	18.33	33.33	0	1	0	0	
	s		0.5		2.51	4.72						
Lunel-Viel I - inferior												AU
H. mediterraneus	m	104	1.65	40	16.1	8.05	30	0	1	0	9.23	
	s		0.86		4.95	1.69						
C. elaphus	m	40	2.11	17	19.85	16.7	17.65	0	1	0	100	
	s		0.82		3.82	2.31						
Megaloceros sp.	#9.23124	1	3	1	15.5	18.5	0	0	1	0	100	
Lunel-Viel I - superior												AU
H. mediterraneus	m	27	1.59	23	26.6	9.6	56.52	0	0.65	0	78.26	
	s		0.79		6.05	2.45						
C. elaphus	m	6	2.83	4	26	17.25	25	0	1	0	100	
	s		0.98		3.19	0.96						
PRERESA												AU
H. mediterraneus	# 05/88/414a 421	1	1	1	13	12	0	0	1	0	100	
Rinoceront												FR
H. mediterraneus	m	17	1.29	19	15.58	16.47	52.63	5.26	1.26	0	5.26	
	s		0.68		4.99	2.57						
C. elaphus	m	2	3.5	2	10.75	20.5	50	0	1	0	0	
	s				0.35	0.7						

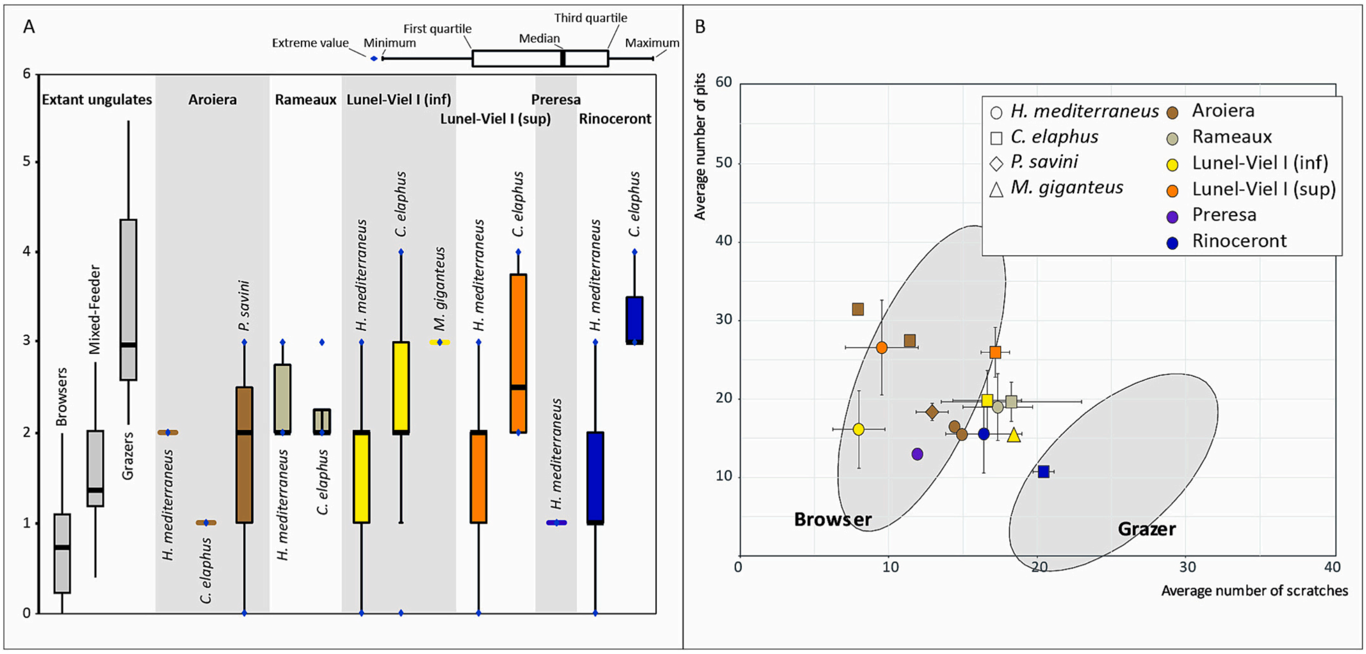

Fig. 2. A: Mesowear scores (MWS) of the cervids from Gruta da Aroeira, Igue des Rameaux, Lunel-Viel, PRERESA and Cova del Rinoceront compared to the values of recent ungulates published by Fortelius and Solounias, 2000, Rivals et al., 2014, Rivals et al., 2010. B: Bivariate plot of the mean number of pits and scratches of the cervids from Gruta da Aroeira, Igue des Rameaux, Lunel-Viel, PRERESA and Cova del Rinoceront. The error bars correspond to the standard deviation (±1 SD). The ellipses correspond to the Gaussian confidence ellipse (p. = 0.95) on the centroids of current grazers and browsers published by Solounias and Semprebon, 2002.

diet (Rivals and Semprebon, 2017). In Lunel-Viel I-inferior and PRERESA, no large pits, gouges or hypercoarse scratches were observed and the texture of the scratches was moderate (SWS = 1) (Table 2).

Red deer from Rameaux-Amont and Lunel-Viel I-inferior display a moderate quantity of pits and scratches and plot with the extant mixed-feeders (Fig. 2). They also show a moderate percentage of specimens with large pits (Rameaux-Amont = 33.33 % and Lunel-Viel I-inferior = 17.65 %), no gouges or hypercoarse scratches, and a mixed scratch texture (Table 2), which matches a mixed-feeding diet (Semprebon et al., 2011) similar to the characteristics of the mixed-feeding *Haploidoceros* from Rameaux-Amont and Rinoceront. Because of the highest number of pits from the Lunel-Viel I-superior sample, this *C. elaphus* population falls within the ellipse of the extant browsers. Their other dental microwear features are similar to that of the previous group (Table 2). They can be considered, therefore, as browsers that include a small quantity of abrasive intake into their diet. The two red deer individuals from Aroeira display a much-limited number of scratches and fall within the category of the browsers. They are also characterized by a high number of pits, percentage of large pits, gouges and hypercoarse scratches, and a high scratch width score (SWS = 1.5) (Table 2) which can indicate the ingestion of dust or soil and feeding on bark from small branches or twigs (Rivals and Semprebon, 2017; Semprebon et al., 2004, 2011). Finally, the red deer from Rinoceront display a high number of scratches and plot in the ellipse of the grazers (Fig. 2). They also display a moderate percentage of specimens with large pits, no gouges or hypercoarse scratches, and a mixed SWS (Table 2).

Four teeth of *P.* cf. *savini* were available for dental microwear. With a moderate number of pits and scratches, they fall within the variability of the mixed-feeder (Fig. 2). They also have a high percentage of specimens with large pits, no gouges or hypercoarse scratches, and a moderate SWS (Table 2). Their characteristics are very similar to those of *H. mediterraneus* from the same site and they must, as well, have included a small portion of abrasive components in their diet (Semprebon et al., 2011). The unique individuals of *Megaloceros* sp. from Lunel-Viel I-inferior (Brugal et al., 2021: Fig. 4) also display intermediate values for scratches and pits, and therefore, are classified among the mixed-feeders (Fig. 2). The teeth bear no large pits, gouges or hypercoarse scratches and the scratch width score is intermediate (SWS = 1) (Table 2). *Megaloceros* sp. dietary traits are therefore similar to that of *C. elaphus* from the same site and to *H. mediterraneus* from Rameaux-Amont and Rinoceront.

4.2. Co-occurrence of Haploidoceros mediterraneus with the other contemporaneous cervids

To date, five fossil populations of *H. mediterraneus* are known from the Middle Pleistocene of southern France and Iberia. The absence of this species is displayed very near the centre of the MCA, which indicates almost no influence on the analysis (Fig. 3). On the first axis which represents 31.04 % of the inertia, *H. mediterraneus* seems to be more commonly present when *C. capreolus* is also present and when *Praedama/Megaloceros* and *Dama* sp. are absent.

During the Late Pleistocene, only one population of *H. mediterraneus* is documented (Cova del Rinoceront). The absence of this species is displayed very near the centre on the second and third axis, which indicate no influence on the analysis (Fig. 4). The presence of *H. mediterraneus* has, however, an important impact on the first axis, which corresponds to 42.78 % of the inertia. *Haploidoceros mediterraneus* appears to be present when *Capreolus capreolus*, *Megaloceros giganteus*, *Dama* sp. and *Rangifer tarandus* are absent.

5. Discussion

5.1. Haploidoceros mediterraneus ecological niche

Haploidoceros mediterraneus general dietary behavior, according to dental mesowear, ranges between the strict browsers at PRERESA to mixed-feeders at Rameaux-Amont through mixed-feeders with a browsing trend in Aroeira and Lunel-Viel I inferior and superior and in Rinoceront (Fig. 2; Table 3). The mesowear results from our study are consistent with the narrow and pointed premaxillary bones observed in *Haploidoceros mediterraneus* (Croitor et al., 2018). The MWS of the Late Pleistocene population of Rinoceront is significantly different from those of the Middle Pleistocene (Wilcoxon test, $p = 0.03$). *Haploidoceros mediterraneus* mesowear data could indicate a chronological shift with a diet more focused on soft woody herbs, bushes or trees (while still including few abrasive items) during the Late Pleistocene.

At the time of death (dental microwear), *Haploidoceros mediterraneus*

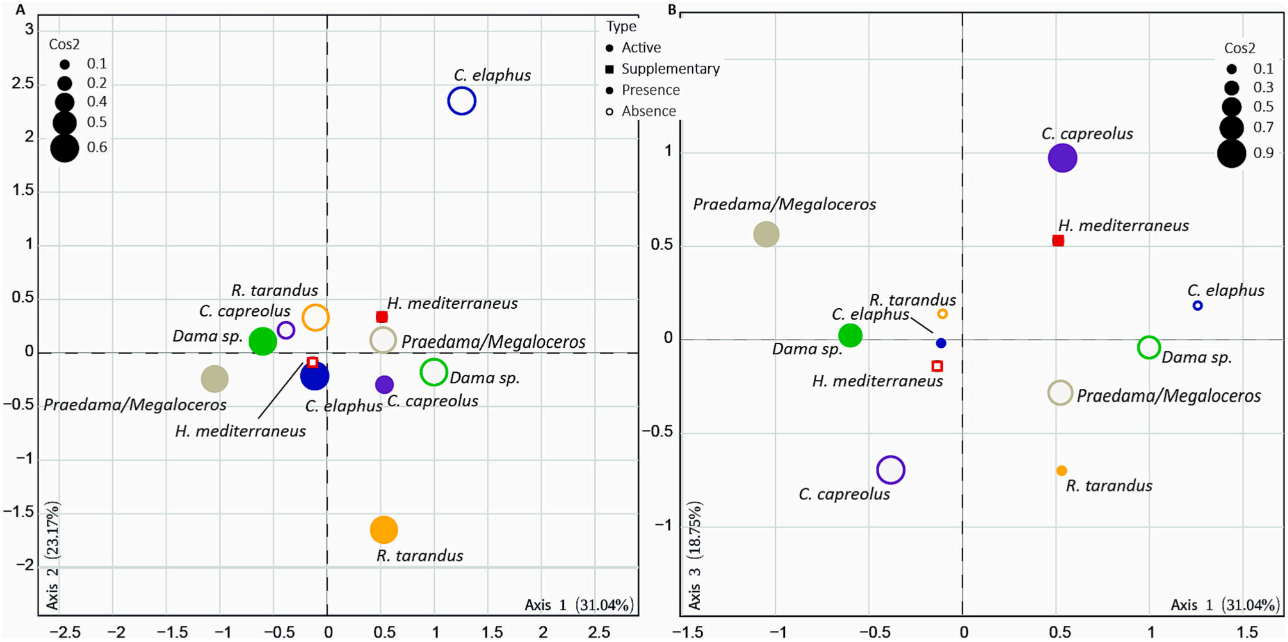

Fig. 3. Multiple correspondence analysis of the co-occurrence of the cervid taxa in southern France and Iberia during the Middle Pleistocene. Circle = active variables; square = illustrative variables; black = presence; white = absence. A: axis 1 (31.04 %) × axis 2 (23.71 %); B: axis 1 (31.04 %) × axis 3 (18.75 %).

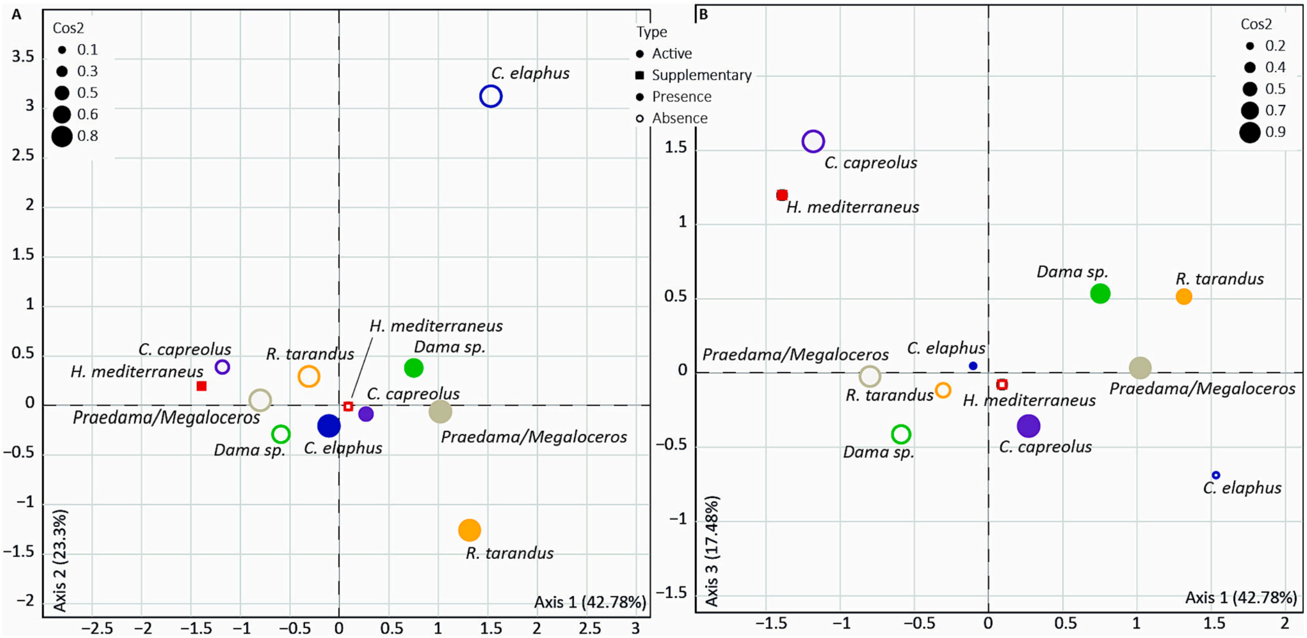

Fig. 4. Multiple correspondence analysis of the co-occurrence of the cervid taxa in southern France and Iberia during the Late Pleistocene. Circle = active variables; square = illustrative variables; black = presence; white = absence. A: axis 1 (42.78 %) × axis 2 (23.3 %); B: axis 1 (42.78 %) × axis 3 (17.48 %).

Table 3
Summary of co-occurring cervid species with *H. mediterraneus* and of their life-trend diet (dental mesowear) and period of death-diet (dental microwear) according to the geological period (Middle or Late Pleistocene). ND = No data.

Period	Contemporaneous cervid species	Locality	Life-trend diet	Period of death-diet
Middle Pleistocene				
	C. elaphus	Aroeira	Browser to mixed-feeder	Browser
		Rameaux-Amont	Mixed-feeder to grazer	Mixed-feeder
		Lunel-Viel I - inferior	Mixed-feeder to grazer	Browser
		Lunel-Viel I - superior	Mixed-feeder to grazer	Browser
	P. cf. *savini*	Aroeira	Mixed-feeder	Mixed-feeder
	M. giganteus	Lunel-Viel I - inferior	Mixed-feeder	Mixed-feeder
	Dama cf. *vallonnetensis*	Aroeira	ND	ND
	C. capreolus	Lunel-Viel I - inferior	ND	ND
		Lunel-Viel I - superior	ND	ND
		PRERESA	ND	ND
	H. mediterraneus	Aroeira	Mixed-feeder	Browser
		Rameaux-Amont	Mixed-feeder to grazer	Mixed-feeder
		Lunel-Viel I - inferior	Mixed-feeder	Browser
		Lunel-Viel I - superior	Mixed-feeder	Browser
		PRERESA	Browser to mixed-feeder	Browser
Late Pleistocene				
	C. elaphus	Rinoceront	Grazer	Grazer
	H. mediterraneus	Rinoceront	Browser to mixed-feeder	Mixed-feeder

populations fall within the same range between browsers and mixed-feeders (Fig. 2; Table 3). Their seasonal signal at the time of death can differ from their annual one. At Aroeira, they focused slightly more on soft dicot plants, and they were very focused on this type of vegetation in Lunel-Viel I compared to their general tendencies. At Cova del Rinoceront, they included more abrasive food at their time of death. The specific dietary characteristics of *Haploidoceros mediterraneus* at this latter site, as revealed by microwear analysis, are likely to be related to the specific characteristics of this site. The Cova del Rinoceront site functioned as a trap for young males seeking forage during the winter season when food supplies were limited (Croitor et al., 2018). Yearly and monthly dietary signals, however, match in Rameaux-Amont and PRERESA. *Haploidoceros mediterraneus* can therefore be classified as a flexible browser: a browser that can incorporate a small proportion of grass.

The six known occurrences of *H. mediterraneus* are dated from the mid-Middle Pleistocene (Gruta da Aroeira, ≈ 400 ka) to the beginning of the Late Pleistocene (Cova del Rinoceront, between 74 and 147 ka, Daura et al., 2015). The climatic conditions of the sites where *H. mediterraneus* is present share some similarities. They were either semi-continental (Aroeira, Rameaux-Amont, PRERESA) or Mediterranean (Lunel-Viel I and Cova del Rinoceront), always temperate and more humid than the current-day climate (Blain et al., 2019; Brugal et al., 2021; Daura et al., 2015; Jeannet and Mein, 2016; López-García et al., 2018; Sesé et al., 2011). The environments for the six faunal associations were also very similar and correspond to open woodland where the forested cover never exceeded 60 % of the vegetal composition. The simplification of *H. mediterraneus* antlers may be a reflection of an adaptation to low and unstable ecosystem productivity (Croitor et al., 2019). Within open-woodland landscapes, *H. mediterraneus* appears to have, generally, selected more of the browse component of this environment while being able to incorporate some monocots in its diet.

From the mid-Middle Pleistocene, new research has demonstrated a cervid specific diversity higher than expected within the Iberian Peninsula, especially in Gruta da Aroeira (Croitor et al., 2019) and the Manzanares valleys (Van der Made et al., 2023). Among those cervids, two species are currently known only in the Iberian peninsula (*Megaloceros matritensis* and *Dama celia* Van der Made, 2019; Van der Made et al., 2023) while *H. mediterraneus* was able to expand across the Pyrenees mountains with the northernmost occurrence at Igue des Rameaux and the easternmost one at Lunel-Viel. The emergence of those species may be related to the geographical position of the Iberian Peninsula, which has a long process of endemism (Hewitt, 2011) combined with favorable climatic conditions, for the cervid lineages, especially here

(Croitor et al., 2018).

5.2. *Haploidoceros mediterraneus* relationships with other contemporaneous cervids

In general, *Haploidoceros mediterraneus* is more of a browser than the other contemporaneous cervids. Significant differences (Wilcoxon test, $p < 0.0001$) can be observed in the MWS of *C. elaphus* that had a more abrasive diet than *H. mediterraneus* (Fig. 2; Table 3). Exceptions can be observed at the Gruta da Aroeira and at Rameaux-Amont. In the first site, *H. mediterraneus* MWS is similar to that of *P.* cf. *savini* and higher than that of *C. elaphus*. In the second, the MWS of *H. mediterraneus* and *C. elaphus* are similar. However, very few individuals are represented in each of those sites.

This diet segregation among cervids is not strictly observable at the microwear scale (Fig. 2; Table 3). Several patterns can be observed in the Middle Pleistocene populations. At Rameaux-Amont, the dietary characteristics of *C. elaphus* and *H. mediterraneus* are similar. At Gruta da Aroeira, the diets of *H. mediterraneus* and *P.* cf. *savini* are very similar while *C. elaphus* was more of a browser. In the more recent sites from the end of the Middle Pleistocene and the beginning of the Late Pleistocene (Lunel-Viel I, PRERESA and Cova del Rinoceront), *H. mediterraneus* always had a dicots-focused diet while *C. elaphus*, when present, had a more abrasive diet (from browser with mixed-feeder tendencies to grazer). Dental microwear, however, is a very short-window proxy that corresponds to the last month to days of life of the individuals (Winkler et al., 2020) that can be strongly affected by seasonal changes in the vegetation (Sánchez-Hernández et al., 2016; Uzunidis and Rivals, 2023). Currently, the season of death of the individuals has only been estimated at Rameaux-Amont where both *C. elaphus* and *H. mediterraneus* died in summer (Coumont, 2006), Lunel-Viel I-inferior where *C. elaphus* died mostly in summer and autumn, and *H. mediterraneus* in winter (Brugal et al., 2021), PRERESA where *H. mediterraneus* died in autumn (Yravedra et al., 2019), and Cova del Rhinoceront where the estimation was only possible for *H. mediterraneus* and indicated a death period between autumn and late winter (Croitor et al., 2018; Sanz et al., 2018). Thus, only two sites provide an estimation for more than one taxon, Rameaux-Amont and Lunel-Viel I-inferior. In Rameaux-Amont, the diet of both *C. elaphus* and *H. mediterraneus* included dicots and monocots at the time of death. The wide range of plants they consumed may have allowed them to share the same territory at least during summer and avoid competition. In Lunel-Viel I-inferior, the differences observed in the two cervid diets may either be linked to the seasonal vegetation turnover or to the species preferences.

From the Middle to the Late Pleistocene, the diet of *H. mediterraneus* shifted from mixed-feeder with a browsing trend to more specialized browsing. The dietary change of *H. mediterraneus* could have followed the evolution of vegetation accompanying the climate change of MIS 5. In the Iberian Peninsula especially, the forest density increases and dicots species became very predominant (Ochando et al., 2022). In the same timespan, its relationships with other cervids changed. During the Middle Pleistocene (Fig. 3; Table 3), *H. mediterraneus* co-occurred regularly with *C. capreolus*, while these two species very rarely coexisted with *Praedama/Megaloceros* and *Dama* sp. However, during the Late Pleistocene (Fig. 4; Table 3), *H. mediterranus*'s presence correlates with the absence of *C. capreolus*, *Megaloceros giganteus*, *Rangifer tarandus* and *Dama dama*. Its negative relationship with *R. tarandus* was strongly expected since reindeer are more commonly associated with a colder climate (Rivals and Semprebon, 2017), which was avoided by *H. mediterraneus*. Similarly, *M. giganteus* is a very uncommon species south of the Pyrenees (Uzunidis et al., 2023b), while for now, Iberia appears as the last refugium for *H. mediterraneus*. Consequently, their co-occurrence during the Late Pleistocene is highly unlikely. *Capreolus capreolus* and *Dama dama*, however, are common species of the beginning of the Late Pleistocene in Iberia (Table 1). *Capreolus capreolus* is a browser specialist (Rivals and Lister, 2016; Saarinen et al., 2016; Tixier and Duncan, 1996), which can seasonally incorporate grass in its diet (Merceron et al., 2004) but which will focus generally on fruits and leaves. Extant *Dama dama* has been classified among the mixed-feeders (Hofmann, 1989). Currently monocots constitute a high proportion of the fallow deer diet compared to other cervids, notably red deer (Azorit et al., 2012; Esattore et al., 2022; Filella et al., 2024; García-González and Cuartas, 1992; Putman et al., 1993; Spitzer et al., 2020), even if some populations favored browsing (Berlioz et al., 2017; Esattore et al., 2022; Rivals et al., 2020). The high intake of abrasive plants in the current fallow deer diet, however, is not recorded among Pleistocene populations. They were either classified as browser or mixed feeder during the Middle and Late Pleistocene through dental wear and isotopic analysis (García García et al., 2009; Rivals et al., 2020; Rivals et al., 2008; Rivals and Lister, 2016). Moreover, its dietary and morphological characteristics have been shown to be very close to those of *H. mediterraneus* (Croitor et al., 2018; Rivals et al., 2016). The dietary shift of *H. mediterraneus* toward a more specialized diet may have led to direct competition with *D. dama* and *C. capreolus* for the same dietary resources. No negative relationship was observed with *C. elaphus* which has a more flexible diet (Uzunidis et al., 2022b). In Cova del Rinoceront, the diets of the two cervids, *C. elaphus* and *H. mediterraneus*, are highly partitioned: the former focus on monocots, while the latter focus on dicots. The significant reduction in the abundance of monocots during MIS 5 (Ochando et al., 2022) may have exacerbated competition among herbivores during this period. More flexible herbivores, such as red deer, may have been outcompeted on dicots by more specialized taxa like *H. mediterraneus* or *Dama* sp., and were thus restricted to graminoids. Graminoid plants, already scarce, could possibly no longer be occasionally used by specialist species. The competition between ecomorphologically similar taxa like *Dama* and *Haploidoceros* may have been mediated and intensified by flexible species like red deer. The narrow distribution of *H. mediterraneus*, associated with a reduction of its ecological niche which has led to direct competition with other cervids, could be one for the factors of its disappearance during the Late Pleistocene.

6. Conclusions

The ecological and geographical conditions in Iberia during the mid-Middle Pleistocene have led to the appearance of several cervid species characterized by their short temporal and small geographical expansion. Among them, *H. mediterraneus* was the most successful within a timeframe that spans from the mid-Middle Pleistocene to the beginning of the Late Pleistocene and a distribution that extended beyond the Pyrenees Mountains (i.e., to the South of France).

Six populations of *H. mediterraneus* are currently known: three in France and three in Iberia, which allow for the reconstruction of the ecological niche it has favored and its relationships with the other cervids. *Haploidoceros mediterraneus* habitat corresponded to open forests where the woody component did not exceed 60 %, with temperate, mildly humid, semi-continental or mediterranean climatic conditions. During the Middle Pleistocene, *H. mediterraneus* was relatively flexible with a diet corresponding to mixed-feeders with browsing tendencies. It co-occurred commonly with *C. elaphus* and *C. capreolus* and only exceptionally with other cervid taxa (*Praedama/Megaloceros* and *Dama* sp.) which led most of the time to a partition of the dietary vegetal resources. During the Late Pleistocene, it became more specialized toward browsing. It may have been led to direct competition with other deer species, notably *C. capreolus* and *D. dama*. This competition may be one of the factors which constrained *H. mediterraneus'* distribution and led to its disappearance after the MIS 5.

CRediT authorship contribution statement

Antigone Uzunidis: Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Jean-Philip Brugal: Writing – review & editing. **Roman Croitor:** Writing – review & editing. **Joan Daura:** Writing – review & editing. **Pierre Magniez:** Writing – review & editing. **Joaquín Panera:** Writing – review & editing. **Susana Rubio-Jara:** Writing – review & editing. **Montserrat Sanz:** Writing – review & editing. **Jose Yravedra:** Writing – review & editing. **Florent Rivals:** Writing – original draft, Validation, Supervision, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

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

Data availability

Data are available in Open Access on Zenodo: https://doi.org/10.5281/zenodo.13380761.

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