



THE HYENA DEN OF CUEVA VICTORIA (LATE EARLY PLEISTOCENE, SPAIN): ADDITIONAL EVIDENCE OF THE ACTIVITY OF *PACHYCROCUTA BREVIROSTRIS* AND A DISCUSSION ON HYENAS FORAGING ON SEALS IN THE PLEISTOCENE OF MEDITERRANEAN EUROPE

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ABSTRACT: Cueva Victoria is a paleontological site of late Early Pleistocene age (ca. 0.9 Ma) located in the southeast of the Iberian Peninsula (Cartagena, Region de Murcia), which yielded diverse and abundant fossil remains, especially of large mammals. This accumulation is regarded as mainly deriving from the action of the giant hyena *Pachycrocuta brevirostris*, which used the cave as a den. Here, we present some preliminary taphonomic information deriving from the study of a portion of the large mammal collection from Cueva Victoria, including formerly uncatalogued material collected since the 1980s, which has not been considered in previous research. The study of this material started in 2018, when, owing to a suspension of the excavation activities in the cave, permissions were obtained to examine the uncatalogued specimens recovered during previous campaigns. Alongside a large number of remains of terrestrial mammals such as equids and cervids, *Pachycrocuta brevirostris* carried into the cave remains of groups uncommon in continental settings, such as marine mammals (cetaceans, seals). Beginning with the description of the seal remains of Cueva Victoria (assigned to *Monachus* sp.), with then discuss the relevance of hyena-seal interactions in the Pleistocene of Europe in terms of ecology, as well as of seal documentation in the fossil record. From a critical review of the available evidence, Cueva Victoria stands out as a clear example of the consumption of seal by hyenas, with another likely case being represented by the much younger site of Lunel-Viel (late Middle Pleistocene, France). In other known cases of co-occurrence of hyenas and seals, the presence of seals is either due to other factors (e.g., hominins, deposition of marine sediments) or its origin cannot be ascertained for sure.

Keywords: *Crocuta crocuta*; '*Hyaena*' *prisca*; *Monachus monachus*; Phocidae; Epivillafranchian.

1. INTRODUCTION

Hyenas (Hyaenidae, Carnivora) are a group of large mammals today greatly reduced in diversity and geographic distribution, being represented by only four living species mainly limited to Africa, except for the striped hyena *Hyaena hyaena* (Linnaeus, 1758), which is also present west of Africa up to the Indian Subcontinent (Kasperek et al., 2004; Akash et al., 2021; Hadad et al., 2023; Wilkinson et al., 2024). This is in sharp contrast with the large number of species and "ecomorphs" known from the Miocene fossil record (e.g., Kurtén, 1956; Howell & Petter, 1980; Qiu, 1987; Werdelin & Solounias, 1991, 1996; Semenov, 2008; Turner et al., 2008; Tseng et al., 2013; Coca-Ortega & Pérez-Claros, 2019; Morlo et al., 2019; Pérez-Claros & Coca-Ortega, 2020; Koufos, 2021; Iurino et al., 2022; Kargopoulos et al., 2023a, 2023b). Although the decrease in the diversity and distribution of hyenas was already evident in the Pleistocene, hyenas were still present in Europe at the time with several species. The so-called "hunting hyena" *Chasmaporthetes lunensis* (Del Campaña, 1914) was the last representative of a

once widespread group (even reaching North America) that differed from the coeval and following hyenas inhabiting Europe in a series of anatomical features, from the more trenchant dentition to the slenderer limbs, which indicate a greater propensity to active hunting (Berta, 1981; Kurtén & Werdelin, 1988; Ferretti, 1999; Antón et al., 2006; Turner, 2009; Tseng et al., 2011, 2013; Pérez-Claros et al., 2021; Konidaris, 2022; Marciszak et al., 2022; Iannucci, 2024a). All other European hyenas recorded during the Pleistocene are regarded as "bone-crackers", being closely related and aligning morphologically to three out of four of the extant species (Turner & Antón, 1996; Iannucci et al., 2021, 2022; Lewis & Werdelin, 2022; Pérez-Claros, 2024), the exception being the aardwolf, a specialized termite-eater belonging to a divergent clade (Kruuk & Sands, 1972; Cooper & Skinner, 1979; Werdelin & Solounias, 1991; Westbury et al., 2021; Rajmil et al., 2023). The bone-cracking hyenas known from the Pleistocene of Europe are *Pliocrocuta perrieri* (Croizet & Jobert, 1828), *Pachycrocuta brevirostris* (Gervais, 1850), '*Hyaena*' *prisca* de Serres et al., 1828, and *Crocuta* Kaup, 1828 – the latter either assigned altogether to the same taxon of the extant spot-

ted hyena, *C. crocuta* (Erxleben, 1777), or separated in multiple (sub)species (e.g., Bonifay, 1971; Schütt, 1971; Sardella & Petrucci, 2012; Lewis & Werdelin, 2022). All these species share remarkably similar proportions in their dentition, apart from *Crocota*, which mainly differs from the others in having a relatively elongated carnassial (Iannucci et al., 2021; Lewis & Werdelin, 2022; Pérez-Claros, 2024). Indeed, several authors placed *Pliocrocota perrieri* and *Pachycrocota brevirostris* in the same genus (i.e., *Pachycrocota* Kretzoi, 1938) (Qiu et al., 2004; Liu et al., 2021), and it has been argued even for '*Hyaena*' *prisca* (Pérez-Claros, 2024). In any case, bone-cracking hyenas are documented throughout the European Pleistocene. *Pliocrocota perrieri* endured the *Equus* event (Iannucci & Sardella, 2023) and survived until at least ca. 1.8 Ma, chronologically overlapping with the earliest representatives of the giant hyena *P. brevirostris* (Iannucci et al., 2022). *Pachycrocota brevirostris* is then widely documented for the rest of the Early Pleistocene, until ca. 0.8 Ma in Europe, when *Crocota* and '*H.*' *prisca* dispersed in the region (Iannucci et al., 2021). The bioevents represented by the appearance and disappearance of bone-cracking hyenas from the fossil record of Europe are considered of great biochronological significance, especially for the faunal turnovers of the middle Villafranchian-late Villafranchian – with the spread into Europe of *P. brevirostris* – and of the Epivillafranchian-Galerian – with the local extinction of *P. brevirostris* and the arrival of *Crocota* and '*H.*' *prisca* (Palombo et al., 2008; Martínez-Navarro, 2010; Iannucci et al., 2021, 2023; Croitor et al., 2024; Konidaris & Kostopoulos, 2024; Spassov, 2024).

For instance, during the 1.2-0.9 Ma time span, around the Jaramillo Subchron, a marked faunal turnover followed the shift of the climate from 41 ka obliquity orbital cycles to a highly non-linear system dominated by a 100 ka periodicity with asymmetric glacial/interglacial cycles (Clark et al., 2006). The faunal assemblages of this time span (1.2-0.8 Ma) are assigned to the Epivillafranchian biochron (Bellucci et al., 2015), which includes among the others Untermassfeld in Germany, Le Vallonnet in France, Colle Curti, Scoppito/Madonna della Strada and Slivia in Italy, Trinchera Elefante and Vallparadís Estació in Spain. The *C. crocuta* event marks the end of this biochron and represents a further renewal in European faunas, when most of the Villafranchian large carnivores became extinct. The severe glaciation of the "0.9 Ma event" might have been particularly influential in promoting the observed changes in the mammalian fauna (Head & Gibbard, 2015; Strani et al., 2019; Strani, 2021). In the Italian fossil record, the large mammal assemblage of Slivia includes the latest occurrence of the giant hyena *P. brevirostris*, while the occurrence of *C. crocuta* is documented at Casal Selce 1 (Rome, ca. 0.75-0.7 Ma; Sardella & Petrucci, 2012). This agrees with what is known in Spain, where the replacement between *P. brevirostris* and *C. crocuta* (and roughly '*H.*' *prisca*) is documented ca. 0.8 Ma with the appearance of the latter in the strati-



Fig. 1 - Geographic location of the late Early Pleistocene paleontological site of Cueva Victoria.

graphic section of Gran Dolina (García & Arsuaga, 2001; Iannucci et al., 2021; Gibert et al., 2024).

Bone-cracking hyenas are responsible for mass accumulations of bones, which are of fundamental importance for gaining insights into Pleistocene ecosystems (e.g., Kuhn et al., 2010; Mangano, 2011; Fourvel et al., 2015). Here, we present some preliminary taphonomic information deriving from the study a portion of the large mammal collection from the late Early Pleistocene site of Cueva Victoria (Cartagena, Spain) which has not been considered in previous research. At Cueva Victoria, the giant hyena *P. brevirostris* played a major role in the fossil accumulation, besides carrying into the cave remains of groups uncommon in terrestrial deposits, such as marine mammals. Beginning with the case of the presence at Cueva Victoria of seal remains related to the monk seal, (*Monachus* Fleming, 1822), of which we provide a description, with then discuss the relevance of hyena-seal interactions in the Pleistocene of Europe in terms of ecology, as well as of seal documentation in the fossil record.

2. CUEVA VICTORIA

Cueva Victoria is a paleontological site located in the mining Sierra de La Unión, in the Cerro de San Ginés de la Jara, near the towns of the Strait of San Ginés and the Llano del Beal, in Cartagena (SE Spain) (Fig. 1). The karstic origin of Cueva Victoria led to the formation of cavities that opened to the outside during the Early Pleistocene (Vilá-Vinyet et al., 2015). As a consequence, the cave was filled with sediment from the outside through several entrances, forming the fossil gap continuously until it was filled (Ferrández et al., 1989; Gibert et al., 2006). It was during this filling time interval that the hyena *Pachycrocota brevirostris* used it as its den. After total clogging, the cave was sealed, producing a cementation process due to the calcium carbonate contained in the runoff water that was entering, forming a speleothem layer (Gibert et al., 2016).

The deposit is altered by the action of the miners, who, looking mainly for manganese, destroyed a good part of the fossiliferous breccia. In this way, the original cave underwent modifications and large blocks can be seen, which fell from the ceiling and contain a breccia, as a result of the use of explosives. Therefore, it is a cave that in turn is a mine exploited from the end of the 19th century to the middle of the 20th century, approximately (Pérez De Perceval et al., 2015).

At the beginning of the 1980s, systematic paleontological excavations began at Cueva Victoria, which is dated at ca. 0.9 Ma (Gibert et al., 2016). The site presents one of the best records of fossil fauna from the European Early Pleistocene, with approximately one hundred identified vertebrate species (Gibert & Ferrández-Cañadell, 2015), mainly due to its condition as a den for the hyena *P. brevirostris* (Gibert et al., 1992). It is also noteworthy that taxa new to science have been discovered in Cueva Victoria, such as the lagomorph *Oryctolagus giberti* de Marfà, 2008, the arvicolid *Victoriamys chalinei* Martin, 2012, and the giant deer *Megaloceros novocarthaginiensis* Van der Made, 2015.

Another matter of great importance is the presence in the cavity of remains of primates of African origin; in different excavation campaigns, a total of five teeth belonging to *Theropithecus oswaldi* were found, constituting to date the only place in Europe where fossils of this primate have been found (Gibert et al., 1995, 1999; Ferrández-Cañadell et al., 2014; Ribot et al., 2015; Martínez et al., 2020). Rook et al. (2004) cited the presence of this taxon in the Pirro Nord site represented by three cervical vertebrae, which caused some discussion (Patel et al., 2007; Rook & Martínez-Navarro, 2013), eventually settled in 2014 with the publication of Alba et al. (2014), who showed that they were three vertebrae of *Hystrix refossa*, an abundant porcupine in this site. On the other hand, a second phalanx of the fifth finger of the right hand was also found, classified as *Homo* sp. (CV-0) (Gibert 1985; Gibert and Pons-Moyà, 1985; Pons-Moyà, 1985; Gibert et al., 2008; Ribot et al., 2015).

Another peculiarity within the abundance and diversity of taxa in Cueva Victoria is the fossil record of marine fauna. The cave is currently about 3.3 km from the sea. According to the study by Goy et al. (1990) during the Early Pleistocene the coastline would be similar to the current one, although with a different morphology; therefore, the sea could never invade the cave. Inside the cavity, four vertebral centra belonging to an indeterminate cetacean were found, as well as an incomplete hemimandible and a fragment of monk seal maxilla initially cited as a sirenid (Gibert et al., 1992) and later assigned to the genus *Monachus* (Gibert et al., 1999; Ferrández-Cañadell, 2015). The fact that the seal hemimandible is bitten at its proximal end confirms its transport to the interior of the cavity by hyenas, which did not limit their hunting-scavenging activity to land

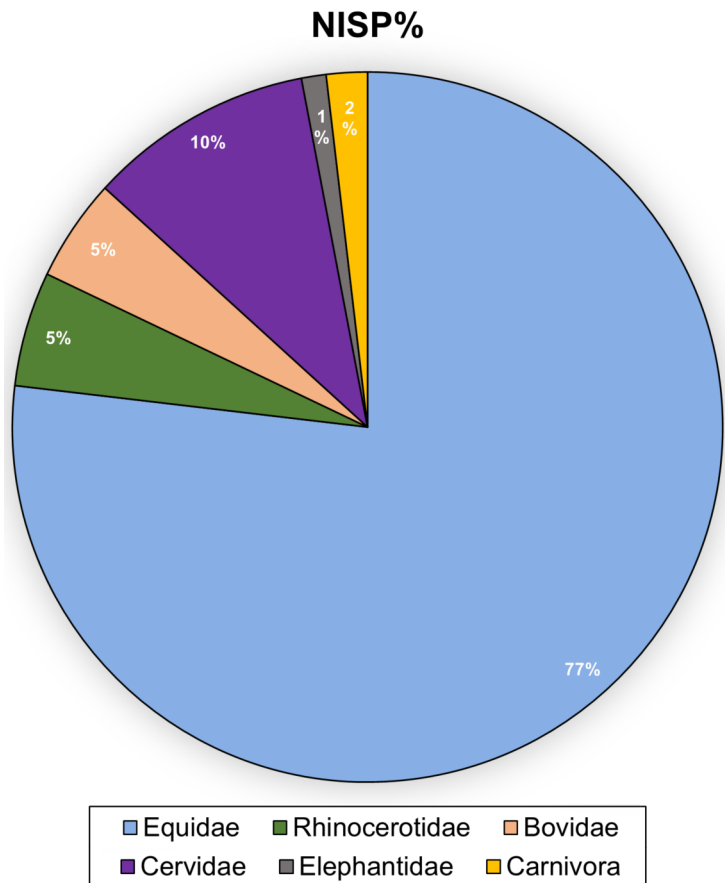


Fig. 2 - Distribution of the number of identified specimens (NISP) of the studied mammal remains from Cueva Victoria by taxonomic group.

mammals. The cave was interpreted as a den of hyenas after studying various aspects that left no room for doubt, such as: the presence of milk teeth of *P. brevirostris*, the abundance of accumulated coprolites of hyenas, the presence of the aforementioned marine fauna, bones digested and the enormous amount of remains with different tooth marks and fractures resulting from the action of these carnivores (Gibert et al., 1992). In this sense, the splinters and fragments of bones of different sizes stand out. The review of the material has also revealed the presence of marks on a large part of the abundant number of splinters in the fossil collection deposited in the Museo Arqueológico Municipal Enrique Escudero de Castro, in Cartagena. These marks provide information of taphonomic value that complements that of the whole bones (García-Nos & Ribot Trafí, 2021).

3. MATERIALS AND METHODS

We studied 4235 complete or (mainly) fragmented skeletal elements of medium and large size (> 2 cm for bone fragments), part of the fossil collection of Cueva Victoria, housed in the Museo Arqueológico Municipal Enrique Escudero de Castro, in Cartagena. The study of this material started in 2018, when, owing to a suspen-

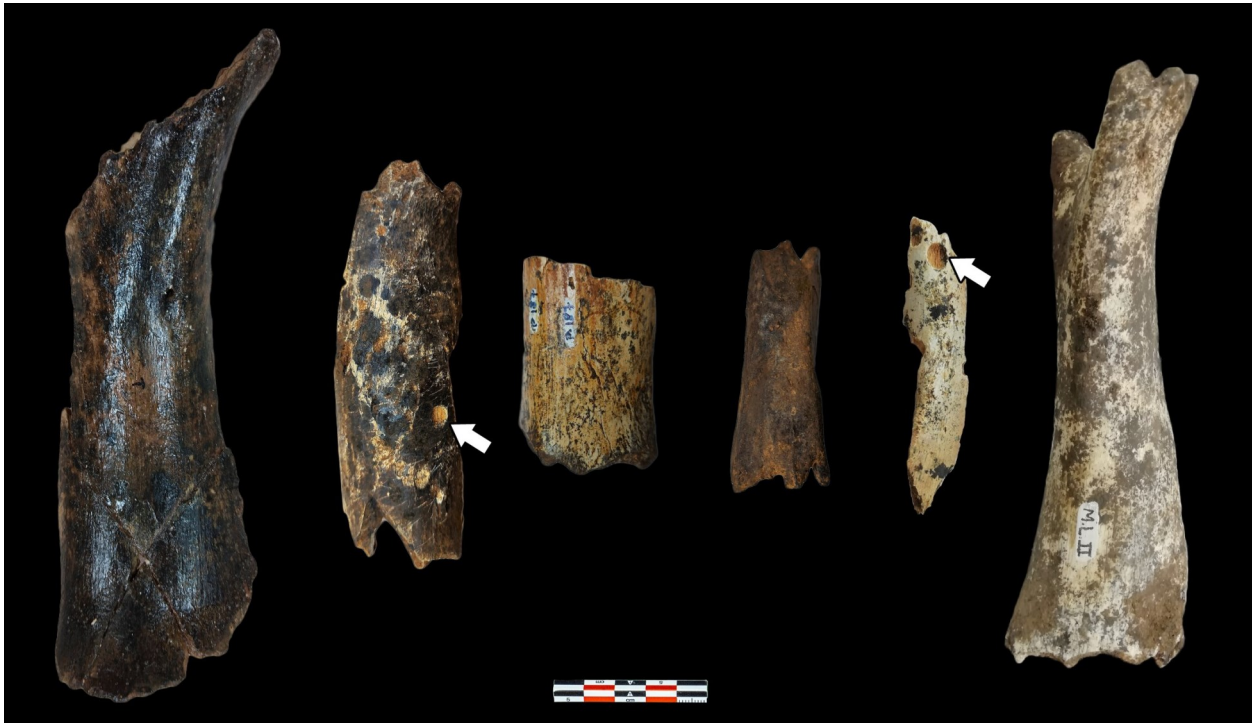


Fig. 3 - Example of bone fragments from Cueva Victoria showing traces of the activity of hyenas (Museo Arqueológico Municipal Enrique Escudero de Castro, Cartagena). Arrows point to some large pits. Photos: Eulalia García-Nos.

sion of the excavation activities in the cave, permissions were obtained to examine the uncatalogued specimens recovered during previous campaigns (García-Nos et al., 2020). We considered only large mammal remains, excluding lagomorphs and smaller species. Given the fragmentary nature of the studied material, taxonomic identifications and considerations are limited to the family or order level.

Nomenclature, taxonomy, and comparative discussion on the seal remains of Cueva Victoria is mainly based on Scheel et al. (2014) and Berta et al. (2015), including reference to the fossil species *Pliophoca etrusca* Tavani, 1941 and the extant monk seals *Monachus monachus* (Hermann, 1779) and *Neomonachus Slater & Helgen, 2014* (in Scheel et al., 2014).

4. RESULTS

Of the total sample of 4235 specimens considered in this work, 906 (21.4%) remains have been anatomically and taxonomically identified (Fig. 2). Isolated and fragmented teeth account for 46% ($n = 417$) of the total, primarily belonging to equids ($n = 310$). Mandibular fragments are not abundant ($n = 26$; 2.9%), while maxillae and cranial remains are totally absent. There are 63 vertebrae (only 5 of which are roughly complete) and 13 costae. Distal epiphyses of metapodials are the most common skeletal element ($n = 199$), with other fragments of bones being represented by astragali ($n = 53$), calcanei ($n = 46$), proximal tibiae ($n = 23$), proximal radii ($n = 16$), femoral shafts ($n = 12$), and rotulas ($n = 7$), with equid specimens being dominant and several inde-

terminate remains belonging to middle-sized ungulates. Complete bones are quite limited in the sample, including only small elements such phalanges ($n = 25$), calcanei ($n = 6$), and one cervid astragalus.

Signs of the activity of hyenas are observable in 76% of the 4235 remains, including W-shaped fractures, corrosion due to digestion, and tooth marks of large size (pits of 7-10 mm) (Fig. 3). There is no evidence of cut marks or other traces potentially indicating an anthropic influence on the accumulation. Those specimens where signs of the activity of carnivorans are not recorded are generally those whose size or preservation preclude a clear evaluation.

5. SYSTEMATIC PALEONTOLOGY

Family PHOCIDAE Gray, 1825
Subfamily MONACHINAE Gray, 1869
Tribe MONACHINI Gray, 1869
MONACHUS Fleming, 1822

Monachus sp.
(Fig. 4)

5.1. Description

The presence of seals at Cueva Victoria is documented by two specimens, a right maxilla (CV-MC-67) and a left hemimandible (CV-MC-66). Both specimens are in good state of preservation (the maxilla better) and belong to adult individuals with differentially worn teeth. Postcanine teeth are formed by a large single central cusp/cuspid, with accessory cuspules/cuspidids better

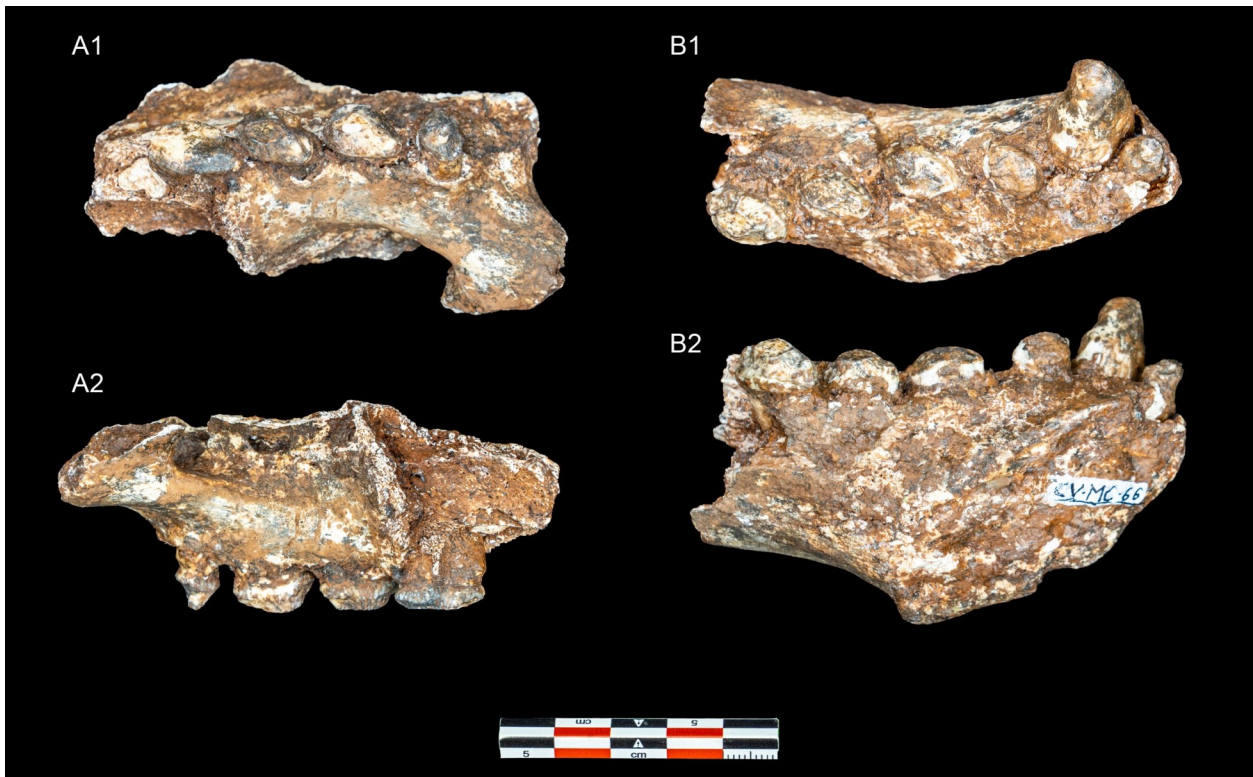


Fig. 4 - Seal remains (*Monachus* sp.) from Cueva Victoria, including a right maxilla CV-MC-67 (A) figured in occlusal (A1) and buccal (A2) views and a left mandible CV-MC-66 (B) figured in occlusal (B1) and lingual (B2) views (Museo Arqueológico Municipal Enrique Escudero de Castro, Cartagena). Photos: Miguel Camino and Eulalia García-Nos.

expressed distally. These teeth are oriented obliquely with respect to the mesio-distal axis of the tooth row. They are separated by diastemata, which are shorter in the maxilla, so that teeth overlap in lateral view. In the maxilla, P1 is broken but the rest of the postcanine dentition is preserved. P1 would have been placed very close to the upper canine and lingually to it. P2, P3, and P4 are large (the latter less than the others) and worn, while M1 is markedly smaller and less worn than the premolars, preserving a pointed cusp with more evident vertical striae that connects it to the cingulum. In the hemimandible, i2 is broken, while the specimen preserves i1, a large canine, and four postcanine teeth (p1-p4). The mandibular ramus is robust with a wide symphysis. Premolars are large (but p1 is smaller) but preservation and wear do not always allow us to evaluate the finer morphological details. The last premolar, p4, has clear accessory cusplids and a marked lingual cingulum.

5.2. Remarks

The fossil record of seals is rather patchy in time and space (Valenzuela-Toro & Pyenson, 2019). In particular, apart from some monachine remains of uncertain taxonomic placement, an important gap (ca. 2 Ma) separates the holotype partial skeleton of *Pliophoca etrusca* of the Late Pliocene (Piacenzian) of Casa Nuova, Orciano Pisano (Tuscany, Italy; Berta et al., 2015) from the late Early Pleistocene occurrence of *Monachus* at Cueva

Victoria (and Le Vallonnet). *Pliophoca etrusca* is closely related to extant monk seals and shares a large number of morphological traits with *M. monachus* (Berta et al., 2015). In these species (including material assigned to *Pliophoca* cf. *etrusca* by Berta et al., 2015) and in the seal of Cueva Victoria, premolars are large, oriented obliquely, and separated by short diastemata, and the mandibular ramus is robust with a wide symphysis. The seal of Cueva Victoria differs from *P. etrusca* and *Neomonachus* in the more crowded positioning and the related more oblique orientation of postcanine teeth along the mesio-distal axis of the tooth row, also resulting in a larger overlap (especially) between P2 and P3. Collectively, the morphological features observable on the seal remains from Cueva Victoria point to an attribution to *Monachus* and most likely to the Mediterranean monk seal *M. monachus*, although, since the available sample does not allow us to evaluate traits which have been considered diagnostic for the identification of the species in previous studies (Scheel et al., 2014; Berta et al., 2015), we favor an assignment to *Monachus* sp.

6. DISCUSSION

Considering the richness of the fossil record of Cueva Victoria, in terms of diversity and number of remains, it is not surprising that the material studied herein has not been included in the latest systematic revision of the locality (Gibert & Ferràndez-Cañadell, 2015), but it allowed us to complement previous information on the

site while promoting the valorization of its important museum collection. We refrain from detailed taphonomic considerations, as the studied material represents a sub-sample, besides biased towards elements regarded as least significant (hence uncatalogued) in previous research, of the large mammal assemblage known from the site. For instance, equids are abundant at Cueva Victoria (Alberdi & Piñero, 2015) but proportionally even more in the studied sample, probably because there are several remains which are not diagnostic at a species level – and therefore could belong to one or the other of the two species present at the site (Alberdi & Piñero, 2015). The majority of the remains revealed traces of the activity of carnivorans and, when this is not verified, it is generally limited to the smallest and least preserved specimens, corroborating the view that the giant hyena *Pachycrocuta brevirostris* was the primary agent responsible for the accumulation of large mammal remains (Gibert et al., 1992). Indeed, some species recorded at Cueva Victoria evidently did not live in the cave, but their remains were carried inside by the hyenas. Most notably, this is the case with marine mammals such as cetaceans (of which some vertebrae are known) and seals (Fig. 4; Ferrández-Cañadell, 2015). The latter offer the occasion to discuss the potential prey-acquisition-strategy adopted by hyenas when foraging on seals, that is, to attempt to evaluate whether hyenas actively hunted seals, at Cueva Victoria and other Pleistocene sites, or they just scavenged carcasses available in the surrounding.

Today, the populations of brown hyena, *Parahyaena brunnea* (Thunberg, 1820) that live along the Namibian Coast offer an interesting case study, as they indeed actively hunt seals, otherwise being primarily scavengers (Mills, 1982, 1990; Wiesel, 2006). However, although seals represent the main food source for the brown hyenas of the coast of Namibia, they rely on a wide range of resources, and active hunting is mainly directed towards seal pups, while not disregarding the ingestion of carrions (Skinner et al., 1995; Wiesel, 2006; Kuhn et al., 2008). It is also worth noting that Namibian seal colonies represent a resource abundant and available all year round (though with seasonal fluctuations) in an otherwise challenging and unproductive environment, with the Namib Desert on the background. In this situation, brown hyenas adapted to habitually forage on seals, with a greater proportion of killings than observed elsewhere in other populations of the species, and besides also modified their period of activity, being active during day and night, while the species is usually mainly nocturnal (Skinner et al., 1995; Wiesel, 2006; Kuhn et al., 2008).

The fossil assemblage of Cueva Victoria suggests a rather different context. The variety of species recorded at the site indicates, on one hand, the diversity of habitats that were present in the area (e.g., Blain, 2015; Furió, 2015; Sánchez Marco, 2015; García-Nos et al., 2023) and, on the other, that the populations of *P. brevirostris* did not specialize in the consumption of one or few species. Considering the large mammals, Cueva Victoria offers a wide picture of the fauna of the late Early Pleistocene of Europe, besides including some unique elements such as *Theropithecus oswaldi*. In-

deed, apart from relatively rare groups such as suids (Iannucci, 2024b), other absences, for instance, that of hippopotamuses (Ferrández-Cañadell, 2015) are probably of paleoecological significance. In this context, though it is impossible to state it for sure, it seems more likely that the seal remains recovered from Cueva Victoria derived from carcasses exploited by hyenas, rather than from actively hunted individuals. Perhaps, benefiting from a favorable beaching, as is certainly the case with the cetacean remains.

The occurrence of seal remains referable to the genus *Monachus* is documented in the Pleistocene of Mediterranean region in a few sites. Apart from Cueva Victoria, another site of late Early Pleistocene age that yielded seal remains is the cave of Le Vallonnet, along the southern coast of France (de Lumley et al., 1963; 1988). As for Cueva Victoria, the Vallonnet Cave is interpreted has been used as den by hyenas, but also other carnivorans and, most importantly, hominins were also present at the site, as documented by a series of more than 100 lithic pieces and some bones with anthropogenic traces (Echassoux, 2004; Michel et al., 2017; Cauche, 2022). In any case, neither hominins nor hyenas were probably responsible for carrying seal remains inside the cave at Le Vallonnet, as the occurrence of *Monachus* is limited to the stratigraphic ensemble II recognized by the authors, and this unit consists of marine sands which documents the passage of the sea inside the cave (Echassoux, 2004; Michel et al., 2017; Cauche, 2022).

A rather long chronological gap separates the findings from Cueva Victoria and Le Vallonnet from the following seal occurrences in the European Mediterranean, which are known from late Middle Pleistocene sites. One of these, which is not so far from Le Vallonnet, is Lunel-Viel, from which Brugal et al. (2021) reported the presence of three seal teeth assigned to cf. *Phoca* sp.?.; here, however, the faunal assemblage comes entirely from continental deposits, hence suggesting that hyenas were responsible for the accumulation of seal remains (Brugal et al., 2021). At Lunel-Viel, the remains of hyenas are quite abundant and two species are part of the faunal assemblage, *Crocota crocuta* (or *C. intermedia*, or *C. spelaea intermedia*, depending on different taxonomic approaches) and '*Hyaena*' *prisca* (Bonifay, 1971; Brugal et al., 2021). '*Hyaena*' *prisca* is the fossil hyena from the Pleistocene of Europe which is arguably the most intriguing to discuss in relation to the potential foraging on seals. For a start, the species is very close in dental size and proportions to the brown hyena (e.g., Iannucci et al., 2021, Pérez-Claros, 2024), besides, while its fossil record is rather patchy, several occurrences of '*H.*' *prisca* are known from sites located not far from the sea, especially in southern France (Iannucci et al., 2021). On the other hand, Lunel-Viel represents the only site where the co-occurrence of '*H.*' *prisca* and seals is documented so far (Brugal et al., 2021).

In general, there is only one other Middle Pleistocene finding of seal in Mediterranean Europe, based on a phalanx assigned to *Monachus monachus* recovered during recent excavations at Grotta Romanelli, in Apulia, southeastern Italy (Mecozzi et al., 2024). Recent research at Grotta Romanelli led to the revision of the

stratigraphic setting and chronology of this site, which played an important role for the correlations of the European Late Pleistocene (Sardella et al., 2018, 2019; Mecozzi et al., 2021, 2022, and references therein), revealing an older (i.e., late Middle Pleistocene) initial frequentation of the cave by hominins and fauna than previously assumed (Pieruccini et al., 2022). The new seal finding comes from the late Middle Pleistocene levels of Grotta Romanelli (ISU2; Mecozzi et al., 2024), while previous reports listed the presence of the species from the Late Pleistocene (ISU3) and Holocene (ISU5) units (Blanc, 1920, 1928; Sardella et al., 2018; Pieruccini et al., 2022). Although hyenas, here represented by *Crocota*, are known from Grotta Romanelli, their rarity in the fossil assemblage (Blanc, 1920, 1928; Mecozzi et al., 2024) suggests that they were not responsible for the presence of *Monachus*, but rather other carnivores or hominins played a role.

It is worth mentioning the occurrence of *Monachus* cf. *monachus* from a fossiliferous breccia recovered on the small island Formica di Burano (Tuscany, Italy), which was considered of Late Pleistocene age based on the presence of continental mammals, namely, *Cervus elaphus* and *Dama dama* (Azzaroli et al., 1990).

Finally, *Monachus* remains are known from several Late Pleistocene to Holocene localities of Mediterranean Europe, mainly from archaeological sites of Mousterian or Late Glacial-Holocene context, for instance, evidence of monk seal hunting by Epipalaeolithic humans have been discovered in the Nerja Cave in Spain (Morales-Pérez et al., 2019, and references therein).

In brief, conclusive evidence for hyenas foraging on seals in the Pleistocene of Europe is limited to the activity of *P. brevisrostris* at the late Early Pleistocene site Cueva Victoria, with another likely case being represented by the late Middle Pleistocene of Lunel-Viel, where either *Crocota* or '*H. prisca*' might have been responsible for the consumption. Other co-occurrences of hyenas and seals are known (e.g., Grotta Romanelli), but, although this possibility cannot be ruled out, evidence for the direct interaction between the two groups is currently lacking. Still, if not for the action of bone-cracking hyenas, the fossil record of seals (which is biased chronologically and geographically, see Valenzuela-Toro & Pyenson, 2019) in the Pleistocene of Europe would be even scarcer than it is. The occurrence of *Monachus* at Cueva Victoria provides robust evidence of the presence of monk seals in the Mediterranean since at least the late Early Pleistocene.

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