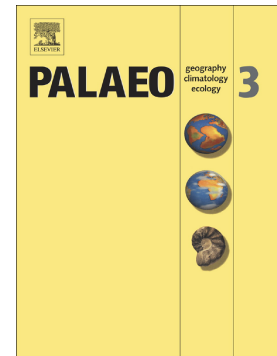


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Palynology and chronology of hyaena coprolites from the Piñar karstic Caves Las Ventanas and Carihuela, southern Spain

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Abstract

This paper presents pollen analyses and radiocarbon dating on *Crocota* coprolites from Las Ventanas (LV) and Carihuela (Car) Caves in southern Spain (Granada), with the aim of reconstructing the environmental conditions of these hominin sites. The LV coprolites are radiocarbon dated from c. 37890 to 6980 cal yr BP, and the Car coprolites from c. 31063 to 7861 cal yr BP. Overall, the palaeoecological scenario inferred from both coprolite series display similar patterns, with *Pinus*, *Poaceae*, and *Artemisia* as dominant during the full Pleistocene, and an important contribution of *Quercus* in the most recently dated coprolite samples. While the palynology is consistent with results of former investigations on the past environments in the region as obtained from other deposits (peat bogs, cave infills), the Late Glacial and Holocene chronology of several

coprolites in both sites is in conflict with the generally accepted timing of extinction of *Crocota* in western Europe. A discussion on the taphonomical processes and potential sources of carbon contamination of the radiocarbon samples is provided. The correlation between pollen from coprolites and from sedimentary records, and the paucity of the fossil bone record suggests nevertheless, that a late survival of *Crocota* in southern Spain should not be categorically discarded.

Keywords: palaeoecology, palaeoanthropology, *Crocota*, Quaternary, Pleistocene, Holocene

1. Introduction

Pollen analysis of coprolites and other fossil faecal materials, although useful in the reconstruction of past flora and vegetation (Scott, 1987; Horwitz and Goldberg, 1989; Carrión et al., 1995a, 1995b, 1999, 2004, 2006, 2007, 2008, 2018; Scott, 1994; Latorre et al., 2002; González-Sampériz et al., 2003; Yll et al., 2006; Marais et al., 2015; Gatta et al., 2016; Daura et al., 2017; De Porras et al., 2017; Williams et al., 2018) and cave taphonomy (Navarro et al., 2000, 2001; Scott et al., 2003; Hunt and Fiacconi, 2018), remains an underutilized resource in palaeoecology. Some of the problems associated with their use include uncertainty about the chronostratigraphic and biological origin of the coprolite. Post-depositional pollen corrosion, biases due to pollen transport, contamination and reworking of palynomorphs complicate the investigation (Carrión et al., 2009; Gatta et al., 2016). Here we report pollen analyses and radiocarbon dating of coprolites plausibly attributed to the spotted hyaena (*Crocota crocuta*) from two adjacent Paleolithic caves in southern Spain, Las Ventanas (LV) and Carihuela (Car) (Fig. 1). With the aforementioned methodological limitations in mind,

our goal is twofold, viz., to decipher the palaeoenvironmental signals of the palynomorphs, and to investigate the age of the coprolites and the demise of *Crocota crocuta* in the region.

2. Physical setting

Las Ventanas Cave (3° 25' 17''W, 37° 24' 54''N) and Carihuela Cave (3° 25' 47''W, 37° 26' 56''N) are located 500 metres apart in Píñar, 45 km northeast of Granada city in southern Spain (Fig. 1). The regional climate is Mediterranean, with a mean annual temperature of 12-15 °C, and a mean annual precipitation of 250-600 mm. The modern landscape is largely utilized for agriculture (wheat, barley, olives, wine grapes) (Wigand 1978). Local woodlands are characterized by *Quercus rotundifolia*, with *Q. faginea* in the wettest areas. Oaks mix with pines at higher elevations while scrub with *Quercus coccifera* is locally more common, with *Pistacia lentiscus*, *Phillyrea angustifolia*, and *Olea europaea* (Carrión, 1990, 1992). Open forests with *Pinus sylvestris* and *P. nigra* are typical above 1600-1800 m (Carrión et al., 1998).

3. The Caves and excavation finds

3.1. Las Ventanas

Las Ventanas and Carihuela are just two of the many caves located in this karstic region (Fig. 1). Las Ventanas Cave, some 1,200 m deep, gets its name from its three entrances (Fig. 2). The main cave axis is orientated easterly from the main entrance. The archaeology dates from before the Upper Palaeolithic to the present, and includes lithics, pottery, and bone remains of different animals and anatomically modern humans (Riquelme and Moreno, 1999; Riquelme, 2002). A palynological study of coprolites

was carried out by Carrión et al. (2001) (revisited by Scott et al., 2003, and Riquelme and Carrión, 2010). A recent study by Cortés-Sánchez et al. (2018) reported pre-Solutrean rock art, including trilinear hind figures, with stylistic and technical traits showing similarities with engravings in the Cantabrian Palaeolithic.

Las Ventanas Cave contains thousands of coprolites in the clayey sediments exposed in a near-to-entrance pit of c. 4 m depth and c. 5 m diameter. The sediments containing the coprolites contain also bone remains of spotted hyaena (*Crocota crocuta* subsp. *spelaea*) and herbivores (*Equus hydruntinus*, *Bos primigenius*, *Cervus elaphus*). Gnawing damage is visible on bone fragments (Riquelme, 1999; Riquelme and Carrión, 2010) (Table 1). A specific latrine area may have been responsible for the great accumulation of coprolites (Brain, 1981).

3.2. Carihuela

Carihuela Cave has acquired relevance as it has been proposed as one of the youngest sites with Neanderthal settlements in Europe (Vega-Toscano, 1993; Carrión et al., 2019). From a geographic point of view, Carihuela and Las Ventanas Caves are both located in the same olistolith (named Píñar) and very close from each other (c. 500 m) (Fig. 1). Nowadays, Carihuela presents three entrances. The main entrance runs in direction N-S and reaches immediately the named Chamber III (CIII) (Fig. 3). A secondary entrance located very close to the main one ends into Chamber I (CI). An abrupt change of direction (towards W) connects CI with Chamber II (CII). This chamber and CIII are connected by a narrow and short corridor. CIII narrows and leads to Chamber IV which opens in NW-SE direction. From the south wall of CIV an eastward opening leads down into Chamber V (CV).

Carihuela has been excavated by four teams. The first systematic excavations

were carried out by J.-Ch. Spahni (1954-1955) (Spahni, 1955a, 1955b) who was interested in the Pleistocene fillings. As the fruit of his works, thousands of Mousterian lithics, as well as bones of Neanderthal and anatomically-modern humans were collected (García-Sánchez, 1960). In addition, the first stratigraphic sequence of Carihuela was proposed. At the end of that decade (1959-1960), M. Pellicer focused a research project on Neolithic and Bronze Age units in CIV Pellicer (1964a, 1964b) (Fig. 3). The interest for the Pleistocene record returns at the end of the Sixties decade. An international team directed by the Washington State University and University Complutense of Madrid excavated from 1969 to 1971 in the Exterior Area (AE), CIII, and CIV (Almagro et al., 1970; Garralda, 1970). The last research project was extended between 1979 and 1992 (Table 1). G. Vega Toscano (University Complutense of Madrid) led a multidisciplinary team that put forward, based on the former proposals, a chronostratigraphical interpretation with 12 lithostratigraphical units (Vega-Toscano et al., 1988) covering the whole Quaternary sequence. The new proposed sequence includes some 50 archaeological levels with Mousterian artefacts (Vega-Toscano, 1990), the uppermost layers in unit IV-3 providing a Middle Palaeolithic (*sensu lato*) assemblage. In addition, a supposed Upper Paleolithic assemblage has been associated to unit III. Nevertheless, such set remains unknown. Units II and I mainly contained recent prehistory material, the most of them being associated with Neolithic times. Notwithstanding, some of them at Unit I are ascribed to Bronze Age (Pellicer, 1964a; Wigand, 1978).

Homo neanderthalensis remains are mainly placed at CIII and are encompassed between VIII and lowermost IV (García Sánchez, 1960; Jiménez-Arenas et al., 2019). In addition, some of them were collected at CII unit VIII (García Sánchez, 1960; De Lumley and García Sánchez, 1971), CI AE (García-Sánchez et al., 1990, 1994), CIII 1

unit VI, and CIV 1 unit VI (Vega-Toscano, 1988). At least two molars and a premolar from CI, CIII and CIV appear to be Neanderthal (du Souich Henrici and Jiménez Brobeil, 2011). Lastly, three Neanderthal teeth corresponding to a right mandibular series are stored at the Granada's Archaeological Museum (GAM) (Jiménez-Arenas et al., 2016). Concerning pre-Neolithic anatomically modern human, two fragments are housed at the GAM. The first one is a small fragment of parietal collected at CIII, uppermost unit IV, assigned to *Homo sapiens fossilis* (sic.) based on tabular bone thickness (García-Sánchez, 1960; Vega-Toscano, 1988, Jiménez-Arenas et al., 2019). The second one is a right hemimandible excavated at the same chamber unit III that conserves the postcanine series. DNA analysis has revealed an Epipaleolithic genomic structure of the latter individual (Olalde et al., 2019). Finally, a rich collection of anthropological remains have been collected from the Neolithic and Bronze Age levels in CIV and CV (Wigand, 1978).

In a recent review, the chronology and palaeoecology of Carihuela has been reported by Carrión et al. (2019). It is worth to note that the archaeological deposits of the Carihuela Cave have provided an excellent palynological record. From a quantitative point of view there are relatively high pollen concentrations, and a considerable number of pollen taxa. Besides, it has allowed to establish correlations between the percentages and concentrations of pollen with the ecological consistency of the pollen assemblages. Significantly, there is a good level of correspondence between pollen spectra from different sections of the same lithological units. In addition, most sections are polleniferous, allowing much to be done in the difficult context of cave palynology (Carrión and Scott, 1999; Carrión et al., 1999; Navarro et al., 2001, Hunt and Fiacconi, 2018).

The first palaeoecological reconstruction from palynomorphs was carried out by

Carrión (1992) who encompassed five CIII sections containing Middle Palaeolithic artefacts (units XI–IV). Later, CIV Sections 1 and 2 were studied by Carrión et al. (1998). This study included the area excavated by Pellicer (1964a) (Sections 3, 4 and 5 in CIV) and provided both a detailed palynological record and an accurate palaeoecological reconstruction for the Late Glacial and Holocene (Fernández et al., 2007). This research investigated units III-I, which are dated between the Last Glacial Maximum (LGM) (c. 19 cal year BP) and the end of the Bronze Age (c. 1.17 cal year BP) (Fig. 3). Recently, Carrión et al. (2018) focused on pollen analysis of three Pleistocene hyaena coprolites housed at the Archaeological Museum of Granada.

4. Material and methods

The coprolites (LV) sampling was conducted near the cave entrance from the pit where they were preserved in outcrop sediments (Table 2, Fig. 2), the same area sampled by Carrión et al. (2001). All the Carihuela coprolite samples were taken from specimens at Granada's Archaeological Museum (Carrión et al., 2019) (Table 3).

The colour of the coprolites varied on the outside from brown to yellowish, and inside from pale brown to white (Fig. 4). The morphology of these pellets are coherent with those described by Diedrich (2012) for ice age spotted hyaena (*Crocota crocuta spelaea*) coprolite granulates from the European Pleistocene. In addition, their association with bone fragments of spotted hyaena and the prey of the hyaenas is manifestly shown in LV (Carrión et al., 2001; Riquelme, 2002; Cortés et al., 2018), confirming that these animals were present at the locality. Furthermore, other carnivore species are unlikely to be responsible for these fossil scats. Droppings of *Hyaena* (striped hyaena) are discernibly smaller than those of *Crocota*, and bone fragments are rarely visible (Horwitz and Goldberg, 1989). Some droppings with bone fragments

better preserved may belong to *Canis lupus* (Larkin et al., 2000). On the other hand, large felids are excluded, as Turner (1992) suggests, as their dentition only allows them to consume flesh, not bone. In LV, *Crocota* is the main carnivore (Riquelme, 2002), but in Carihuela, there are bone remains of *Crocota*, *Canis*, *Vulpes* and *Panthera* in the Pleistocene levels (Vega-Toscano, 1988). Likewise, *Vulpes* and *Canis* persist in the Neolithic (Wigand, 1978). The two caves are nevertheless very close, and it is therefore likely that the carnivores explored the vicinity of both caves, regardless of where they established and made their dens.

In addition, surface layers of the coprolites were cut open with a steel spatula, and a large amount of material from the centre was scraped out to minimize contamination from external face. For the extraction of palynomorphs, the "Classic Chemical Method" was followed (Dimbleby, 1985; Erdtman, 1969), with the modifications proposed by Girard and Renault-Miskovsky (1969). The pollen sum varied between 118 and 496 pollen grains. The pollen count data was treated with the *p-simpoll* software in order to obtain the pollen diagrams (Bennett, 2000) (Figs. 5-8). Along with spores and non-pollen microfossils, we excluded the pollen grains of Asteraceae from the total pollen sum because it is assumed that this group is overrepresented in some of the samples studied, as a consequence of local overdeposition. Fungal spores were not counted as they were largely sordariaceous ascospores, customarily occurring in different kinds of fossil dung (van Geel et al., 1989).

5. Chronology

Radiocarbon dating for LV coprolites achieved here conform to a period from 37,890 to 6980 cal yr BP approximately (Table 2, Figs. 5-8). *Crocota* teeth give three

radiocarbon dates of c. 43,004 (TLV2), 42,596 (TLV1) and 31,444 cal yr BP (TLV3) (Table 2). Dates on coprolites by Carrión et al. (2001) gave 12,780, and 10,871 cal yr BP, suggested that the coprolite collection would span a period of at least 1000 years at the transition between the Upper Pleistocene and the Holocene. However, each of those dates derived from a group of coprolites, and in view of the dating results presented here, it is more likely that the time interval they represent is wider than previously published. In other words, those two determinations might represent average ages.

For the current study, most determinations are on total organic carbon in AMS or conventional radiocarbon dating. However, in five of the LV samples, the coprolites were analysed segregating the carbon and organic fractions, leading to two determinations per sample. In these five coprolites, the carbonate fraction gave ages considerably younger than the organic fraction. LV16, LV18, LV19, LV20 and LV23 respectively gave ages of c. 25,341, 23,098, 22,773, 21,162, and 7146 cal yr BP for the organic fractions, and c. 5664, 6868, 6516, 4172, and 4595 cal yr BP for the carbonate fractions (suggesting that the carbonate was precipitated considerably later than the formation of the coprolites). The chronology of the Carihuela coprolites range from c. 31,063 to 7861 cal yr BP approximately (Table 3). All Carihuela determinations were AMS measurements on total organic carbon.

Several possibilities arise for interpreting the coprolite chronology (Tables 2 and 3). Firstly, that the hyaenas were living in the cave over the period represented by the radiocarbon dating series, e.g. from final MIS 3 (43-30 ka) to mid Holocene. This long survival is unexpected in view of the lack of fossil bone evidence of hyaenas in Europe. It is currently accepted that European spotted hyaenas disappeared by the end of the Pleistocene (Varela et al., 2010; Stuart and Lister, 2014). However, available dates for the last hyaenas in central and northern Europe may not reflect what happened in the

southern Iberian Peninsula where their survival lasted longer in an area that served as a geographical refuge for Pleistocene mammal populations (O'Regan et al., 2002). Figure 9 shows all the direct (dates on bones of the species) and associated (dates on material in the same layer) dates of *Crocota crocuta* in Europe uncal yr BP (based on uncalibrated radiocarbon dates) (modified and updated from Knul, 2018). This confirms the general view that hyaenas did not survive the LGM in northern Europe confirming the results published by Stuart and Lister (2014). The associated dates are most likely to be unreliable as they will include dates on younger material associated with reworked hyaena remains. Stuart and Lister (2014) rejected all the late occurrences they redated but as shown by the Holocene dates for mammoth on Wrangel Island the latest dates of megafaunal species can change (Vartanyan et al., 1993). The direct dates show an absence of *Crocota* dates outside of Mediterranean Europe post 20 thousand years ago. Both late dates, one on a coprolite from Italy and one from the United Kingdom on a hyaena mandible, are deemed too young (Dinnis et al., 2016; Gatta and Rolfo, 2017). It is interesting to note that Iberia has a low number of dates compared to northern Europe. It is therefore possible that dating of new materials in the next future bring more dates supporting the late survival of *Crocota*.

Another possible problem with the dating of the coprolites at Carihuela and Las Ventanas Cave may be that they may have been produced during a shorter interval within the Pleistocene than the time represented by the dated hyaena teeth at the cave (c. 43-31 cal yr BP). In this case, the younger dates, in fact the majority, would have been affected by contamination. Several authors have emphasized that contamination by recent carbon assimilation might be common in coprolites and therefore, dating of these may be a poor choice (Bon et al., 2012; Gatta, 2017).

A third, intermediate possibility is that the hyaenas persisted for an unknown length of time after 31000 cal yr BP. Interestingly, *Homo neanderthalensis* remains disappeared from Carihuela after deposition of basal unit IV (García-Sánchez, 1960; Vega-Toscano, 1988; Jiménez-Arenas et al., 2019), which according to Carrión et al. (2019), is late MIS 3 (Fig. 8). *Homo sapiens* occupied caves only from Neolithic and Bronze Age times onward (Wigand, 1978; Fernández et al., 2007). Carnivorous scavenging is thought to be responsible for carrion derived from modern human remains in uppermost unit IV, where the bones were found in a highly modified flint assemblage with hyaena coprolites in the absence of hearths (Vega-Toscano, 1988). The artefacts could have been derived from colluvial reworking of underlying sediments in the entrance area of the cave (Fig. 3). Whether hyaenas alone frequented the cave at this time and for how long, is an interesting matter of future taphonomical research. We know little about the complex interaction of cave hyaenas and humans during the late Pleistocene (Rosell et al., 2012) and how they differed between the two caves.

6. Palynology and past vegetation

In LV, 8 out of 27 coprolite analysed samples contained pollen grains, and the corresponding pollen spectra were added to the 10 samples (LV1-LV10) reported by Carrión et al. (2001) (Figs. 5, 6 and 8). The dominant pollen across all samples is that of Poaceae, *Pinus*, *Artemisia*, *Quercus* (evergreen and deciduous), and to a lesser extent, Asteraceae (Asteroideae and Cichorioideae), *Juniperus*, Amaranthaceae, *Ephedra distachya*, *Plantago* and Lamiaceae. Other taxa, generally below 2%, occur frequently such as *Alnus*, *Olea*, *Cistus*, *Helianthemum*, *Buxus*, *Betula*, *Rhamnus*, Brassicaceae, Liliaceae and Ranunculaceae. Other woody plants (*Pinus pinaster*, *Abies*, *Acer*, *Salix*,

Ulmus, *Juglans*, *Corylus*, *Taxus*, *Sorbus*, *Myrtus*, *Pistacia*, *Viburnum*, *Ephedra fragilis*, *Sambucus nigra*, *Hedera*, *Berberis*) and herbs occur more sporadically.

Most LV coprolite pollen spectra are co-dominated by two or three of the main pollen contributors, with particular relevance of Poaceae. However, there are exceptions such as LV13 (dominated by *Pinus*), LV5, LV6, LV8 (*Artemisia*), LV2 (*Plantago*), LV11 (Cichorioideae), and LV16 (Poaceae). The samples LV23, LV22 and LV21 show high percentages of deciduous and to a lesser extent, evergreen *Quercus*.

A mosaic landscape can be inferred from the LV pollen spectra, with grasslands, pine forests, and *Artemisia* steppe with juniper. The abundance of *Quercus* in several samples, and the presence of *Abies*, *Betula*, *Corylus*, *Alnus*, *Salix*, *Acer*, *Juglans*, *Sorbus*, *Taxus*, *Myrtus*, *Olea*, *Pistacia*, *Myrtus*, *Buxus*, *Viburnum*, *Cistus*, and *Ephedra fragilis*, among others, suggested that oak forests with temperate trees and thermo-Mediterranean scrub persisted during the upper Pleistocene in some locations, plausibly in the valleys under less continental conditions of the Betic mountains.

Regardless of the expected mosaic nature of the pollen-producing vegetation landscape and the taphonomical disparity between LV pollen assemblages (Carrión et al., 1999, 2009; Hunt and Fiacconi, 2018; Navarro et al., 2000, 2001) the dating of the coprolites raises the question of whether the pollen diagram (Figs. 5-8) reflects (i) a temporal sequence of events from MIS 3 to Holocene, or (ii) a shorter time interval in the late Pleistocene. The alternative is that it represents (iii) an indeterminable time framework after 31,000 cal yr BP (Table 2). It is interesting, however, that samples LV23 (7146 cal yr BP), LV22 (18,062 cal yr BP), and LV21 (19,236 cal yr BP) are oak dominated, similar to their chronological counterpart in the Carihuela sediment pollen sequence (Carrión et al., 2019) (Figs. 7, 8).

In Carihuela, 5 out of 13 coprolite samples contained pollen. Characteristically accompanied by *Amaranthaceae* and *Ephedra*, *Artemisia* predominates in Car6 and Car2, and is still abundant in Car1. Conversely, *Pinus* and *Poaceae* rise when *Artemisia* declines. The few indicators of Mediterranean and temperate forest in Car1 (*Quercus*, *Corylus*, *Myrtus*, *Salix*, *Phillyrea*) are absent in Car6 and Car2. In contrast, Car11 and Car13 are dominated by deciduous and evergreen *Quercus* with continuous occurrences of *Corylus*, *Taxus*, *Betula*, *Alnus*, *Berberis*, *Myrtus*, *Salix*, and important contributions of *Poaceae*, *Olea*, *Phillyrea*, *Pistacia*, *Genista*, and *Ericaceae* in Car13, and *Juniperus* and *Olea* in Car11.

The pollen spectra from coprolites in both caves reflect some of the pollen zones described in the cave sediment pollen sequence of Carihuela Cave (Carrión, 1992; Carrión et al., 1998, 1999, 2019; Fernández et al., 2007) which has been correlated with the reference pollen sequence of the Padul peatbog (Camuera et al., 2019) (Fig. 8). Thus, Car6, Car2, and LV11 resemble sediment pollen zones 13 and 14 (unit V) (Carrión et al., 2019). LV13 contains pollen spectra similar to the sediment pollen zone 15 (unit V). Car1, LV16 and LV19 correlate well with sediment pollen zones 15-17 (unit IV), while LV15 is closer to pollen zone 16. The pollen spectra found in Car13, Car11, and LV23 are similar to those in the Holocene pollen zone 20. Similarly, the pollen spectra from LV21 and LV22 show high oak frequencies such as pollen zone 17 (Fig. 8).

In general, full Pleistocene samples are dominated or co-dominated by *Pinus*, *Poaceae*, and *Artemisia*, while Late Glacial and Holocene records are dominated by *Quercus*. Admittedly, contamination may have affected pollen assemblages post-depositionally. This explanation cannot be categorically discarded although precautions were taken to avoid contamination. However, there are no features of recent or

reworked palynomorphs in the LV and Car coprolite pollen spectra. Thus, while taphonomical studies are being carried out, the correlation between coprolite and sediment pollen supports the view that *Crocota crocuta* survived for a long time during the Pleistocene and even survived up to the early Holocene of southern Spain.

7. Conclusions

It is clear that the use of radiocarbon dating of hyaena coprolites, or of bones of other carnivores where available, may be troublesome. It may be that the cortical cracks of coprolites and/or other post-depositional processes such as their exposure to the open air, movement into the cave or sedimentary context, may facilitate carbon contamination. Therefore in this study we relied on the organic contents for dating. Similarly, we do not know if this may involve pollen that is not contemporary with the original production of the coprolite but we utilised the centre of coprolites for pollen analyses to avoid contamination as far as possible. Karstic contexts pose an additional problem, as carbonate carbon can distort the actual age of the coprolites. However, notwithstanding the possible problems, the chronology of the coprolites of Las Ventanas and Carihuela includes recent dates as young as Holocene, and the palynological characteristics support this attribution. Therefore, we present evidence for a later survival of *Crocota* in southern Spain than previously inferred. This is interesting if considered in the context of an alternation between human and carnivore occupations in the cave system. This study sheds some light on the complexity of the human occupations at Las Ventanas and Carihuela Caves. A long continuous Neanderthal occupation should have finished at the end of the MIS 3. The increase of *Crocota* occupation could be indicative of a dramatic reduction of the human occupation from c. 43,000 yr BP onwards. Nevertheless there is a late persistence of the Mousterian

technocomplex at Carihuela followed by a significant human occupation hiatus during the end of the Pleistocene and the beginning of the Holocene. Lastly, by the Neolithic, modern humans occupied intensively the site and left an important archaeological record. We cannot determine precisely when the Píñar hyaena occupation ended, but if it happened as late as the early Holocene as indicated here, a review of the chronology of the European extinction of *Crocota* should be considered. According to literature, *Crocota* became extinct in north-west and southern Europe between c. 31000 and 21000 cal year BP. A new dating program, possibly accompanied by a phylogeographic study using aDNA across the region, may clarify these uncertainties. This, in turn, may have important implications for the human occupation of Iberia where there appears to be exclusive occurrences with cave systems of the two species.

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FIGURE LEGENDS

Figure 1. Location of Las Ventanas and Carihuela Caves in the Monte del Castillo de Piñar, and the Padul peat-bog in the Sierra Nevada (Granada, southern Spain). Redrawn from Fernández et al. (2007) and Carrión et al. (2019).

Figure 2. Longitudinal section of Las Ventanas Cave, showing the situation of the pit where coprolites were sampled, near the entrance. Modified from Riquelme (2002).

Figure 3. Longitudinal section of Carihuela Cave, showing the situation of the chambers, stratigraphical sections and sedimentological units studied palynologically (Carrión, 1992; Carrión et al., 1998, 2019; Fernández et al., 2007). Redrawn from Fernández et al. (2007).

Figure 4. Coprolite specimens from Carihuela Cave (a-f) and Las Ventanas Cave (g-l).

Figure 5. Percentage pollen diagram of coprolite samples from Las Ventanas Cave (trees and shrubs).

Figure 6. Percentage pollen diagram of coprolite samples from Las Ventanas Cave (herbaceous types, spores and non-pollen palynomorphs; Asteraceae and spores excluded from pollen sum).

Figure 7. Percentage pollen diagram of coprolite samples from Carihuela Cave. Coprolites Car-1, Car-2 and Car-6 formerly published in Carrión et al. (2019). Asteraceae and spores excluded from pollen sum.

Figure 8. Coprolite chronology of Las Ventanas and Carihuela in the framework of a tentative correlation between the pollen sequences of Carihuela (Carrión, 1992; Carrión et al., 1998; Fernández et al., 2007) and Padul (Camuera et al., 2018). Red and blue numbers indicate forest and steppe maxima, respectively, in the Padul pollen sequence and their counterparts at Carihuela. Redrawn from Carrión et al. (2019). Also, a synthetic pollen diagram of coprolites from Carihuela and Las Ventanas (Figs. 5, 6, 7)

has been drawn including *Pinus* (*Pinus* and *Pinus pinaster*), Poaceae, and Mediterranean forest (evergreen *Quercus*, *Pinus pinaster*, *Viburnum*, *Buxus*, *Olea*, *Pistacia*, *Myrtus*, *Phillyrea*, *Ephedra fragilis*, Ericaceae, *Cistus* and *Helianthemum*).

Figure 9. Sites with all the direct (bones of the species) and associated (material in the same layer) dates of *Crocota crocuta* in Europe between 60000 and 10000 years (based on uncalibrated radiocarbon dates) (modified and updated from Knul, 2018).

Table 1 Fossil vertebrate remains from Piñar Caves (Ruiz-Bustos and García-Sánchez, 1977; Sevilla García, 1988, 1989; Vega-Toscano, 1988).

Carihuela
<i>Testudo</i> sp. (Vega Toscano, 1988)
<i>Lacerta</i> sp. (Vega Toscano, 1988)
<i>Pyrrhocorax alpinus</i> (Vega Toscano, 1988) (reported by Koby and Spahni, without additional confirmation)
<i>Turdus viscivorus</i> (Vega Toscano, 1988) (reported by Koby and Spahni, without additional confirmation)
<i>Merula</i> sp. (Vega Toscano, 1988) (reported by Koby and Spahni, without additional confirmation)
<i>Apodemus</i> cf. <i>flavicollis</i> (Ruiz Bustos and García Sánchez, 1977) <i>A. sylvaticus</i> (Vega Toscano, 1988)
<i>Eliomys quercinus</i> (Ruiz Bustos and García Sánchez, 1977) <i>E. q. quercinus</i> (Vega Toscano, 1988) <i>E. q. lusitanicus</i> (Vega Toscano, 1988)
<i>Arvicola sapidus</i> (Ruiz Bustos and García Sánchez, 1977)
<i>Pitymys duodecimcostatus</i> (Ruiz Bustos and García Sánchez, 1977)
<i>Clethrionomys glareolus</i> (Vega Toscano, 1988)
<i>Sorex araneus</i> (Ruiz Bustos and García Sánchez, 1977) <i>S. cf. minutus</i> (Vega Toscano, 1988)
<i>Microtus nivalis</i> (Ruiz Bustos and García Sánchez, 1977) <i>M. arvalis</i> (Ruiz Bustos and García Sánchez, 1977) <i>M. cf. Dentatus</i> (Ruiz Bustos and García Sánchez, 1977) <i>M. cabreræ</i> (Vega Toscano, 1988)
<i>Pliomys lenki</i> (only one upper M3) (Ruiz Bustos and García Sánchez, 1977)
<i>Dicrostonyx andaluciensis</i> (Ruiz Bustos and García Sánchez, 1977)
<i>Allocricetus bursae</i> (Ruiz Bustos and García Sánchez, 1977)
<i>Erinaceus europaeus</i> (Ruiz Bustos and García Sánchez, 1977)
<i>Crocidura</i> sp. (Ruiz Bustos and García Sánchez, 1977) <i>C. suaveolens</i> (Vega Toscano, 1988) <i>C. russula</i> (Vega Toscano, 1988)
<i>Neomys</i> cf. <i>anomalus</i> (Vega Toscano, 1988)
<i>Suncus</i> sp. (Vega Toscano, 1988)
<i>Equus caballus</i> cf. <i>germanicus</i> (Vega Toscano, 1988) <i>E. hydruntinus</i> (Vega Toscano, 1988)
<i>Sus scrofa</i> (Vega Toscano, 1988)
<i>Stephanorhinus</i> (<i>Dicerorhinus</i>) <i>kirchbergensis</i>
<i>Coelodonta antiquitatis</i> (reported by Koby and Spahni, without additional confirmation) (Vega Toscano, 1988)
<i>Cervus elaphus</i> (Vega Toscano, 1988)
<i>Capreolus</i> sp. (Vega Toscano, 1988)
<i>Capra</i> sp. (Vega Toscano, 1988)
<i>Bison</i> sp. (Vega Toscano, 1988)
<i>Bos primigenius</i> (Vega Toscano, 1988)
<i>Crocota</i> sp. (Vega Toscano, 1988)

<i>Canis lupus</i> (Vega Toscano, 1988)
<i>Ursus</i> sp. (Vega Toscano, 1988)
<i>Panthera</i> sp. (Vega Toscano, 1988)
<i>Vulpes</i> sp. (Vega Toscano, 1988)
<i>Lepus capensis</i> (Vega Toscano, 1988)
<i>Oryctolagus cuniculus</i> (Vega Toscano, 1988)
<i>Myotis myotis</i> (Sevilla García, 1988, 1989)
<i>M. myotis/blythi</i> (Sevilla García, 1988, 1989)
<i>M. natterei</i> (Sevilla García, 1988, 1989)
<i>M. emarginatus</i> (Vega Toscano, 1988)
<i>M bechsteini</i> (Sevilla García, 1988, 1989)
<i>Plecotus auritus/austriacus</i> (Sevilla García, 1988, 1989)
<i>P. austriacus</i> (Sevilla García, 1988, 1989)
<i>Rinolophus euryale</i> (Sevilla García, 1988, 1989)
<i>R. mehelyi</i> (Sevilla García, 1988, 1989)
<i>R. euryale/mehelyi</i> (Sevilla García, 1988, 1989)
<i>R. hipposideros</i> (Sevilla García, 1988, 1989)
<i>R. ferrumequinum</i> (Sevilla García, 1988, 1989)
<i>Barbastrella bastastellus</i> (Sevilla García, 1988, 1989)
<i>Eptesicus serotinus</i> (Vega Toscano, 1988) (reported by Koby and Spahni, without additional confirmation)
<i>Miniopterus schreibersi</i> (Sevilla García, 1988, 1989)

Table 2 Radiocarbon dating results of hyaena samples from Las Ventanas Cave. Radiocarbon Laboratory: (CNA) Centro Nacional de Aceleradores Sevilla, (Poz) Poznan Radiocarbon Laboratory, (Beta) Beta Analytic Miami, (GrA) Groningen Accelerator. Calibration: OxCal v4.3.2 Bronk Ramsey (2017); r:5; IntCal13 atmospheric curve (Reimer et al. 2013). HTc=hyaena tooth collagen (*published in Cortés et al., 2018). TOC=coprolite total organic carbon. OF=coprolite organic fraction. CF=coprolite carbonate fraction. S=coprolite collection (** published in Riquelme and Carrión, 2010). P=polleniferous, NP=palynologically sterile. In bold specimens dated for both CF and OF.

Sample	Lab N°	Method	Material	yr BP	cal yr BP	Midpo cal yr	Pollen
CV-8B	CNA-674c	AMS	TOC	6095 ± 45	6805 - 7156	6980	-
LV-23	Beta-286454	AMS	CF	4010 ± 40	4410 - 4780	4595	P
LV-23	Beta-284644	AMS	OF	6260 ± 40	7024 - 7268	7146	P
CV-8	CNA-674R	AMS	TOC	7530 ± 35	8215 - 8409	8312	-
7 items	Gra-13533	AMS	S**	9500 ± 50	10589 - 11080	10834	P
CV-7	CNA-673R	AMS	TOC	10410 ± 60	12061 - 12529	12295	-
5 items	Beta-141051	AMS	S**	10670 ± 40	12567 - 12707	12637	P
CV-6	CNA-672R	AMS	TOC	11730 ± 90	13401 - 13755	13578	-
LV-22	Poz-43338	Conventional	TOC	14840 ± 70	17857 - 18267	18062	P
LV-36	Poz-57792	Conventional	TOC	15040 ± 50	18077 - 18446	18261	NP
LV-21	Poz-43336	Conventional	TOC	15940 ± 120	18932 - 19540	19236	P
LV-20	Beta-286452	AMS	CF	3790 ± 40	3994 - 4350	4172	NP
LV-20	Beta-284642	AMS	OF	17520 ± 60	20921 - 21403	21162	NP
LV-28	Poz-57788	Conventional	TOC	18750 ± 60	22426 - 22817	22621	NP
LV-19	Beta-285846	AMS	CF	5700 ± 40	6405 - 6628	6516	P
LV-19	Beta-284646	AMS	OF	18920 ± 80	22525 - 23021	22773	P
LV-18	Beta-285845	AMS	CF	6030 ± 40	6755 - 6981	6868	NP
LV-18	Beta-284645	AMS	OF	19140 ± 70	22822 - 23374	23098	NP
LV-33	Poz-	Conventional	CF	19270	22949 -	23219	NP

	57791			± 80	23490		
LV-16	Beta-286453	AMS	CF	4930 \pm 40	5595 - 5733	5664	P
LV-16	Beta-284643	AMS	OF	20990 \pm 80	25107 - 25576	25341	P
LV-30	Poz-57789	Conventional	OF	21350 \pm 100	25455 - 25901	25678	NP
LV-15	Poz-43335	Conventional	TOC	23140 \pm 100	27221 - 27642	27431	P
LV-31	Poz-57790	Conventional	TOC	25750 \pm 130	29499 - 30409	29954	NP
TLV3	CNA-669	AMS	HTc *	27500 \pm 300	30913 - 31976	31444	-
LV-12	Poz-38318	Conventional	TOC	28800 \pm 500	31566 - 33831	32698	NP
LV-13	Poz-38279	Conventional	TOC	29380 \pm 320	32808 - 34121	33464	P
LV-14	Poz-38280	Conventional	TOC	29730 \pm 290	33337 - 34423	33880	NP
LV-11	Poz-37429	Conventional	TOC	33700 \pm 600	36393 - 39388	37890	P
TLV1	Beta-289558	AMS	HTc	38590 \pm 370	42085 - 43107	42596	-
TLV2	Beta-289559	AMS	HTc	39150 \pm 420	42346 - 43663	43004	-

Table 3 AMS radiocarbon dating results of Carihuela Cave coprolites according to Carrión et al. (2019). Car-1 to Car-12: specimens obtained from stored material at the Granada Archaeological Museum, derived from excavation campaigns between 1970 and 1971 (Almagro et al. 1970; Garralda, 1970; Vega-Toscano, 1988). Car-13 was sampled by us from the profile where it was embedded. Calibration: OxCal v4.3.2 Bronk Ramsey (2017); r:5; IntCal13 atmospheric curve (Reimer et al. 2013). Suggestions about coprolite-embedded units follow correspondence with WSU excavation levels by Vega-Toscano (1988). The precise position of specimens is unknown. *Coprolites in materials removed from trenches between two current stratigraphical sections

Sample	Lab Nº	Chamber-Section/s	Unit (suggested intervals)	Coordinates (excavation notes)	yr BP	cal yr BP	Midpoint cal yr BP	Industry in "excavation labels"
Car 13	Poz-55205	CIV-3	I-II	701S / 701W	7040 ± 50	7965-7757	7861	Neolithic
Car 11	ETH-49314	CIV-2	I-III	696S / 702W	9543 ± 33	11081-10713	10897	Recent Prehistory
Car 3	ETH-49306	CIV-2	II-III	697S / 701W	11407 ± 36	13323-13143	13233	Neolithic (?)
Car 4	ETH-49307	CIV-2	II-III	697S / 701W	11417 ± 36	13338-13146	13242	Neolithic (?)
Car 10	ETH-49313	CIV-1	I-III	694S / 702W	12100 ± 37	14105-13799	13952	Recent Prehistory
Car 9	ETH-49312	CIV-2	I-IV	698S / 701W	14836 ± 43	18210-17875	18043	"Bronze"
Car 12	ETH-49315	CIV-2-3*	III-V	699S / 701W	16139 ± 48	19644-19277	19461	Final Middle Palaeolithic
Car 5	ETH-49308	CIV 2-3 *	III-V	700S / 701W	16711 ± 74	20405-19939	20172	Early Upper Palaeolithic
Car 8	ETH-49	CIV-2	IV-V	698S / 701W	17691 ± 50	21656-211	21410	Final Middle Palaeolithic

	31 1					64		olithic
Car 1	ET H- 49 30 4	CIII 2-3*	IV-V	507,45S / 508,87W	19499 ± 89	237 81- 231 41	2346 1	Palae olithic
Car 7	ET H- 49 31 0	CIV-2-3 *	III-V	699S / 701W	20551 ± 247	254 04- 241 30	2476 7	Final Middle Palae olithic
Car 2	ET H- 49 30 5	CIII 2-3*	IV-VI	507,45S / 507,50W	26158 ± 188	308 74- 298 66	3037 0	Middle Palae olithic
Car 6	ET H- 49 30 9	CIV-2-3 *	III-V	700S / 701W	27027 ± 205	313 22- 308 03	3106 3	Early Upper Palae olithic

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.

Journal Pre-proof

Highlights

- New pollen analyses and radiocarbon dating on *Crocota* coprolites from Las Ventanas (LV) and Carihuela (Car) Caves.
- The palaeoecological scenario inferred from both coprolite series display similar patterns.
- Timing of extinction of *Crocota* in western Europe.
- A late survival of *Crocota* in southern Spain should not be categorically discarded.

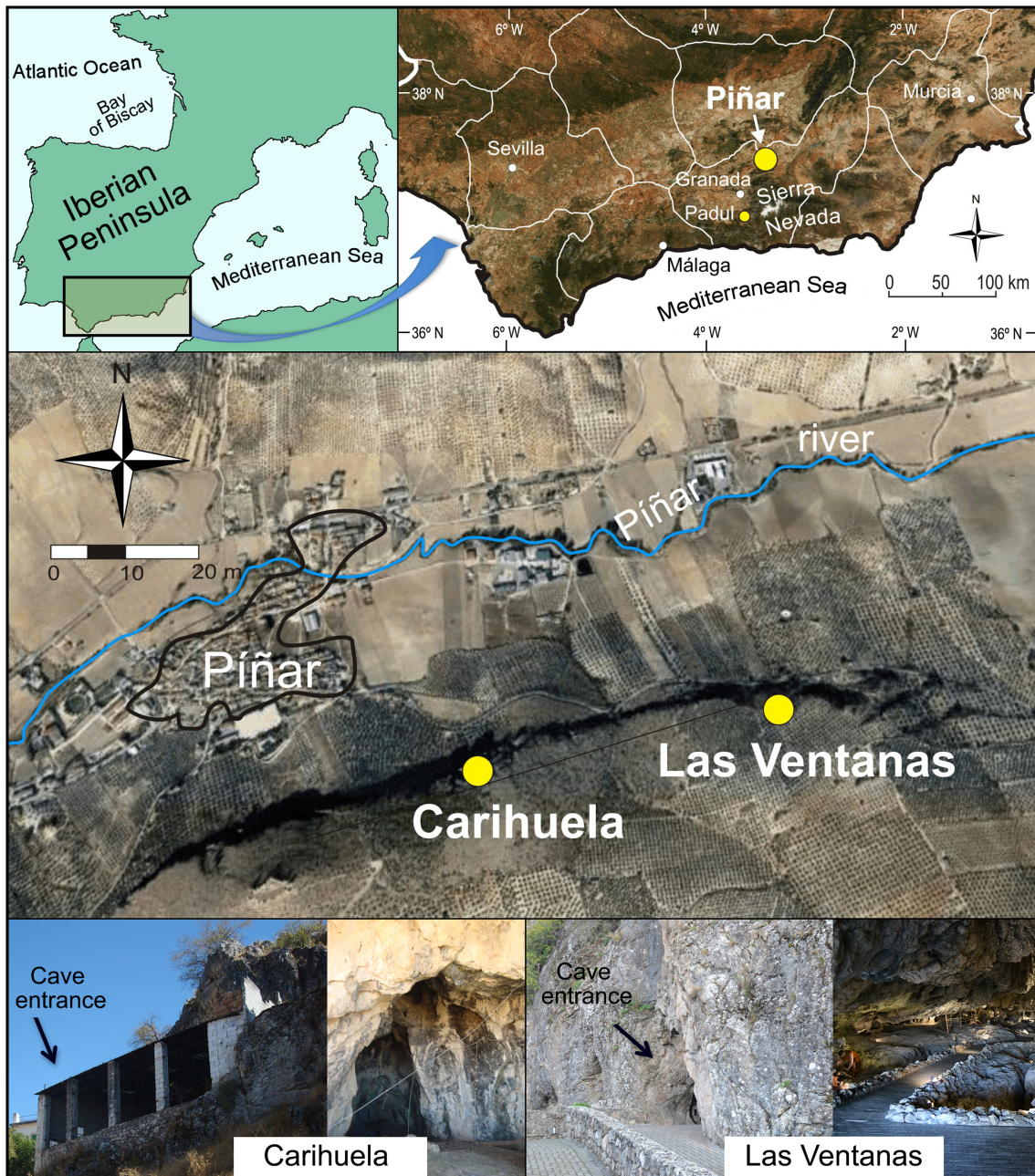


Figure 1

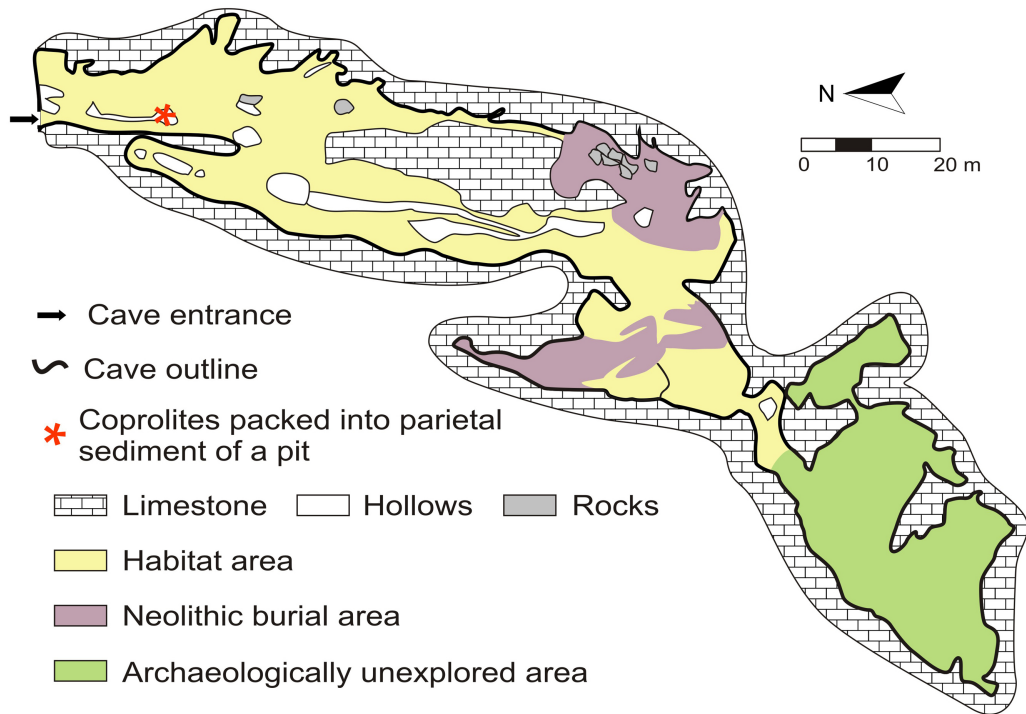


Figure 2

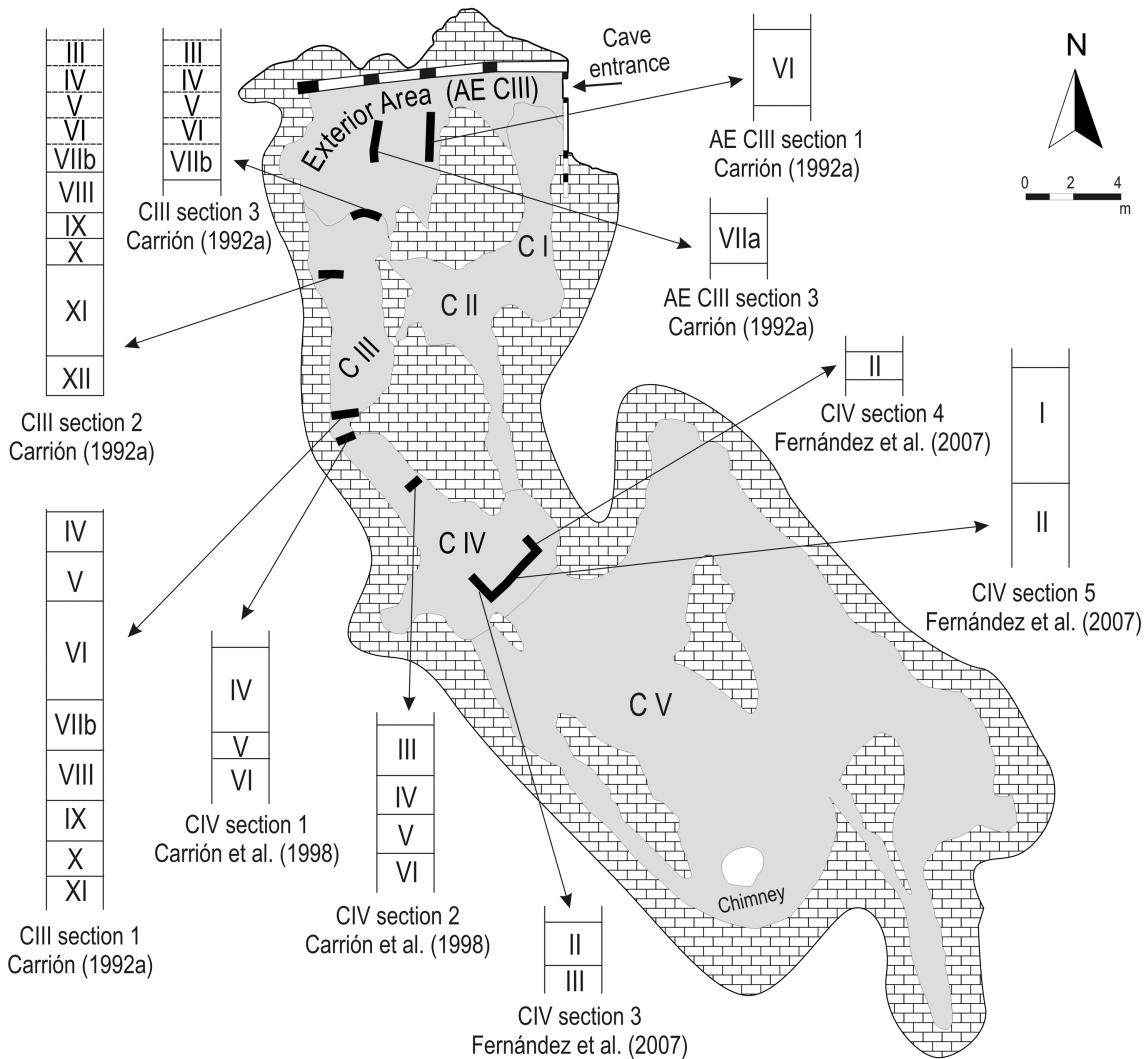


Figure 3

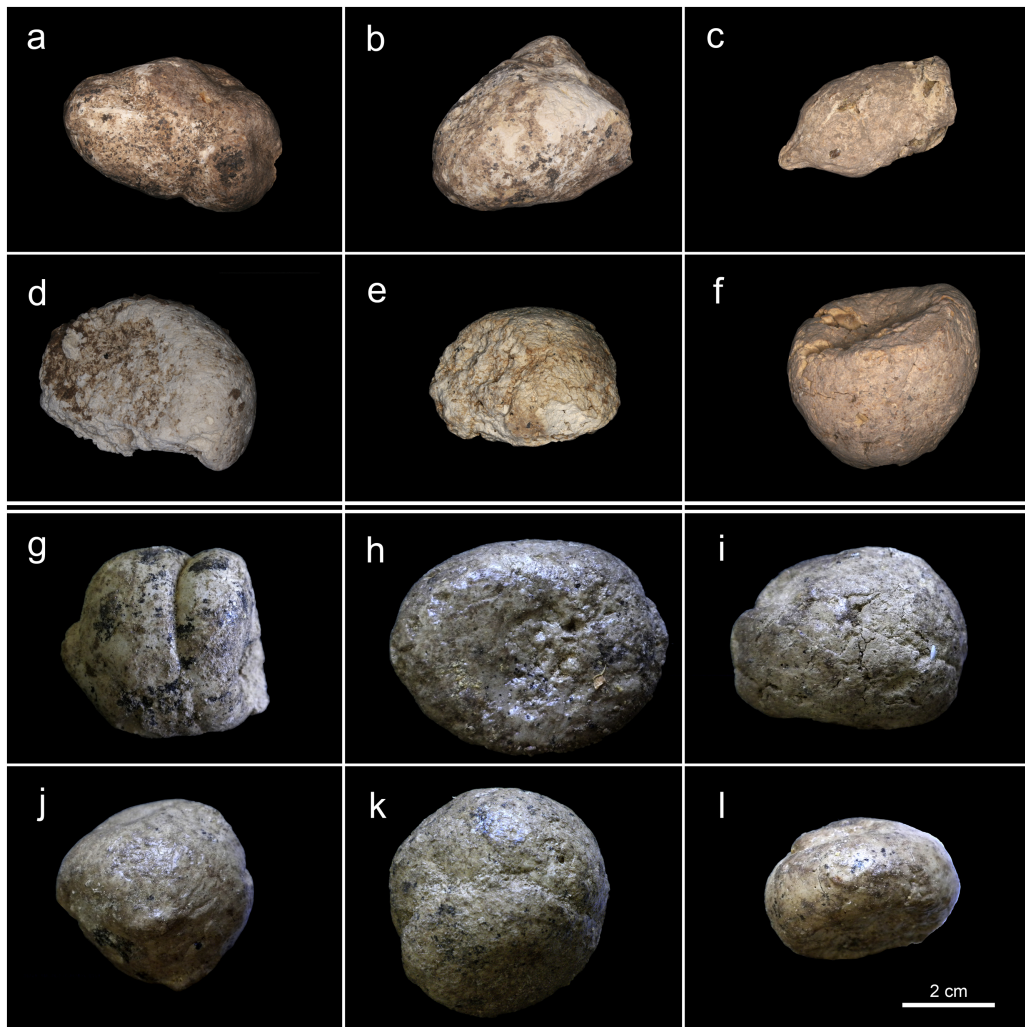


Figure 4

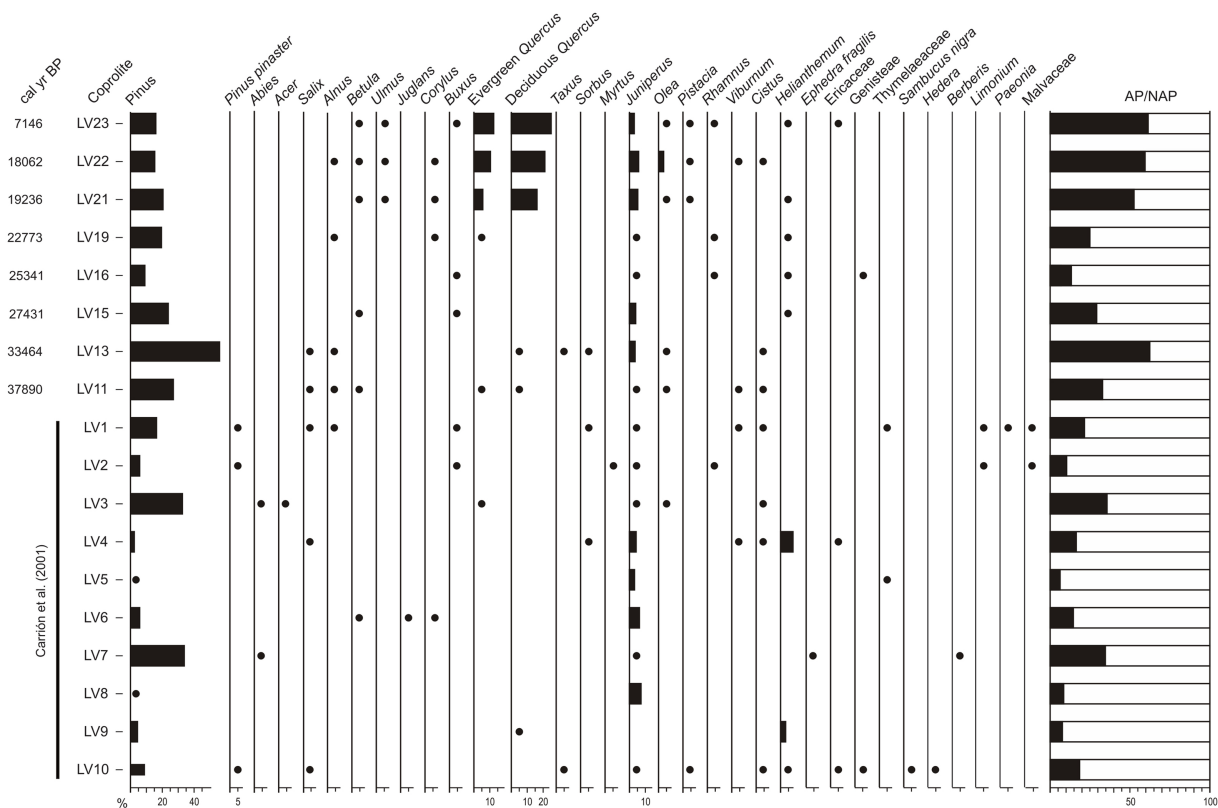


Figure 5

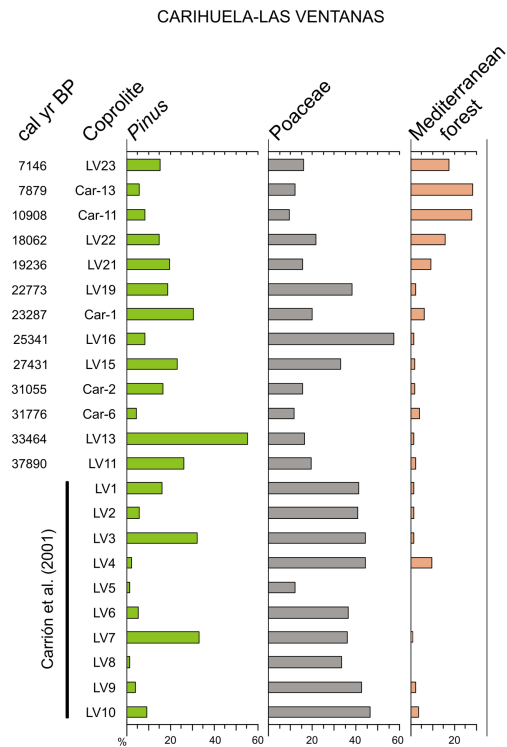
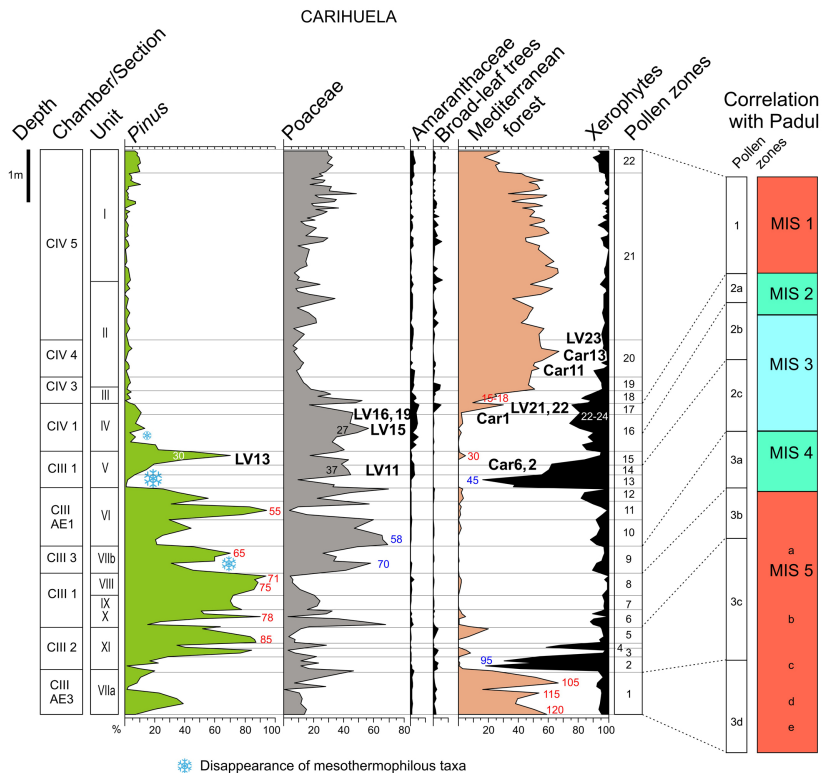
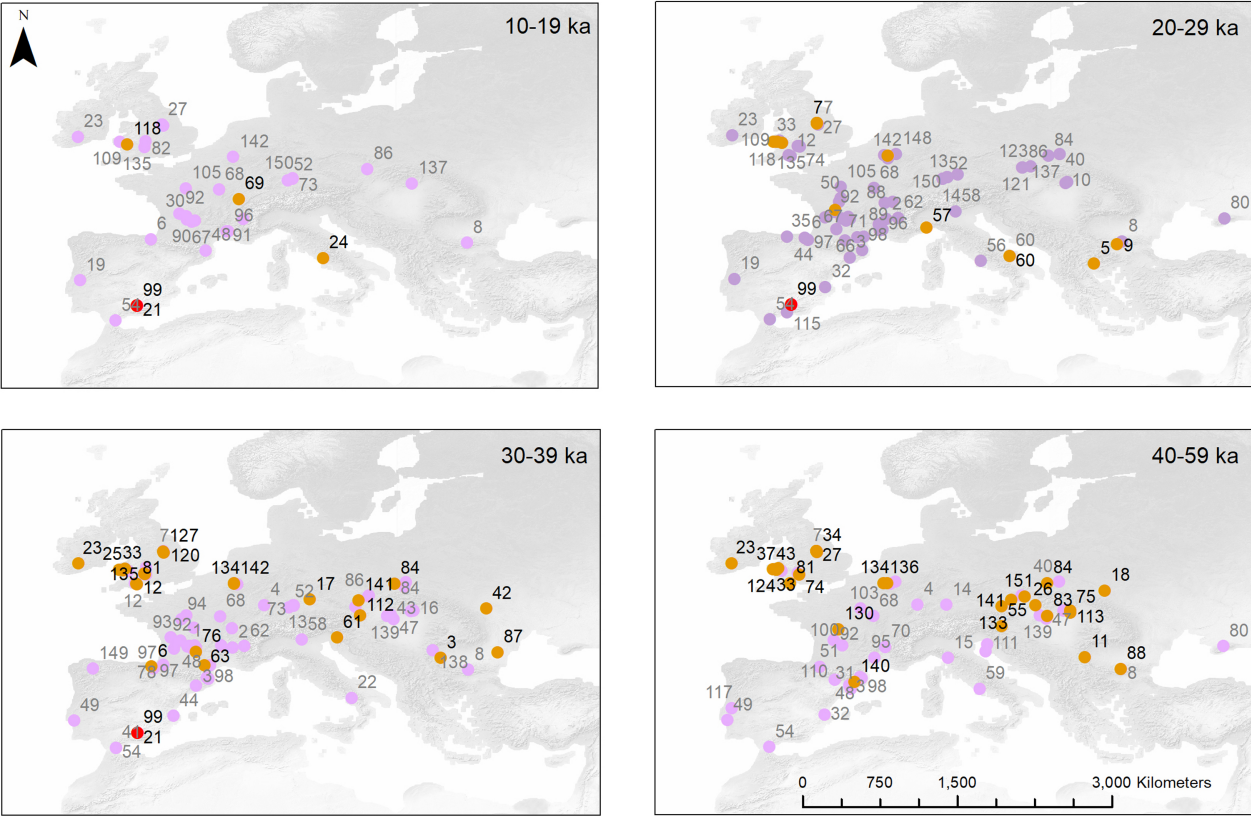


Figure 8



- Carihuela y Las Ventanas
 - Crocuta dated directly
 - Crocuta dated by association
- | | | | | |
|---------------------------|--------------------------------|-----------------------------|------------------------|----------------------------|
| 1, Abri Castanet | 28, Ciemna | 61, Grotta Pocala | 92, La Quina | 121, Pod Hradem Cave |
| 2, Abri Moula | 29, Combe Grenal | 62, Grotte Chauvet | 93, La Roche a Pierrot | 122, Potters Cave |
| 3, Abric Romani | 30, Combe Sauniere I | 64, Grotte de Canecaude I | 94, La Roche Cotard | 123, Predmosti |
| 4, Achenheim | 31, Cova del Gegant | 65, Grotte de Conives | 95, La Roquette II | 124, Priory Farm Cave |
| 5, Agios Georgios Cave | 32, Cova Negra | 66, Grotte de la Nauterie I | 96, La Salpêtrière | 125, Reclau Viver |
| 6, Amalda Cave | 33, Coygan Cave | 67, Grotte des Fieux | 97, Labeko Koba Cave | 126, Rexidora Cave |
| 7, Ash Tree Cave | 35, Cueva Morin | 68, Grotte du Renne | 98, l'Arbreda | 127, Robin Hood's Cave |
| 8, Bacho Kiro | 37, Daylight Rock | 69, Grotte Grappin | 99, Las Ventanas | 128, Roc de Combe |
| 9, Balkan Range | 39, Desnisukhi Peck Cave | 70, Grotte Neron | 100, Le Moustier | 129, Roc de Marcamps |
| 10, Balla Cave | 40, Deszczowa Cave | 71, Grotte Tournal | 101, Le Plage | 130, Rochers-de-Villeneuve |
| 11, Baranica Cave | 41, Devil's Tower | 72, Grotte Velars Etrigny | 102, L'Ermitage | 131, Romualdo Cave |
| 12, Bench Quarry Cave | 42, Duruitoarea Veche | 73, Höhlenstein-Stadel | 103, Les Bossats | 132, Sandford Hill |
| 13, Bockstein-Törle | 43, Eel Point | 74, Hyaena Den | 104, Les Canalettes | 133, Schusterlucke cave |
| 14, Brillenhöhle | 44, Ekain Cave | 75, Igric | 105, Les Cottés | 134, Scladina Cave |
| 15, Buca della Iena | 44, Ekain Cave | 76, Igue du Gral | 106, Les Garennes | 135, Soldier's Hole |
| 16, Budospest | 45, El Castillo | 77, Istalosko cave | 107, Les Pêcheurs | 136, Spy |
| 17, Windener Barenhöhle | 46, Enlène | 78, Isturitz | 108, Les Rivaux | 137, Szeleta Cave |
| 18, Bukovinka Cave | 47, Erd | 79, Jaurens | 109, Little Hoyle Cave | 138, Tabula Traiana Cave |
| 19, Caldeirão | 48, Ermitons | 80, Karabi Tamchin | 110, Los Moros I | 139, Tata |
| 20, Camiac [-et-St-Denis] | 49, Figueira Brava Cave | 81, Kent's Cavern | 111, Marlera | 140, Teixonerés Cave |
| 21, Carihuela | 50, Fontenioux | 82, King Arthur's Cave | 112, Melwurmhöhle | 141, Teufelslucke |
| 22, Castelcivita | 51, Gatzarria | 83, Kiskevelyi | 113, Miskolc III | 143, Tokod |
| 23, Castlepook Cave | 52, Geissenklösterle | 84, Komarowa Cave | 114, Nanna's Cave | 144, Tornewton Cave |
| 24, Cava Muracci | 54, Gorham's Cave | 85, Krems-Hundssteig | 115, Nerja | 145, Trou Al'Wesse |
| 25, Cefn Cave | 55, Griifen Cave | 86, Kulna Cave | 116, Ogof-yr-Ichen | 146, Trou du Docteur |
| 26, Certova Pec | 56, Grotta del Fossellone | 87, La Adam Cave | 117, Oliveira Cave | 147, Trou du Renard |
| 27, Church Hole Cave | 57, Grotta delle Arene Candide | 88, La Balme d'Epy | 118, Paviland Cave | 148, Trou Walou |
| | 58, Grotta di Fumane | 89, La Baume Longue | 119, Picken's Hole | 149, Valina |
| | 59, Grotta Guattari | 90, La Ferrassie | 120, Pin Hole West | 150, Vogelherd |
| | 60, Grotta Paglicci | 91, La Lauza | 120, Pin Hole Cave | 151, Vypustek |
| | | | | 152, Weinberghöhlen |

Figure 9