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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 *Crocuta* 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. 37,890 to 6980 cal yr BP, and the Car coprolites from c. 31,063 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 *Crocuta* 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 *Crocuta* in southern Spain should not be categorically discarded.

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 (*Crocuta crocuta*) from two adjacent Palaeolithic 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 *Crocuta crocuta* in the region.

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

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 m 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 1200 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

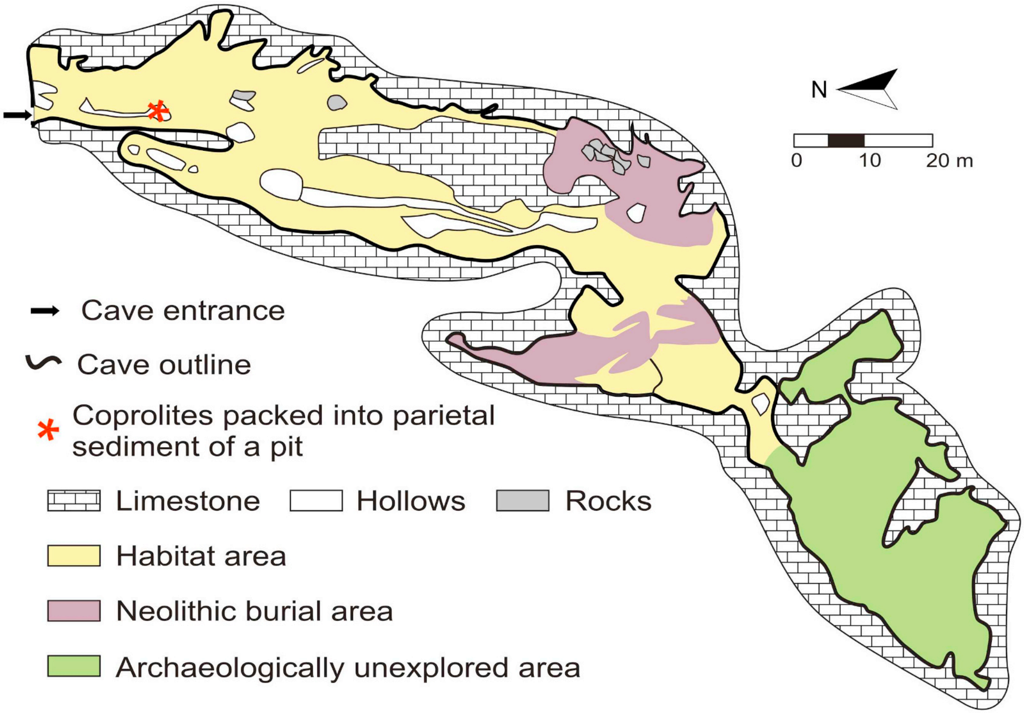


Fig. 2. Longitudinal section of Las Ventanas Cave, showing the situation of the pit where coprolites were sampled, near the entrance. Modified from Riquelme (2002).

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 (*Crocuta 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 adquired 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 reachs inmediately 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 Palaeolithic assemblage has been associated to unit III. Nevertheless, such set remains unkown. 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 adscribed 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., 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

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

Carihuela
Allocricetus bursae (Ruiz-Bustos and García-Sánchez, 1977)
Apodemus cf. *flavicollis* (Ruiz-Bustos and García-Sánchez, 1977)
A. sylvaticus (Vega-Toscano, 1988
Arvicola sapidus (Ruiz-Bustos and García-Sánchez, 1977)
Barbastrella bastastellus (Sevilla García, 1988, 1989)
Bison sp. (Vega-Toscano, 1988)
Bos primigenius (Vega-Toscano, 1988)
Canis lupus (Vega-Toscano, 1988)
Capra sp. (Vega-Toscano, 1988)
Capreolus sp. (Vega-Toscano, 1988)
Cervus elaphus (Vega-Toscano, 1988)
Clethrionomys glareolus (Vega-Toscano, 1988)
Coelodonta antiquitatis (reported by Koby and Spahni, without additional confirmation) (Vega Toscano, 1988)
Crocidura sp. (Ruiz-Bustos and García-Sánchez, 1977)
C. suaveolens (Vega-Toscano, 1988)
C. russula (Vega-Toscano, 1988)
Crocuta sp. (Vega-Toscano, 1988)
Dicrostonyx andaluciensis (Ruiz-Bustos and García-Sánchez, 1977)
Eliomys quercinus (Ruiz-Bustos and García-Sánchez, 1977)
E. q. quercinus (Vega-Toscano, 1988)
E. q. lusitanicus (Vega-Toscano, 1988)
Eptesicus serotinus (Vega-Toscano, 1988) (reported by Koby and Spahni, without additional confirmation)
Equus caballus cf. *germanicus* (Vega-Toscano, 1988)
E. hydruntinus (Vega-Toscano, 1988)
Erinaceus europaeus (Ruiz-Bustos and García-Sánchez, 1977)
Lacerta sp. (Vega-Toscano, 1988)
Lepus capensis (Vega-Toscano, 1988)
Merula sp. (Vega-Toscano, 1988) (reported by Koby and Spahni, without additional confirmation)
Microtus nivalis (Ruiz-Bustos and García-Sánchez, 1977)
M. arvalis (Ruiz-Bustos and García-Sánchez, 1977)
M. cf. *Dentatus* (Ruiz-Bustos and García-Sánchez, 1977)
M. cabrerae (Vega-Toscano, 1988)
Miniopterus schreibersi (Sevilla García, 1988, 1989)
Myotis myotis (Sevilla García, 1988, 1989)
M. myotis/blythi (Sevilla García, 1988, 1989)
M. natterei (Sevilla García, 1988, 1989)
M. emarginatus (Vega-Toscano, 1988)
M bechsteini (Sevilla García, 1988, 1989)
Neomys cf. *anomalus* (Vega-Toscano, 1988)
Oryctolagus cuniculus (Vega-Toscano, 1988)
Panthera sp. (Vega-Toscano, 1988)
Pitymys duodecimcostatus (Ruiz-Bustos and García-Sánchez, 1977)
Plecotus auritus/austriacus (Sevilla García, 1988, 1989)
P. austriacus (Sevilla García, 1988, 1989)
Pliomys lenki (only one upper M3) (Ruiz-Bustos and García-Sánchez, 1977)
Pyrrhocorax alpinus (Vega-Toscano, 1988) (reported by Koby and Spahni, without additional confirmation)
Rinolophus euryale (Sevilla García, 1988, 1989)
R. mehelyi (Sevilla García, 1988, 1989)
R. euryale/mehelyi (Sevilla García, 1988, 1989)
R. hipposideros (Sevilla García, 1988, 1989)
R. ferrumequinum (Sevilla García, 1988, 1989)
Stephanorhinus (Dicerorhinus) kirchbergensis (Vega-Toscano, 1988)
Sorex araneus (Ruiz-Bustos and García-Sánchez, 1977)
S. cf. *minutus* (Vega-Toscano, 1988)
Suncus sp. (Vega-Toscano, 1988)
Sus scrofa (Vega-Toscano, 1988)
Testudo sp. (Vega-Toscano, 1988)
Turdus viscivorus (Vega-Toscano, 1988) (reported by Koby and Spahni, without additional confirmation)
Ursus sp. (Vega-Toscano, 1988)
Vulpes sp. (Vega-Toscano, 1988)

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 establishing 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 (*Crocuta 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-Sánchez et al., 2018), confirming that these animals were present at the locality. Furthermore, other carnivore species are unlikely to be responsable for these fossil scats. Droppings of *Hyaena* (striped hyaena) are discernibly smaller than those of *Crocuta*, 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, *Crocuta* is the main carnivore (Riquelme, 2002), but in Carihuela, there are bone remains of *Crocuta, 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).

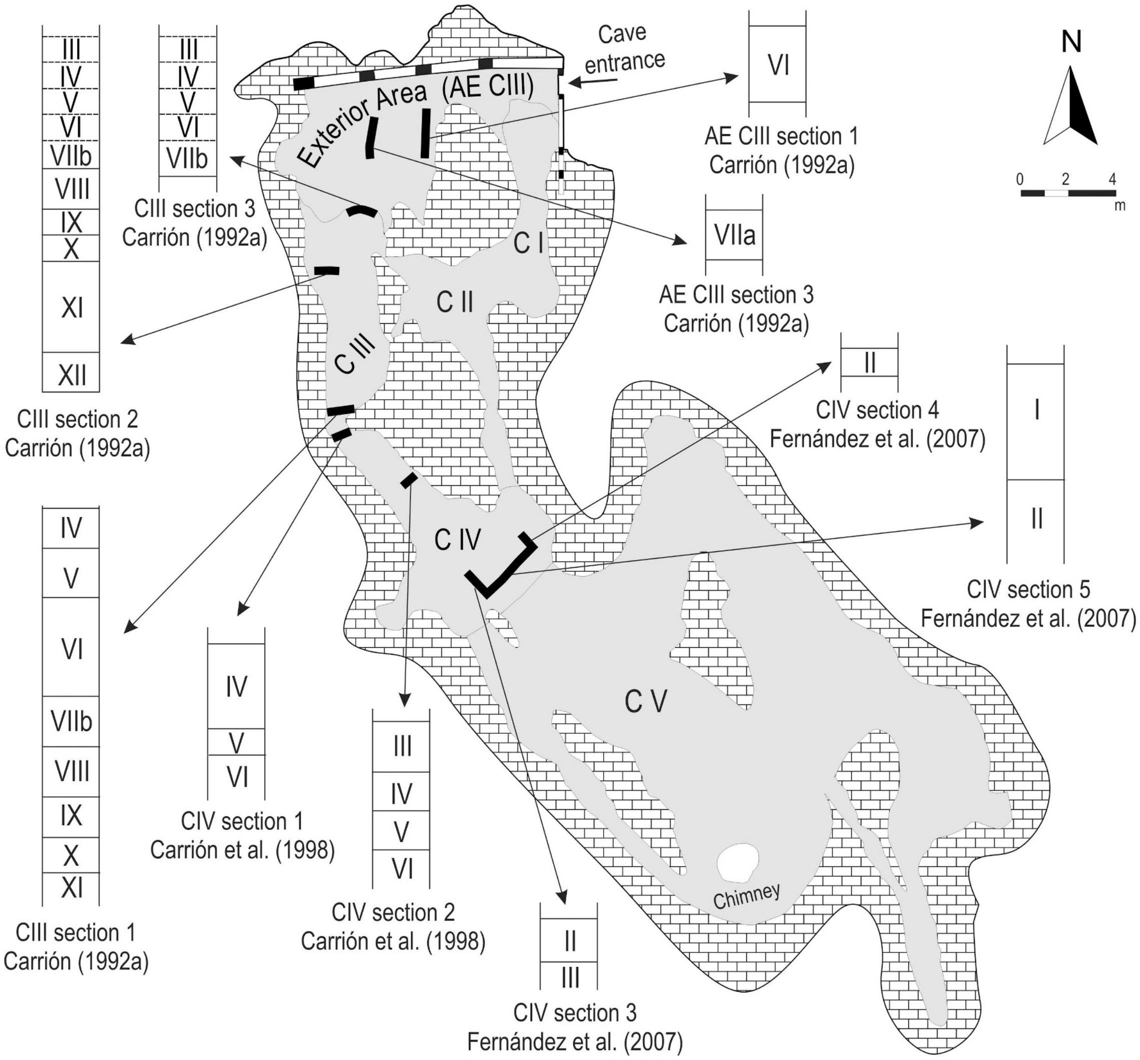


Fig. 3. Longitudinal section of Carihuela Cave, showing the situation of the chambers, stratigraphical sections and sedimentological units studied palynologically (Carrión, 1992; Carrión et al., 1998, 2019; Fernández et al., 2007).
Redrawn from Fernández et al. (2007).

5. Chronology

Radiocarbon dating for LV coprolites achieved here conforms to a period from 37,890 to 6980 cal yr BP approximately (Table 2, Figs. 5-8). *Crocuta* 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). Fig. 9 shows all the direct (dates on bones of the species) and associated (dates on material in the same layer) dates of *Crocuta 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

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	Midpoint cal yr BP (midpoint)	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	10,589–11,080	10,834	P
CV-7	CNA-673R	AMS	TOC	10,410 ± 60	12,061–12,529	12,295	–
5 items	Beta-141051	AMS	S**	10,670 ± 40	12,567–12,707	12,637	P
CV-6	CNA-672R	AMS	TOC	11,730 ± 90	13,401–13,755	13,578	–
LV-22	Poz-43338	Conventional	TOC	14,840 ± 70	17,857–18,267	18,062	P
LV-36	Poz-57792	Conventional	TOC	15,040 ± 50	18,077–18,446	18,261	NP
LV-21	Poz-43336	Conventional	TOC	15,940 ± 120	18,932–19,540	19,236	P
LV-20	**Beta-286452**	**AMS**	**CF**	**3790 ± 40**	**3994–4350**	**4172**	**NP**
LV-20	**Beta-284642**	**AMS**	**OF**	**17,520 ± 60**	**20,921–21,403**	**21,162**	**NP**
LV-28	Poz-57788	Conventional	TOC	18,750 ± 60	22,426–22,817	22,621	NP
LV-19	**Beta-285846**	**AMS**	**CF**	**5700 ± 40**	**6405–6628**	**6516**	**P**
LV-19	**Beta-284646**	**AMS**	**OF**	**18,920 ± 80**	**22,525–23,021**	**22,773**	**P**
LV-18	**Beta-285845**	**AMS**	**CF**	**6030 ± 40**	**6755–6981**	**6868**	**NP**
LV-18	**Beta-284645**	**AMS**	**OF**	**19,140 ± 70**	**22,822–23,374**	**23,098**	**NP**
LV-33	Poz-57791	Conventional	CF	19,270 ± 80	22,949–23,490	23,219	NP
LV-16	**Beta-286453**	**AMS**	**CF**	**4930 ± 40**	**5595–5733**	**5664**	**P**
LV-16	**Beta-284643**	**AMS**	**OF**	**20,990 ± 80**	**25,107–25,576**	**25,341**	**P**
LV-30	Poz-57789	Conventional	OF	21,350 ± 100	25,455–25,901	25,678	NP
LV-15	Poz-43335	Conventional	TOC	23,140 ± 100	27,221–27,642	27,431	P
LV-31	Poz-57790	Conventional	TOC	25,750 ± 130	29,499–30,409	29,954	NP
TLV3	CNA-669	AMS	HTc *	27,500 ± 300	30,913–31,976	31,444	–
LV-12	Poz-38318	Conventional	TOC	28,800 ± 500	31,566–33,831	32,698	NP
LV-13	Poz-38279	Conventional	TOC	29,380 ± 320	32,808–34,121	33,464	P
LV-14	Poz-38280	Conventional	TOC	29,730 ± 290	33,337–34,423	33,880	NP
LV-11	Poz-37429	Conventional	TOC	33,700 ± 600	36,393–39,388	37,890	P
TLV1	Beta-289558	AMS	HTc	38,590 ± 370	42,085–43,107	42,596	–
TLV2	Beta-289559	AMS	HTc	39,150 ± 420	42,346–43,663	43,004	–

and Lister (2014) rejected all the late occurences 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 *Crocuta* 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 *Crocuta*.

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

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.

Sample	Lab N°	Chamber-section/s	Unit (suggested intervals)	Coordinates (excavation notes)	yr BP	cal yr BP	Midpoint cal yr BP	Industry in “excavation labels”
Car13	Poz-55,205	CIV-3	I-II	701S/701W	7040 ± 50	7965–7757	7861	Neolithic
Car11	ETH-49314	CIV-2	I-III	696S/702W	9543 ± 33	11,081–10,713	10,897	Recent Prehistory
Car3	ETH-49306	CIV-2	II-III	697S/701W	11,407 ± 36	13,323–13,143	13,233	Neolithic (?)
Car4	ETH-49307	CIV-2	II-III	697S/701W	11,417 ± 36	13,338–13,146	13,242	Neolithic (?)
Car10	ETH-49313	CIV-1	I-III	694S/702W	12,100 ± 37	14,105–13,799	13,952	Recent Prehistory
Car9	ETH-49312	CIV-2	I-IV	698S/701W	14,836 ± 43	18,210–17,875	18,043	“Bronze”
Car12	ETH-49315	CIV-2-3[a]	III-V	699S/701W	16,139 ± 48	19,644–19,277	19,461	Final Middle Palaeolithic
Car5	ETH-49308	CIV 2-3[a]	III-V	700S/701W	16,711 ± 74	20,405–19,939	20,172	Early Upper Palaeolithic
Car8	ETH-49311	CIV-2	IV-V	698S/701W	17,691 ± 50	21,656–21,164	21,410	Final Middle Palaeolithic
Car1	ETH-49304	CIII 2-3[a]	IV-V	507,45S/508,87W	19,499 ± 89	23,781–23,141	23,461	Palaeolithic
Car7	ETH-49310	CIV-2-3[a]	III-V	699S/701W	20,551 ± 247	25,404–24,130	24,767	Final Middle Palaeolithic
Car2	ETH-49305	CIII 2-3[a]	IV-VI	507,45S/507,50W	26,158 ± 188	30,874–29,866	30,370	Middle Palaeolithic
Car6	ETH-49309	CIV-2-3[a]	III-V	700S/701W	27,027 ± 205	31,322–30,803	31,063	Early Upper Palaeolithic

[a] Coprolites in materials removed from trenches between two current stratigraphical sections.

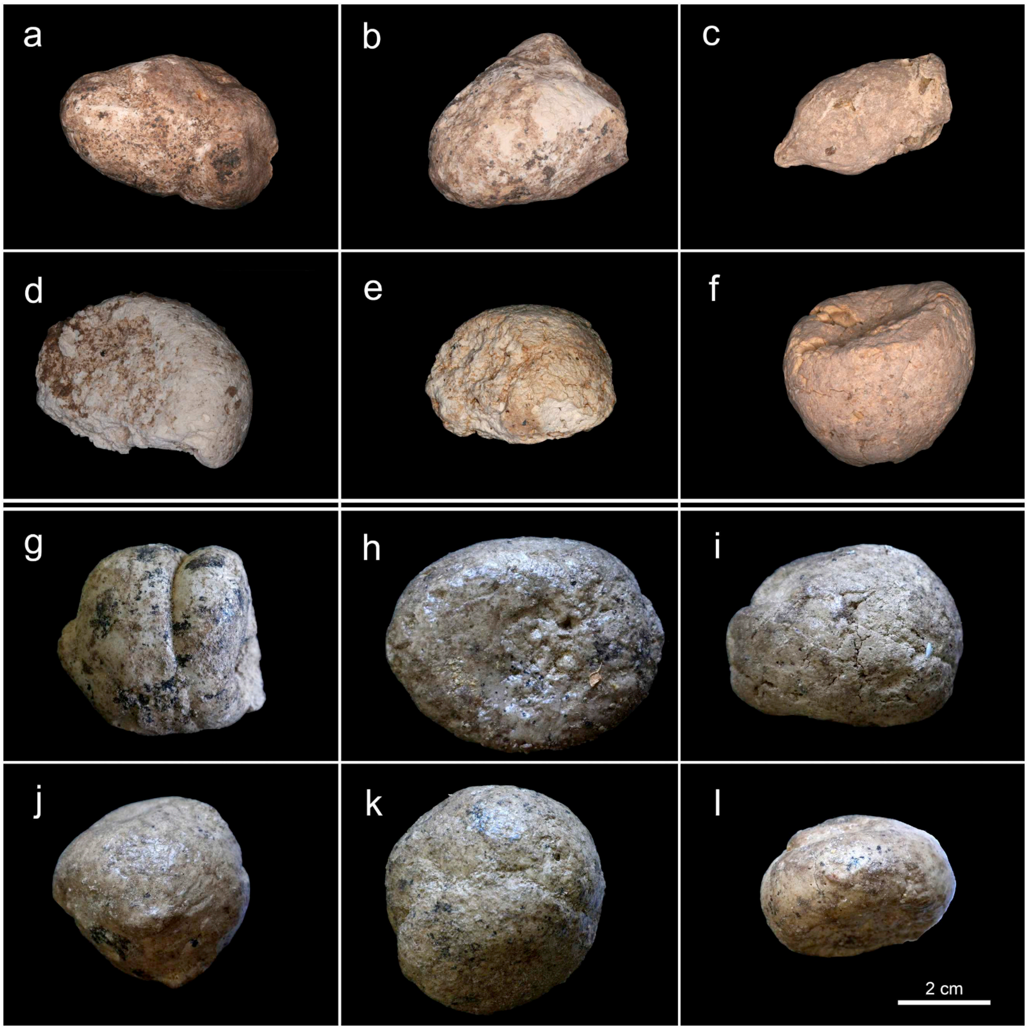


Fig. 4. Coprolite specimens from Carihuela Cave (a-f) and Las Ventanas Cave (g-l).

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 31,000 cal yr BP. Interestingly, *Homo neanderthalensis* remains dissappeared 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

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

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

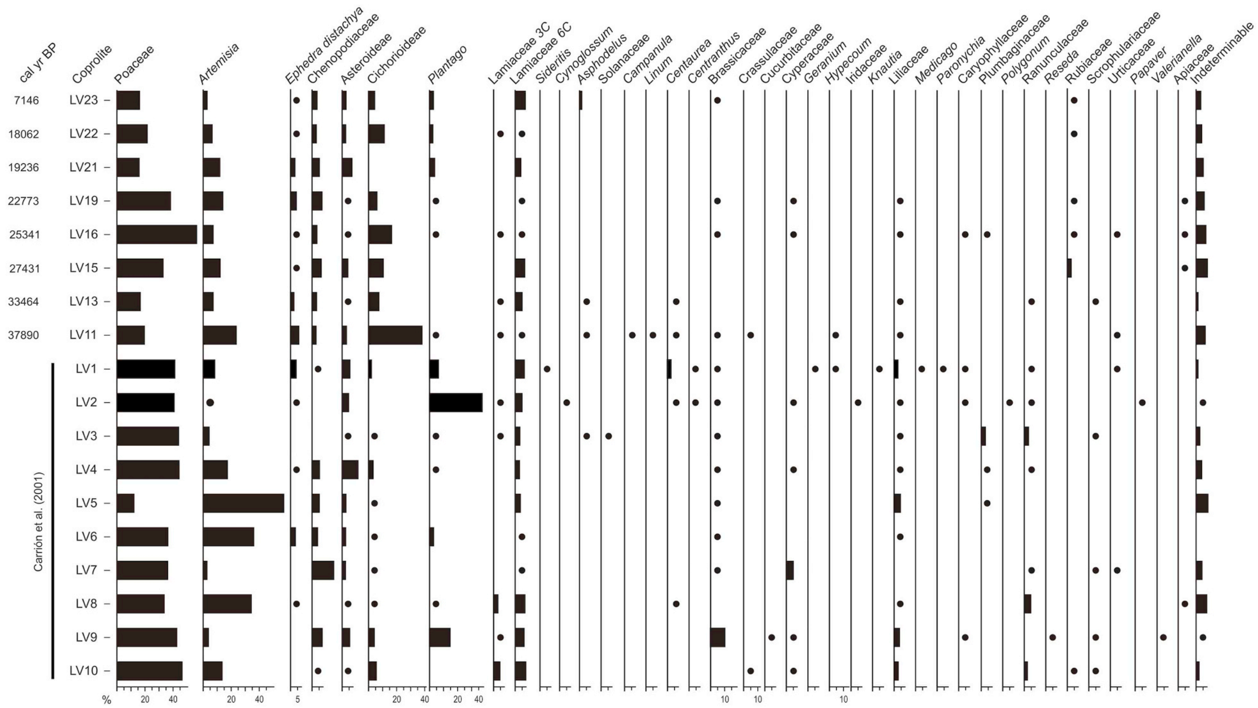


Fig. 6. Percentage pollen diagram of coprolite samples from Las Ventanas Cave (herbaceous types, spores and non-pollen palynomorphs; Asteraceae and spores excluded from pollen sum).

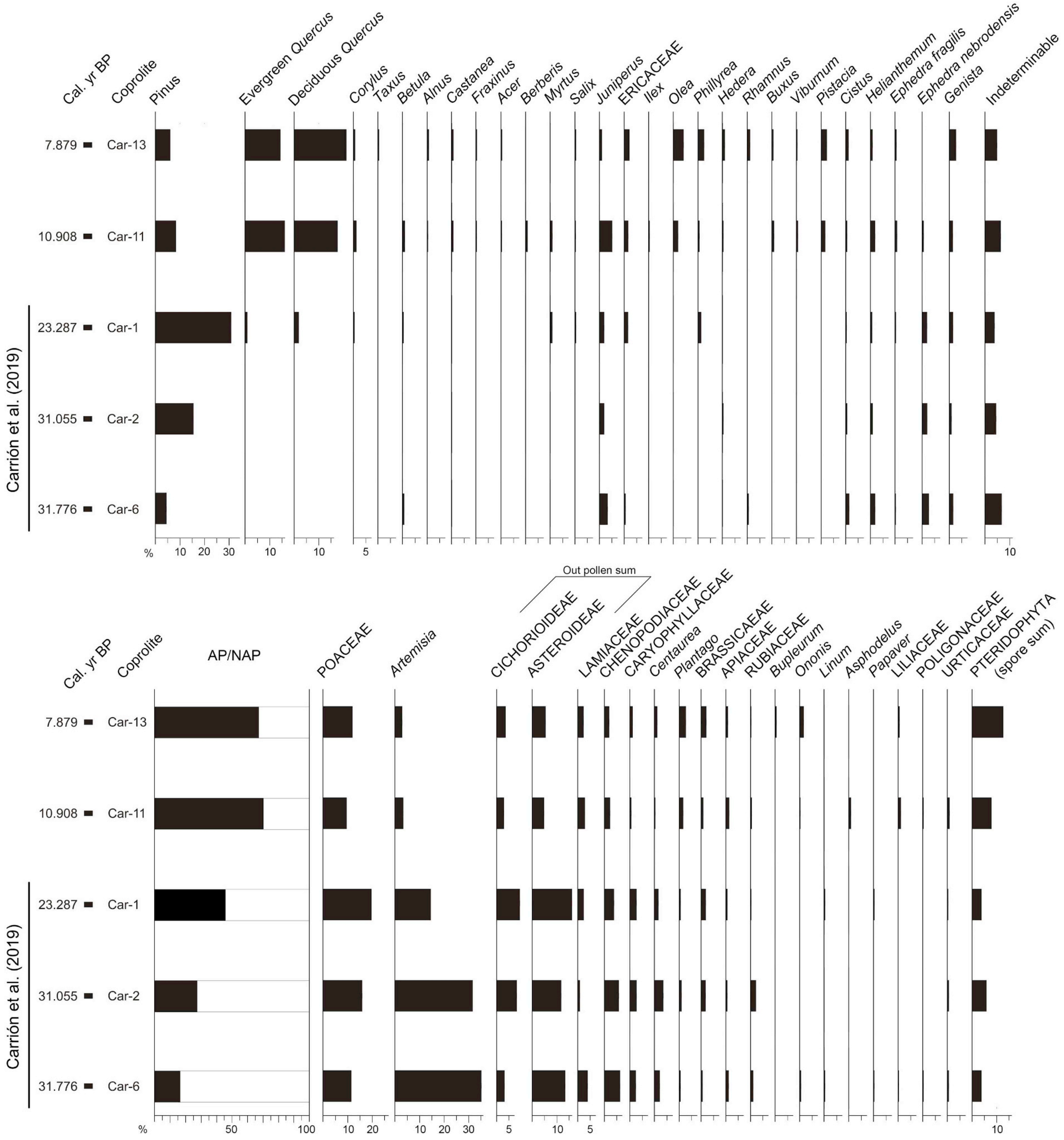


Fig. 7. Percentage pollen diagram of coprolite samples from Carihuela Cave. Coprolites Car-1, Car-2 and Car-6 formerly published in Carrión et al. (2019). Asteraceae and spores excluded from pollen sum.

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

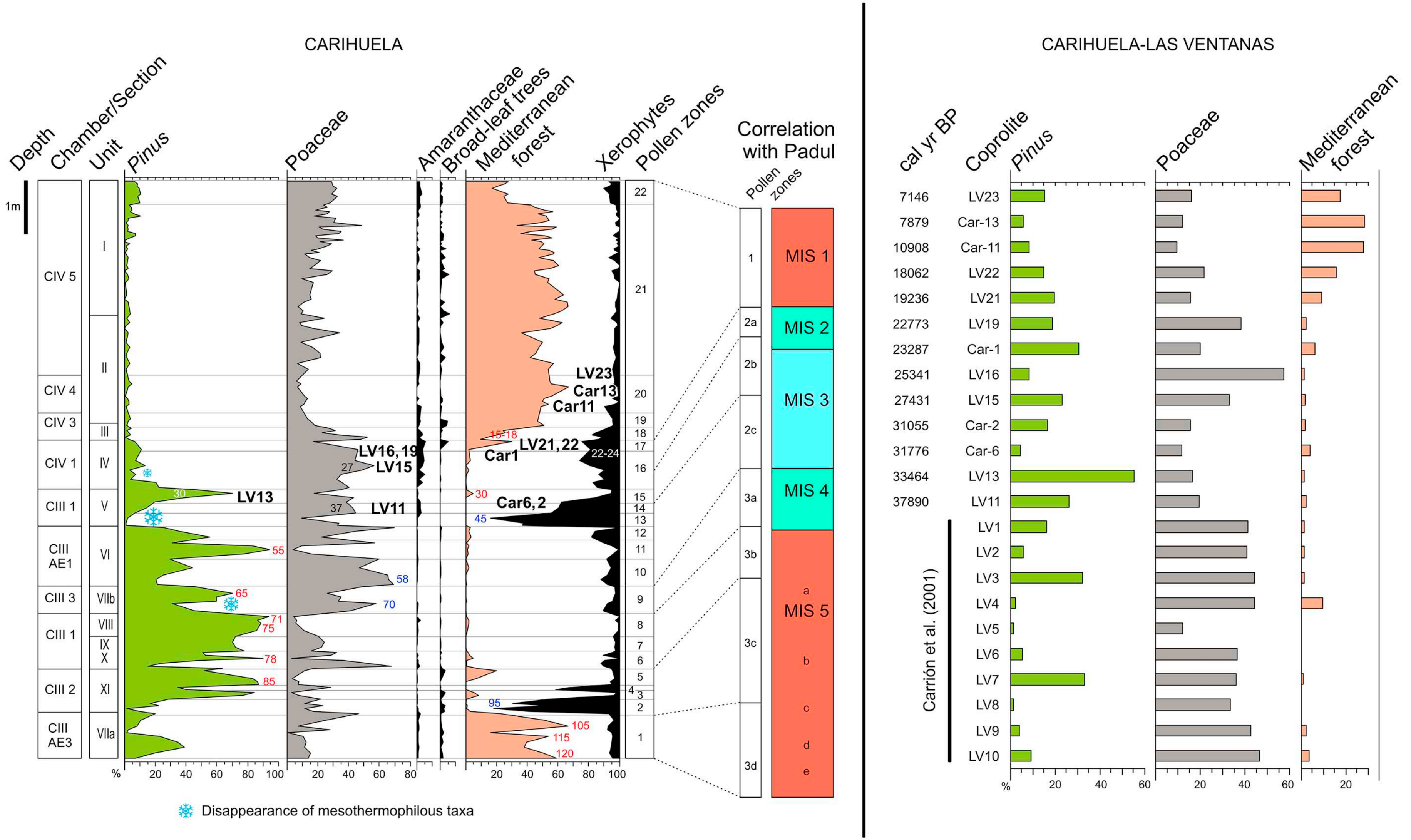
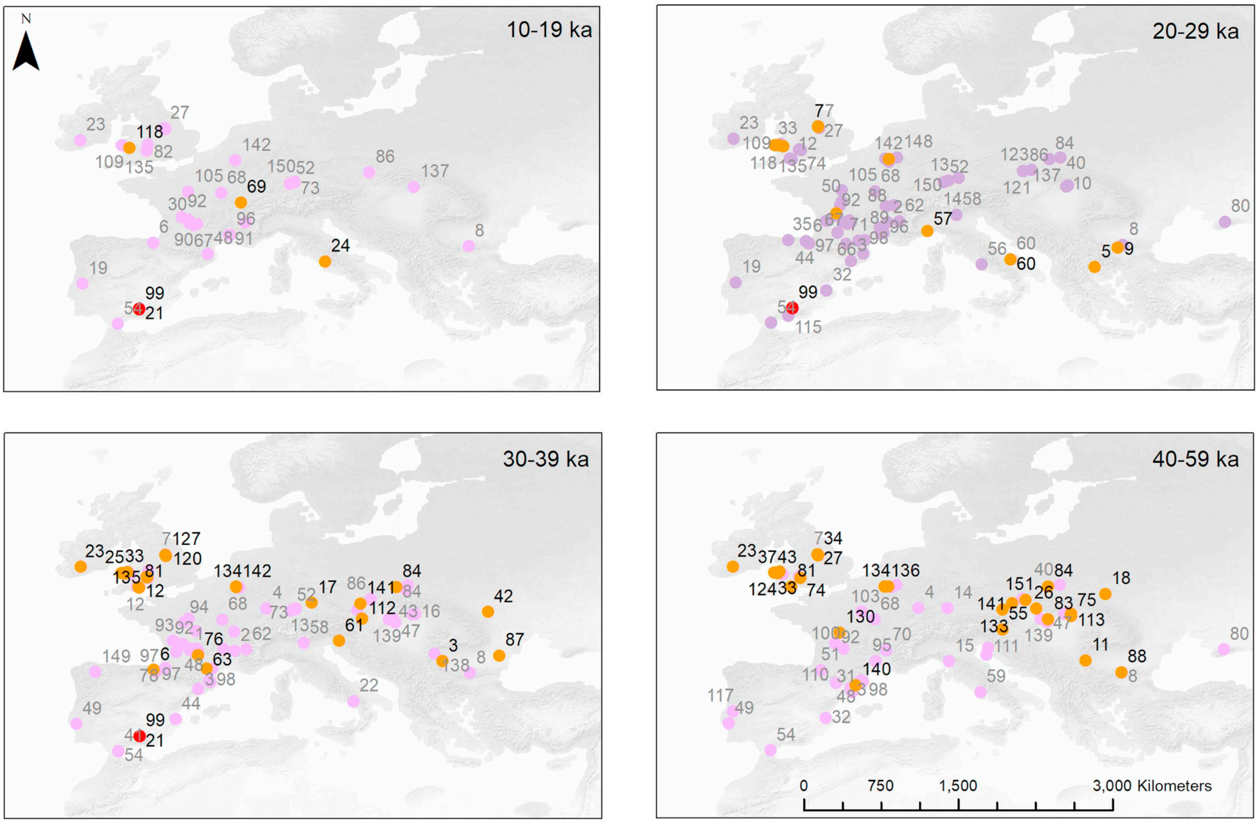


Fig. 8. Coprolite chronology of Las Ventanas and Carihuela in the framework of a tentative correlation between the pollen sequences of Carihuela (Carrión, 1992; Carrión et al., 1998; Fernández et al., 2007) and Padul (Camuera et al., 2019). Red and blue numbers indicate forest and steppe maxima, respectively, 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*). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



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

(caption on next page)

Fig. 9. Sites with all the direct (bones of the species) and associated (material in the same layer) dates of *Crocuta crocuta* in Europe between 60,000 and 10,000 years (based on uncalibrated radiocarbon dates) (modified and updated from Knul, 2018).

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 *Crocuta 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 utilized 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 *Crocuta* 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 *Crocuta* 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 *Crocuta* should be considered. According to literature, *Crocuta* became extinct in northwest and southern Europe between c. 31,000 and 21,000 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 occurences with cave systems of the two species.

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.

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References

Almagro, M., Fryxell, R., Irwin, H.T., Serna, M., 1970. Avance a la investigación arqueológica, geocronológica y ecológica de la Cueva de la Carigüela de Píñar (Granada). Trab. Prehist. 27, 45–60.

Bennett, K.D., 2000. Psimpoll and pscomb: computer programs for data plotting and analysis. Available on the internet at. http://www.kv.geo.uu.se/software.html.

Bon, C., Berthonaud, V., Maksud, F., Labadie, K., Poulain, J., Artiguenave, F., Wincker, P., Aury, J.M., Elalouf, J.M., 2012. Coprolites as a source of information on the genome and diet of the cave hyena. Proc. R. Soc. B Biol. Sci. 279, 2825–2830.

Brain, C.K., 1981. The Hunters or the Hunted? An Introduction to African Cave Taphonomy. University of Chicago Press, Chicago, IL.

Camuera, J., Jiménez-Moreno, G., Ramos-Román, M.J., García-Alix, A., Toney, J.L., Scott-Anderson, R., Jiménez-Espejo, F., Bright, J., Webster, C., Yanes, Y., Carrión, J.S., 2019. Vegetation and climate changes during the last two glacial-interglacial cycles in the Western Mediterranean: a new long pollen record from Padul (Southern Iberian Peninsula). Quat. Sci. Rev. 205, 86–105.

Carrión, J.S., 1990. Evolución paleoambiental durante el Pleistoceno superior en el sureste de España. In: Las secuencias polínicas de las Cuevas de la Carihuela (Granada) y Beneito (Alicante). Universidad de Murcia Tesis doctoral. (167 pp).

Carrión, J.S., 1992. Late Quaternary pollen sequence from Carihuela Cave, Southern Spain. Rev. Palaeobot. Palynol. 71, 37–77.

Carrión, J.S., Scott, L., 1999. The challenge of pollen analysis in palaeoenvironmental studies of hominid beds. The record from Sterkfontein Caves. J. Hum. Evol. 36, 401–408.

Carrión, J.S., Dupré, M., Fumanal, M.P., Montes, R., 1995a. A palaeoenvironmental study in the semiarid south-eastern Spain: the palynological and sedimentological sequence at Perneras Cave (Lorca, Murcia). J. Archeol. Sci. 22, 355–367.

Carrión, J.S., Munuera, M., Dupré, M., 1995b. Estudios de Palinología arqueológica en el sureste ibérico semiárido. Cuat Geomorf 9, 17–31.

Carrión, J.S., Munuera, M., Navarro, C., 1998. Palaeonvironmental reconstructions of cave sediments on the basis palynology: an example from Carihuela Cave (Granada). Rev. Palaeobot. Palynol. 99, 17–31.

Carrión, J.S., Scott, L., Vogel, J.C., 1999. Twentieth-century changes in montane vegetation in the eastern Free State, South Africa, derived from palynology of hyrax dung middens. J. Quat. Sci. 14, 1–16.

Carrión, J.S., Riquelme, J.A., Navarro, C., Munuera, M., 2001. Pollen in hyaena coprolites reflects late glacial landscape in southern Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 176, 193–205.

Carrión, J.S., Yll, R., Riquelme, J.A., González, P., 2004. Perspectivas del análisis polínico de coprolitos y otros depósitos biogénicos útiles en la inferencia paleoambiental. In: Miscelanea en Homenaje a Emiliano Aguirre. Volumen II: Paleontología, Museo Arqueológico Regional, Alcalá de Henares, pp. 129–140.

Carrión, J.S., Scott, L., Marais, E., 2006. Environmental implications of pollen spectra in bat droppings from south-eastern Spain and potential for palaeoenvironmental reconstructions. Rev. Palaeobot. Palynol. 140, 175–186.

Carrión, J.S., Scott, L., Arribas, A., Fuentes, N., Gil-Romera, G., Montoya, E., 2007. Pleistocene landscapes in central Iberia inferred from pollen analysis of hyena coprolites. J. Quat. Sci. 22, 191–202.

Carrión, J.S., Finlayson, C., Fernández, S., Finlayson, G., Allué, E., López-Sáez, A., López-García, P., Fuentes, N., Gil, G., González-Sampériz, P., 2008. A coastal reservoir of biodiversity for Upper Pleistocene human populations: palaeoecological investigations in Gorham's Cave (Gibraltar) in the context of the Iberian Peninsula. Quat. Sci. Rev. 27, 2118–2135.

Carrión, J.S., Fernández, S., González-Sampériz, P., Leroy, S.A.G., Bailey, G.N., López-Sáez, J.A., Burjachs, F., Gil-Romera, G., García-Antón, M., Gil-García, M.J., Parra, I., Santos, L., López-García, P., Yll, E.I., Dupré, M., 2009. Quaternary pollen analysis in the Iberian Peninsula: the value of negative results. Internet Archaeology 25, 1–53. http://intarch.ac.uk/journal/issue25/5/toc.html.

Carrión, J.S., Ochando, J., Fernández, S., Munuera, M., Amorós, G., Blasco, R., Rosell, J., Finlayson, S., Giles, F., Jennings, R., Finlayson, G., Giles-Pacheco, F., Rodríguez-Vidal, J., Finlayson, C., 2018. Last Neanderthals in the warmest refugium of Europe: palynological data from Vanguard Cave. Review of Palaeobotany and Palynology, Special Issue (Carrión, J. S., deMenocal, P., Scott, L., eds.): Human evolution and palaeofloras: the contribution and potential of palaeobotany in the environmental reconstruction of hominin-bearing sites. Rev. Palaeobot. Palynol. 259, 63–80.

Carrión, J.S., Fernández, S., Jiménez, J., Munuera Giner, M., Ochando, J., Amorós, G., Ponce de León, M., Zollikofer, Ch., Martín-Lerma, I., Toro-Moyano, I., Hajdas, I., Walker, M.J., 2019. The sequence at Carihuela Cave and its potential for research into Neanderthal ecology and the Mousterian in southern Spain. Quat. Sci. Rev. 217, 194–216.

Cortés-Sánchez, M., Riquelme, J.A., Simón, M.D., Parrilla, R., Odriozola, C.P., Calle, L., Carrión, J.S., Monge, G., Rodríguez-Vidal, J., Moyano, J.J., Rico, F., Nieto, J.E., Antón, D., Aranzazu, M., Jiménez-Barredo, F., Cantero-Chinchilla, F., 2018. Pre-solutrean rock art in southernmost Europe: evidence from las Ventanas cave (Andalusia, Spain). PLoS One 13, e0204651. https://doi.org/10.1371/journal.pone. 0204651.

Daura, J., Sanz, M., Allué, E., Vaquero, M., López-García, J.M., Julià, R., Ortiz, E., Sánchez Marco, A., Skinner, A.R., Domenech, R., Martinell, J., Arnold, L.J., Carrión, J.S., 2017. Cova del Coll Verdaguer (Cervelló, Barcelona): the palaeoenvironmental reconstruction of the MIS 3 based on a terrestrial archive and the implications for the last Neanderthals's landscape in the Mediterranean coast of the Iberian Peninsula.

Quat. Sci. Rev. 177, 34–56.
De Lumley, M.A., García-Sánchez, M., 1971. L'enfant néandertalien de Carigüela a Piñar (Andalousie). L'Anthropologie 75, 29–56.
De Porras, M.E., Maldonado, A., Latorre, C., Betancourt, J.L., 2017. Late Quaternary environmental dynamics in the Atacama Desert reconstructed from rodent midden pollen records. J. Quat. Sci. 32, 665–684.
Diedrich, C., 2012. Typology of Ice Age spotted hyena Crocuta crocuta spelaea (Goldfuss, 1823) coprolite aggregate pellets from the European Late Pleistocene and their significance at dens and scavenging sites. New Mexico Museum of Natural History and Science, Bulletin 57, 369–377.
Dimbleby, G.W., 1985. The Palynology of Archaeological Sites. Academic Press, London.
Dinnis, R., Pate, A., Reynolds, N., 2016. Mid-to-late Marine Isotope Stage 3 mammal faunas of Britain: a new look. Proc. Geol. Assoc. 127, 435–444.
du Souich Henrici, F., Jiménez Brobeil, S., 2011. Algunos dientes humanos musterienses de la Carigüela (Granada). In: Alemán-Aguilera, I., Jiménez-Brobeil, S., Pérez-Pérez, A., Ruiz-Rodríguez, L., du Souich Henrici, F. (Eds.), Cinco trabajos de Antropología Física. Al Prof. Dr. D. Miguel Guirao Pérez in Memoriam 2010. Lulu Enterprises, Raleigh, USA, pp. 51–61.
Erdtman, G., 1969. Handbook of Palynology. Hafner Publishing Company, Nueva York.
Fernández, S., Carrión, J.S., Fuentes, N., González-Sampériz, P., Montoya, E., Gil-Romera, G., Vega-Toscano, L.G., Riquelme, J.A., 2007. Palynology of Carihuela Cave, southern Spain: completing the record. Geobios 40, 75–90.
García-Sánchez, M., 1960. Restos humanos del Paleolítico Medio y Superior y del Neo-Eneolítico de Píñar (Granada). Trabajos del Instituto "Bernardino de Sahagún" de Antropología y Etnografía. 15. pp. 19–78.
García-Sánchez, M., Tillier, A.-M., Garralda, M.-D., Vega-Toscano, G., 1994. Les dents d'enfant des niveaux moustériens de la grotte de Carihuela (Grenade-Espagne). Paléo 6, 79–88.
Garralda, M.D., 1970. Problemas en torno al Paleolítico de la Cueva de la Carigüela, en Píñar (Granada). In: Crónica del XI Congreso Nacional de Arqueología, Mérida, pp. 190–198.
Gatta, M., 2017. Understanding Late Pleistocene Landscapes of Central Italy: A Multidisciplinary Approach. PhD thesis. University of York.
Gatta, M., Rolfo, M.F., 2017. Cava Muracci: a new Middle Palaeolithic site in West-Central Italy. Mediterr. Archaeo. Archaeome. 17, 105–116.
Gatta, M., Sinopoli, G., Giardini, M., Giaccio, B., Hajdas, I., Pandolfi, L., Bailey, G., Spikins, P., Rolfo, M.F., Sadori, L., 2016. Pollen from Late Pleistocene hyena (Crocuta crocuta spelaea) coprolites: an interdisciplinary approach from two Italian sites. Rev. Palaeobot. Palynol. 233, 56–66.
Girard, M., Renault-Miskovsky, J., 1969. Nouvelles techniques de preparation en palynologie appliques a trois sediments du Quaternaire final de l'Abri Corneille (Istres-Bouches-du-Rhone). In: Bulletin de l'Association Francaise pour l'Etude du Quaternaire. 4. pp. 275–284.
González-Sampériz, P., Montes, L., Utrilla, P., 2003. Pollen in hyena coprolites from Gabasa Cave (northern Spain). Rev. Palaeobot. Palynol. 12, 7–15.
Horwitz, L.K., Goldberg, P., 1989. A study of Pleistocene and Holocene hyaena coprolites. J. Archeol. Sci. 16, 71–94.
Hunt, C.O., Fiacconi, M., 2018. Pollen taphonomy of cave sediments: what does the pollen record in caves tell us about external environments and how do we assess its reliability? Quat. Int. 485, 68–75.
Jiménez-Arenas, J.M., Toro, I., Margvelashvili, A., Ponce de León, M., Alba, J., Carrión, J.S., Cortés, M., Lalueza, C., Riquelme, J.A., Zollikofer, Z., 2016. Digging in the museum. Preliminary report of three unpublished Neanderthal teeth from Carigüela Cave (Píñar, Granada, Spain). Am. J. Phys. Anthropol. 159, 185–186.
Jiménez-Arenas, J.M., Bienvenu, T., Toro-Moyano, I., Ponce de León, M., Zollikofer, C., 2019. Virtual reconstruction and re-evaluation of the neanderthal frontal bone from Carigüela cave (Granada, Spain). Quat. Sci. Rev. 217, 89–97.
Knul, M.V., 2018. Faunal and Human Biogeography and Terminal Ice Age Climate Change. PhD Thesis. Bournemouth University.
Larkin, N.R., Alexander, J., Lewis, M.D., 2000. Using experimental studies of recent faecal material to examine hyaena coprolites from the West Runton Freshwater Bed, Norfolk, UK. J. Archeol. Sci. 27, 19–31.
Latorre, C., Betancourt, J.L., Rylander, K.A., Quade, J., 2002. Vegetation invasions into absolute desert: a 45,000 year rodent midden record from the Calama-Salar de Atacama basins, northern Chile (lat 22°–24°S). Bull. Geol. Soc. America 114, 349–366.
Marais, E., Scott, L., Gil-Romera, G., Carrión, J., 2015. The potential of palynology in fossil bat-dung from Arnhem Cave, Namibia. Trans. R. Soc. S. Afr. 70, 1–7.
Navarro, C., Carrión, J.S., Navarro, J., Munuera, M., Prieto, A.R., 2000. An experimental approach to the palynology of cave deposits. J. Quat. Sci. 15, 603–619.
Navarro, C., Carrión, J.S., Munuera, M., Prieto, A.R., 2001. Cave surface pollen and the palynological potential of karstic cave sediments in palaeoecology. Rev. Palaeobot. Palynol. 117, 245–265.
Olalde, I., Mallick, S., Patterson, N., Rohland, N., Villalba-Mouco, V., Silva, M., Dulias, K., 2019. The genomic history of the Iberian Peninsula over the past 8000 years. Science 363, 1230–1234.
O'Regan, H.J., Turner, A., Wilkinson, D.M., 2002. European Quaternary refugia: a factor in large carnivore extinction? J. Quat. Sci. 17, 789–795.
Pellicer, M., 1964a. Actividades de la delegación de zona de la provincia de Granada durante los años 1957-62. Not. Arq. Hisp. 6, 304–350.
Pellicer, M., 1964b. El Neolítico y el Bronce de la Cueva de la Carihuela de Píñar (Granada). Trab. Prehist. 15, 7–71.
Ramsey, C., 2017. Methods for summarizing radiocarbon datasets. Radiocarbon 59, 1809–1833.
Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Grootes, P.M., Guilderson, T.P., Haflidason, H., Hajdas, I., HattZ, C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Staff, R.A., Turney, C.S.M., van der Plicht, J., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0-50,000 years cal BP. Radiocarbon 55, 1869–1887.
Riquelme, J.A., 1999. La Cueva de las Ventanas, Píñar (Granada). Recuperación e investigación del Patrimonio Arqueológico. Rev. Arqueol. 22, 12–19.
Riquelme, J.A., 2002. Cueva de Las Ventanas. In: Historia y arqueología. Excmo. Ayuntamiento de Píñar, Granada.
Riquelme, J.A., Carrión, J.S., 2010. Las Ventanas Cave, Píñar, Granada: Archaeological Reconstruction of a hyaena Den for Lateglacial Southern Iberia. In: First Meeting on Hyaena Dens in Archaeological Sites of the Iberian Peninsula. Museo Arqueológico Regional, Alcalá de Henares, pp. 345–351.
Riquelme, J.A., Moreno, F., 1999. Cueva de las Ventanas: difusión del Patrimonio Arqueológico. Rev. Arqueol. 224, 6–13.
Rosell, J., Baquedano, E., Blasco, R., Camarós, E., 2012. New insights on hominid-carnivore interactions during the Pleistocene. J. Taphonomy 10, 125–128.
Ruiz-Bustos, A., García-Sánchez, M., 1977. Las condiciones ecológicas del Musteriense en las depresiones granadinas. La fauna de micromamíferos en la cueva de la Carihuela (Píñar, Granada). In: Cuadernos de Prehistoria. 2. pp. 7–17.
Scott, L., 1987. Pollen analysis of hyena coprolites and sediments from Equus cave, Taung, southern Kalahari (South Africa). Quat. Res. 28, 144–156.
Scott, L., 1994. Palynology of Late Pleistocene hyrax middens, southwestern Cape Province, South Africa: a preliminary report. Hist. Biol. 9, 71–81.
Scott, L., Fernández Jalvo, Y., Carrión, J.S., Brink, J., 2003. Preservation and interpretation of pollen in hyaena coprolites: taphonomic observations from Spain and southern Africa. Palaeontol. Afr. 39, 83–91.
Sevilla García, P., 1988. Estudio paleontológico de los Quirópteros del Cuaternario español. Paleontologia i Evolució 22, 113–233.
Sevilla García, P., 1989. Quaternary fauna of bats in Spain. Paleoecologi and biogeographic interest. In: Hanák, V., Horáček, I., Gaisler, J. (Eds.), European Bat Research 1987, pp. 349–355.
Spahni, J.C., 1955a. Grotte de la Campana à Píñar (Grenade, Espagne), LII. Bull. Soc. Prehistor. Françaisepp. 248–249.
Spahni, J.C., 1955b. Vestiges néandertaliens de Píñar, LII. Bull. Soc. Prehistor. Française. (540 pp).
Stuart, A.J., Lister, A., 2014. New radiocarbon evidence on the extirpation of the spotted hyaena (Crocuta crocuta (Erx1.)) in northern Eurasia. Quat. Sci. Rev. 96, 108–116.
Turner, A., 1992. Large carnivores and earliest European hominids: changing determinants of resource availability during the Lower and Middle Pleistocene. J. Hum. Evol. 22, 109–126.
van Geel, B., Coope, G.R., Van der Hammen, T., 1989. Palaeoecology and stratigraphy of the Lateglacial type section at Usselo (The Netherlands). Rev. Palaeobot. Palynol. 60, 25–129.
Varela, S., Lobo, J.M., Rodríguez, J., Batra, P., 2010. Were the Late Pleistocene climatic changes responsible for the disappearance of the European spotted hyena populations? Quat. Sci. Rev. 29, 2027–2035.
Vartanyan, S.L., Garutt, V.E., Sher, A.V., 1993. Holocene dwarf mammoths from Wrangel Island in the Siberian Arctic. Nature 362 (6418), 337–340.
Vega-Toscano, G., 1988. El Paleolítico medio del sureste español y Andalucía oriental. Tesis Doctoral. Departamento de Prehistoria. Universidad Complutense, Madrid.
Vega-Toscano, G., 1990. La fin du Paléolithique moyen récent au sud de L'Éspagne (ses implications dans le contexte de la Péninsule Ibérique). In: Farizy, C. (Ed.), Actes du Colloque International de Nemours. Mémoire du Musée de Préhistoire de l'Ile de France. 3. A.P.R.A.I.F., Nemours, pp. 169–176.
Vega-Toscano, G., 1993. El tránsito del Paleolítico Medio al Paleolítico Superior en el sur de la Península Ibérica. In: Cabrera Valdés, V. (Ed.), El origen del hombre moderno en el suroeste de Europa. UNED. Universidad Nacional de Educación a Distancia, Madrid, pp. 147–170.
Vega-Toscano, G., Hoyos, M., Ruiz Bustos, A., Laville, H., 1988. La séquence de la grotte de la Carihuela (Piñar,Grenade). In: Otte, M. (Ed.), L'homme de néandertal, vol 2, L'environnement. ERAUL 29, Études et Recherches Archeólogiques de l'Université de Liège, Liège, pp. 169–178.
Wigand, P.E., 1978. The Neolithic and Bronze Age Levels of Cariguela de la Pinar, Granada, Spain. Tesis doctoral. Washington State University, Inédita.
Williams, J., Grimm, E.C., Blois, J.L., Charles, D.F., Davis, E.B., Goring, S.J., Graham, R.W., Smith, A.J., Anderson, M., Arroyo-Cabrales, J., Ashworth, A.C., Betancourt, J.L., Bills, B.W., Booth, R.K., Buckland, P.I., Curry, B.B., Giesecke, T., Jackson, S.T., Latorre, C., Nichols, J., Purdum, T., Roth, R.E., Stryker, M., Takahara, H., 2018. The Neotoma paleoecology database, a multiproxy, international, community-curated data resource. Quat. Res. 89, 156–177.
Yll, R., Carrión, J.S., Marra, A.C., Bonfiglio, L., 2006. Pollen in late Pleistocene hyena coprolites from San Teodoro Cave (Sicily, Italy). Palaeogeogr. Palaeoclimatol. Palaeoecol. 237, 32–39.