Pollen in hyaena coprolites reflects late glacial landscape in southern Spain

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Abstract

The presence of coprolites and bone remains of spotted hyaena (*Crocuta crocuta*) together with bone remains of alleged preys in Las Ventanas Cave (Granada) indicates that the spotted hyaena persisted in southern Spain until the Lateglacial. Pollen analysis of hyaena coprolites is used in conjunction with existing pollen records to improve our picture of the vegetation in the region at c. 12 780 cal yr BP. Although many coprolites were sterile, 10 of them showed good pollen preservation, relatively high pollen concentration and diversity of both herbaceous and arboreal types. Because of the relatively high pollen concentration of several coprolites, it is postulated that pollen is largely incorporated into the coprolite through the stomach contents of plant-consuming prey. Dietary behaviour does not preclude palaeoenvironmental reconstruction. The coprolite pollen record compares closely with pollen spectra from lateglacial sediments in the adjacent Carihuela Cave and other regional pollen records. It depicts a mosaic landscape comprising pine forests, steppes of *Artemisia* with juniper, and grassland. Lower frequencies of *Quercus*, *Betula*, *Abies*, *Corylus*, *Alnus*, *Acer*, *Taxus*, *Myrtus*, *Olea*, *Pistacia*, *Ephedra fragilis*, and *Rhamnus*, among others, suggest that oak forests with temperate trees and thermo-Mediterranean scrub persisted in less continental situations of the Betic cordilleras. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: palaeoecology; pollen analysis; coprolites; hyaena; Quaternary; Spain

1. Introduction

Examination of pollen in fossil faecal materials may yield valuable palaeoenvironmental information (Martin et al., 1961; Bryant and Holloway, 1983; Davis and Anderson, 1987; Davis, 1990; Scott and Cooremans, 1992; James and Burney, 1997; Carrión et al., 1999b). Hyaena coprolites have been a reliable source of evidence on animal diet (Siegfried, 1984) and animal–human relations in the past (Horwitz and Goldberg, 1989). However, except for Scott (1987), research has been rarely addressed towards palaeo-vegetation issues. Here we report a pollen-analytical investigation of Late Quaternary hyaena coprolites from Las Ven-

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tanas Cave in southern Spain. The interpretative potential assigned to the palynology of hyaena coprolites is based upon the working hypothesis that coprolite pollen spectra can be compared with available pollen records in order to improve our knowledge about the regional palaeo-landscape at particular times of the Quaternary. Two facts justify this approach. First, available studies from southern Africa corroborate the coincidence of coprolite spectra with well-established regional pollen records from open sites (Scott, 1995). Second, there is a need to depend upon faecal materials and cave infillings in arid and semi-arid areas where conventional open pollen-rich deposits are rare, and where the abundance of entomophilous plants may complicate interpretation (Carrión et al., 1999b).

2. Setting

Las Ventanas Cave (3°25′17′W, 37°24′54′N, 1040 m asl) is located 45 km northeast of Granada city in southern Spain. It lies on the north slope of the Sierra Arana mountains in the valley of the southwesterly flowing Río Piñar (Fig. 1). The climate of the region is continental Mediterranean, with mean annual temperature of 12–15°C, and mean annual precipitation of 250–600 mm. Regional vegetation includes mixed oak forests of *Quercus rotundifolia* and *Quercus faginea*, Mediterranean scrub with *Pistacia–Quercus cocci-fera* understorey, pine forests (*Pinus halepensis, Pinus pinaster, Pinus nigra, Pinus sylvestris*), and steppe-like communities dominated by *Lygeum spartum*, several species of *Artemisia*, and *Stipa tenacissima* (Carrión, 1992).

3. The cave and depositional environment

The local relief reflects primarily the karstic nature of the region, and Las Ventanas is just one of the many caves located in the area. Carihuela Cave, one of the latest Neanderthal settlements of Europe (Vega-Toscano, 1993), lies only c. 500 m distant (Fig. 1). The cavern axis is orientated in a generally easterly direction from the single main

entrance, which faces northwest. The cave is renowned because of its spectacular endokarst, and the archaeological materials exhibited in the adjacent museum. The collection dates from back beyond the Upper Palaeolithic to the present, and includes abundant lithics, pottery, and bone remains of extinct animals and anatomically modern man (Riquelme and Moreno, 1999). Unfortunately, systematic excavation has not been yet undertaken, and most of the findings come from sediments removed by looters, who have pillaged the cave over the last century.

Thousands of well-preserved coprolites and fragmented specimens occur packed into parietal sediment of a pit c. 4 m depth and c. 5 m diameter, located close behind the main entrance. The bed comprises clay, silt and sand without evidences of plant macrofossils. Abundant bone remains of spotted hyaena (*Crocuta crocuta* subsp. *spelaea*) and herbivores (*Bos primigenius, Cervus elaphus, Equus hydruntinus*) have been found assembled in the same pit, and scattered deeper into the cave. Hyaena remains correspond to at least five individuals differing in age, as is characteristic within hyaena dens. Gnawing damage typical of hyaenids is visible in a number of bone fragments (Riquelme, 1999).

Understanding the depositional environment and history of preservation of the coprolites and animal remains is not simple. The skeletal remains may be the result of different interactions among hyaenas, humans, and other carnivores present in the cave such as the brown bear. The simplest explanation involves the existence of a conical talus acting as a collecting place for all kind of materials falling in from above and transported by water during karst reactivations. A specific 'latrine area' might have been responsible for the great accumulation of coprolites. In living spotted hyaenas, social defecation tends to occur not far from the cave opening (Brain, 1981). Excavations must be undertaken to resolve this and similar questions.

4. Description of the coprolites

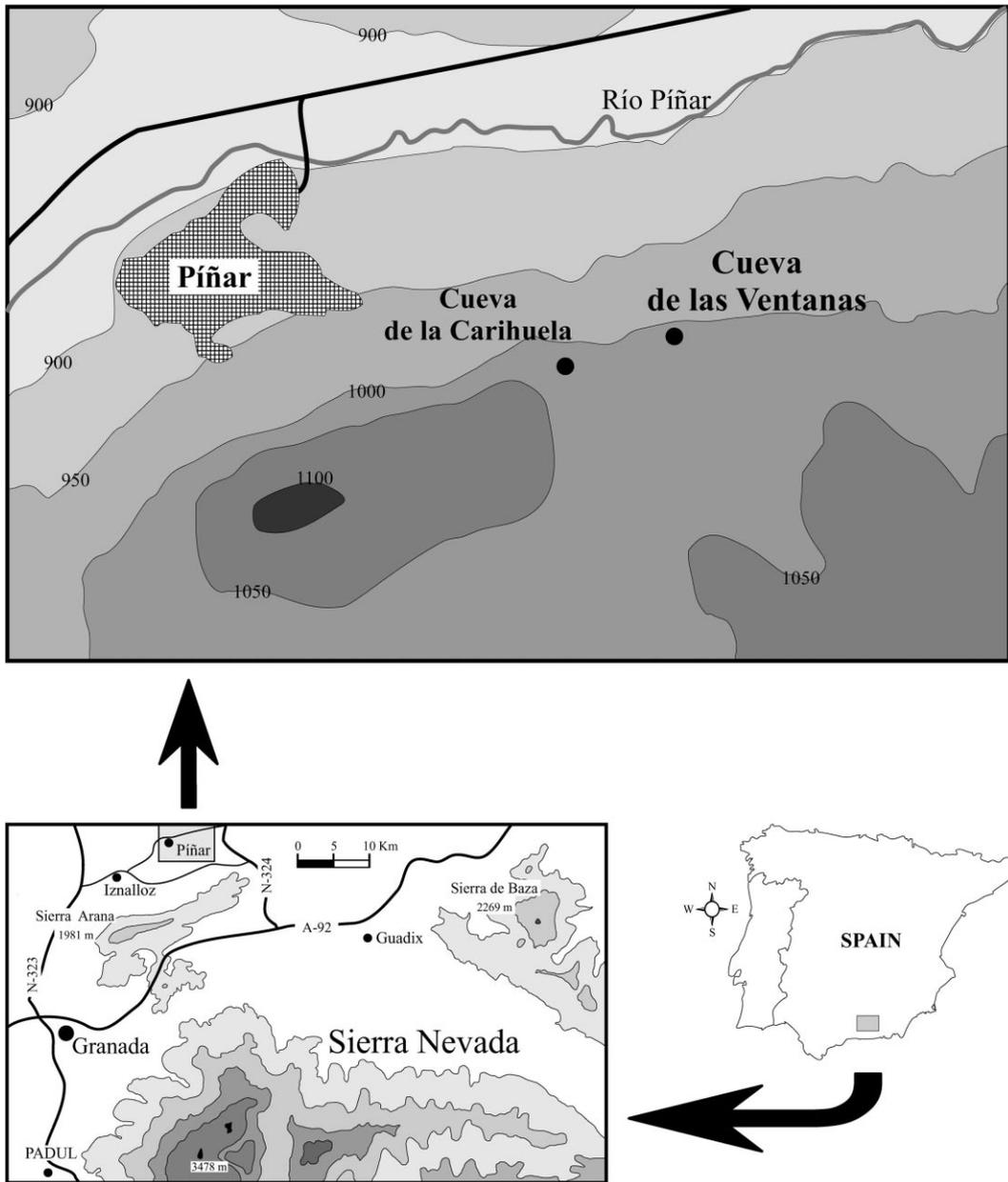Coprolites were externally pale brown to yellow-

Fig. 1. Location of Las Ventanas Cave, and the Carihuela and Padul pollen sites in southeastern Spain.

ish, and internally pale brown to white. Most were hard, although not permineralised, and sometimes broke easily. Their surface showed straight cracks, up to 5 cm in length, sometimes intersecting each other in the inner region, giving a polygonal appearance to the matrix. A denser cortex, probably related to the intestinal lubricant (Horwitz and Goldberg, 1989), was macroscopically discernible from the inner region of the coprolite. Several specimens contained small, highly corroded fragments of partially digested prey bones. A great majority of the coprolite specimens consisted of

Table 1
Measurements of hyaena coprolites and fresh droppings at several fossil and recent sites, including the case study at Las Ventanas

Site/species	Widest diameter mean, mm (range)	Shorter diameter mean, mm (range)
Las Ventanas, south Spain	40.1 (31–50)	38.7 (30–49)
La Valiña, north Spain, *Crocuta crocuta* coprolites (Fernández-Rodríguez et al., 1995)	40.5	–
West Runton, UK, *Crocuta crocuta* coprolites (Larkin et al., 2000)	41 (27–55)	33 (19–50)
Geula, Israel, *Crocuta crocuta* coprolites (Horwitz and Goldberg, 1989)	40 (36–44)	–
Kebara, Israel, *Crocuta crocuta* coprolites (Horwitz and Goldberg, 1989)	41 (38–44)	–
Colchester Zoo, UK, fresh *Crocuta crocuta* droppings (Larkin et al., 2000)	31 (17–43)	26 (12–36)
Oyster Bay, South Africa, *Parahyaena brunnea* coprolites (Carrión et al., 2000c)	29 (25–40)	24 (16–34)
Arad, Israel, sub-recent *Hyaena hyaena* droppings (Horwitz and Goldberg, 1989)	21 (15–26)	–
Tel-Aviv Zoological Garden, Israel, fresh *Hyaena hyaena* droppings (Horwitz and Goldberg, 1989)	18	–

individual segments of 31–50 mm (mean 40.1) in their widest diameter (Table 1, Fig. 2).

5. Assessment of the coprolite-producing species

Several facts support the attribution of faecal materials found in Las Ventanas Cave to fossil droppings of *Crocuta crocuta*. Firstly, there is little doubt that these materials are defecated remains containing a great amount of transformed bone, and as such are likely to have been produced by carnivores with a diet similar to that of modern *C. crocuta* (Kruuk, 1972). Secondly,
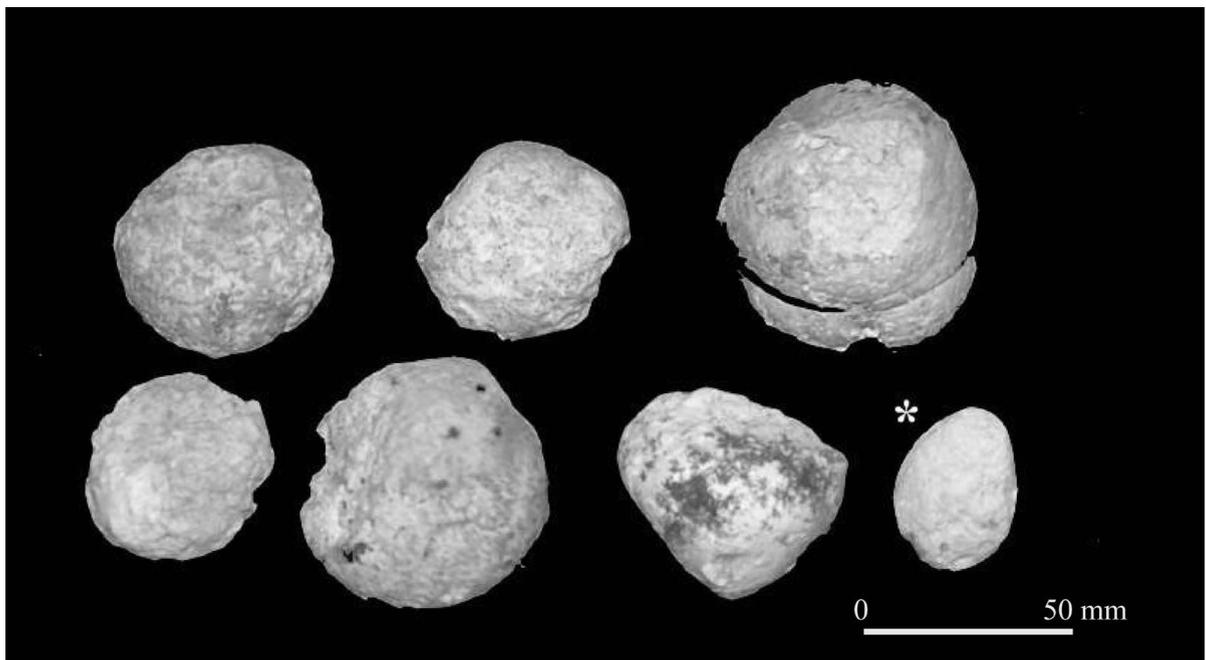

Fig. 2. Spotted hyaena coprolites from Las Ventanas Cave. Asterisk next to brown hyaena coprolite from Oyster Bay, South Africa.

Table 2
Pleistocene stratigraphy of Spanish hyaenids (Arribas and Jordá, 1999)

Stage	Characteristics	Fossil type sites	Other sites
Upper Pleistocene	*Crocuta crocuta* var. *spelaea*	Torrejones Pinarillo-1	Morín Carihuela Cova Negra
Middle Pleistocene	*Crocuta crocuta* var. *intermedia*	Villacastín Congosto	Cúllar
Lower Pleistocene	*Pachycrocuta brevirostris*	Venta Micena Cueva Victoria	Huéscar

the coprolites found were extremely large and conform in shape and size to descriptions of spotted hyaena coprolites from elsewhere in Europe and Israel (Table 1). It is interesting that they are larger on average than recent droppings, in agreement with the interpretation that European spotted hyaenas of the Upper Pleistocene were larger than modern African equivalents (Kurtén, 1968). Thirdly, their association with bone remains of spotted hyaena and the prey of the hyaenas confirms that these animals were present at the site (Sutcliffe, 1970). Fourthly, skeleton fragments associated with coprolites showed evidence of post-mortem disturbance including chewing by scavengers. Finally, other carnivore species are unlikely to be responsible for the coprolites. The species *Parahyaena brunnea* and *Hyaena hyaena* provide droppings of a discernibly smaller size (Table 1), with bone fragments rarely visible (Horwitz and Goldberg, 1989; Carrión et al., 2000c). Furthermore, there is no record of *P. brunnea* and *H. hyaena* in Iberia during the Quaternary (Arribas and Jordá, 1999). Other bone-cracking scavengers such as the lion-sized hyaena (*Pachycrocuta brevirostris*) dominate the hyaenid bone spectrum in Lower Pleistocene sites of Iberia (Arribas and Palmqvist, 1998) (Table 2). *Canis lupus* droppings may contain bone fragments, but differently to *Crocuta*, these are sharp and

well-preserved (Larkin et al., 2000). Large felids are excluded as their dentition only allows them to consume flesh, not bone (Turner, 1992).

6. Chronology of the coprolites and palaeontological relevance

Two samples comprising five and seven coprolites were submitted respectively to the CSIR (Pretoria), and Beta Analytic (Miami) for radiocarbon dating (Table 3). Previous samples consisting of individual coprolites were not datable because of insufficient concentration of organics. Although the cortex was surely richer in organic matter and thus hypothetically datable, it was removed from the coprolite samples submitted for dating with the goal of reducing the chance of contamination by extraneous carbon. At first sight, the dates suggest that the coprolite collection spans a period of at least 1000 years at the transition between the Upper Pleistocene and the Holocene. That these dates derive each from a set of coprolites implies that the time interval they represent could be wider, but the difference in calculated ages may well be due to inaccuracy of one or both dates. In view of palynological results discussed below, it seems likely that the date at c. 10 750 cal yr BP is too young.

Table 3
Radiocarbon dating of coprolites from Las Ventanas

Laboratory No.	^{14}C age yr BP	Calibrated age cal yr BP	Method
Beta-141051	10 670 ± 40	12 780 (12 949–12 618)	AMS
GrA-13533	9 500 ± 50	10 750 (10 871–10 636)	AMS

Calibrations were carried out following Stuiver et al. (1998).

It is generally assumed in the literature that
spotted hyaenas became extinct in Europe at the
end of the Pleistocene (Sutcliffe, 1970), but the
chronology of the extinction is unclear for most
regions. In the case of the Iberian Peninsula, *Cro-
cuta crocuta* is principally documented in bone
samples of the Middle and Upper Pleistocene (Ar-
ribas, 1994; Arribas and Jordá, 1999), with the
latest records dating from Cueva Morín, northern
Spain, at c. 23 900 cal yr BP (Altuna, 1971). Las
Ventanas Cave appears therefore as a key site to
document the lateglacial survival of Iberian spot-
ted hyaenas.

7. Pollen analysis

7.1. Methods

Twenty-five coprolite specimens were collected
for pollen analysis. After clearing away the outer
5 cm to expose a fresh surface in the pit wall, five
sediment samples were collected along a vertical
column. In another work, 10 sediment samples
have been collected from the cave surface and
analysed for pollen (Navarro, 2000). In the lab-
oratory, to minimise contamination from exter-
nal surfaces, the coprolites were cut open with a
steel spatula, and material from the centre was
scraped out and weighed. Laboratory treatment
was performed following the conventional HCl,
HF and KOH method and *Lycopodium clavatum*
tablets containing a known quantity of spores
were added to each sample prepared to enable
estimation of pollen concentration. Pollen identi-
fication was performed by comparison with the
reference collection of the Plant Biology Depart-
ment at Murcia University. Percentages of each
taxon for each sample were based on a pollen
sum excluding non-pollen palynomorphs (Figs. 3
and 4).

7.2. Results

No sediment sample was polliniferous,
although surface sediment showed quantities of
fungal spores (Navarro, 2000). Ten coprolite
specimens showed good preservation of pollen,
and allowed average counts of 349 grains, with
only one sample (VL7) not exceeding 250 grains
(Table 4). These 10 samples were the only con-
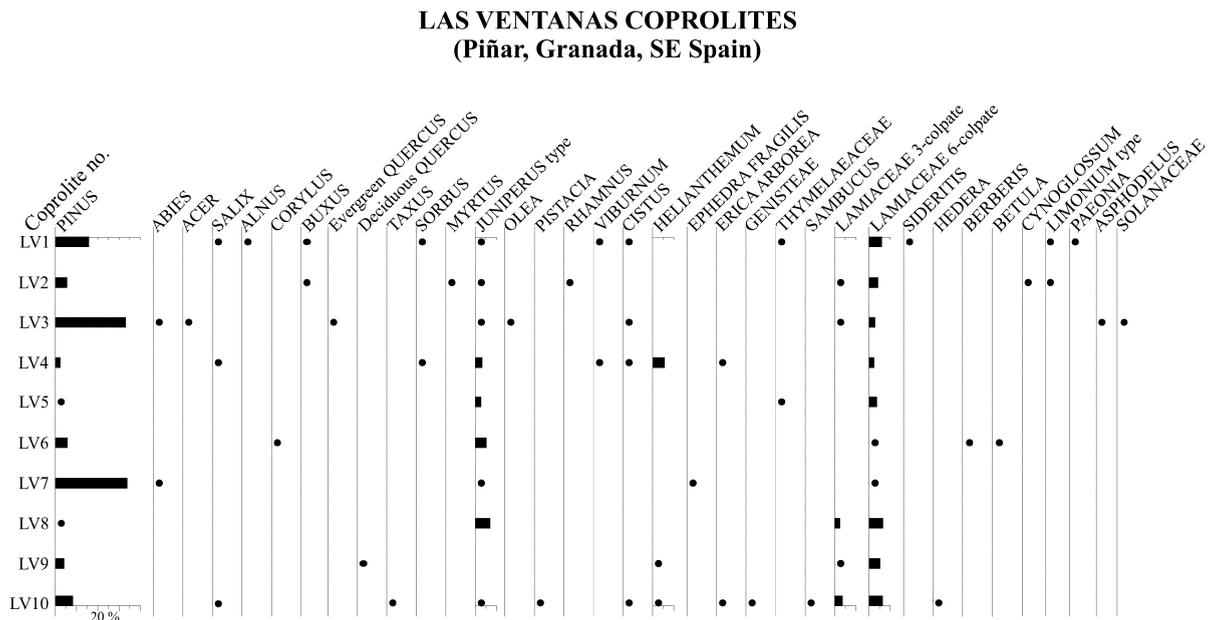sidered reliable for palaeoecological reconstruc

LAS VENTANAS COPROLITES
(Piñar, Granada, SE Spain)

Fig. 3. Percentage pollen diagram of coprolites from Las Ventanas Cave. Black spots indicate pollen percentages below 2%.
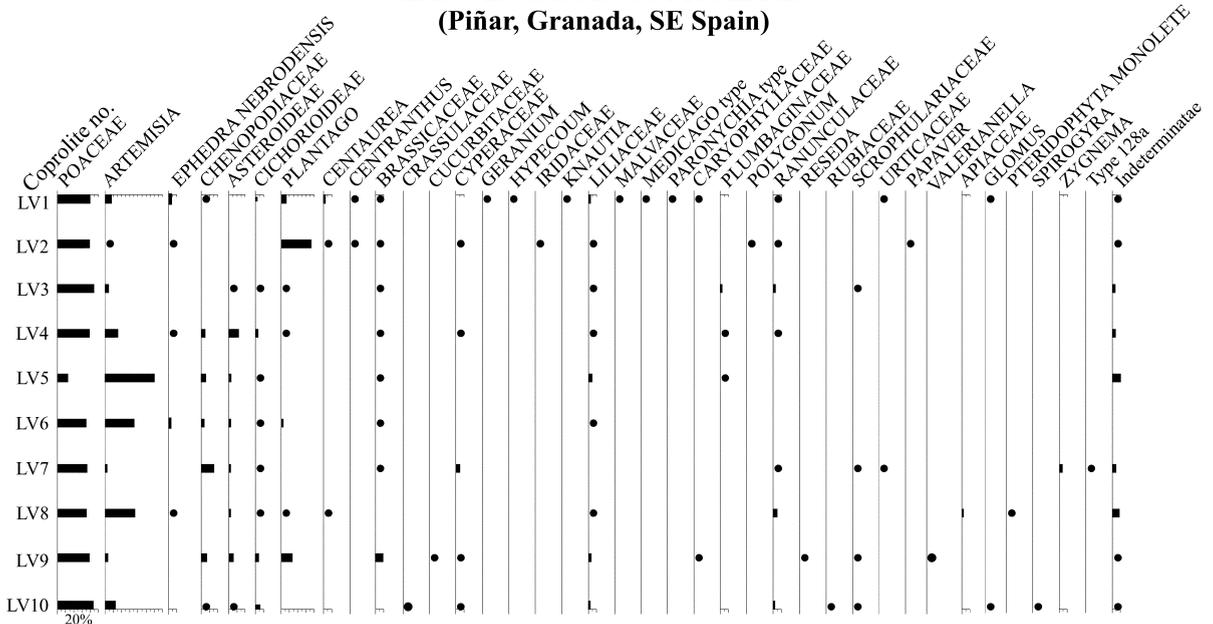
Fig. 4. Percentage pollen diagram of coprolites from Las Ventanas Cave (continuation). Black spots indicate pollen percentages below 2%.

tion (Figs. 3 and 4). The remaining 15 coprolites either were totally sterile or contained few grains, although these were well preserved. There was no relationship between the polliniferous character and the macroscopic appearance of the coprolite (e.g. colour, size, presence of surface cracks). Values of total pollen concentration, pollen sum, number of pollen taxa, and percentages of indeterminable pollen are shown in Table 4. The number of palynomorphs extracted from the coprolites ranges between 0 and 287 777 grains/g. Pollen preservation was generally good, allowing reliable pollen identifications and frequencies of indeterminable grains below 4%. Pollen taxa diversity is high, with 71 types in total, exceeding 15 types in most sam-

Table 4
Palynological characteristics of hyaena coprolites from Las Ventanas Cave: pollen concentration, percentage of indeterminable pollen, pollen sum, and number of taxa

Sample	Concentration (grains/g)	Indeterminable (%)	Pollen sum	Number of taxa
LV1	199 657	1.2	342	33
LV2	287 777	0.3	451	25
LV3	51 001	2.2	280	21
LV4	60 089	2.1	276	21
LV5	42 987	3.4	444	13
LV6	20 901	0.0	397	16
LV7	87 654	1.9	201	18
LV8	90 023	2.9	321	16
LV9	145 876	1.1	433	20
LV10	171 112	1.5	348	27
Mean	115 707	1.6	349	21

ples. The great diversity of herbaceous types is remarkable (Fig. 4).

The main pollen dominants in the coprolites are *Pinus*, Poaceae, *Artemisia* and, to a lesser extent, *Juniperus* and Lamiaceae (Figs. 3 and 4). Other pollen taxa reach relatively high values in some samples, such as *Helianthemum* (VL4), Chenopodiaceae (VL7), Asteroideae (VL4) and *Plantago* (VL2 and VL9). Other common types are *Ephedra nebrodensis*, Brassicaceae, and Liliaceae. Ecologically interesting arboreal types such as *Quercus*, *Betula*, *Abies*, *Acer*, *Corylus*, *Taxus*, *Myrtus*, *Olea*, *Pistacia*, *Viburnum*, *Ephedra fragilis*, *Erica arborea* and *Sambucus nigra* occur sparsely in low percentages. Zygospores and aplanospores of *Spirogyra* and *Zygnema* were identified in samples LV10 and LV7 respectively. *Glomus* chlamydospores occur in samples VL1 and VL2. The pollen spectra show great percentage variability, with the most distinctive differences being relative to the percentages of *Pinus* and *Artemisia*. In contrast, Poaceae are generally abundant, with the exception of sample VL5. It is worth mentioning that *Juniperus* reaches the highest frequencies in VL4, VL5, VL6 and VL8, conforming with the highest records of *Artemisia*.

8. Discussion

8.1. Pollen-analytic potential of hyaena coprolites

That most coprolites in Las Ventanas Cave are well preserved is surprising, because the deposit has been subject to episodic floods, instead of the more usual dry conditions known to favour Quaternary dung preservation (Martin et al., 1961; Davis et al., 1984). However, studies about the integrity and transportability of *Crocuta* droppings (Larkin et al., 2000) have shown that these droppings are hard and durable, sink rapidly through water and are able to withstand considerable trampling into sediment whilst maintaining a coherent form.

Equally surprising is the good pollen preservation within the humid cave environment. In these samples, exine thinning was not observed as has been shown for brown hyaena coprolites of South Africa (Scott, 1987; Carrión et al., 2000c), and spotted hyaena coprolites of north Spain (Fernández-Rodríguez et al., 1995) and southern Africa (Scott and Brink, 1992). Indeterminable pollen frequencies were also comparatively lower in Las Ventanas (Table 5). As pollen in coprolites con-

Table 5

Palynological characteristics of an average pollen spectrum of Las Ventanas as compared with other fossil hyaena sites in Spain and South Africa

Site	Concentration (grains/g)	Indeterminable (%)	Number of taxa	Pollen dominants
Las Ventanas	0–287 777	1.6	71	Poaceae, *Artemisia, Pinus, Juniperus*, Lamiaceae
La Valiña, north Spain, *Crocuta crocuta* (Fernández-Rodríguez et al., 1995)	0–570	–	16	*Trifolium, Lythrum*
Florisbad, South Africa, *Crocuta crocuta* (Scott and Brink, 1992)	–	–	–	Poaceae, Asteraceae
Equus Cave, South Africa, *Parahyaena brunnea* (Scott, 1987)	0–1000	18	63	Poaceae, Asteraceae, *Tarchonanthus, Rhus, Celtis, Stoebe*, Campanulaceae
Oyster Bay, South Africa, *Parahyaena brunnea* (Carrión et al., 2000c)	0–56	4	32	*Myrica*, Poaceae *Stoebe/ Elytropappus*
Deelpan, South Africa, *Parahyaena brunnea* (Scott and Klein, 1981)	–	–	6	Poaceae, Asteraceae, Chenopodiaceae

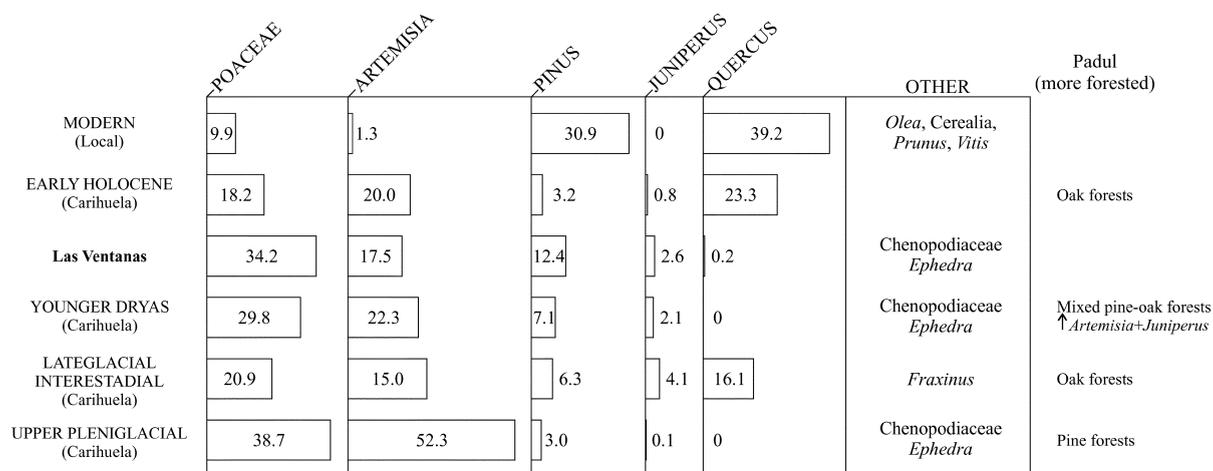|	POACEAE	ARTEMISIA	PINUS	JUNIPERUS	QUERCUS	OTHER	Padul (more forested)
MODERN (Local)	9.9	1.3	30.9	0	39.2	*Olea*, Cerealia, *Prunus*, *Vitis*	
EARLY HOLOCENE (Carihuela)	18.2	20.0	3.2	0.8	23.3		Oak forests
Las Ventanas	34.2	17.5	12.4	2.6	0.2	Chenopodiaceae *Ephedra*	
YOUNGER DRYAS (Carihuela)	29.8	22.3	7.1	2.1	0	Chenopodiaceae *Ephedra*	Mixed pine-oak forests ↑*Artemisia+Juniperus*
LATEGLACIAL INTERESTADIAL (Carihuela)	20.9	15.0	6.3	4.1	16.1	*Fraxinus*	Oak forests
UPPER PLENIGLACIAL (Carihuela)	38.7	52.3	3.0	0.1	0	Chenopodiaceae *Ephedra*	Pine forests

Fig. 5. Comparison of a mean coprolite pollen spectrum from Las Ventanas with average pollen spectra in local modern sediment, and with cave sediments of the adjacent Carihuela site during Upper Pleniglacial, Lateglacial Interstadial, Younger Dryas, and early Holocene phases. Las Ventanas compares closely with the Younger Dryas in Carihuela. References: Carihuela (Carrión, 1992; Carrión et al., 1998); Padul (Pons and Reille, 1988).

taining only few grains was well preserved, we postulate that the limiting factor for the occurrence of pollen in a coprolite is pollen input rather than post-depositional processes. Another possibility is that the cortex provided some kind of protection. In cow dung, burning induces the formation of a dense superficial layer able to seal the pollen (Carrión et al., 2000b). It is finally possible that coprolites were consolidated in dry sediment conditions and only brought to the actual deposit by recent floods. Ongoing research using fresh droppings will try to elucidate the relative influence of digestion processes, depositional environment, and post-depositional alteration on the pollen preservation in coprolite context.

It is worth questioning if the presence of well-preserved pollen is not partially the result of post-depositional contamination. Could, for instance, *Plantago* be indicative of recent contamination in samples VL2 and VL9 (Fig. 4)? Contamination of pollen spectra in cave environments by recent or reworked palynomorphs is very difficult to be categorically discarded (Navarro et al., 2000). However, contamination is unlikely in this case study, because (i) palaeoecological concordance of the coprolite spectra with lateglacial pollen records from adjacent Carihuela (Fig. 5), (ii) modern pollen spectra are different from coprolite pollen spectra, the former with higher values of *Quercus* and *Olea*, and constant presence of Cerealia, *Vitis*, *Fraxinus*, and *Prunus*, while *Plantago* is insignificant (Fig. 5), (iii) there are no differences in susceptibility to staining within the coprolite pollen spectra, something noticeable when pollen is derived from different ages (Carrión et al., 1995), (iv) we know that pollen in the cave sediment of Las Ventanas is rapidly removed or destroyed (Navarro, 2000), (v) coprolite pollen spectra do not show fungal spores that characterise the sediment (Figs. 3 and 4), (vi) *Plantago* is not an unquestionable anthropogenic indicator in southern Spain, because its pollen can occur in relatively high frequencies during the Pleistocene and early Holocene (Pantaleón-Cano, 1997; Carrión et al., 2000a).

8.2. Sources of pollen

Hypothetically, pollen may be incorporated into the hyaena coprolite (i) by ingestion of water, (ii) incidentally from the air, (iii) adhered to any item of the diet, (iv) by ingestion of vegetable matter, and (v) from the stomach contents of preys. However, determining the relative role of each will continue speculative until basic taphonomic research develops. Considering the be-

haviour of the species responsible for the copro-
lite accumulation may shed some light on this
problem (Scott, 1987). Most hyaenas will try to
eat almost everything, and subsist on a broad
omnivorous diet including carrion, vegetable
matter, mammals, and bird eggs (Mills, 1989).
Brown hyaenas may even consume grass (Skin-
ner, 1976). However, when there is abundant sup-
ply, the spotted hyaena seems to subsist primarily
on meat, with a preference for large mammals,
being frequent as primary defleshers (Kruuk,
1972). In this case, a most important pollen
source must be the stomach content of these large
herbivores. In Las Ventanas, this hypothesis finds
support in the fact that pollen concentrations are
similarly high to those found in fossil cow dung
(Carrión et al., 2000b). Dietary information con-
tained in the coprolites must therefore be related
to the prey, and palatable species are often over-
represented. However, if preys mainly consume
grasses, it is clear that the coprolites will provide
a pollen record of regional vegetation sources.
Grass swards are excellent traps of regional pol-
len not influenced by the flowering season (Gu-
tiérrez et al., 1998).

The ingestion of stagnant water by the hyaenas
or their prey is clear from the presence of Type
128 (Carrión and van Geel, 1999) and Zygnema-
taceae spores (Fig. 4). Spotted hyaenas range in
the Namib Desert following the distribution of
freshwater pools (Skinner and van Aarde, 1980).
Prey's diet would be partially reflected in the
abundance of grasses, and especially the high di-
versity of herbs. The abundance of grasses is rel-
atively general to pollen records in hyaena copro-
lites (Table 5). The influence of vegetation is
evident in that airborne pollen is not different in
the coprolite and conventional pollen records of
the Pleistocene and early Holocene in the region
(Pons and Reille, 1988; Munuera and Carrión,
1991; Carrión, 1992; Pantaleón-Cano, 1997; Car-
rión et al., 1998). We infer that dietary input does
not substantially bias the pollen record. This is
not to deny the influence of the behaviour of spot-
ted hyaenas on coprolite pollen spectra, as these
might reflect the vegetation of particular areas
visited. Spotted hyaenas are known to range up
to 50 km from their dens (Mills, 1989).

8.3. Reconstruction of past vegetation

The differences in particular pollen spectra from
the coprolites admit two basic interpretations:
they reflect the coexistence of different vegetation
formations within a patchy landscape, or alterna-
tively, they reflect a temporal record of different
vegetation stages in unknown sequence. In view of
data shown in Fig. 5, we favour the hypothesis
that only the date at c. 12 780 cal yr BP is correct,
and thus the coprolites were produced in phase
contemporary of the Younger Dryas chronozone.
Coprolites are characterised by Poaceae and *Arte-
misia*, with moderate *Pinus* values, *Juniperus* rela-
tively important, and *Quercus* scanty. These are all
characteristics shared by pollen spectra of the
Younger Dryas in Carihuela (Fig. 5). If the cop-
rolites had been produced during either early Ho-
locene or Lateglacial Interstadial stage, their pol-
len spectra would contain more *Quercus* and
mesothermophilous taxa. *Quercus* increases in
Carihuela long before c. 14 700 cal yr BP, and
regional spread is demonstrated to occur from
c. 15 900 cal yr BP (Pons and Reille, 1988). In
Padul, this pattern of lateglacial expansion is
only interrupted shortly during the Younger
Dryas, and continues during the early Holocene.
In Carihuela, trends are similar but oscillations are
sharper, as *Quercus* disappears locally during the
Younger Dryas (Fig. 5). On the other hand, if the
coprolites had been produced during any plenigla-
cial stage, *Artemisia* and Chenopodiaceae would
be more frequent, while *Juniperus*, a lateglacial
characteristic, would have been almost absent.

There are of course several differences between
the pollen spectra in the coprolites and the
Younger Dryas pollen spectra from Carihuela.
For instance, the coprolite samples show,
although in very low frequencies, a higher number
of mesothermophilous taxa. This is probably due
to the fact that coprolites reflect somewhat more
regional pollen sources than sediments, as has
been demonstrated by Scott and Klein (1981)
and Scott (1987) in the southern African hyaena
sites of Deelpan, Free State, and Equus Cave,
Kalahari region.

The overall record suggests the existence of pine
forests (LV3, LV7), steppes of *Artemisia* with ju-

niper (LV5, LV6, LV8), grasslands (LV1, LV2, LV4, LV9, LV10), and floristically rich herbaceous communities, these latter perhaps close to water bodies. Given the physiography of the territory, it is likely that herbaceous-dominated vegetation prevailed in the surrounding plateau and vast Guadix-Baza depression to the east, while pine forests were widespread over the Sierra Arana and Sierra de Baza continental mountains (Fig. 1). Further distant, probably in Sierra Nevada and the more coastal Sierra de Filabres, deciduous oak forests may have developed such as today's *Quercus faginea* and *Quercus pyrenaica* forests, with *Betula celtiberica, Taxus baccata, Corylus avellana, Acer opalus* and *Alnus glutinosa* in the most humid biotopes. *Abies pinsapo* rather than the northern Spanish species *Abies alba* appears responsible for the pollen occurrences at LV3 and LV7. Mediterranean scrub is also discernible from the pollen occurrence of evergreen *Quercus, Pistacia, Myrtus, Rhamnus, Viburnum* and *Ephedra fragilis*. This landscape reconstruction is coherent with that obtained from comparison of lateglacial pollen records of Mediterranean Spain, which match modern bioclimatic contrasts (Carrión et al., 1999a). Additional support might come from faunal association of forest (*Cervus*), and steppe–grassland (*Bos, Equus*) indicators, if ongoing excavations were to demonstrate in-phase relationships. How our findings on the coprolites apply to resolving the puzzle of lateglacial and early Holocene vegetation developments in southern Spain (Carrión et al., 2000a) must remain in question until additional data are published.

It has been shown in this paper that pollen analysis of hyaena coprolites may certainly provide valuable information on past vegetation and landscape. But there are surely many pitfalls behind our interpretation, because very little is known on how pollen is incorporated and preserved into hyaena droppings and coprolites, and we have to rely on comparison with pollen sequence of cave infill, which limits the quality of correlation. It bears emphasis that, dealing with pollen analysis of biogenic deposits, negative results, thought to be less interesting or more inconclusive, have tended to be massively under-re-

ported. We suspect that the pollen analysis of hyaena coprolites mentioned in this paper represents only a small and skewed subset of the total number of studies.

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