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Pollen in hyena coprolites from Gabasa Cave (northern Spain)

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Abstract

Pollen from hyena coprolites are useful to describe palaeovegetation and to infer palaeoclimatic conditions. In previous studies, sedimentological and palynological analyses of the Mousterian Gabasa Cave (Pyrenean foothill region, northeast Spain) have not been able to provide detailed palaeoenvironmental information. In this study, coprolites of the extinct cavern hyena (*Crocuta crocuta*) from Gabasa Cave were used for pollen analysis with the goal of establishing the regional environmental history between > 50 700 and > 39 900 yr BP ^{14}C (AMS). Eight of the twelve coprolites analyzed contained well-preserved and rich pollen assemblages. They indicated the development of a mosaic glacial landscape that included *Pinus* and *Juniperus* woodlands and steppes of *Chenopodiaceae*, *Poaceae*, *Artemisia*, and *Asteraceae*. Pollen for mesophilous and thermophilous trees and shrubs are also present, suggesting the location of nearby refugia of temperate and Mediterranean vegetation.

Keywords: coprolites; hyena; palaeoecology; Spain; Pleistocene; Palaeolithic; glacial refugia

1. Introduction

Pollen from peat bog, lacustrine and fluvial environments, archaeological sites and even stratified slope deposits are usually studied for palaeoenvironmental interpretation (González-Sampériz et al., 2002). The analysis of coprolites may also provide useful information about palaeoclimate, palaeovegetation and even palaeoethnology (Bryant and Holloway, 1983; Davis, 1990; Scott and Cooremans, 1992; Carrión et al., 2000, 2001), especially in arid environments without lakes or swamps. Coprolites can be used to analyze parasites, the main plant taxa used for food and even the season of ingestion. The results are not always as informative as in conventional palynology of lakes and peat bog sites, but notwithstanding coprolite palynology has proven its potential in recent studies (Carrión et al., 2000, 2001).

This paper discusses the study of a collection of twelve coprolites from a Mousterian cave site in northeast Spain of which eight specimens yielded very well-preserved pollen. Previous studies did not find good correlations among the macrofaunal, microfaunal, palynological and sedimentological evidence from this site (Azanza et al., 1988; Hoyos et al., 1992). Besides, pollen percolation in the cave impeded more accurate interpretations (Hoyos et al., 1992). Our results help to clarify

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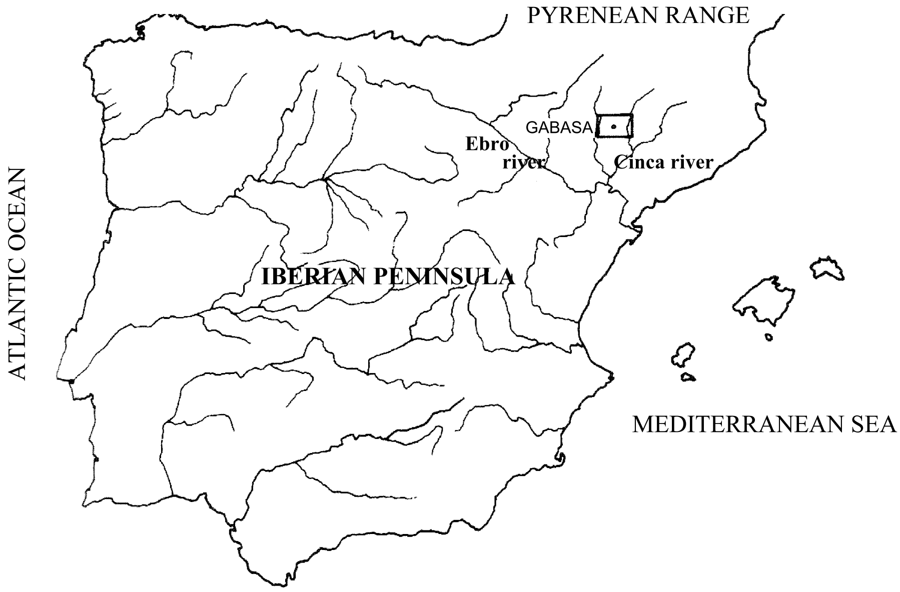

Fig. 1. Location of the Mousterian Gabasa Cave (northern Spain).

uncertainties regarding the plant cover in the vicinity of the Mousterian Gabasa Cave site. We selected samples from abundant hyena coprolites in the archaeological excavation (Blasco and Montes, 1997) in order to perform a palynological analysis in an attempt to provide a complete and coherent picture of past regional environmental and climate change. It is worth stressing that the pollen in hyena coprolites give a regional perspective of the palaeoenvironment, since these animals travel long distances in search of food (Scott, 1995; Carrión et al., 2001). Hyena coprolites reflect more regional pollen sources than sediment analysis, as is demonstrated by Scott and Klein (1981) and Scott (1987) in the South African hyena sites of Deelpan, Free State and Equus Cave, Kalahari region. The results are especially interesting when compared to the pollen analyses of the sedimentary matrices.

2. Physical setting

Gabasa Cave (42°00′20″N, 4°06′20″E, 780 m above sea level) faces south at 150 m above the channel in the headwater of the Sosa River – a tributary of the Cinca River – in the Pyrenean foothill region of northeast Spain (Fig. 1). The basal lithology is composed of Cretaceous and Palaeocene limestones, resulting in a karstic relief with abundant caves, many of them containing prehistoric artifacts.

The climate of the region is of a mountain continental Mediterranean type. Mean annual temperature is 14°C, with a large range (July 30°C and January −5°C). Mean annual precipitation is about 550 mm. Maximum rainfall occurs in spring and autumn (García-Ruiz et al., 2000). Modern vegetation includes a Mediterranean mixed oak forest with *Quercus rotundifolia* and *Q. faginea*, especially in the shady aspects, accompanied by scrubs of *Juniperus communis*, *J. sabina*, *Buxus sempervirens*, *Pistacia lentiscus*, and *Rosmarinus officinalis*. The most frequent species of the adjacent riparian communities are *Populus nigra*, *P. alba*, *Salix alba* and *Ulmus campestris*.

3. Stratigraphy of the cave

Gabasa Cave has two small chambers (each measuring ca. 30 m^2) with remnants of human

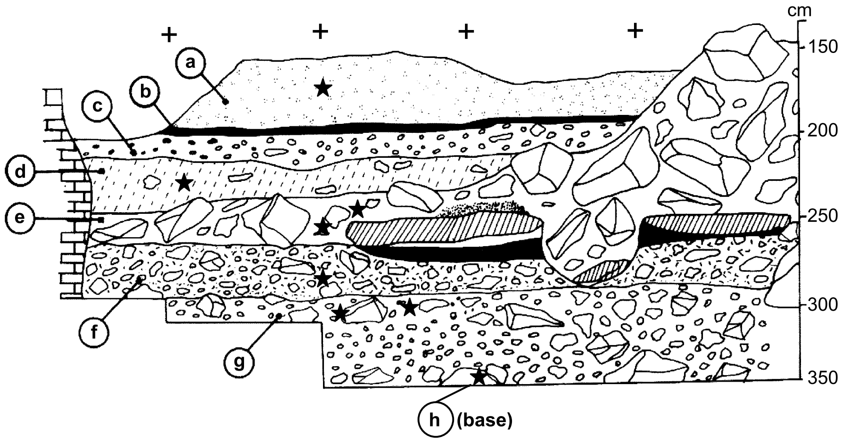

Fig. 2. Stratigraphy of Gabasa Cave. Location of the coprolites analyzed in the stratigraphic layers indicated by stars.

settlement located in the inner room. The stratigraphy (Fig. 2) shows eight archaeologically defined beds (Hoyos et al., 1992). Layer 'b' is thin, sterile, and discontinuous. The whole deposit is very homogeneous (except for layer 'h'), which makes it difficult to separate layers based on color and texture. According to several authors, each layer corresponds to long periods of intermittent occupation as revealed by the artifact contents (Montes, 1988; Utrilla and Montes, 1989, 1993; Blasco, 1995; Blasco et al., 1996; Montes et al., 2000).

Chronology and climatic interpretation used in the first sedimentological study of Gabasa Cave (Hoyos et al., 1992) were based on preliminary data. After new radiocarbon dating, Montes et al. (2000) attributed the sediment of Gabasa Cave to the central part of the curve of Ruddiman and McIntyre (1981) and not to the beginning of Isotopic Stage 3. The absolute chronology of the cave sequence (Table 1) is somewhat imprecise (minimum age), since the dates are beyond the ^{14}C time scale (Montes et al., 2000). The Gabasa sequence could be included in Oxygen Isotope or Marine Isotope Stage (OIS) 3 of Ruddiman and McIntyre (1981), but an older age cannot be ruled out. The absence of human structures (except for a fireplace in the 'h' layer), the nature of the sediment and the presence of Mousterian lithic tools suggest a sporadic, though persistent use of the cave by one or a few human groups during the Mousterian period. The animal remains suggest that the cave was used by humans during seasonal hunting (Blasco, 1995; Blasco et al., 1996), alternating with use as an animal shelter by hyenas, bears and cavern lions.

Table 1
Radiocarbon dating of Gabasa Cave

Gabasa Cave layers	Radiocarbon dating (BP)	Coprolite samples
Layer a	> 39 900	H.A.1
Layer b	> 45 900	No coprolite
Layer c	> 46 900 and > 47 800	No coprolite
Layer d		H.D.1
Layer e	> 45 600 and > 51 900	H.E.2, H.E.4
Layer f		H.F.4
Layer g	> 50 700	H.G.4, H.G.8
Layer h		H.H.2

4. Hyena coprolites: description and methodology

Fifty-four coprolites or fragments were found in the sediment of the Gabasa Cave pit (Plate I). The 12 largest samples were used for pollen analysis. Most coprolites weighed less than 30 g (Table 2). Their characteristics and the associated skeleton fragments of at least 13 individuals correspond with an age distribution that was typical of hyena dens (adults and sub-adults) of *Crocuta crocuta spelaea*, the cavern hyena from the Würm

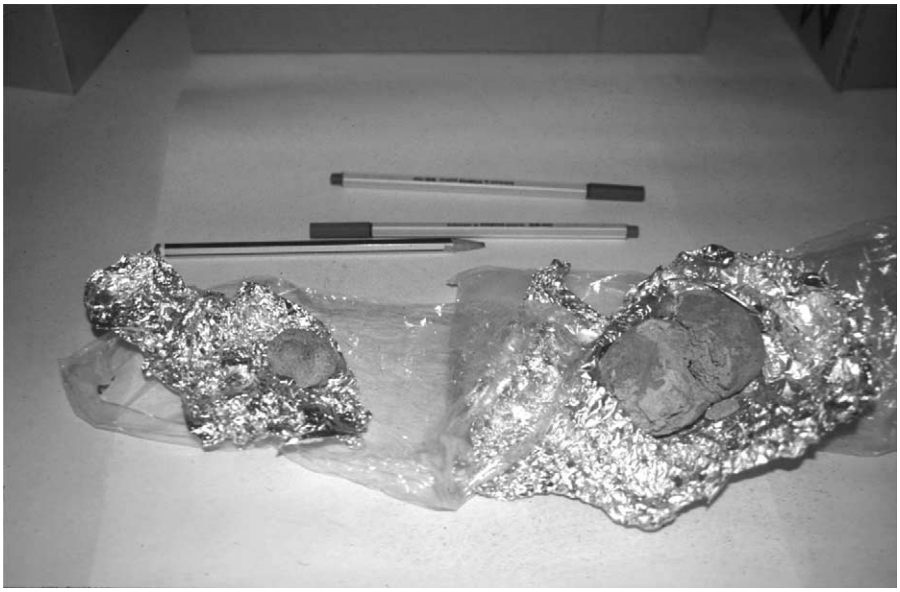

Plate I. Spotted hyena coprolites of Gabasa Cave.

period (Blasco, 1995). This animal was larger than the modern spotted hyena (Kurtén, 1968) and perhaps it was a hunter and not a scavenger. This possibility becomes crucial in the interpretation of the pollen spectra.

The coprolite surfaces are yellowish to pale brown and they are whitish inside. The surfaces form a dense-hard cortex that presumably preserved the pollen. Thus, each coprolite was treated as a whole and was not split (Carrión et al., 2001). In the laboratory, the coprolites were washed with distilled water to minimize contamination from external sources. This method appears valid since we verified the absence of pollen contamination in the first coprolites. Chemical treatment followed the conventional method (Delcourt et al., 1959; Moore et al., 1991; Dupré, 1992): HF, HCl, KOH, concentration with Thoulet solution with density 2, and *Lycopodium clavatum* tablets (Stockmarr, 1971) to calculate the pollen concentrations.

Hyenas digest sufficient organic and plant matter, including pollen, that is preserved in their faecal material (Wernet, 1955). In favourable cases, it is possible to compare the sediment and coprolite pollen contents from the same locations (southern Spain; Carrión et al., 2001), and even with coprolites of different species (*Canis* and

Table 2
Description and pollen characteristics of the coprolites analyzed

Hyena coprolite samples	Weight (g)	Taxa numbers	Pollen concentration (grains/g)	Indeterminate (%)
H.A.1	30	30	12 720	6
H.D.1	38	37	1 707	5
H.E.2	25	26	3 990	3
H.E.4	44	26	1 304	6
H.F.4	23	37	4 289	5
H.G.4	32	17	3 606	9
H.G.8	23	16	12 275	4
H.H.2	35	31	3 383	4

Capra in pre-Roman settlements (González-Sampériz, 2001). This approach provides useful data to test the validity of the results from both types of pollen analysis: sediments and coprolites (González-Sampériz, 2001). The coprolite pollen spectra of herbivorous animals are theoretically influenced by diet regime and plant availability. In archaeological settlements on the island of Mallorca, coprolite pollen analysis from the endemic goat, *Myotragus balearicus*, demonstrated that this extinct ruminant had a monospecific diet based on *Buxus*. Thus, the extinction of *M. balearicus* has been related with the extinction of *Buxus* in the island (Yll Aguirre et al., 2001). Since hyenas are not herbivorous, the ingestion of pollen and spores might be accidental or indirect through respiration (air) in addition to the oral system (water, ingestion of vegetable matter via the stomach contents of prey) (Carrión et al., 2001). In this study, the information obtained from coprolites is not used to describe the diet but to help understand the palaeoenvironment.

The pollen spectra of hyena coprolites in two Palaeolithic settlements in Auvergne – Saint-Hippolyte (Puy-de-Dôme) and Châtelperron (Allier) – in France also proved to be representative of the pollen rain as they compared well with the pollen spectra of the sediment samples (Vivent, 1989). This author observed the absence of pollen contamination during the digestive process in the hyena. Frequently, there is no over- or underrepresentation of specific taxa in the spore–pollen contents of coprolites, but there may be a slight enrichment in entomophilous pollen and shrubs (Girard, 1987; Burjachs, 1988).

5. Palynological results

In general, the pollen spectra in the studied coprolites (Fig. 3) indicate a patchy landscape composed of steppe and forest areas distributed according to topography (especially altitude and aspect) similar to the current foothill landscape of the Pyrenees. The region is transitional between the Ebro Valley and the mountains. The steppes were composed of chenopods, composites, grasses, and *Artemisia*, with patches of pines and junipers. Overall, it suggests a cold, arid climate, typical of the last glacial period in continental Iberia (Pons and Reille, 1986; Turner and Hannon, 1988; Peñalba, 1989; Montserrat, 1992; Pérez-Obiol and Julià, 1994; Carrión and van Geel, 1999).

Mesophilous vegetation occurred in the pollen catchments. It includes *Betula*, *Corylus*, *Ulmus*, *Fagus*, and the Mediterranean *Quercus ilex–coccifera* type and *Quercus faginea–pubescens* type. The pollen content of the hyena coprolites is probably derived from a complex landscape, including a number of biotopes, and trapped by hyenas while traveling up to 50 km away from their dens and eating a variety of fauna (Mills, 1989). In the same archaeological layer, the pollen spectra show a large variability. Other studies of pollen in spotted hyena coprolites also provide information about a regional, heterogeneous plant composition, as in Las Ventanas Cave, southern Spain (Carrión et al., 2001), dated to the end of the Pleistocene. This site was characterized by patchy grass vegetation, heliophytic herbaceous plants like *Artemisia* and *Chenopodiaceae*, pine forests and glacial plant refugia. All these features were present in several hyena coprolites from the same layer.

The suggested plant composition varies in all layers at Gabasa, but the climatic conditions interpreted were similar. In the top layer ('a' layer), pollen analysis suggests more temperate and humid conditions (Fig. 3) instead of arid and cold/cool conditions. The 'a' layer had a higher proportion of arboreal pollen, especially *Pinus* (60% of the total pollen content) and *Quercus ilex–coccifera* type (10%). In Mediterranean Europe, except in the case of glacial refugia situations, the increase of *Quercus ilex–coccifera* type is usually interpreted as belonging to interglacial or relatively warm periods (Wijmstra, 1969; Woillard, 1978; Pérez-Obiol, 1987; Dupré, 1988; Burjachs, 1989; Carrión et al., 1993).

It is interesting that the bottom and middle of the sequence had an unusual proportion of Chenopodiaceae in the first case, and *Plantago* in layer 'e'. These plants are appreciated by ruminants, particularly *Plantago*, because their leaves are very nutritious. The high percentages of these

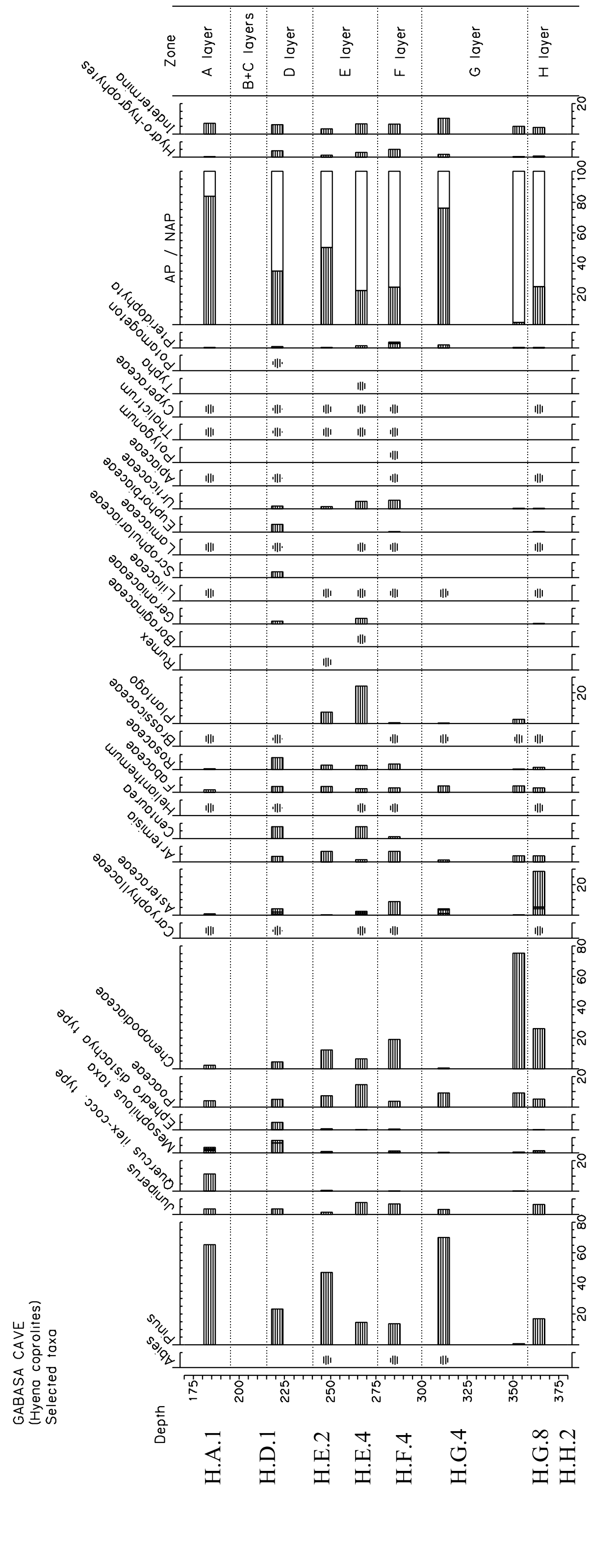

Fig. 3. Pollen diagram of hyena coprolites from Gabasa Cave (northern Spain).

two taxa in hyena coprolites are interpreted as the result of consumption of some ruminant stomach contents. The Mousterian cavern hyena was larger than the modern hyena and it could have chosen its meat food before other mammals (except felines). These hyenas would have been able to eat more stomachs and intestines and, consequently, ingest more pollen grains from these selected taxa (Kruuk, 1972). On the other hand, the prey of the hyena mainly consumed grasses, and grass swards are excellent traps for regional pollen (Gutiérrez et al., 1998).

6. Conclusions

Pollen analysis can be performed on samples from many types of sites and materials, including faecal material or coprolites. In this paper, the pollen content of hyena coprolites from the Mousterian Gabasa Cave (northern Spain) provided information about the palaeoenvironment and palaeoclimate, and reinforced previous archaeological, palynological, sedimentological and chronological studies. It also showed the existence of pollen percolation in the stratigraphy of the cave.

Our results are in agreement with the revised chronology (Montes et al., 2000) for the cave and various regional environmental and climatic interpretations (Pérez-Obiol, 1987; Dupré, 1988; Burjachs, 1989; Carrión et al., 1993, 2001).

The pollen analysis of hyena coprolites in Gabasa Cave suggests an arid and cold/cool climate except in the upper layer ('a'), which suggests a probably warmer climate due to the relatively high proportion of *Quercus ilex–coccifera* type. The rest of the layers show a complex landscape formed by xerophyte-steppe herbaceous plants and forester patches (essentially coniferous). The presence of a proportion of mesophilous vegetation suggests the occurrence of refugia of temperate trees which were probably related with favorable topographic conditions in the Ebro valley. The varied composition of the regional vegetation is probably reflected in the pollen composition of the hyena coprolites due to the mobility of these animals. It is clear that hyena coprolites reflect more regional pollen sources than the sediment matrix, but very little is known about pollen incorporation and post-depositional processes in hyena coprolites. The pollen analyses presented in this paper are a small new contribution to this debate.

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