

Pleistocene landscapes in central Iberia inferred from pollen analysis of hyena coprolites

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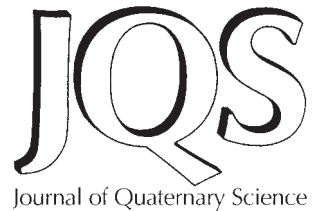
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ABSTRACT: New pollen data from hyena coprolites from central Spain are presented. The fossil faecal material has been recovered from two karstic systems in different localities, Villacastín and Los Torrejones, which are both around 1000 m a.s.l. The combined findings of bone remains and coprolites in both locations suggest the following chronology: late Middle Pleistocene for Villacastín and early Upper Pleistocene for Los Torrejones. The environments inferred from pollen are broadly in keeping with evidence from associated vertebrate fossil remains, and include a shifting mosaic of open and wooded habitats with abundant pine and juniper species, steppe-grassland areas with composites and chenopods, and enclaves with mixed oak forests. However, Los Torrejones appears to have been less forested than Villacastín. The abundance of oaks in Villacastín may imply the presence of refugia within an interconnected network of several enclaves during the glacial stages in the Upper Pleistocene. A possible explanation for the patchiness of the landscape may be in the role of herbivores, although the long distances and variety of habitats that hyenas had to roam through could be another explanation for the heterogeneous pollen contents in their dung. Copyright © 2006 John Wiley & Sons, Ltd.

KEYWORDS: Pleistocene; coprolites; palynology; palaeoecology; Spain.



Introduction

After being largely disregarded by European Quaternary scientists, the study of fossil faecal deposits has gained increased recognition as a palaeoecological tool (Poinar *et al.*, 1998; Pearson and Betancourt, 2002; Carrión *et al.*, 2004; Davis, 2005). The contents of hyena coprolites can provide information on animal diets (Siegfried, 1984) and past animal–human relations (Horwitz and Goldberg, 1989), although originally it was shown that pollen analysis of hyena coprolites could yield valuable palaeoenvironmental data (Scott and Klein, 1981; Scott, 1987). The value of this application of hyena coprolites is demonstrated by:

- 1 Studies showing the correspondence between coprolite pollen spectra and pollen records from open sites in Europe and southern Africa (Scott, 1987; Carrión *et al.*, 2001; González-Sampérez *et al.*, 2003; Scott *et al.*, 2003; Yll *et al.*, 2006).
- 2 Experiments with *Crocuta* droppings have shown that they are hard, durable, will sink rapidly in water and are able to

withstand considerable trampling into sediment without losing integrity (Larkin *et al.*, 2000).

- 3 Pollen in hyena coprolites generally retain good analytical potential due to exine preservation (Scott and Brink, 1992; Fernández-Rodríguez *et al.*, 1995; Carrión *et al.*, 2000a) and therefore allow easy taxonomic discrimination. High total pollen concentrations and few indeterminate pollen are usually recorded in coprolites provided that they did not experience long-term unfavourable sedimentary environments (Scott, 1987; Carrión *et al.*, 2001; González-Sampérez *et al.*, 2003; Scott *et al.*, 2003). Exine thinning (Scott, 1987) in some buried coprolites is thought to be the result of degradation in a sedimentary context and not as a result of hyena gastric action (Scott *et al.*, 2003).
- 4 SEM studies suggest that pollen grains in fresh dung of hyenas, and in fossil hyena coprolites, if preserved under suitable cave conditions, show generally good preservation and only few signs of damage (Scott *et al.*, 2003).
- 5 If preserved, hyena dung pollen assemblages are likely to give relatively unbiased reflections of vegetation of the wide surroundings in which hyenas are active (Scott *et al.*, 2003).

Here we report a pollen-analytical investigation of hyena coprolites from the sites of Villacastín and Los Torrejones in central Spain. In the context of former palaeontological studies, this work aims to help fill a gap existing in the palaeobotanical record

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of the Iberian Pleistocene, especially concerning continental enclaves where pollen-rich pre-Late Glacial deposits are rare (Dupré, 1988; García-Antón and Sainz-Ollero, 1991; Carrión, 1992, 2002; Carrión and van Geel, 1999; Ruiz-Zapata *et al.*, 2003, 2004; Martín-Arroyo *et al.*, 1996a,b; Martín-Arroyo, 1998).

Setting, depositional environments and chronological frameworks

Villacastín

Villacastín (40° 47' 52"N, 4° 22' 20"W, 1123 m a.s.l.) is a rockshelter 6 m wide and 3 m high, SE-facing, occurring in Cretaceous dolomitic sandstones, located 3.5 km northeast of Villacastín village, SW Segovia Province in central Spain (Fig. 1). The climate of the region is continental Mediterranean, with a mean annual temperature of 11–12°C, and mean annual precipitation of 400–500 mm. Present-day vegetation consists of forest patches characterised by *Quercus ilex* subsp. *ballota* trees and scrub, other oaks (*Q. pyrenaica*, *Q. faginea*), and several pine species (*Pinus pinea*, *P. sylvestris*, *P. pinaster*), as well as a notable diversity of shrubs within open to sub-forested areas (*Cytisus scoparius*, *Genista cinerea*, *Lavandula stoechas*, *Thymus* spp.) and a basal layer of grasses (*Stipa gigantea*, *Brachypodium retusum*).

The site was discovered in January 1986, and a series of systematic excavations started soon afterwards (Arribas, 1991) that provided a sedimentological framework (Arribas, 1994a), and up to 1100 animal fossil remains belonging to 35 taxa of amphibia, reptiles, avifauna and mammals. The rockshelter infill is predominantly detritic sand with blocks, both derived from weathering and erosion of the walls and ceiling. Overlying the sandstone bedrock, and overlapped by a calcareous crust, eight lithological units have been defined on a fissure infill under the shelter (Arribas, 1994a). Well-preserved coprolites and fragmented specimens occur packed into the calcareous matrix of Level 2 (Fig. 2). Bone remains of spotted hyena (*Crocuta crocuta* subsp. *intermedia*), and herbivorous species (*Cervus elaphus*, *Equus caballus*, *E. hydruntinus*) have been found assembled in the same infill, especially concentrated in Levels 2 and 3. A specific 'latrine area' appears to have been responsible for the great accumulation of coprolites.

The chronological placing of Villacastín in the late Middle Pleistocene is based on bio-correlation with Iberian and, to a lesser extent, French sites involving the joint occurrence of *Microtus brecciensis*, *Oryctolagus cuniculus* subsp. *grenalensis*, *Ursus* (arctoid agg.), *Dama clactoniana*, *Equus caballus* cf. *germanicus*, *Lynx spelaea*, *Meles meles* subsp. *atavus*, *Mustela eversmanni* and *Crocuta crocuta* subsp. *intermedia* (Aguirre, 1989; Arribas, 1995). This assemblage parallels Pinilla del Valle (Alfárez *et al.*, 1982), and TD10-11 and TG10-11 levels in Atapuerca (Soto, 1987), and the French sites of Lazaret, Pech de l'Ache II, Combe-Grenal, and Gavaudun.

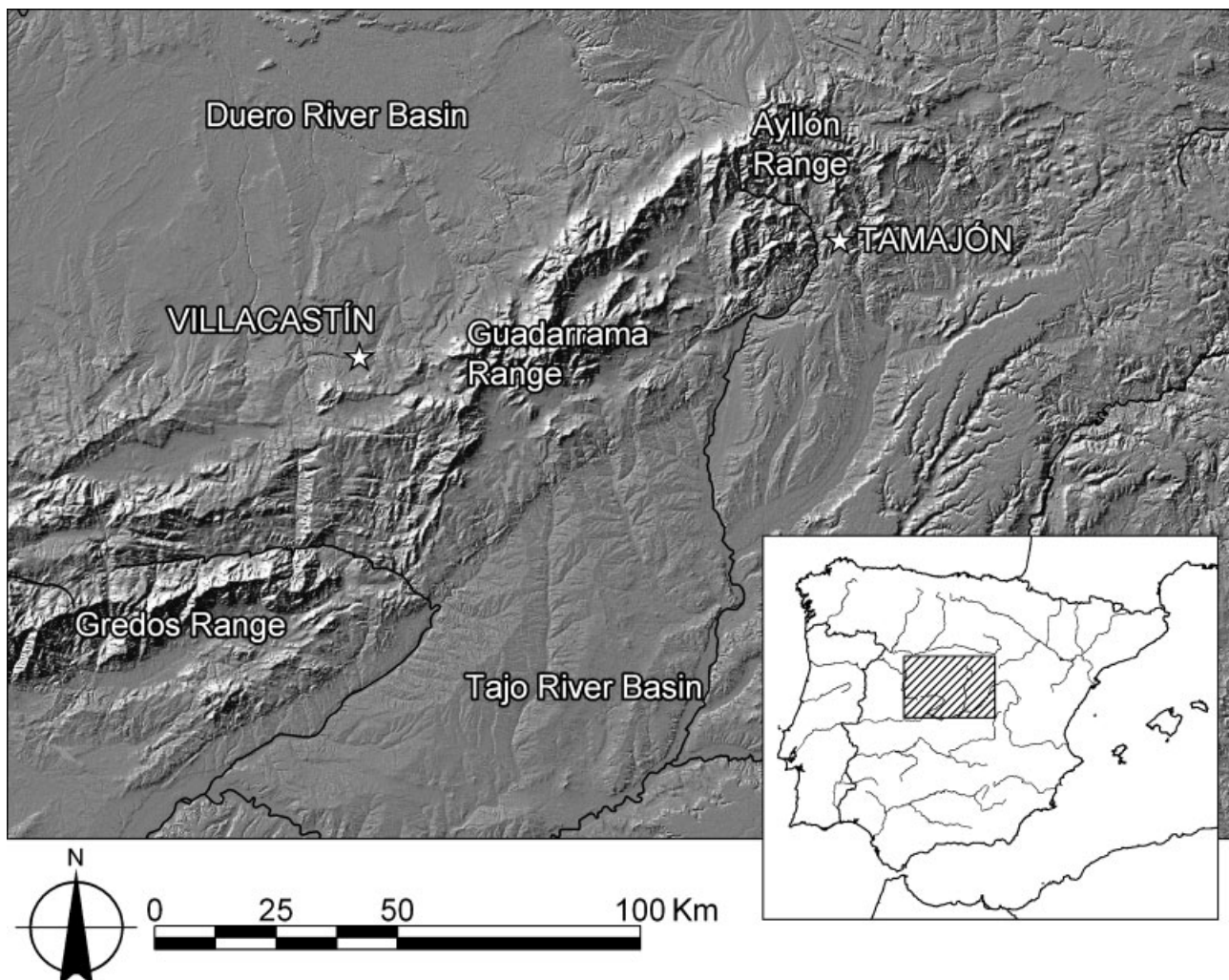


Figure 1 Location of the palaeontological sites of Villacastín and Los Torrejones in the Central Mountain System of Iberia

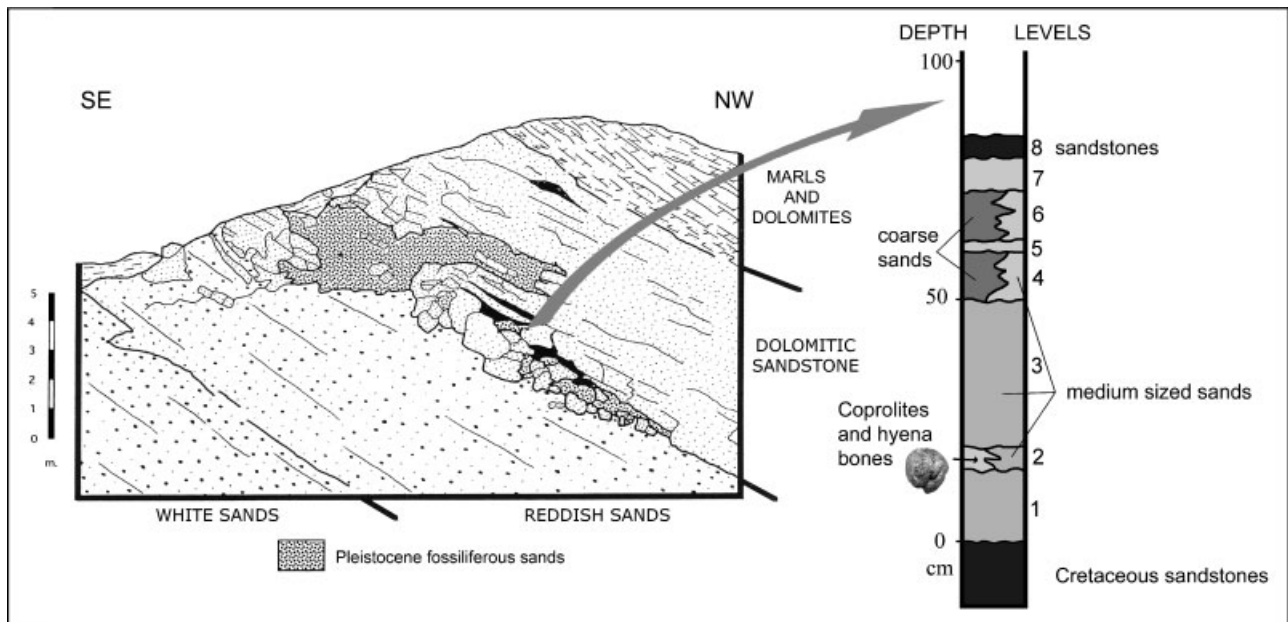


Figure 2 Site of Villacastín: geological section, and stratigraphy of the fissure infill where hyena coprolites were located (packaged in Level 2)

On the basis of these comparisons, Arribas (1995) postulates an approximate age of 150 000 to 120 000 yr BP (MIS 6—glacial) for the Villacastín faunal assemblages. The occurrence of the typical Mid-Pleistocene spotted hyena, *Crocota crocuta* subsp. *intermedia*, described formerly from materials in Cueva del Congosto (Guadalajara), and Pinilla del Valle, Madrid (Alfárez *et al.*, 1982), supports this estimate.

Los Torrejones

Los Torrejones (41° 0' 41" N, 3° 5' 17" W, 1100 m a.s.l.) is a karstic cavern, south-facing in Upper Cretaceous limestones of the Sistema Central mountain range, near the village of Tamajón, northwest of Guadalajara province, central Spain (Fig. 1). Mean annual temperature measured at the nearby meteorological station is 12.4 °C and average yearly precipitation is 785 mm. The main vegetation types around the site include *Juniperus thurifera* open woodlands with stands of *Quercus faginea*, evergreen oak (*Q. ilex* subsp. *ballota*) forests, mixed forests of *Pinus halepensis*, Cistaceae-dominated open areas and *Alnus glutinosa* riverine communities, as well as extensive agricultural, afforestation and pasture areas.

The cave is part of a two-entranced, 60 m deep karst network with several chambers that are interlinked by a complex system of galleries (Fig. 3). The cavity is partially filled and the ceiling height ranges from 1 to 5 m. Around 600 highly fragmented, but well-preserved bones were recovered, among them both herbivores and hyenids. This assemblage includes *Equus caballus*, *Bos/Bison* sp., *Sus scrofa*, *Stephanorhinus hemitoechus*, *Cervus elaphus*, *Capreolus capreolus*, *Crocota crocuta* subsp. *spelaea*, *Ursus arctos*, *Panthera pardus*, *Vulpes vulpes*, *Homo* cf. *neanderthalensis*, *Canis lupus*, *Lacerta lepida*, *Microtus nivalis*, *Microtus arvalis*, *Eliomys*, *Oryctolagus cuniculus*, *Meles meles*, *Erinaceus europaeus* and *Testudo hermanni*. These remains showed little evidence of drip dissolution or weathering cracks, suggesting they were not exposed to frequent moistening and drying (Arribas *et al.*, 1997; Arribas and Jordá, 1999).

During the 1993–1995 excavations of a 16 m² area in the Entrance gallery, a lithostratigraphy with five levels was

established for a 130 cm deep section overlying dolomitic limestone bedrock (Díez *et al.*, 1998) (Fig. 3). Level 5 is formed by sands and shows circumstantial evidence of human occupation consisting of a few remains of *Homo* cf. *neanderthalensis*, the use of leopard bones (Arribas, 1997) and remains of turtle consumption (*Testudo hermanni*). A scanty lithic industry was assigned to the Middle Palaeolithic. This bed grades into Level 4 above it, which is made up of reddish brown clayey sands with angular blocks and organic-rich clay lutites.

The activity of hyenids is most clear in Level 4 (Fig. 4). The bones show signs of gnawing, fractures derived from impact by premolars and molars of adult hyenids, scarring by deciduous teeth of immature individuals and regular digestive corrosion, all of which are associated with numerous isolated coprolite lobes from hyenids.

In erosive contact above the former, is Level 3, a yellow silty bed with altered limestone gravels. Level 2 is mainly sandy and reddish brown in colour, rich in organic matter, roots, wood fragments and removed faunal remains and artefacts. The top layer, Level 1, is a disturbed greyish horizon, with thermoclastic scree, burnt woods and bones.

Middle Palaeolithic materials are not particularly helpful to assign a chronology for the coprolite bearing Level 4. Faunal assemblages in Levels 5 and 4, especially the occurrence of *Panthera pardus*, *Stephanorhinus hemitoechus* and *Crocota crocuta* subsp. *spelaea*, coincide with other Lower Pleniglacial records of the Upper Pleistocene in continental Spain, especially Casares B, but also Carihueta, Cueva del Buho, Cova Negra, Pinarillo-1 and Morín (Altuna, 1971; Aguirre, 1989; Vega-Toscano, 1988). These finds suggest an age between 80 000 and 60 000 yr BP (Arribas *et al.*, 1997; Arribas and Jordá, 1999).

Description of the coprolites and assessment of the coprolite-producing species

In both sites, coprolites were externally pale brown to yellowish, and internally pale brown to white (Fig. 5). They were hard, although not permineralised, and sometimes broke easily

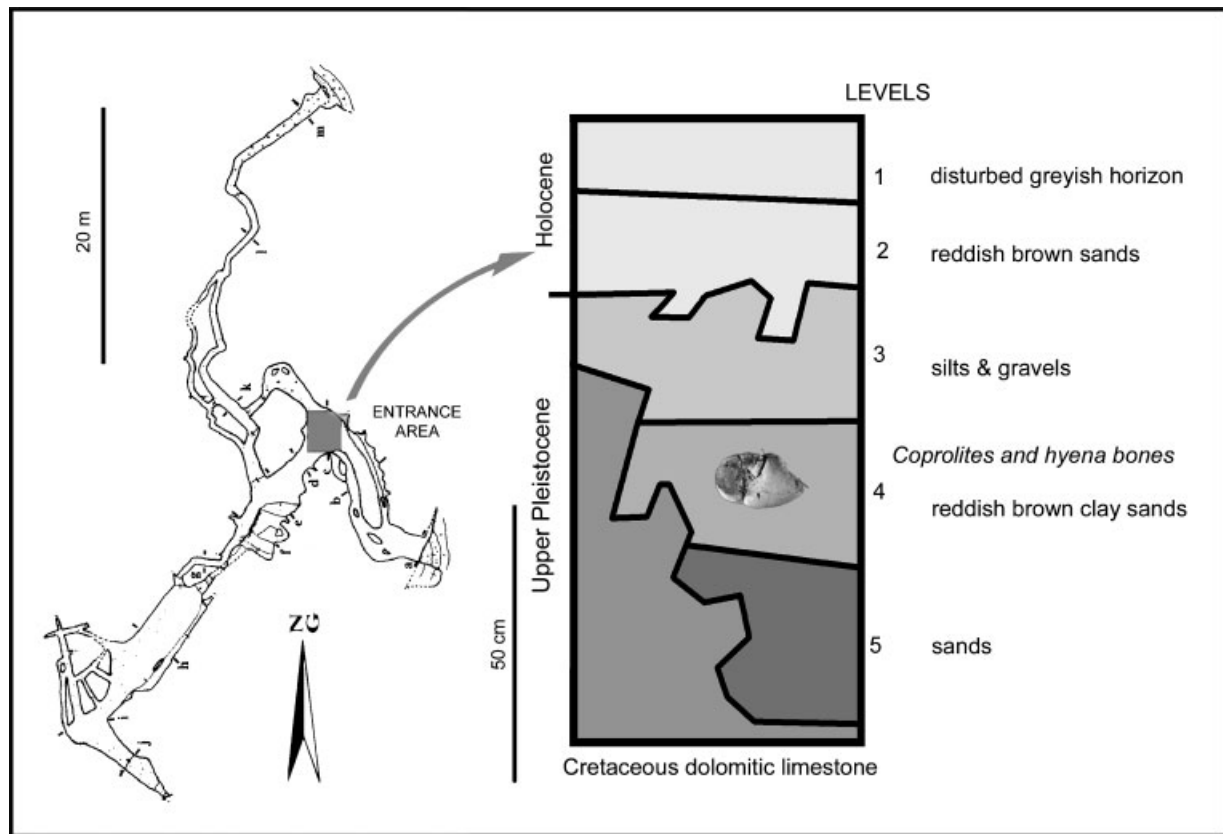


Figure 3 Site of Los Torrejones: longitudinal section of the cave showing the stratigraphy of the Entrance Area where hyena coprolites were recovered (Level 4)

through cortex cracks. The inner portion of the coprolites often contained small, highly corroded fragments of partially digested prey bones. A great majority of the coprolite specimens consisted of individual pellet segments with their widest diameter averaging 4.8 cm at Villacastín and 5.2 cm at Los Torrejones.

Following Arribas (1994b) and Arribas *et al.* (1997), we attribute the studied coprolites to fossil droppings of *Crocuta crocuta*, based on: (i) content of a great amount of transformed bone (Kruuk, 1972); (ii) shape and large size conforming with descriptions of spotted hyena coprolites from elsewhere in Europe (Fernández-Rodríguez *et al.*, 1995; Larkin *et al.*,

2000; Carrión *et al.*, 2001), Africa (Scott *et al.*, 2003), and Israel (Horwitz and Goldberg, 1989); (iii) their association in both sites with bone remains of spotted hyena (Fig. 4) and their prey; and (iv) the fact that associated skeleton fragments showed evidence of post-mortem disturbance including chewing by scavengers.

Other carnivore species are unlikely to be responsible for the coprolites (Fig. 5). The species *Hyaena brunnea*, *Chasmaporthetes lunensis* and *Hyaena hyaena* have smaller droppings and very rarely contain bone fragments (Horwitz and Goldberg, 1989; Carrión *et al.*, 2001; Fonelas Project: (<http://www.igme.es/internet/museo/investigacion/paleontologia/fonelas/index.htm>)). Furthermore, there is no record of *H. hyaena* in Iberia during the Quaternary (Arribas and Jordá, 1999) (Table 1). Other bone-cracking scavengers such as the lion-sized hyena (*Pachycrocuta brevirostris*) dominate the hyenid bone spectrum in Lower Pleistocene sites of Iberia (Arribas and Palmqvist, 1998). *Canis lupus* droppings may contain bone fragments, but in contrast with *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).

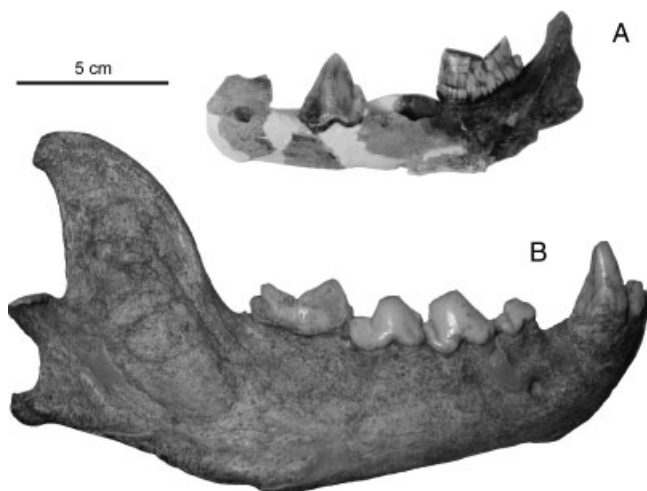


Figure 4 Hemimandibles of the Mid-Pleistocene Villacastín *intermedia* and Upper Pleistocene *spelaea* subspecies of the Iberian spotted hyena (*Crocuta crocuta*)

Palynological methods

Ten coprolite specimens for each site were taken for pollen analysis from the Museo Geominero, Madrid, where excavation materials are curated by Alfonso Arribas. In the laboratory, the coprolites were cut open with a steel spatula, and material from the centre was scraped out to minimise contamination from external surfaces, and weighed. Laboratory treatment

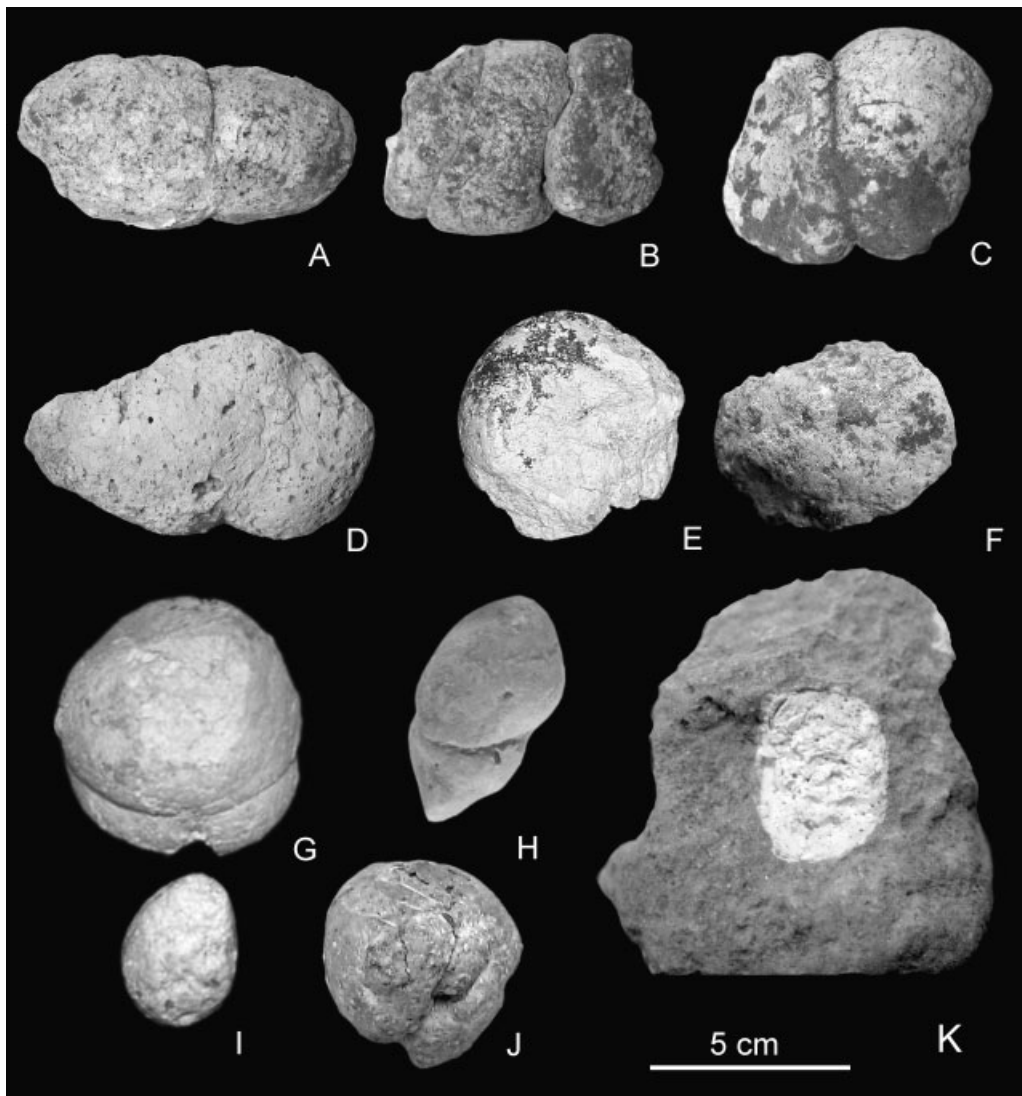


Figure 5 Coprolites of hyenids. (A)–(D): *Crocuta crocuta* subsp. *intermedia* from the Mid-Pleistocene site of Villacastín; (E)–(F): *Crocuta crocuta* subsp. *spelaea* from the Upper Pleistocene site of Los Torrejones; (G): *Crocuta crocuta* subsp. *spelaea* from the Lateglacial southern Spanish site of Las Ventanas; (H): Brown hyena (*Hyaena brunnea*) from the Cape Region Oyster Bay of South Africa; (I): *Hyaena brunnea* from Equus Cave (South Africa); (J): *Pachycrocuta brevirostris* from the lower Pleistocene site of Venta Micena in southern Spain; (K): *Chasmaporthetes lunensis* from Fonelas in southern Spain

was performed following the conventional HCl, HF and KOH method. Tablets with known numbers of *Lycopodium clavatum* spores were added to each sample to enable estimation of pollen concentrations. Pollen identification was performed

by comparison with the reference collection of the Plant Biology Department at Murcia University. A percentage pollen diagram was constructed using Tilia, TiliaGraph and CorelDraw software (Fig. 6). Percentages of each taxon for each sample

Table 1 Late Cenozoic stratigraphy of Spanish hyenids

Stage	Characteristics	Fossil-type sites	Other sites
Upper Pleistocene	<i>Crocuta crocuta</i> subsp. <i>spelaea</i>	Torrejones, Pinarillo-1	Cueva del Búho Morin, Carihuela, Cova Negra Casares-B, Zafarraya
Middle Pleistocene	<i>Crocuta crocuta</i> subsp. <i>intermedia</i>	Pinilla del Valle, Villacastín, Congosto	Cuevas de Pedraza, Atapuerca TD-4, Cúllar
Lower Pleistocene	<i>Pachycrocuta brevirostris</i>	Venta Micena, Cueva Victoria	Incarcal, Pontón de la Oliva, Fonelas SCC-1, Fonelas SCC-1
Pliocene–Pleistocene boundary	<i>Pachycrocuta brevirostris</i>	Fonelas P-1	—
Pliocene–Pleistocene boundary	<i>Hyaena brunnea</i>	Fonelas P-1	—
Pliocene	<i>Chasmaporthetes lunensis</i>	Villarroya	La Puebla de Valverde, Las Higuieruelas, Fonelas PB-4
Pliocene	<i>Pachycrocuta perrieri</i>	Villarroya	La Puebla de Valverde, Las Higuieruelas
Upper Miocene–Lower Pliocene	<i>Pachycrocuta pyrenaica</i>	Layna	La Calera II, La Gloria 4

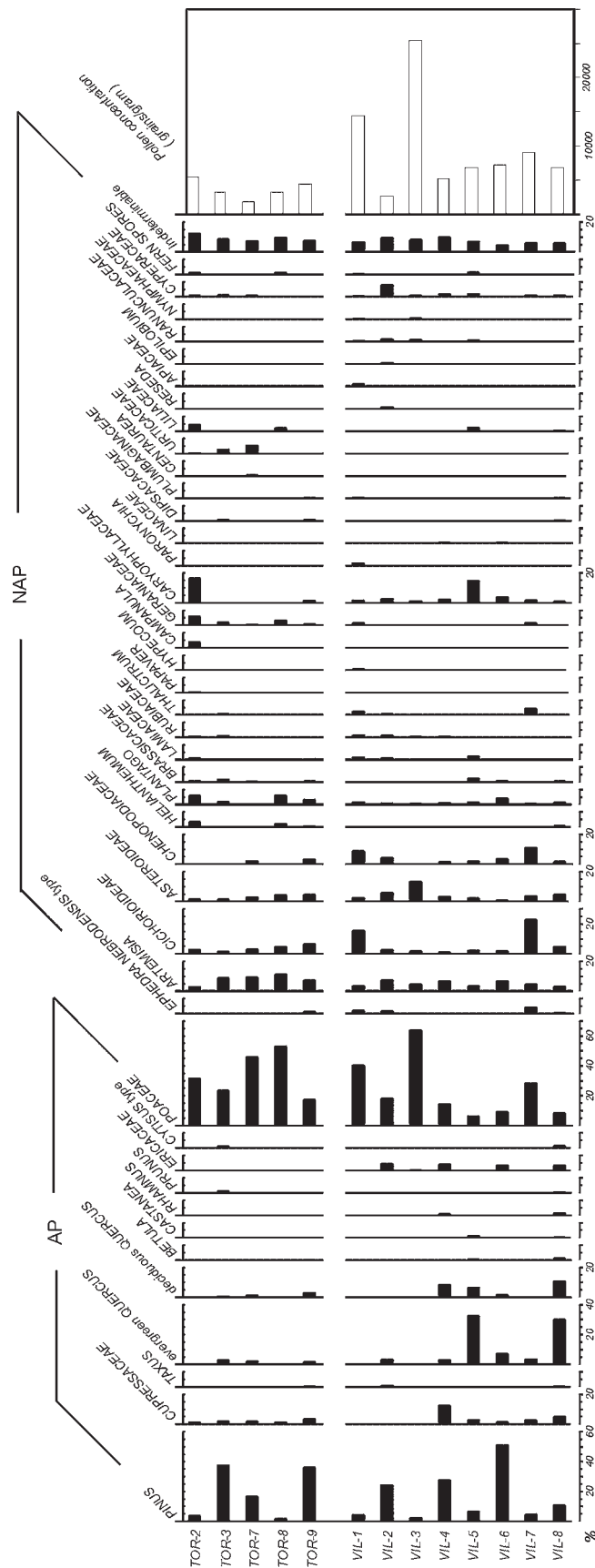


Figure 6 Combined pollen diagram of hyena coprolites from the Mid-Pleistocene site of Villacastín and the Upper Pleistocene site of Los Torrejones

DCA shows the distribution of the samples along Axis 1 and Axis 2 which have eigenvalues of 0.3617 and 0.2034 respectively (Fig. 7). Axis 1 represents a contrast between forested and more open vegetation. The results indicate a certain degree of pollen variation between the two sites with Los Torrejones representing generally more open vegetation and Villacastín more forested conditions. Some overlap in pollen composition in the two sites seems to be indicated, suggesting that comparable conditions occurred at the two places at times (Fig. 7).

Palaeoenvironmental reconstruction

Middle Pleistocene landscapes at Villacastín

Pollen-analytical data indicate different vegetation types in Villacastín, from grasslands (VIL-1, VIL-3, VIL-7) to more or less open forests dominated by either oaks (VIL-5, VIL-8) or pines (VIL-2, VIL-4, VIL-6) (Fig. 6; Table 3). Among oaks, the evergreen species (*Q. ilex*, *rotundifolia*, *coccifera*) are dominant. Apart from junipers, pollen of temperate, mesophilous taxa (*Taxus*, *Quercus*, *Betula*, *Castanea*) occur mainly within pollen assemblages dominated by arboreal pollen, but this component is absent from VIL-1 and VIL-3 grassland samples.

Steppe landscapes and herbaceous layers of forests were dominated by grasses, composites, chenopods, *Artemisia*, *Ephedra nebrodensis-distachya*, Caryophyllaceae, and a diversity of other shrubs and herbs. Humid biotopes are suggested by the occurrence of *Epilobium*, Ranunculaceae, Nymphaeaceae, ferns and Cyperaceae. Palynological discrimination is not good enough to discern whether the habit of Ericaceae was shrubby or arboreal, or whether their ecology was steppic, understorey or riparian.

The former reconstruction is broadly in keeping with Arribas (1995), who depicted a palaeoenvironmental picture from the fossil remains of 25 vertebrate species. Open (50.87%) and forested (49.12%) landscapes were inferred, with five biotopes, namely forests, wet prairies, dry prairies, riparian vegetation and steppes. Arribas (1995) also suggested a continental temperate climate with Atlantic influence for the time of Villacastín faunal assemblage. This suggestion is based on the dominance of microtids over murids among the rodents, together with the presence of *Sus scrofa*, *Cervus elaphus*, *Lynx spelaea*, *Crocota* and *Ursus*, and the occurrence of garden dormouse, water vole and wood mouse (Vernet *et al.*, 1984). Mediterranean summer dryness was also inferred on the basis of breccia vole, fallow deer, *Lacerta lepida* (Sanz and Sanchiz, 1980), *Pitymys*

subterraneus, and the gastropod *Jaminia quadridens* (Vernet *et al.*, 1984).

Regional and extra-regional correlation is hindered by insufficient chronological control of the Middle Pleistocene sites of Iberia. In addition, the available pollen sequences are scarce, mostly uneven, and with few exceptions, display problems with pollen preservation. In any case, within the vague context of 'late Middle Pleistocene', the results reported here do not contradict the palaeo-vegetation picture previously suggested. Firstly, the Villacastín pollen flora fits into the post-Waalian environment, characterised by the extinction in Iberia of *Keteleeria*, *Cathaya*, *Tsuga*, *Symplocos*, *Nyssa*, *Parthenocissus*, *Parrotia*, *Pterocarya*, *Engelhardia*, *Eucommia*, *Zelkova* and *Liquidambar* (Postigo, 2003). Additionally, the pollen record lacks *Carya* and *Ostrya* pollen, which suggests a post-Cromerian age (García-Antón *et al.*, 1990).

The cave sediment pollen record of Atapuerca, covering Cromerian to early Saalian times (García-Antón and Sainz-Ollero, 1991) shows the predominance of deciduous and evergreen *Quercus*, and eventually high frequencies of *Pinus* and Cupressaceae, together with a series of Mediterranean (*Olea*, *Ceratonia*, *Celtis*, *Pistacia*, *Phyllirea*, *Myrtus*, *Ligustrum*) and temperate arboreal taxa (*Betula*, *Picea*, *Fagus*, *Ulmus*, *Acer*, *Corylus*, *Fraxinus*, *Alnus*, *Salix*, *Juglans*, *Platanus*, *Carpinus*, *Castanea*). In the case of levels TD-10 and TG-11 from Atapuerca that possibly correlate with Villacastín (Arribas, 1995), the reconstructed landscapes were warm temperate, *Quercus*-dominated forests, although the uppermost pollen samples in TD-10 show increases of *Pinus*, and thus suggest more xeric conditions. In comparison with Atapuerca (García-Antón and Sainz-Ollero, 1991), the Villacastín flora displays a lower diversity in the woody component, which would be in keeping with a picture of progressive extinction of populations across the Middle Pleistocene of central Iberia.

The remaining Mid-Pleistocene pollen diagrams of the Iberian Peninsula indicate that open pinewoods must have been quite general among the landscapes adjacent to excavation sites. This can be seen in the diagrams of Menéndez Amor and Florschütz (1959) for Torralba and Villaverde, as well as in western localities of Porto Covo, Mealhada, Sines, Ribeira da Provença and Alpiarça (Andrade, 1944).

The fluvio-lacustrine, Acheulean palaeontological sites of Ambrona and Torralba in the northern Iberian System (Conquezueta polje, ca. 1100-1200 m a.s.l., Soria) (Ruiz-Zapata *et al.*, 2003) show a predominance of *Pinus*, alternating with *Juniperus*, occasional increases of Poaceae, *Artemisia* and other composites, a great diversity of herbs and shrubs, and, notably, the occurrence of *Quercus*, *Alnus*, *Betula*, *Castanea*, *Corylus*, *Fagus*, *Juglans*, *Olea*, *Salix* and *Ulmus*. The presence

Table 3 Main features of the inferred vegetation from pollen analysis in Los Torrejones (TOR) and Villacastín (VIL)

Sample	Vegetation	Mesophilous woods
TOR-2	Steppe-grassland with diversity of herbs	—
TOR-3	Open pine forest	Oaks, <i>Prunus</i> , Genisteeae
TOR-7	Steppe-grassland with sparse pine stands	Oaks
TOR-8	Steppe-grassland with <i>Artemisia</i>	—
TOR-9	Open pine forest with junipers and oaks	Oaks, birch, yew
VIL-1	Treeless steppe-grassland with abundant composites and chenopods, and diversity of herbs	—
VIL-2	Steppe-grassland with sparse pines, evergreen oaks and hearths	Oaks, yew
VIL-3	Treeless grassland with abundance of composites	—
VIL-4	Semi-forested landscape, with abundant junipers, deciduous oaks and pines	Oaks, birch
VIL-5	Mixed, evergreen oak-dominated forests	Oaks, birch, chestnut
VIL-6	Pine forests with oaks and hearths	Oaks
VIL-7	Steppe-grassland with composites, chenopods and <i>Ephedra</i>	Oaks
VIL-8	Mixed, evergreen-dominated oak forests with junipers, hearths and Genisteeae understorey	Oaks, birch, chestnut, <i>Prunus</i>

of these taxa during the Middle Pleistocene, despite the dominance of pinewoods, suggests a temperate climate less continental than at present. Recently, Postigo (2003) has identified fossil wood of *Pinus sylvestris* at the site of Torralba.

Several pollen analyses in a series of overbank deposits that developed over the Tagus terraces (Martín-Arroyo, 1998; Martín-Arroyo *et al.*, 1996a,b, Ruiz-Zapata *et al.*, 2004) also show a Mid-Pleistocene mosaic landscape that was eventually dominated by *Pinus*, or evergreen *Quercus*, but also accompanied by *Olea*, *Juniperus* and Cistaceae, and less *Betula*, *Castanea*, *Ulmus*, *Juglans*, *Alnus*, *Fraxinus* and *Salix*.

Upper Pleistocene landscapes at Los Torrejones

Vegetation types reconstructed for the Los Torrejones region include steppe-grasslands (TOR-2, TOR-8), open pine forests (TOR-3, TOR-9) and parkland/savanna vegetation of pine stands (TOR-7) (Fig. 6; Table 3). As in Villacastín, pollen of temperate trees (*Taxus*, *Quercus*, *Betula*) occurs, within pollen assemblages dominated by arboreal pollen. However, there is no evidence for angiosperm forests, and mesophilous trees and junipers are comparatively less frequent. As regards steppe landscapes, these are mainly dominated by grasses, with an abundance of *Artemisia* and other composites, and occasional *Ephedra nebrodensis* and Caryophyllaceae, together with other minor herbaceous and sub-shrubby taxa.

This landscape reconstruction conforms to that derived from the Lower Pleniglacial pollen record of lacustrine and cave fills in continental Spain (Dupré, 1988; Pons and Reille, 1988; Carrión, 1992; Carrión *et al.*, 1999), thus supporting the chronology suggested by the faunal association of between 80 000 and 50 000 yr BP. It is in keeping with the occurrence in Los Torrejones of *Microtus nivalis*, although the faunal assemblage of Level 4 (Fig. 3) is present in both cold and warm intervals of the Pleistocene record of Iberia (Díez *et al.*, 1998). This predominantly herbaceous vegetation may also have been partially conditioned by the montane conditions surrounding the site.

In relation to the landscape reconstruction by Peñalba (1994) (Table 3) the contention that central Spain contained oak populations during glacial stages is supported by our results. Thus, the presence of *Quercus* pollen in Los Torrejones (Fig. 6) may well be an indication of the regional occurrence of sexually reproducing oak populations during the onset of the last glacial stage, perhaps at lower altitudes of the meso-mediterranean belt.

According to the data discussed above, glacial refugia for oaks and other temperate and Mediterranean flora in central Spain existed in the Middle Pleistocene (García-Antón, 1992). In contrast with the Upper Pleistocene, the available Mid-Pleistocene pollen sequences, owing to glacial–interglacial dynamics, do not show sharp oscillations of thermophytes, and less contrasting climatic conditions may be expected during this phase.

During the cold stages of the Upper Pleistocene the southern and eastern territories of Iberia certainly included phytodiversity reservoirs for woody species (Burjachs and Julià, 1994; Carrión *et al.*, 1995, 2003; González-Sampériz *et al.*, 2003, 2004, Finlayson 2004), even at relatively high elevations within steep mountain valleys (Carrión, 2002). Evidence of vegetation in the Cantabrian coast and adjacent mountain ranges reveals low arboreal pollen percentages (Ramil-Rego *et al.*, 1998), but are supported by macroscopic charcoal (Uzquiano, 1992) and megafaunal models (Altuna, 1972).

Owing to the scarcity of data, central Spain has rarely been considered in this debate. However, the findings in this paper

agree with indications of the genetic structure of populations of Iberian oaks (Olalde *et al.*, 2002, Petit *et al.*, 2002; Arroyo *et al.*, 2004) suggesting the existence of multiple refugia, eventually connected by a complex network of migration routes that became active during climate ameliorations. Plausibly, oak and pine species could have enjoyed suitable habitats over wide areas of the Iberian, Betic and Central mountain systems, perhaps by forming meta-populations that were able to survive even if local areas suffered climatic stress. This scenario is in keeping with charcoal and pollen evidence from central Europe (Willis *et al.*, 2000).

Conclusions

Given marked inter-site dissimilarities in the coprolite pollen spectra, one could conclude that each site represents a different climatic phase of the Pleistocene. For example, the mild-climate episodes with forest developments in Villacastín, may represent interglacials and/or interstadials (e.g. VL-5, VL-6 and VL-8), while steppe episodes reflect full glacial stages (e.g. VL-1 and VL-3). However, the stratigraphic correspondence between coprolites and hyena bones, suggests that both fossil types are contemporaneous. More importantly, the whole assemblage of bones and coprolites must have been deposited in a relatively short time during a phase of hyenid activity. This is supported by the low number of remains within relatively thin lithostratigraphical units, which were formed in a reduced endokarstic space (Arribas and Jordá, 1999). Hence, for each site, instead of reflecting a temporal record of different vegetation stages in an unknown sequence, we believe that the reconstructed environments coexisted within a patchy landscape.

In support of the inferred patchiness, previous palynological investigations show that hyena coprolites produced *in situ* are likely to represent mosaic characteristics of landscapes, in physiographically complex territories (Carrión *et al.*, 2001; Scott *et al.*, 2003; Yll *et al.*, 2006). Experimental studies further suggest that most pollen is collected during hyena movements away from home sites, with the composition of the pollen spectra depending on vegetation of the particular areas visited (Scott, 1987; Scott and Brink, 1992). Spotted hyenas are known to range up to 50 km from their dens (Mills, 1989). The distinction between forest and non-forest communities is blurred owing to mixing of pollen in hyena coprolites.

Despite the poor knowledge of the Middle and Upper Pleistocene landscapes of central Iberia, it is quite likely that, even during cold episodes at relatively high altitudes, a grassland–savanna–forest mosaic occurred, unlike southernmost sites where dense forests. *Artemisia* steppes are clearly shown by pollen diagrams (Pons and Reille, 1988; Carrión *et al.*, 2000c; Carrión, 2002; Sánchez-Goñi *et al.*, 2002; Pantaleón-Cano *et al.*, 2003). The picture is one of a shifting mosaic of open and wooded habitats with abundant juniper and pine, and enclaves where other trees and shrubs could locally develop to mature populations of, for example, evergreen and deciduous oaks, broadleaf trees and Mediterranean scrub.

Such a mixture of open and closed habitats would be favourable to mammalian diversity, in particular ungulate faunas including those recovered in the caves such as red deer (*Cervus elaphus*), fallow deer (*Dama clactoniana*), roe deer (*Capreolus capreolus*), horses (*Equus caballus*), ass-like horses (*Equus hydruntinus*), narrow-nosed rhinoceros (*Stephanorhinus hemitoechus*), large bovids (*Bos primigenius*, *Bison* sp.), wild boar (*Sus scrofa*), etc. Diverse and productive grasslands may account for the abundance of grazers such as horses, while



Figure 8 Palaeontological localities of hyenids in Spain since the Pliocene. A number of these sites contain coprolites and, thus, offer potential for palaeoecological reconstruction through pollen analysis. (Redrawn from <http://www.igme.es/internet/museo/investigacion/paleontologia/fonelas/index.htm>)

more densely forested episodes tempered by locally open spaces are in keeping with the appearance of mixed-feeding ungulates such as the fallow deer and narrow-nosed rhino.

Although Quaternary palynologists commonly make palaeoclimatic inferences from vegetation, we believe caution is necessary because mosaics of plant communities can partly be maintained by the activities of the herbivores themselves, as has been stressed by Bradshaw *et al.* (2003). To test this hypothesis more pollen analyses on Pleistocene sites of Iberia are needed. A major challenge is the scarcity of available continuous peatbogs and lacustrine sequences through the Quaternary. However, palaeontological sites with remains of hyenas and their prey are abundant (Fig. 8) and clearly under-exploited in terms of pollen analysis. Coprolites are also common in these sites, including those produced by hyenas and other smaller carnivores (Fig. 5). We have recently, but unsuccessfully attempted pollen analyses on *Chasmaporthetes* coprolites from Fonelas and *Pachycrocuta* coprolites from Cueva Victoria, Murcia. *Crocuta* coprolites are also often palynologically sterile, as seen in several specimens from Nerja Cave, Málaga (Carrión, unpublished), but this has not prevented us from using them in other sites. Like other palaeobiological methods, pollen analysis is a time-consuming activity and, in the case of the palynology of coprolites, luck is often needed to reach its full potential.

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