

# Pollen Taphonomy of hyaena coprolites: an experimental approach.

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## Introduction

Interpreting past environments has been mainly based on pollen as the most direct source of information about vegetation. Pollen-vegetation relationships are investigated by palynologists through direct observation in modern environments. However, apart from complications derived from climatic parameters (e.g. wind currents, diurnal/nocturnal or seasonal temperatures, relative humidity, sun exposure) or interspecific differences (pollen productivity or variability), additional biases may be introduced by taphonomic processes in fossil sites, especially where predation is a factor. Some environments are better for concentration and preservation of pollen, such as lakes or peatbogs than others. Pollen spectra from sediments may or may not give an accurate representation of the environment because transport and depositional patterns (e.g. air and water transport, insect-pollination, or predation) influence pollen distribution (dispersal and/or concentration). This is particularly true in those environments where pollen preservation and abundance is not appropriate as in caves, open air sites and drylands. In these sites and regions, coprolites of past hyaena scats have been proved as an important vegetation archive,

as pollen gets trapped due to ingestion and the sticky surface of dung (Scott 1987, 2000; Scott and Brink, 1992; Carrión *et alii* 2000; Carrión *et alii*, 2001; Scott *et alii*, 2003). Pollen spectra from biogenic materials of animal origin are considered to be the best analogues of local and regional vegetation, and show the best analytical potential in terms of pollen concentration and taxon diversity, both at modern or historical (Figure 1) and fossil (Figure 2) sites.

Some investigations focused on the extent that pollen and spores reach the accumulating sediment surfaces in caves and reflect the vegetation near cave entrances and the regional environments beyond the caves (Coles and Gilbertstone, 1994; Navarro *et alii*, 2001; Hunt & Rushworth, 2005). Rates of pollen production by different plants (past and present) and representation in open air sediments have also been established related to taphonomic agents that influence preservation (Hoffman, 2002; Martín-Closas & Gómez, 2004). However, to our knowledge, no previous

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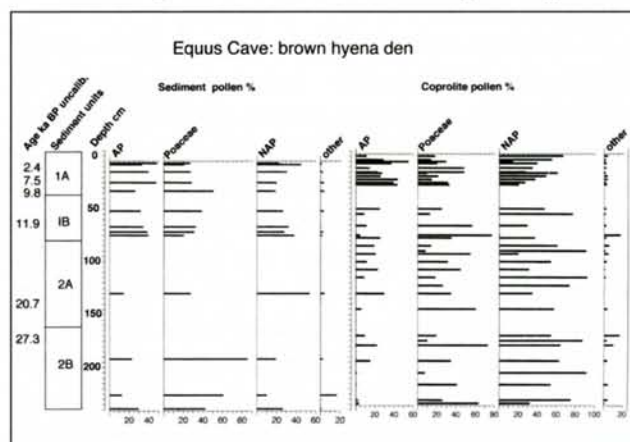


Figure 1. Equus Cave (Brown hyaena 35ka BP). Pollen could be found in several more levels in coprolites than in sediment samples and the latter had very low concentrations of pollen. Pollen content in coprolites is generally richer than in the surrounding sediments from which they came. The same has been found in the case of phytolith contents (L. Rossouw, unpublished data).

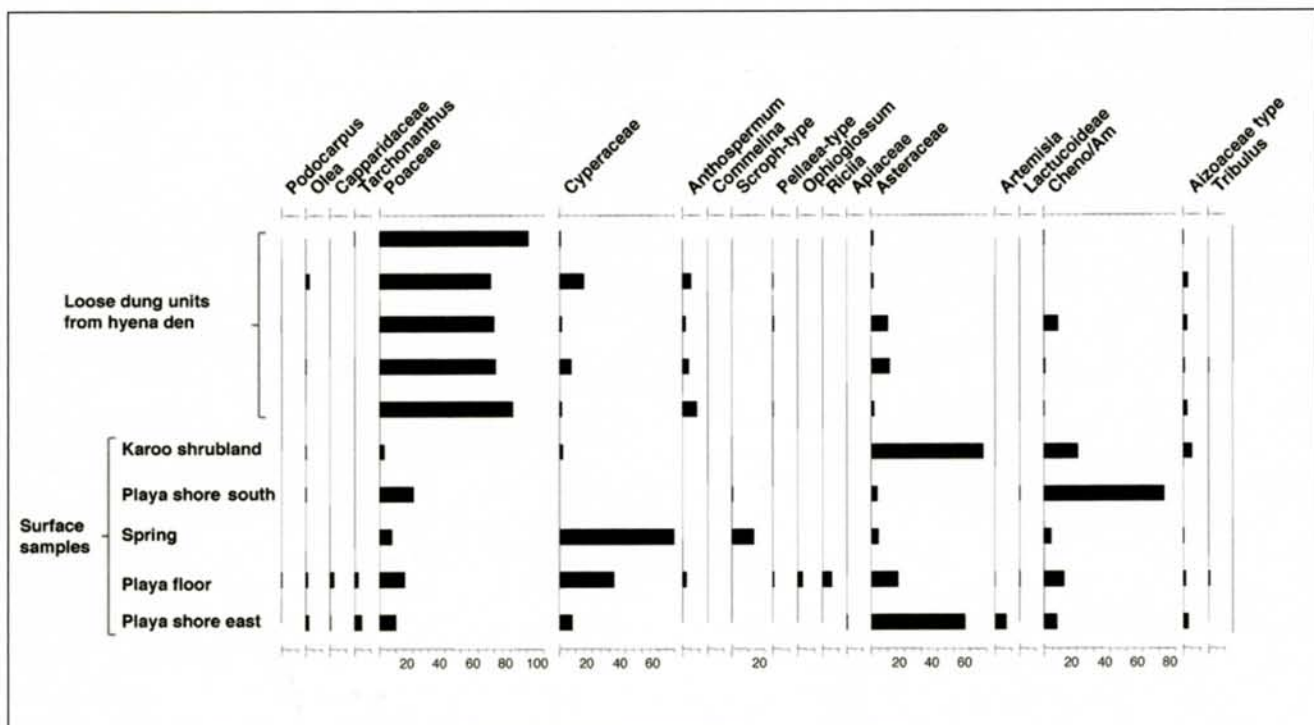


Fig. 2. Delpán (playa) a brown hyaena den 200 years old. Comparison of pollen content from the dust surface (bottom) and loose dung from brown hyaena den (top).

study on pollen representation in coprolites has been accomplished to the date.

Differential preservation during fossilization affects a specific pollen type (due to particular histological traits,) or all pollen grains at a certain environment, site or depositional conditions (Campbell, 1999). Therefore, the question is, if pollen-spectra obtained from sediments are representative of the past pollen rain.

Environments of exposure as well as fossilization determine preservation/destruction of pollen grains (Scott *et alii*, 2003). Both these environments are less severe for pollen in hyaena coprolites. The slightly acid environment provided by the coprolite is constant and the structure of the coprolite seals the pollen from the weathering and probably reduces the variation of humidity and temperature as long as the coprolite structure is intact. Hyaena droppings are hard and durable even under sun exposure, sink rapidly into water and resist trampling into sediment whilst maintaining a coherent form.

The source of palynomorphs may also be inferred from taxonomic investigations of potential prey animals recorded at sites that bear taphonomic evidence of hyaena activity, such as fossil bones chewed and broken. Where predation is involved, pollen transport/deposition may not be fully subjected to insect-pollination or hydrodynamic/aerodynamic

properties, but to predator-prey physiological relationships and consumer preferences (browser-grazing).

Vegetation in the surroundings can be inferred in general from the taxonomy, predominance of prey in the site and their usual diet (browser/grazer). The latter (the herbivore diet) can also be deduced from fossil bone isotopic ( $\delta C^{13}/\delta C^{14}$ ) analyses.

Hypothetically, pollen may be incorporated into the hyaena coprolite by (i) ingestion of water, (ii) adhered to any item of the diet, (iii) ingestion of vegetable matter/grass, (iv) the stomach contents of preys, and (v) adhered pollen from the air trapped by the sticky mucus of the dung surface (Scott, 1987). Determining the actual relative role of each source needs taphonomic research, and it is our intention to do taphonomic investigation both through experimental and palaeontological approaches.

Further, the geographical distribution of hyaenas, their behaviour, and, most importantly, the extent of areas visited and feeding habits differ in each species of hyaena (Hofer & Mills, 1998). **Brown hyaena** (*Hyaena brunnea*) is omnivorous and more of a scavenger than spotted hyaena (*Crocuta crocuta*), although it will also hunt small mammals (G. Avery, pers. com., Williams *et alii*, in prep). It lives mainly in the Kalahari Desert and Namibia. Because of the scarcity of food in the desert, the brown hyaena supple-



ments its diet with fruit and vegetables. It lives in clans but less hierarchical and smaller than those of spotted hyaena, and individuals do not hunt cooperatively. The area visited by brown hyaena is usually more reduced than spotted hyaena's home ranges. **Spotted hyaena** are the biggest hunters among hyaenas, they live in big clans (of up to 80 individuals) hierarchically organized with some female members looking after the puppies in large communal dens when the rest of the group hunts. **Striped hyaena** (*Hyaena hyaena*) is the smallest hyaena species, reduced to some areas of Africa and to the Middle East up to East India. Today, striped hyaenas are largely scavengers, but will also eat small animals, fruit and insects. They are nomadic but stay in areas not larger than 10 km. They have smaller home ranges than brown and spotted.

Most hyaenas will try to eat almost everything, and subsist on a broad-sized omnivorous diet including carrion, vegetable matter, mammals, and bird eggs. Brown hyaenas may even graze grass. However, when there is abundant food supply, the spotted hyaena seems to subsist primarily on meat, with preference for large mammals, being frequent as primary defleshers, but also secondary scavengers. In this case, the stomach content of these large herbivores must be a most important pollen source.

### The goal of the project

Our main aim in this project is to find out whether pollen spectra obtained from hyaena coprolites are representative of the real pollen rain. Pollen research intends to provide the basis to confirm the climate and environment in which the past ecosystems evolved, and we aim to provide a background for the biodiversity represented at a given site where hyaena coprolites are present.

The main aspects focusing our investigation are: 1) How nutritional preferences of past animals (fossil species recorded in the site) that were prey of other animals (hunters/scavengers) that produced coprolites, influenced the pollen species representation.

2) How microenvironmental traits, as regional or local climatic conditions, influenced pollen preservation. Criteria must be established that allow us to characterize conditions of pollen preservation through predation and local environmental conditions.

#### WORKING HYPOTHESIS (1): Nutritional preferences

- It is assumed that pollen trapped in the interior of coprolites would consist mainly of grains that passed through the digestive system of the prey, of the pre-

dators and the general pollen rain, while the exterior surface could add only air-borne pollen.

In order to test this hypothesis, comparison between internal and external parts of the coprolite should be done to establish differential pollen sources on the final pollen spectrum. Secondly, in order to confirm any biases, pollen contents of modern scat, modern surface soil and pollen traps should be compared as the latest would be equivalent to sediments in fossils sites and caves. This leads us to conduct experimental works in nature.

Experimental approach: hyaenas in nature.

Our approach to this working hypothesis will imply two main phases:

- Search for currently used hyaena dens in natural parks. The experiment in natural conditions will be conducted in Southern Africa where both spotted and brown hyaenas are available (striped hyaenas are at the moment excluded). Many of the fossil sites from South Africa contain brown hyaena coprolites, some both brown and spotted hyaenas, and Spanish sites mainly spotted. This may also show which type of hyaena reflects the environment more accurately through pollen in their dung. This has never been tested before.
- Collection should be planned seasonally, and prior to collection each time the area will be cleaned of previous scats and an aerial pollen trap (Cour filters) (Cour 1974) will be left hanging from non polliniferous support, such as a dead tree or a piece of wire in a fenced area.

At the end of each season, collection will include,

- (1) scats produced during the season (collect using latex gloves) in a cleaned sample sealed bag.
- (2) surface sediment nearby also in a sealed bag. Surface sediment from around scat may give a control for the assemblage we expect on the scat surface.
- (3) pollen trap in a third sealed bag as pollen rain control of sediment and scat.
- (4) Surface sediment from the same environment, but located several metres away from the scat area.

#### WORKING HYPOTHESIS (2) Microenvironmental traits

- Fossil sites with poor or no pollen contents in coprolites are relatively old or have been exposed to environmental (wet and dry moisture or acid/alkaline soils) fluctuations over a very long period (Scott *et*

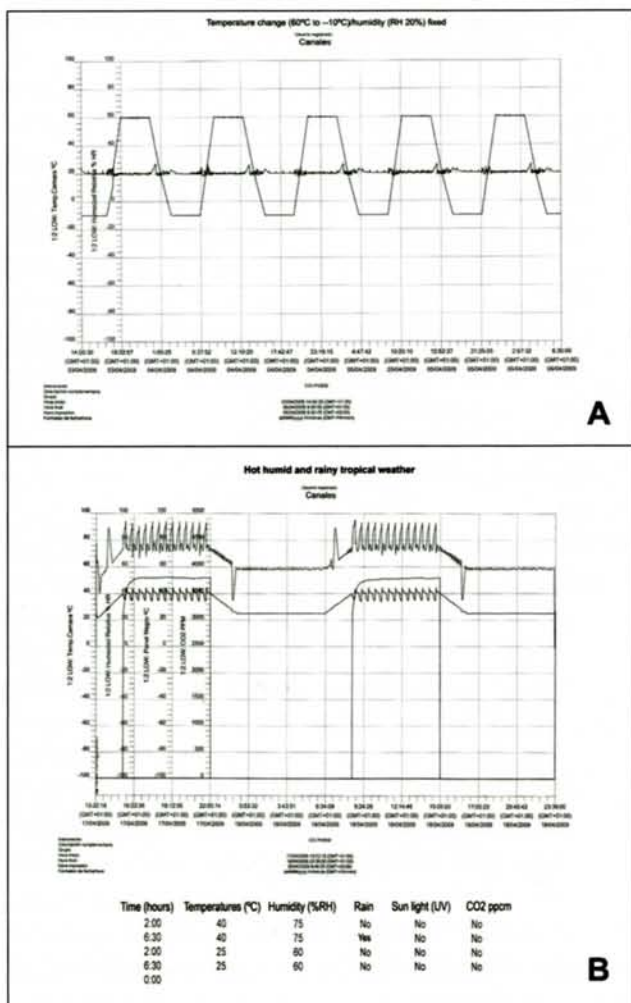


Fig. 3. Example of experiments designed for CCI climatic chamber to control different parameters independently or creating cycles to emulate a particular climate. A. Desert weather. Temperature change: 60°C to -10°C at a constant humidity of 20% RH (Temperature at the CCI chamber can change from 80°C to -60°C using cryogenic conditions). B. Hot humid and rainy tropical weather. Temperatures between 40°C and 25°C at a 75%RH and 60%RH respectively with rain periods.

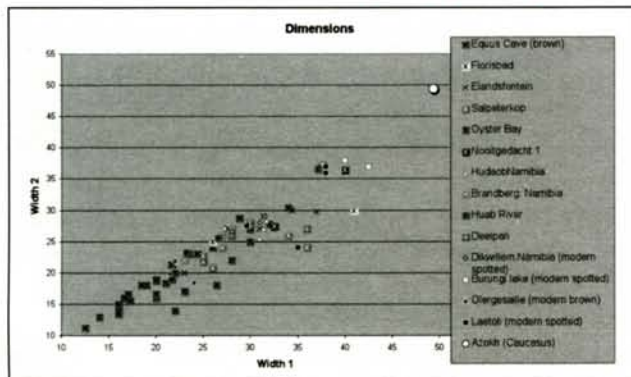


Fig. 4. Dimensions of hyaena dung (modern and fossil) form different sites compared to a coprolite from Azokh Cave site (Caucasus) which is a bear den.

LOCATION	largest dimension	middle dimension	shortest dimension	WIDTH 1	WIDTH 2
Equus Cave	33,2	30	27	30	27
	26	20	16	20	16
	20	16	14	16	14
	26	26	24	26	24
	28	16	15	16	15
	32	25	22	25	22
	30	25	22	30	25
	36,4	18,4	18	18,4	18
	22	20	17	22	20
	23,5	23	13	23,5	23
	35	20	19	20	19
	31,6	23	17	23	17
	29	20	16,6	20	16,6
	21	21	18,3	21	18,3
	32	26,4	18	26,4	18
	30	17	16,6	17	16,6
	20	16,6	16	16,6	16
	28,8	16	13,5	16	13,5
	23,4	17,2	15,5	17,2	15,5
	25	14	13	14	13
	33	20	18,8	20	18,8
	19	18	17,7	19	18
	16	16	15	16	15
21,6	21,3	11,6	21,6	21,3	
17	12,5	11,2	12,5	11,2	
broken	22	14	22	14	
30	28,8	28,7	28,8	28,7	
51	34	30,5	34	30,5	
24,4	23	22	24,4	23	
28	28	22	28	22	
Florisbad	41	30	22	41	30
	39	26	25	26	25
Elandsfontein	43,8	34,4	30	34,4	30
	40	38	32,7	40	38
	49	31	27	31	27
	31,4	29	21	31,4	29
	45	37	29,8	37	29,8
	38,8	23	20	23	20
Salpeterkop	27,7	27	24,4	27,7	27
	34	31	26	34	26
	32	30	28	30	28
	38,5	25	21,8	25	21,8
	41,5	25	22,7	25	22,7
	38,8	26	20,8	26	20,8
	39	36	24	36	24
37,6	37,3	26	37,6	37,3	
Oyster Bay	37,2	36,6	23	37,2	36,6
	41	32	27,8	32	27,8

alii, 2003). This lack of pollen suggests that conditions in the past eventually destroyed them, but we ignore which conditions or environmental/fossilization parameters influenced them most. Some taphonomic studies from modern and fossil sites have been published (Hunt & Rushworth, 2005, Carrión *et alii*, 2009) but further work is needed. Oxidation associated with perennial dampness in sediments, sun exposure and/or temperature oscillations seems to be the most active conditions that may damage pollen to destruction.

In order to test this second hypothesis experiments with a climatic chamber (CCI, series METEOTRON-MQ/ESP) using pollen grains, scats/coprolites and



LOCATION	largest dimension	middle dimension	shortest dimension	WIDTH 1	WIDTH 2
Nooitgedacht 1	49	32,5	27,4	32,5	27,4
	63,6	40	36,5	40	36,5
HudaobNamibia	38,3	27,3	27,2	27,3	27,2
	31	25,5	23,8	31	25,5
	72	31,7	28,3	31,7	28,3
	32	31,4	27	31,4	27
Brandberg. Namibia	42	27	26	27	26
	28	27	27	28	27
	33	27	25	27	24
	86,8	23	22	23	22
Huab River	42,7	26,6	25,6	26,6	25,6
	23,2	23,2	21,7	23,2	23,2
	21,7	19	16	21,7	19
Deelpan	44	36	27	36	27
	30	27,5	19	30	27,5
	31	26	24,7	28	26
Dikwillem. Namibia (modern)	36	31,5	29	31,5	29
	39	28	26,6	28	26,6
	41	31	28	31	28
Burungi lake (modern)	43	38	36	40	38
	43,5	37	32	42,5	37
Olergesaillie (modern)	22	21	20	22	21
	28,8	24	20	24	18,6
	33	22	22	22	22
	26	21,5	20	21,5	20
Laetoli (modern)	35	34	24	35	24
	38	37	21	38	37
	59	38	36	38	36
	29,6	27,5	23	29,6	27,5
Azokh (bear)	49,8	49,4	33	49,8	49,4

sediments will be carried on. Experiments are designed to characterize which environmental parameter acting independently (temperature fluctuations, wet-dry cycles, oxidation-reduction cycles, sun ray exposure, contaminant environments has stronger influence (Figure 3a). Climatic cycles simulating cold climates, deserts or hot humid rainy tropical climates will also be experimented (Figure 3b). All these experiments will allow us to establish under which climatic conditions or weather parameters pollen grains preserve better and which are the most destructive.

Pollen quality after experimentation will be observed at the scanning electron microscope and optical microscopes. Comparison with controlled natural conditions should also be included.

### Application to fossil sites

Many of the fossil sites from South Africa contain brown hyaena coprolites and some both brown and spotted, while Spanish sites contain mainly spotted. The final aim of this project is to apply experimental and natural results to fossil sites where hyaena scats are abundant.

Several new discoveries are available as well as coprolites which have been stored over several years are now available for study. Coprolites from more sites have recently been collected, pictured, measured and

catalogued (Figure 4). Measurement of coprolite diameter does not help distinguishing between brown or spotted hyaenas, but it can do between hyaenas and other coprolite-producing carnivores (Azokh Cave is a Middle Pleistocene cave bear den site in Nagorno-Karabagh, Caucasus). Eventually, taxonomic analysis of pollen might provide an important indication of conditions at these sites. It has further been observed (L. Rossouw unpublished data) that coprolites also preserve phytoliths very effectively and as off-spin of the present project phytoliths will also be observed. The following sites have been identified for future work.

### Florisbad Spring

Middle Pleistocene site that yielded a human skull, contains hyaena coprolites, which might be derived from spotted hyaena. Several coprolites from this Free State grassland site north of Bloemfontein were studied previously but a number of them are still available for future study (Scott and Brink, 1992). The grass-dominated pollen from the coprolites suggests hyaena activity in the grassy surroundings of the spring and saltpan.

### Erfkroon

The site west northwest of Bloemfontein in erosional gulleys along the Modder River and near Florisbad, yielded extensive Middle and Late Pleistocene Stone Age faunal and archaeological remains but pollen preservation is poor. Therefore we hope better preserved pollen derived from coprolites may shed light on palaeoenvironmental conditions. Although previous pollen studies on apparent coprolites from this (Churchil *et alii*, 2000) were unproductive, probably due to open air conditions, new coprolites are now available for study.

### Equus Cave

A rich assemblage of Late Pleistocene and Holocene fossil bones and brown hyaena coprolites was collected from Equus Cave in the southern Kalahari thornveld area produced the first important palynological results of hyaena coprolites in South Africa (Fig. 1) (Scott, 1987). Several more coprolites are available for further study and they are also considered potentially useful in experiments in the environmental chambers.

### Oyster Bay

Several coprolites in a soil horizon on an open-air coastal site at Oyster Bay (Carrion *et alii*, 2000) are still available for study and new ones can potentially be collected from



the site in dunes along the southern coast of South Africa. The coprolites are loosely associated with Howieson's Poort artefacts, representing a unique Middle Stone Age phase dating between 59 and 66 ka (Jacobs *et alii*, 2008) and appearing over a large part of Southern Africa. These coprolites are of interest because of their potential environmental information associated with the Howieson's Poort culture.

#### Wonderwerk Cave

Some hyaena coprolites have recently been discovered in this cave with artefacts indicating the oldest known case of human cave dwelling (Chazan *et alii*, 2008). Although the cave is rich in archaeological material it is not rich in faunal and botanical remains and therefore the accumulation of dung deposits especially hyaena coprolites will prove to be important for environmental reconstructions.

#### Langebaanweg/ Elandsfontein

The two nearby sites from the south western Cape fynbos biome are of Pliocene and middle Pleistocene age respectively, have rich in fossil faunas and have yielded several coprolites. In the case of Elandsfontein, some palynological research has been done (Singer and Wymer, 1968; Klein *et alii*, 2007). Several coprolites have been stored and newly excavated from these sites and are now available for study.

#### Pinnacle Point

Several coprolites are available from Pinnacle Point Site 30 near Mossel Bay on the south African south coast, that contains a large faunal assemblage including many coprolites (C. Marean, pers comm.). The site with a rich faunal assemblage is currently the topic of palaeoenvironmental and palaeoanthropological research (Marean *et alii*, 2007) and it is hoped that the coprolites can make a significant contribution in this regard.

### Homologues sites in Spain and adjacent areas<sup>1</sup>:

#### Las Ventanas (Granada)

The Late Quaternary *Crocota* den site of Las Ventanas in Granada, southern Spain showed hundreds of coprolites and associated bones together with remains of alleged preys. Pollen analysis of coprolites allowed depicting the

lateglacial landscapes in the region at 12 780 cal yr BP, being remarkable the location of glacial refugia for temperate and thermophilous tree species. A number of coprolites were palynologically sterile, while ten of them showed good pollen preservation and relatively high pollen concentration and diversity of both herbaceous and arboreal types (Carrión *et alii*, 2001). These differences in pollen content between coprolites may be due to different seasonal record, and this will be tested in this project.

#### Gorham's Cave (Gibraltar)

Twenty four coprolite specimens, mostly attributable to *Crocota crocuta*, were analysed for pollen in the late-Neanderthal site of Gorham's Cave, Gibraltar. From these, ten were sterile, including three specimens for the Mousterian Level IV, four for the Upper Palaeolithic Level III, and three for the Holocene Level II. The remaining pollen-bearing coprolites showed generally good preservation of pollen, and allowed reliable pollen identifications and counts of 180 to 1993 grains. No relationship was seen between the polleniferous character and the macroscopic appearance of the coprolite (e.g. colour, size, presence of surface cracks). Pollen concentration in the coprolites was highly variable, some surpassed the highest values reported for the hyaena coprolites in the site of Las Ventanas (Carrión *et alii*, 2001).

#### Villacastín (Segovia)

Ten coprolite specimens from the late Mid-Pleistocene cavern of Villacastín (Segovia, central Spain) were analyzed, from which two lacked pollen. Yet, there was no relationship between the polliniferous character and the macroscopic appearance of the coprolite (e.g. colour, size, presence of surface cracks). Pollen taxa diversity indicated, in general, a semi-forested landscape (Carrión *et alii*, 2007).

#### Los Torrejones (Guadalajara)

Pollen analyses from the upper Pleistocene site of Los Torrejones in central Spain showed between 10 and 18 types with variable pollen concentrations. Like in Villacastín, the pollen records of Los Torrejones showed percentage variability, but here the landscapes were shown more open, and the number of thermophilous taxa somewhat lower.

### Summary

Coprolites studied palynologically from several sites in South Africa and Europe showed great promise in

1. Nerja (Málaga) and Cova Negra (Valencia) caves are palynologically sterile. They have been rejected from a former list after Carrión *et al.* (2009). Two new sites, Villacastín and Los Torrejones, have been listed.



reconstructing past vegetation conditions. Preliminary indications are that these coprolites give a relatively regional pollen signal representing a wider source of habitats than the sediments nearby where they come from. Pollen-taphonomic studies have mainly focused on rates of palynomorph dispersal in particular environments (caves, lakes) and rates of pollen preservation to establish how they reflect the vegetation from the immediate vicinity or regional environment. However, there are currently no detailed studies about pollen taphonomy in coprolites over time under changing environmental conditions or different record between the outer and inner part of the coprolite. The background for the diversity, composition and origin and nature of pollen spectra represented at a given site where hyaena coprolites are present, has to be more precise. Therefore, monitoring in the surroundings of hyaena territory/dens will be started to get information about seasonal influx and pollen input. Specific environmental parameters that may affect pollen preservation can be better known through experimental work. In this paper we have described an experimental protocol to tackle pollen deposition and preservation in hyaena coprolites. This implies modern hyaena scat collection to analyse pollen contents using soil surface samples and pollen traps as controls. It also will involve the use of environmental chambers to define the most influential parameters in pollen preservation.

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YOLANDA FERNÁNDEZ-JALVO

## Resumen

Polen, esporas, fitolitos y otros microfósiles en coprolitos de hiena proporcionan una información relevante en la interpretación paleoambiental. Sin embargo, existe una serie de procesos implicados que necesitan ser investigados. Estos procesos pueden modificar el registro palinológico por transporte, incorporación selectiva de plantas-pólenes en la dieta, y selección y estrategias de caza de depredadores. Además, existen condiciones ambientales y preservación selectiva de estos microfósiles en los coprolitos (tanto antes como durante la fosilización) que pueden tener un papel muy importante en la interpretación paleoambiental.

Las hienas, de las cuales tres especies habitan hoy en África, han producido abundantes restos de excrementos que han fosilizado (coprolitos) en sus cubiles, lo que ha proporcionado una importante trampa polínica en yacimientos de Europa y África. Los coprolitos han sido ampliamente empleados por los palinólogos, pero las diferencias en la composición polínica entre los coprolitos y el sedimento, que indica la vegetación en los alrededores donde se acumularon, tienen implicaciones en las interpretaciones paleoambientales. Para investigar cómo los pólenes pueden ser afectados durante la fosilización, proponemos una serie de experimentos a) para comparar coprolitos que puedan estar disponibles y que cubran un rango de ambientes diferentes y b) para determinar sesgos en la preservación de polen por agentes tafonómicos que puedan reproducirse experimentalmente.

**Palabras clave:** contenido polínico en coprolitos, tafonomía, hiena, Sudáfrica, España.

## Abstract

*Pollen, spores, phytoliths, and other non-pollen microfossils in hyaena coprolites provide valuable insights into past environments. There are, however, taphonomic processes involved that need to be investigated. These processes may modify palynological records by transport, selective incorporation of plant-pollen in animal diet, and selection and hunting behaviour of predators.*

*Further, environmental conditions and selective pollen preservation (both before and during fossilization) may also play an important role when interpreting past environments.*

*Hyaenas, of which most species occur in Africa today, have left fossil dung remains in den sites that provided important fossil pollen traps both in Europe and Africa. These pollen traps have been extensively used by palynologists but differences between pollen composition in coprolites and the vegetation in the surroundings of where they accumulate have implications for the interpretation of past environments. In order to investigate how pollen assemblages are affected during fossilization some experiments are proposed a) to compare available coprolites from a range of different environments and b) to determine biases in pollen preservation by taphonomic processes by means of experiments.*

**Keywords:** coprolite pollen content, taphonomy, hyaena, South Africa, Spain.



# ZONA ARQUEOLÓGICA

ACTAS DE LA 1ª REUNIÓN DE CIENTÍFICOS  
SOBRE CUBILES DE HIENA (Y OTROS GRANDES  
CARNÍVOROS) EN LOS YACIMIENTOS  
ARQUEOLÓGICOS DE LA PENÍNSULA IBÉRICA

NÚMERO 13  
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