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Vegetation reconstruction on the basis of pollen in Late Pleistocene hyena coprolites from San Teodoro Cave (Sicily, Italy)

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Abstract

Vegetation reconstruction based on pollen from coprolites of extinct spotted hyena (*Crocuta crocuta spelaea*, Goldfuss 1832) recovered from excavations carried out in 1998 at San Teodoro Cave (Sicily, Italy) supports previous indications of pre-Late Glacial conditions. Eight of the twelve coprolites analysed contained well-preserved pollen grains. There is a general similarity between the pollen contents from the coprolites but they show variability. They suggest a main vegetation type dominated by steppic taxa (Poaceae, *Artemisia*, *Ephedra*, Chenopodiaceae and Asteraceae) but also including arboreal taxa (*Pinus* and Cupressaceae). Low percentages of pollen of mesophilous woody taxa (*Quercus*, *Betula*, *Abies*, *Alnus*, *Pistacia*, among others) are noticeable, suggesting the existence of nearby refugia for temperate and Mediterranean vegetation. A reconstruction of the landscape, using the coprolite pollen record and other pollen records from Sicily and south Italy, shows the predominance, during the pre-Late Glacial, of a wooded steppe biome, with elements representing a variety of local environmental conditions.
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1. Introduction

It is generally assumed in the literature that spotted hyenas become extinct in Europe at the end of the Pleistocene (Sutcliffe, 1970), but the chronology of the extinction is unclear for most regions. During the Upper Pleistocene, Europe was inhabited by two species of hyena: *Hyaena hyaena*, the striped hyena, and *Crocuta crocuta*, the spotted hyena (Davis, 2002). Hyenas are only poorly documented in archaeological sites in Iberia and they disappeared almost completely in Late Palaeolithic (Fernández Rodríguez et al., 1995). In the case of Italy, *C. crocuta* is principally documented in bone samples from the Middle and Upper Pleistocene. Here we present pollen analyses of *Crocuta* coprolites from San Teodoro Cave, a key site that documents one of the last insular refuges of spotted hyenas in the northern side of the Mediterranean basin.

Studies of the integrity of *Crocuta* droppings have shown that they are hard and durable (Larkin et al., 2000). Examination of pollen in fossil faecal remains may yield valuable palaeoclimatic, palaeovegetational and palaeoethnological information (Martin et al., 1961; Bryant and Holloway, 1983; Davis, 1990; Scott and Cooremans, 1992; James and Burney, 1997; Carrión et

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al. 1999, 2001) especially in arid environments without lakes or swamps. Coprolite palynology has proved its potential in recent studies (Scott, 1987; Alcover et al., 1999; Carrión et al., 2000, 2001). Hyena coprolites have been a reliable source of evidence about animal diet (Siegfried, 1984), and animal–human relations in the past (Horwitz and Goldberg, 1989). However, research has rarely been directed towards palaeovegetational issues (except for Scott,1987; Carrión et al., 2001). The interpretative potential attributed to the palynology of hyena 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 in the Quaternary. The pollen from hyena coprolites gives a regional view of the landscape, since these mammals travel long distances (Scott, 1987; Carrión et al., 2001). The available studies from southern Africa corroborate the similarity of coprolite spectra with well-established regional pollen records from open sites (Scott, 1987) and besides 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, with low pollen production, may complicate interpretation (Carrión et al., 1999, 2001).

2. The site and depositional environment

San Teodoro Cave (14° 35′ 48″ E; 38° 2′ 43″ N; 145 m a.s.l.) located at Acquedolci (Messina, Sicily, Italy) (Fig. 1) is an important site for the study of Late Palaeolithic culture and Upper Pleistocene mammal assemblages in the Mediterranean area. It opens into the side of a high calcareous hill, the Pizzo Castellaro, which forms part of the northernmost slopes of Mount San Fratello Formation.

The cave is huge, about 60 m long, 20 m wide and up to 20 m high, with a small entrance and an area of more than 1000 m^2, the longer axis being orientated in accordance with a NNW–SSE fault system (Robillard, 1975; Bonfiglio et al., 2001). In previous excavations (Vaufrey, 1928, 1929; Leonardi, 1941; Maviglia, 1941; Graziosi and Maviglia, 1946; Lona, 1949; Anca, 1959–60) was distinguished an Upper Late Glacial sedimentary unit (unit a) containing human food remains associated with Epigravettian stone artifacts, while a lower sedimentary unit (unit b) contained Late Pleistocene endemic mammal remains. Exceptionally complete and well-preserved articulated skeletons of at least seven humans have been recovered (Graziosi, 1947; Fabbri, 1993), and were buried intrusively in the clayey sands and gravels of the lower stratigraphic unit b (Bonfiglio et al, 2001).

The 1998 excavations were almost exclusively in the sediments of the lower (pre-Late Glacial) unit. The

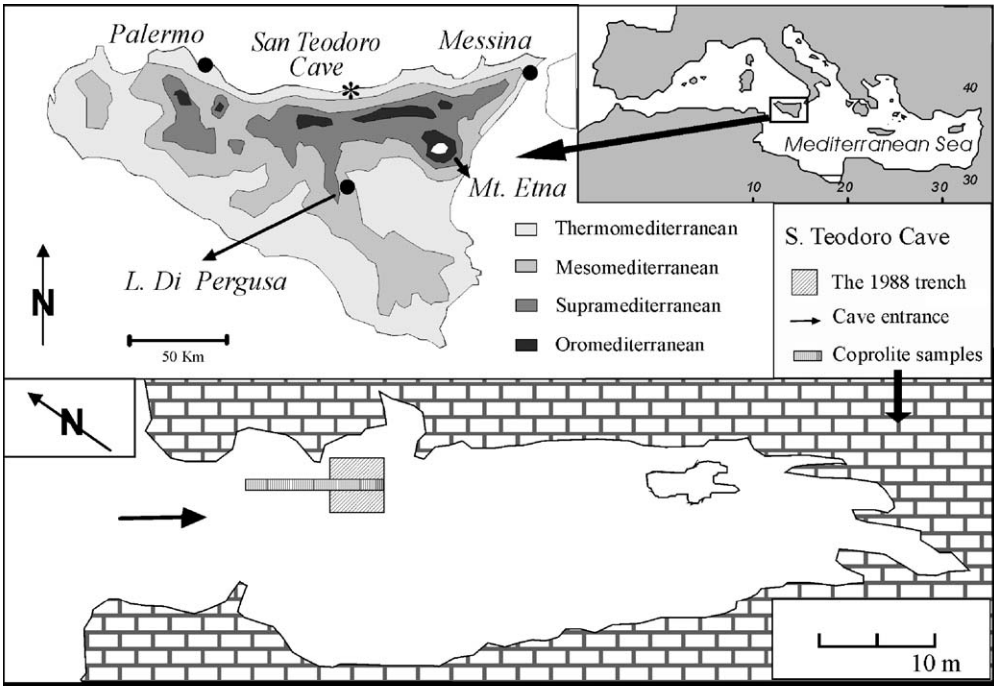

Fig. 1. Location and plan of San Teodoro Cave, Sicily. The map shows the vegetation stages after Ozenda (1994) (simplified and redrawn). The San Teodoro Cave plan is after Bonfiglio et al. (2001) (redrawn).

Table 1
Measurements of hyena coprolites and fresh droppings from several fossil and recent sites, including San Teodoro Cave

Site/species	Widest diameter mean, mm (range)	Shorter diameter mean, mm (range)
San Teodoro (Sicily, south Italy) *Crocuta crocuta*	29 (23–41)	25 (17–35)
Las Ventanas, south Spain *Crocuta crocuta* coprolites (Carrión et al., 2001)	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	29 (25–40)	24 (16–34)
Arad, Israel sub-recent *Hyaena hyaena* droppings (Horwitz and Goldberg, 1989)	21 (15–26)	–
Tel-Aviv Zool. Garden, Israel fresh *Hyaena hyaena* droppings (Horwitz and Goldberg, 1989)	18	–

lithology and fossil content are fairly uniform throughout the depth investigated. The material recovered from washed samples of sediment consists of a large number of mammal bones and hyena coprolites, small vertebrates, small gastropods and seeds (Bonfiglio et al., 2001). The spotted 'cave' hyena is represented by 4 cranial fragments, 4 incomplete hemimandibula fragments, several isolated teeth, 1 distal epiphysis of a humerus, 1 radius, 1 femur and 1 femur shaft. All the hyena bones, except for one larger cranial fragment, show serious damage by conspecific crushing and gnawing (Bonfiglio et al., 2001). The damage to hyena and other mammal bones together with the abundant coprolites testifies to intense hyena activity. The taphonomic features related to the presence of hyena during the deposition of unit b are similar to those known from other cave deposits in Africa and Europe regions although unknown from the islands.

At present the average annual precipitation on the north coast of Sicily is very variable, between 350 and 850 mm. The average annual rainfall at the station of Messina (in the East) is 386 mm and at the station of Palermo (in the West) is 836 mm. At the same stations, the average annual temperatures are 18.2 and 19 °C, respectively.

The thermomediterranean vegetation belt reaches altitudes of up to 400 m in the south of the island, and is characterised by sclerophyllous forest and scrub consisting of *Quercus ilex* accompanied by other woody species such as *Fraxinus ornus* and *Celtis australis*. The shrub layer is composed of *Phillyrea angustifolia*, *Rhamnus alaternus*, *Arbutus unedo*, *Viburnum tinus* and *Laurus nobilis* (Pignatti, 1998).

3. Description of the coprolites

The 1998 excavations reached a maximum depth of 1.50 m in the sandy clays of unit b, over an area of about 12 m^2. The hyena coprolites (*C. crocuta* subsp. *spelaea*, Goldfuss, 1832) come from sieved sediment from different excavation levels. Each level is about 10 cm thick and is labelled as "tg" followed by a number from a

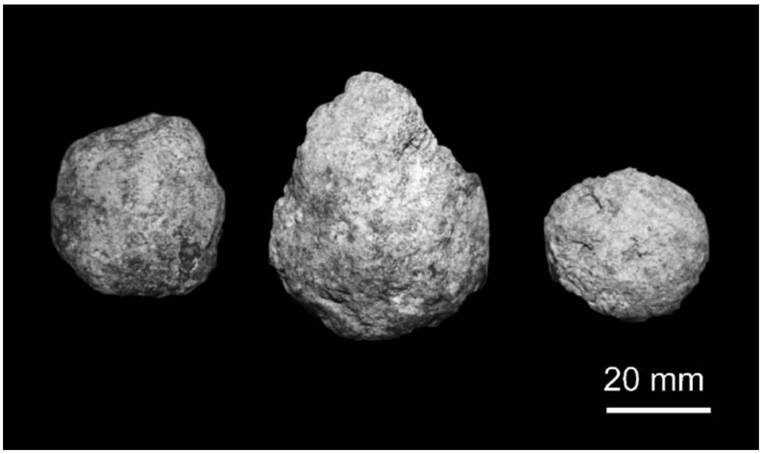

Fig. 2. Spotted hyena coprolites from San Teodoro Cave.

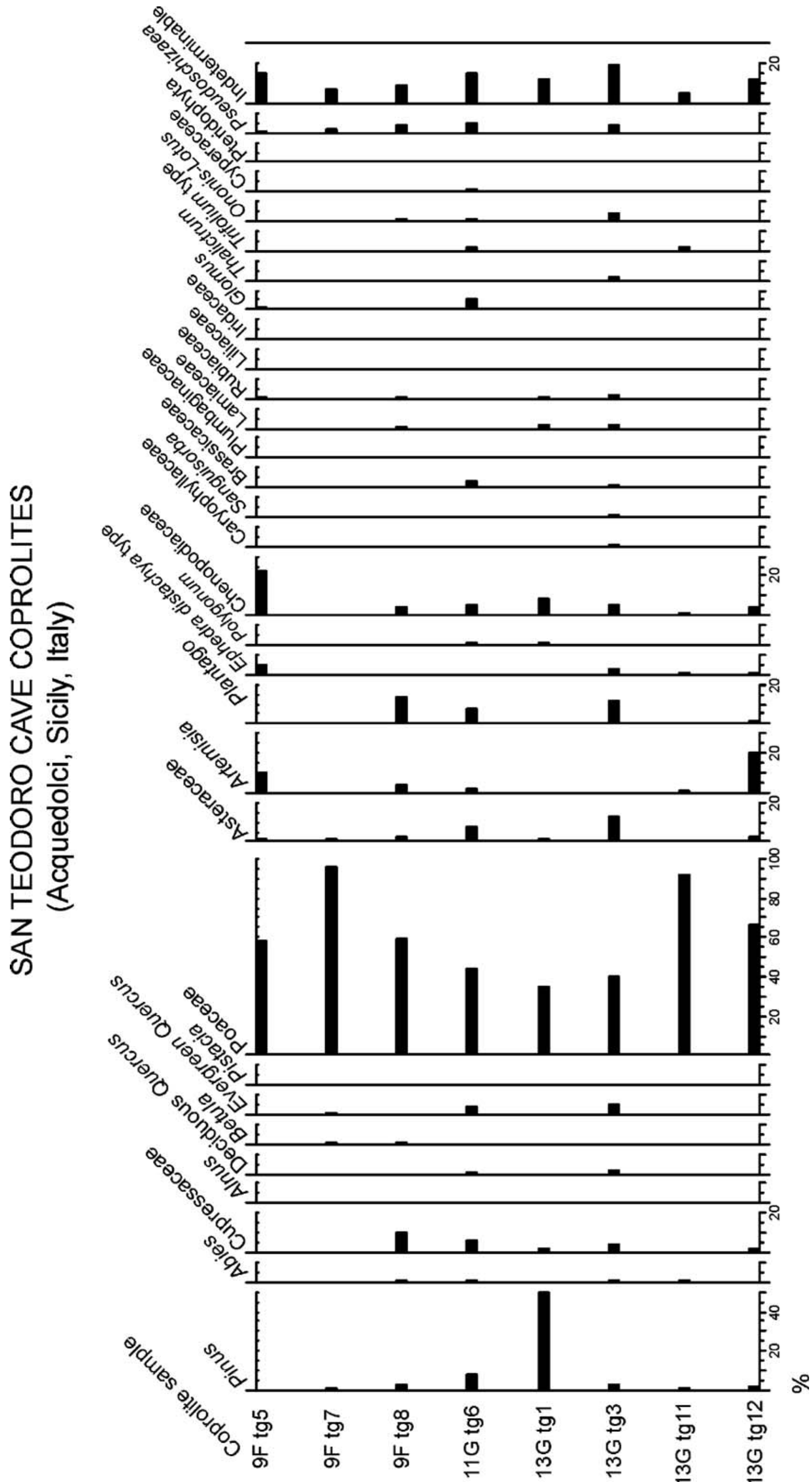

Fig. 3. Pollen diagram of hyena coprolites from San Teodoro Cave.

series that progresses from the top to the bottom of the excavation trench in unit b. The sedimentary unit b is uniform throughout the thickness excavated.

The coprolites were pale yellowish brown externally and pale brown to white internally. Most were hard, although not permineralized, and sometimes broke easily. Their surfaces showed straight cracks, up to 3–4 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 distinguishable from the inner region of the coprolite. The great majority of the coprolite specimens consisted of individual segments with their maximum ranging from 23 to 41 mm (mean 29) (Table 1, Fig. 2). The morphological characteristics of the coprolites identify them as being from *C. crocuta* (Carrión et al., 2001; Horwitz and Goldberg, 1989); in addition, several specimens contained small, highly corroded fragments of partially digested prey bones, an exclusive characteristic of this hyena species.

4. Pollen analysis

4.1. Methods

Twelve coprolite samples from different levels of the excavations were collected for pollen analysis. In the laboratory, to minimise contamination from external surfaces, the coprolites were cut open with a steel spatula and material from the centre was scraped out and weighed. Laboratory treatment was carried out following the conventional method of HCl, HF and KOH digestion. *Lycopodium clavatum* tablets containing a known quantity of spores were added to each sample so that the pollen concentrations could be estimated. Pollen identification was carried out by comparison with the reference collection of the Plant Biology Department at Murcia University. The percentages of each taxon (Fig. 3) for each sample were based on a pollen sum excluding non-pollen palynomorphs (*Glomus* and *Pseudoschizaea*).

4.2. Results

Eight coprolite specimens showed good preservation of pollen, and allowed counts of 115 to 384 grains (mean 243) (Table 2). The remaining four samples were either totally sterile or displaying a few grains. The values for the total pollen concentration, pollen sum, number of pollen taxa, and percentages of indeterminable pollen are shown in Table 2. The number of palynomorphs extracted from the samples ranges between 1476 and 12142 grains per gram. Pollen preservation was variable, but allowed reliable pollen identification with frequencies of indeterminable grains between 2.3% and 10.4%. The samples with good pollen preservation (tg8, tg6, tg3 and tg11) show high concentrations and higher diversity, while those with poor preservation (tg5, tg7, tg1 and tg12) showed a lower pollen diversity with as few as 10 taxa. The diversity of pollen types is not very high, with 31 taxa in total. (Fig. 3).

Table 2
Palynological characteristics of hyena coprolites from San Teodoro Cave: pollen concentration, percentage of indeterminable pollen, pollen sum, and number of taxa

Sample	Concentr. (grains/g)	Indet. (%)	Pollen sum	Taxa no.
9F tg5	1476	8.8	170	10
9F tg7	2639	3.7	187	7
9F tg8	11957	2.8	323	16
11G tg6	9560	3.9	384	22
13G tg1	2265	10.4	115	8
13G tg3	12142	5.4	354	20
13G tg11	2817	2.3	217	12
13G tg12	3359	6.2	192	9

Pollen spectra show variability in the relative percentages of *Pinus*, Cupressaceae, Poaceae, *Artemisia* and *Plantago*. Poaceae is the most abundant pollen taxon, with percentages between 35% (tg1) and 95% (tg7). The main arboreal taxa are *Pinus* and Cupressaceae. The main non-arboreal taxa are Poaceae, Asteraceae, *Artemisia*, *Plantago* and Chenopodiaceae. In some samples, relatively high values are reached by other pollen taxa, such as evergreen *Quercus* (tg6 and tg3)), *Ephedra* (tg5), and *Ononis–Lotus* type (tg3). *Abies*, Lamiaceae and Rubiaceae are common although minor taxa. *Pseudoschizaea* is also well-represented, and especially significant, in samples tg8, tg6 and tg3. *Glomus* chlamydospores occur in sample tg6 (Fig. 3).

5. Environmental implications

Pollen may be incorporated into hyena coprolites in different ways. Spotted hyenas are known to range up to 50 km from their dens (Mills, 1989). Coprolites will generally provide a pollen record representing the regional vegetation (Scott, 1987; Carrión et al., 2001). In this study, contamination seems unlikely (Navarro et al., 2000; Navarro, 2000), mainly because of the similarity between the coprolite spectra and the pre-Late Glacial pollen records for this region (Allen et al., 2000), both of them showing a main vegetational formation dominated by herbs and containing reduced numbers of arboreal taxa. The coprolites are characterised by Poaceae, Asteraceae, *Artemisia* and *Plantago*,

Table 3
Main pollen percentages of Lago Grande di Monticchio, Lago di Pergusa and San Teodoro Cave for representative pollen samples of full Glacial, Late Glacial and Holocene age: (LGM: full Glacial of pollen assemblage 4 (25,900–14,300 years BP); Late Glacial of PAZ 2–3 (14,300–11,200 years BP) and Holocene PAZ 1 (<11,200 years BP)

Taxa	Full Glacial		Late Glacial		Holocene	
	LGM	STC	LGM	LGM	LP1	LP2
Poaceae	25–40	40	15–30	<10	15–45	5–20
Artemisia	20–40	<5	<10	*	5–30	<5
Chenopodiaceae	<20	5	*	*	5–45	<10
Pinus	5–50	8	<5	*	<5	*
Juniperus	5–35	6	*	*	<5	*
Quercus	<5	5	40–60	50–65	10–35	60–90

LP: for LP1: local pollen zones 7–6 (10,815–8950 years BP) and for LP2: LPZ 5–4 (8950–4400 years BP).
*Presence<2%.

with low *Pinus* values (except in sample tg1), Cupressaceae and evergreen *Quercus*.

These characteristics are shared by other coprolite pollen spectra (Carrión et al., 2001), in which grasses are abundant, and by the pre-Late Glacial pollen record (Allen et al., 2000) at Lago Grande di Monticchio (southern Italy). The only dated postglacial record in Sicily (Sadori and Narcisi, 2001) is a pollen diagram from Lago di Pergusa, starting at 10,815 years BP, showing steppe of Chenopodiaceae, *Artemisia* and Gramineae. In this site, lying at 667 m.a.s.l. and 50 km from the sea, forest colonisation started at 10,600 years BP (Sadori and Narcisi, 2001). At a higher altitude, at Urgo di Pietra Giordano (Bertolani Marchetti et al., 1984) the open forest is replaced by deciduous-oak woodland at 9200 years BP. The start of postglacial afforestation is placed at between 10,800 and 10,300 years BP in most pollen records from southern and central Italy (Follieri et al., 1986; Leroy et al., 1996; Watts et al., 1996; Magri, 1999; Magri and Sadori, 1999; Ramrath et al., 2000).

The pre-Late Glacial deposits at Lago Grande de Monticchio (Allen et al., 2000) display similar pollen spectra those from the coprolite samples from San Teodoro Cave. The upper part of pollen zone 4, dated to 14,300 calendar years, shows a predominance of herbaceous taxa (Poaceae, *Artemisia* and Chenopodiaceae), low percentages of *Pinus* and *Juniperus*, and scarcity of other woodland elements (largely *Quercus* and *Betula*). Table 3 shows the 6 main pollen taxa percentages of Lago Grande de Monticchio, Lago di Pergusa and San Teodoro Cave for representative samples of full Glacial, Late Glacial and Holocene age. According to Allen et al. (2000) the climate inferred at Monticchio during the Last Glacial maximum is one of varying intensity of seasonal drought; the greatest drought intensities are inferred for the steppe phases dominated by herbaceous taxa, especially those periods when species of Chenopodiaceae were relatively more abundant.

In San Teodoro Cave, the low abundance of meso-thermophilous taxa is a clear indication of the steppe conditions that dominated a great part of the landscape during the pre-Late Glacial. In this context, it is possible that woodlands developed in the most favourable habitats. The presence of *Betula* at San Teodoro Cave suggests relatively cool summers. Samples from this pollen zone are classified as representing the cool steppe biome (Allen et al., 2000). The pollen spectrum is consistent with the appearance in Sicily of *Equus hydruntinus*, which occurs for the first time in the San Teodoro Cave (Bonfiglio et al., 2001). The palaeobiome reconstruction for southern Italy (Prentice et al., 1992; Huntley et al., 1996; Allen et al., 2000) shows the predominance of the wooded steppe biome during much of the Upper Pleistocene, and it apparently has no extensive modern analogue. It is, however, clear that the data reflect a combination of different environmental conditions.

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