Palynology of badger coprolites from central Spain

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Abstract

This paper presents pollen analysis of badger coprolites from Cueva de los Torrejones, central Spain. Eleven of fourteen coprolite specimens showed good pollen preservation, acceptable pollen concentration, and diversity of both arboreal and herbaceous taxa, together with a number of non-pollen palynomorph types, especially fungal spores. Radiocarbon dating suggests that the coprolite collection derives from badger colonies that established setts and latrines inside the cavern over the last three centuries. The coprolite pollen record depicts a mosaic, anthropogenic landscape very similar to the present-day, comprising pine forests, *Quercus*-dominated formations, woodland patches with *Juniperus thurifera*, and a *Cistaceae*-dominated understorey with heliophytes and nitrophilous assemblages. Although influential, dietary behavior of the badgers does not preclude palaeoenvironmental interpretation of the coprolite pollen spectra.
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Keywords: Palynology; Palaeoecology; Holocene; Coprolites; Badger; Spain

1. Introduction

Copropalynology has greatly contributed to filling the gap of Quaternary landscape reconstruction studies in poorly known territories (Davis, in press). Palynologists have succeeded in extracting pollen from consolidated dung of extinct megafauna (Thompson et al., 1980; Davis and Anderson, 1987; Mead et al., 1986), caprids (Mead et al., 1987; Rasmussen, 1993; Karg, 1998; Akeret et al., 1999; Alcover et al., 1999; Yll et al., 2001), hyenas (Scott, 1987; Carrión et al., 2000b, 2001a; González-Sampériz et al., 2003; Scott et al., 2004; Yll et al., in press), rodents in North America (Davis and Anderson, 1987; Betancourt et al., 1989; Cole, 1990; Smith and Betancourt, 1998), South America (Holmgren et al., 2001; Kuch et al., 2002; Latorre et al., 2002), Australia (Green et al., 1983; Pearson, 1999; Allen et al., 2000; Pearson and Betancourt, 2002), and southern Africa (Scott and Cooremans, 1992), and hyraxes (Scott and Vogel, 1992; Scott, 1994; Carrión et al., 1999). Other promising materials include vitrified cow dung (Carrión et

al., 2000a), owl pellets (Fernández-Jalvo et al., 1999), avian coprolites (James and Burney, 1997), and bat guano (Bui Thi Mai and Girard, 2000; Leroy and Simms, 2002; Maher, 2002; Carrión et al., in press).

This paper presents pollen analysis of Eurasian badger (*Meles meles:*Mustelidae, Carnivora) coprolites from Cueva de los Torrejones, central Spain. To our knowledge, badger coprolites have not been used hitherto for pollen analysis.

2. Setting and present-day vegetation

Los Torrejones is a karstic, sac-like cavern situated at 1100 m asl in Upper Cretaceous limestones of the Ayllón Massif (eastern Sistema Central), near the village of Tamajón, northwest of Guadalajara province, central Spain (Fig. 1). The fluvial basins of the Sorbe, Jarama, and Henares rivers extend southwards

of the massif. 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 and deck pipes (Fig. 2). The cavity is partially filling up, and the ceiling height ranges from 1 to 5 m. A 16 m^2 area in the Entrance gallery was excavated during 1993–1995, discovering abundant bone remains of early Upper Pleistocene faunas, and Middle Palaeolithic utils (Arribas et al., 1997; Arribas and Jordá, 1999).

Hundreds of well-preserved coprolites (Fig. 3), and fragmented specimens occur exposed on the surface of the cave sediments, being especially abundant at the rear in the Tejones Chamber, 25–27 m deep into the cavern (Fig. 2). The bed comprises clays, and brown silts without evidence of plant macrofossils. Abundant bone remains of *M. meles* (Fig. 4) have been found accumulated in the same area with less abundant bone fragments of a diversity of animals like *Erinaceus europaeus*, Chiroptera, *Apodemus*, *Pity-*
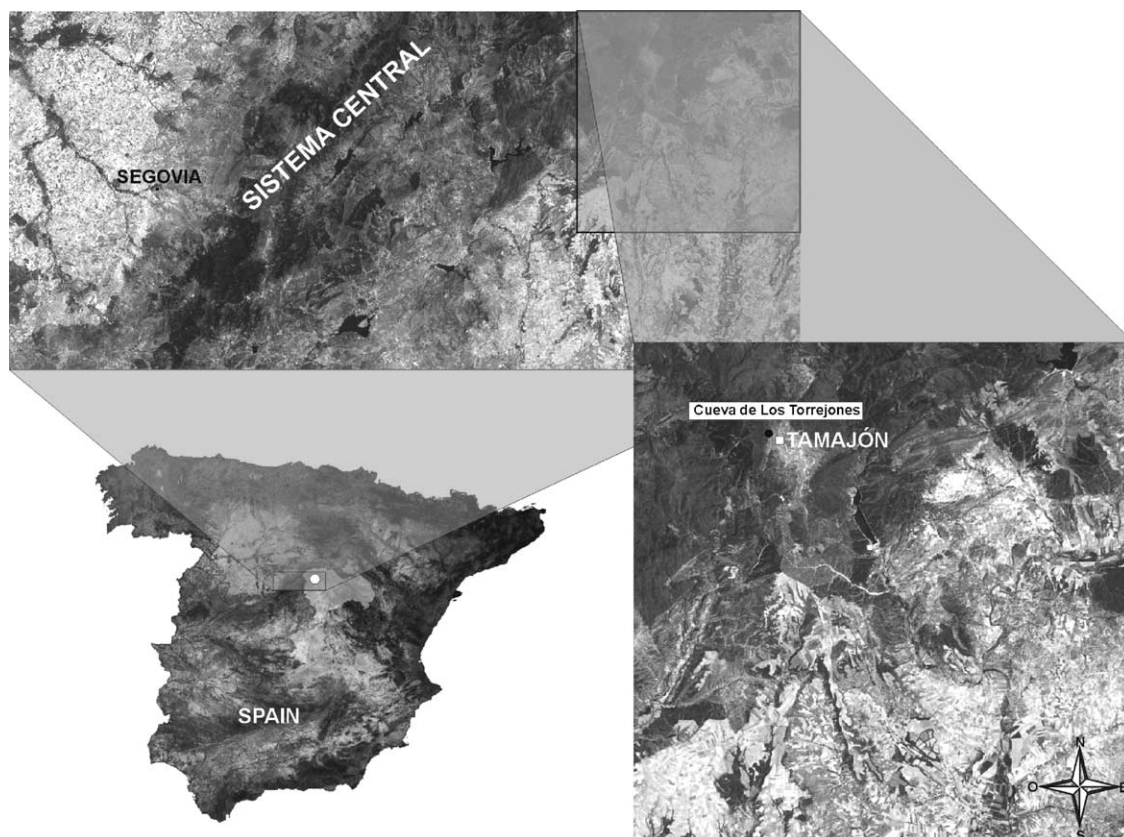

Fig. 1. Location of Cueva de los Torrejones in the eastern plateau of the Sistema Central region of Spain.
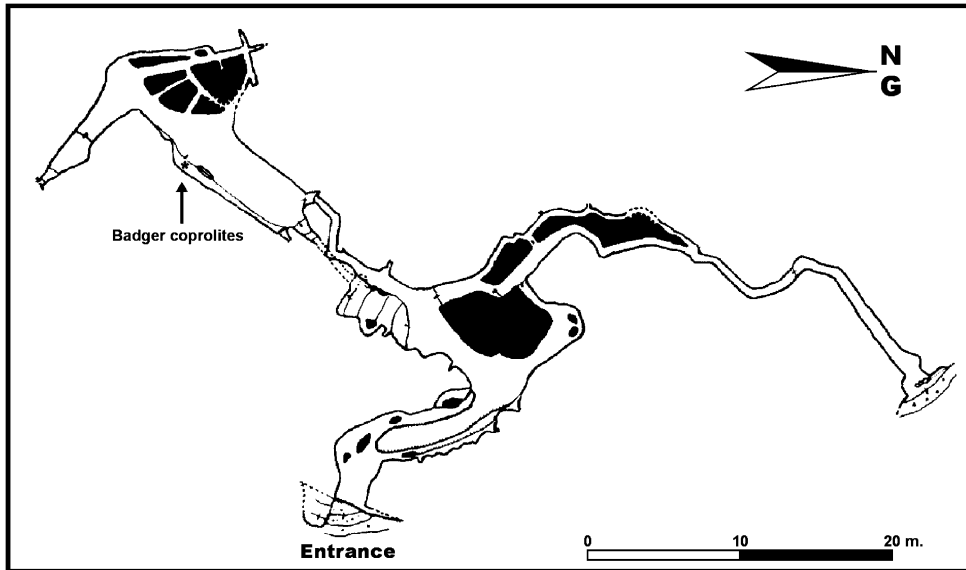
Fig. 2. Situation of the badger coprolites (Tejones Chamber) in the cavern topography.

mys, *Oryctolagus*, *Lepus*, *Vulpes vulpes*, *Cervus ela-phus*, *Capra*, *Lacerta lepida*, *Bufo*, *Coluber*, and Anura (Arribas et al., 1995; Arribas and Jordá, 1999). Understanding the depositional environment and history of preservation of the coprolites and bones is not simple, although one explanation could be that the collecting area of the Tejones Chamber acted as a latrine (dung pit).

The local modern landscape in the vicinity of the site includes a mosaic of plant formations typical of both acidic and calcareous substrates. The cave lies in an orographically complex ecotone between potential forests characterized by deciduous oaks above, and evergreen oaks below. The vegetation mosaic includes patches of oak, pine and juniper woodlands, as well as pastures, cultivated areas, and forest plantations. The main vegetation types are:

(1) *Juniperus thurifera* open woodlands with stands of *Quercus faginea*, *Sambucus nigra*, scrub of *Juniperus communis*, *J. oxycedrus,* spiny shrubs like *Prunus spinosa* and *Genista scorpius*, and heliophytic matorral of *Lavandula latifolia, Thymus zygis, Artemisia glutinosa*, and *Satureja montana*, among others.

Fig. 3. *Meles meles* coprolites from Cueva de los Torrejones.

Fig. 4. Skull of *Meles meles* ssp. from Cueva de los Torrejones.

(2) Evergreen oak (*Q. ilex* subsp. *ballota*) forests with the deciduous *Q. faginea* and *Acer monspessulanum* trees in shaded locations, with a *Phlomis lychnitis* understorey.

(3) Mixed forests of *Pinus halepensis*, with occasional *Quercus pyrenaica*, and *Q. ilex* subsp. *ballota*, and Cistaceae-dominated understorey of *Cistus ladanifer* and *C. laurifolius*, *Lavandula stoechas*, *Erica arborea*, *G. scorpius*, *G. cinerea*, *Thymus mastichina*, and *Daphne gnidium*. This vegetation type has developed on metamorphic-bedrock substrates.

(4) Cistaceae-dominated open areas with a number of chamaephytes and hemicryptophytes, largely Lamiaceae, Poaceae, Asteraceae, and Genisteae species.

(5) *Alnus glutinosa* riverine communities, including *Salix* and *Fraxinus* species.

3. Material and methods

Coprolites were collected from Los Torrejones Cave's excavation materials curated in the Museo Geominero, Madrid, by one of us (A. Arribas) (Fig. 3). The identification of the coprolite-producing ani-

mal, the European badger (*M. meles*), was based on morphological features of the dung and their association with bones of the same species. The coprolites were externally reddish brown to pale brown, and internally pale brown to greyish; most broke easily and showed surface cracks. They largely contained wing cases of beetles, and remains of woodlice, sometimes mammal hairs, but no visible plant remains.

Fourteen coprolite specimens (TORbd1-14) were treated for pollen in the Department of Plant Biology at Murcia. The laboratory preparation techniques followed conventional methods in palynology using HCl, HF, KOH, and a heavy liquid ($ZnCl_2$) mineral separation. At the beginning of the pollen processing, two *Lycopodium clavatum* spore tablets (c. 12,542 spores tablet^{-1}) were added to each sample in order to facilitate concentration calculations (grains per gram dry weight). All slides were mounted in glycerine jelly and stained with safranine.

Identification and counting were performed with light microscopy. The TILIA, TILIAGRAPH and CORELDRAW software programs were used for plotting percentage pollen diagrams. Percentages of each taxon for each sample were based on a pollen sum excluding spores (Figs. 5–7). Nomenclature of fungal spores follows Jarzen and Elsik (1986) and Kalgutkar
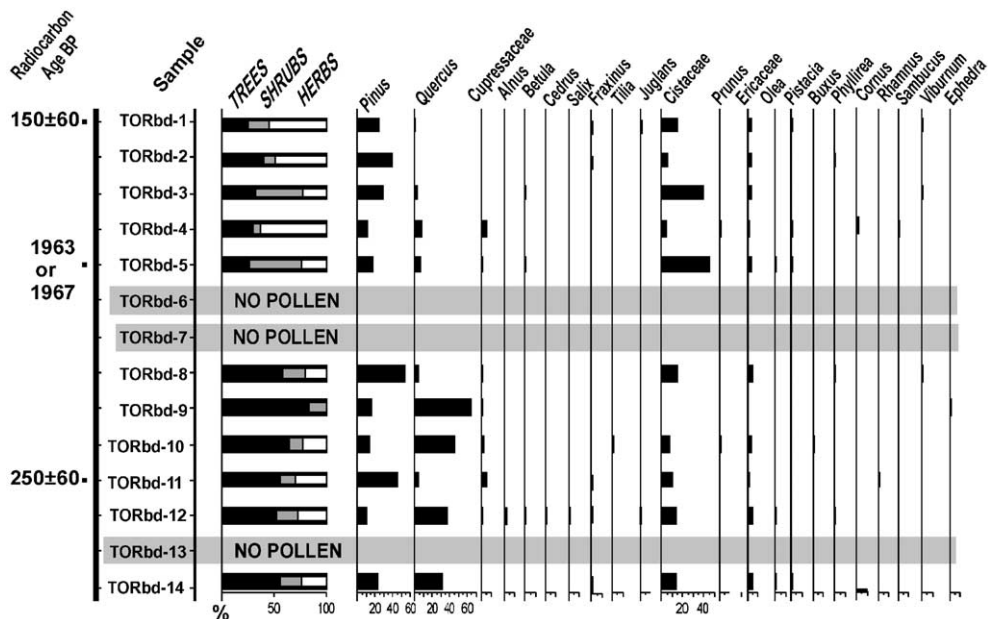

Fig. 5. Percentage pollen diagram of badger coprolites from Cueva de los Torrejones. Arboreal and most woody types.
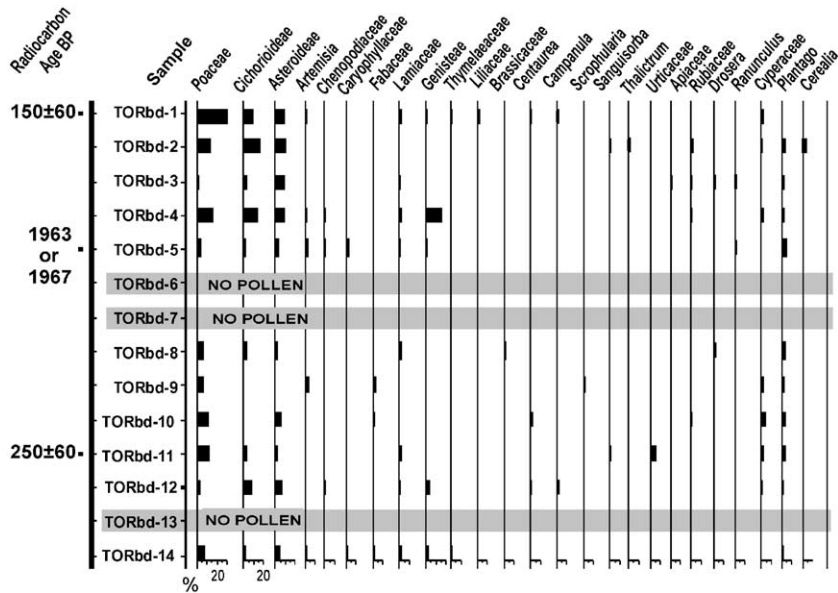
Fig. 6. Percentage pollen diagram of badger coprolites from Cueva de los Torrejones. Non arboreal types.

and Jansonius (2000). The non-pollen palynomorph types 179 and 189 follow the nomenclature by of Van Geel et al. (1981, 1983, 1989).

Three coprolite samples were submitted for radio-carbon dating to QUADRU, CSRI, Pretoria, South Africa (Table 1). Because of their high organic con-
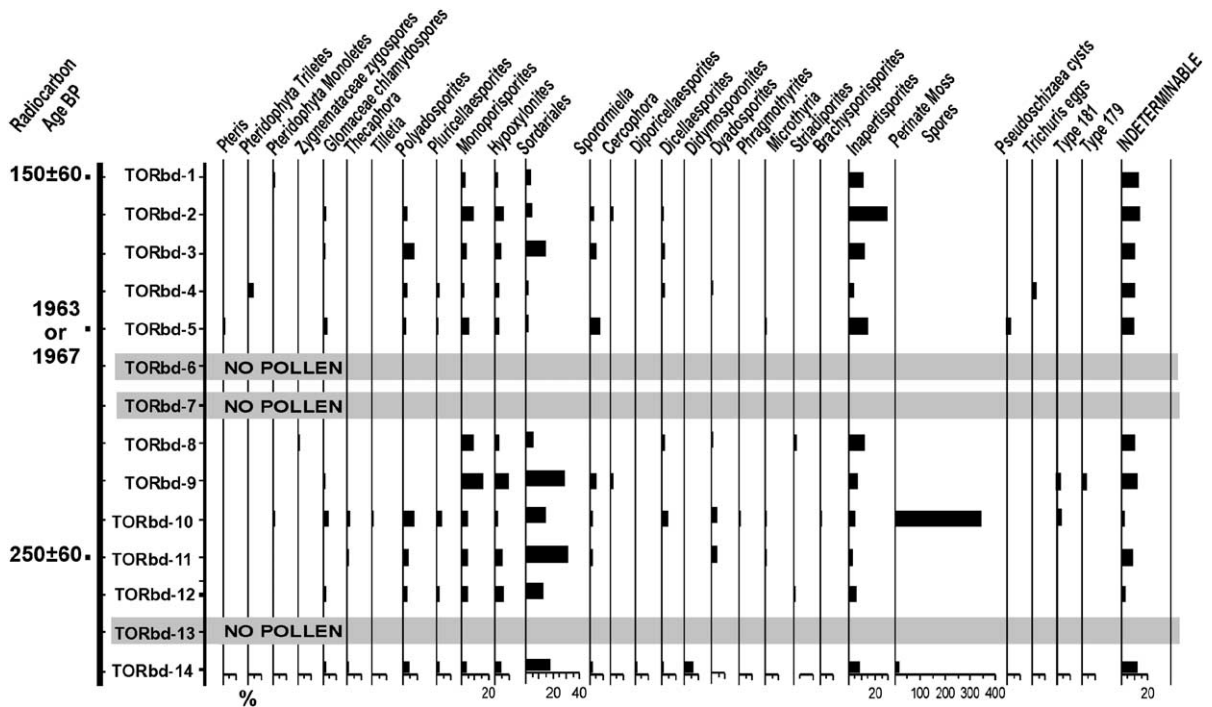

Fig. 7. Percentage pollen diagram of badger coprolites from Cueva de los Torrejones. Non-pollen palynomorphs and indeterminable pollen.

Table 1
Results of radiocarbon analysis of three badger coprolites from Cueva de Los Torrejones (Tamajón, Guadalajara, north-central Spain)

Ref. lab.	Coprolite	$\delta^{13}C$ (‰)	Radiocarbon age (yrs BP)	^{14}C (pmc)	Calibrated date (AD, 1 sigma range)
Pta-9055	TORbd1	25.7	150 ± 60		1665 (1682, 1738, 1806) 1890; 1908 (1931, 1954) 1955
Pta-9060	TORbd5	25.7		169.4 ± 0.5	1963 or 1967
Pta-9050	TORbd11	26.2	250 ± 60		1532–1548; 1634 (1652) 1670; 1779–1796; 1945–1955

pmc = percent modern carbon, where "modern" refers to the year 1950. Calibrated ages are given with the 1 sigma range, with the most probable date between brackets. Laboratory: CSIR Environmentek, South Africa.

tent, the coprolites are a suitable material for radiocarbon dating. Although the cortex was rich in organic matter and thus hypothetically datable, it was removed from the coprolite samples submitted for dating with the goal of reducing the chance of contamination by extraneous carbon.

4. Sources of pollen in the coprolites

Considering the behavior of the species responsible for the coprolite accumulation may shed some light on the pollen sources in the badger scats.

The Eurasian badger is found across Europe and Asia, within a broad range of biotopes including deciduous, coniferous and mixed forests, hedges, scrubs, riverine habitats, agricultural lands, grasslands, and steppes (http://www.badgerland.co.uk). It is mainly nocturnal, territorial, and can be found in clans of up to 12, living in extensive setts. Badger clans regularly defend an area of c. 50 to 150 hectares, which contains their home sett and several foraging areas. Territoriality is depicted through placing latrines, where the badgers urinate and defecate at regular intervals along the borders. Latrines are small pits which in appearance are not unlike those created by badgers when digging for grubs or other underground prey (http://www.badgers.org.uk). In contrast to most mammals, badgers leave their droppings exposed. Often, badgers deposit not only dung, but also secretions from their anal glands. It is worth investigating whether these secretions could favour preservation of pollen by creating chemical or physical microenvironments that reduce the activity of decomposing fungi and bacteria.

In Spain and other southern European countries, badgers can be solitary and do not have the custom of hibernation, but they are less active in winter. Yet,

they remain territorial, and in the chambers inside the setts, make nests for bedding from dry grass, straw, bracken or dead leaves. Nests are almost invariably constructed in forests or other areas with a woody cover, but foraging is mainly done in open areas such as fields. Foraging for worms is most effective in areas of short grass, so well-grazed pastures are preferred (http://www.badgers.org.uk).

The diet of the badger has been widely studied across its range (Pigozzi, 1991; Martín et al., 1995; Neal and Cheeseman, 1996; Goszcynkski et al., 2000; Zabala and Zuberogoitia, 2003). The main food items include insects, earthworms (Lumbricus terrestris), ground-living insect larvae, and fruits. Occasionally small mammals, eggs and nests of birds, reptiles and amphibians are consumed, but rarely fish. Badger scats may contain remains of earthworms, insects, fruits, seeds, vertebrates, larvae, grass, leaves, roots, bark, bulbs, snails, mammal hairs, garbage, etc.

It must be stressed that the European badger is a foraging omnivore that will exploit a wide range of food items. Thus, the badger's diet may vary throughout its geographic range, and according to season, food abundance, climate, and habitat. Although badgers may concentrate on certain food sources that are abundant at a particular place and/or time, they can readily adapt their feeding habits to exploit alternative and novel resources. The American badger (Taxidea taxus) is more carnivorous than M. meles.

Incorporation of pollen into badger coprolites could be via: (i) settlement from the air, (ii) ingestion of vegetable matter, (iii) ingestion of insects that are themselves covered by pollen or whose digestive system contains pollen, (iv) adherence of pollen to any other item of the diet, (v) bedding material, (vi) fragments of badger skin and hair during social grooming, (vii) ingestion of water, and (viii) dust brought by the activity of animals. Determining the

relative role of each of the mechanisms of incorporation of pollen will continue to be speculative until basic taphonomic research is undertaken.

5. Results and discussion

5.1. Chronology of the coprolites

Dates are reported in conventional radiocarbon years, i.e., using a half-life of 5568 years for C-14 (Table 1). Ages are corrected for variations in isotope fractionation. Calibrated ages were calculated by the programme developed by John Vogel in QUADRU, one of the laboratories that is able to measure atmospheric ^{14}C levels throughout the 1954–63 nuclear-bomb interval. The three dates obtained suggest that most of the coprolites are sub-recent, with the whole collection no older than 300 years.

5.2. Pollen-analytical features

Eleven coprolite specimens were polliniferous, showed good preservation of pollen, and allowed average counts of 317 grains, with only one sample (TORbd9) not exceeding 200 grains (Table 2). The remaining three coprolites were palynologically sterile (TORbd6, TORbd7, TORbd13). There was no relationship between the polleniferous character and the

macroscopic appearance of the coprolite (e.g., colour, size, abundance of surface cracks).

Values of 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 coprolites ranges between 5337 and 17415 grains per gram.

Pollen preservation was generally good, allowing reliable pollen identifications and frequencies of indeterminable grains below 10% (Table 2, Fig. 7). Palynomorph taxa diversity is relatively high, with a total of 47 pollen types, 3 fern spore types, 19 fungal types, and 5 further types of non-pollen palynomorphs recorded (Figs. 5–7).

The pollen dominants in the coprolites are *Pinus, Quercus*, and Cistaceae and, to a lesser extent, Poaceae, Cichorioideae, Asteroideae, Cupressaceae, and Ericaceae (Figs. 5–7). Other pollen taxa such as Genisteae (TORbd-4) reach relatively high values in some samples. Other common types are *Plantago*, Lamiaceae, and Cyperaceae. Ecologically interesting woody types such as *Alnus, Betula, Salix, Fraxinus, Tilia, Juglans, Pistacia, Buxus, Phyllirea, Cornus, Rhamnus, Sambucus, Ephedra*, and *Viburnum,* occur infrequently and in low percentages (Fig. 5).

The pollen spectra show great percentage variability among coprolites, with the most distinctive differences being in the percentages of *Pinus, Quercus*, Cistaceae, and Genisteae (Fig. 8). In contrast, the oscillations of Ericaceae, Poaceae, Cichorioideae, Asteroideae and *Plantago* are generally lower. It is worth mentioning that Cistaceae reaches highest frequencies in samples TORbd-3 and TORbd-5, conforming with the lowest records of arboreal pollen (AP) (Fig. 5). The highest amounts of Genisteae (TORbd-4) also coincide with a drop in AP.

Apart from pollen grains, the studied specimens contain a variety of cryptogam spores and other palynomorphs, some of which have proved their value as palaeoecological indicators (Wolf, 1967; Elsik, 1976; Stubblefield and Taylor, 1988; Van Geel et al., 1989, 1994). The most abundant non-pollen palynomorphs are spores of sordariaceous fungi, including *Cercophora*, and *Sporormiella,* which are often coprophilous (Lundqvist, 1972; Davis, 1987, in press; Van Geel et al., 1994). Other spore types found are ubiquitous in a variety of Cenozoic sediments such as *Inapertisporites, Mono-*

Table 2

Palynological characteristics of badger coprolites from Cueva de los Torrejones: percentage of indeterminable pollen, pollen concentration, pollen sum (excluding indeterminable and non-pollen palynomorphs), and number of taxa

| Coprolite sample	% indet.	Pollen concentration (grains/gr)	Pollen sum	Taxa number (incl. extra-fossils)
TORbd-1	10.4	6825	320	27 (35)
TORbd-2	6.1	10 165	329	16 (26)
TORbd-3	5.6	13 579	343	17 (26)
TORbd-4	8.4	17 415	501	24 (37)
TORbd-5	5.8	13 114	314	21 (33)
TORbd-8	6.8	11 629	295	18 (28)
TORbd-9	4.2	5337	194	10 (19)
TORbd-10	0.6	9886	201	16 (36)
TORbd-11	4.1	14 428	309	19 (29)
TORbd-12	1.9	15 811	398	30 (42)
TORbd-14	5.8	14 362	284	24 (40)
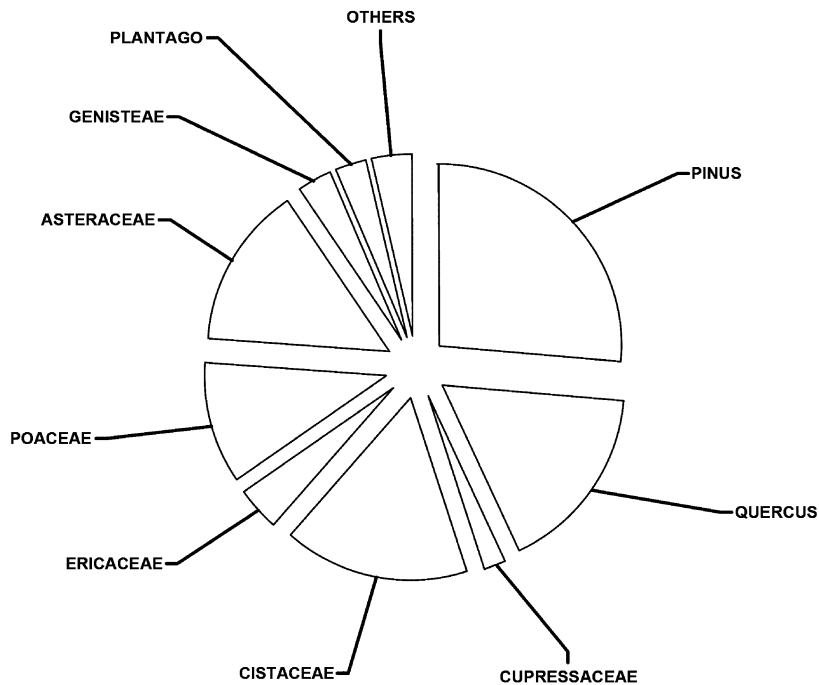
Fig. 8. Average percentages of the main types in the coprolite pollen spectra from Cueva de los Torrejones.

porisporites, *Hypoxylonites*, *Polyadosporites*, and to a lesser extent Glomaceae, *Pluricellaesporites*, *Dicellaesporites*, *Dyadosporites* and *Striadiporites* (Pirozynski et al., 1984, 1988; Jarzen and Elsik, 1986; Rull and Vegas-Villarrubia, 1999; Carrión and Van Geel, 1999; Carrión et al., 1999, 2001b; Kalgutkar and Jansonius, 2000). Other minor, but meaningful types are the fungi *Thecaphora* and *Tilletia*, and the eggs of the parasite *Trichuris*, all of which have been found assembled in fossil and fresh cow dung (Carrión et al., 2000a). The presence of Zygnemataceae spores, Type 179, Type 181, and *Pseudoschizaea* cysts (Scott, 1992) could indicate water ingestion by the badgers. Type 179 (Van Geel et al., 1983) is a vasiform microfossil, 24–60 × 13–38 μm, with a protruding wide opening in one end. It corresponds probably to the remains of some aquatic invertebrate, although a relation with euglenophytes cannot be categorically discounted. Type 181 is a spheric, finely echinate microfossil, often associated with eutrophic lakes and pools (Van Geel et al., 1983; López-Sáez et al., 1998). The sample TORbd-10 contains high concentrations of moss spores prominently perinated, similar to those of *Encalypta*.

5.3. From the pollen record to vegetation

Since only three of the fourteen coprolites have been dated, the differences in pollen spectra from the coprolites allow two alternative interpretations: they reflect the coexistence of different vegetation formations within a patchy landscape, or they provide a temporal record of different vegetation stages in an unknown sequence. Several of the coprolites may be in temporal sequence while others may be synchronous.

Pollen spectra in the dung of other species reflect the usual patchiness of vegetational landscapes (Davis and Anderson, 1987; Scott and Cooremans, 1992; Carrión, 2002; Carrión et al., 2004; Scott et al., 2004). For badgers, we still need to test this potential through the analysis of fresh dung, although our study could roughly serve as a preliminary test since there may have been little landscape change in three centuries. Thus, the comparison of coprolite pollen spectra and present-day vegetation, and, if available, pollen records for the last few centuries, and studies of modern pollen rain, could be of value. In fact, a good agreement would substantiate palaeoecological interpretation of the coprolite pollen spectra.

The composition of pollen spectra from badger coprolites analysed here fits well into modern vegetation in the vicinity of the Cueva de los Torrejones. The samples TORbd-9, TORbd-10, and TORbd-12, and to a lesser extent, TORbd-14 correspond with oak woodlands; the samples TORbd-8, and TORbd-11, with the nearby pinewoods, and the remaining samples reflect the prevalence of open spaces with pine, oak, and juniper stands, together with a variety of shrubs and herbs, among which Cistaceae, Ericaceae, grasses, composites, labiates, and perennial legumes (*Genista*, *Cytisus*, *Adenocarpus*) would be the principal components. The occurrences of *Plantago*, *Artemisia*, *Olea*, *Juglans*, Cerealia, and plausibly composite pollen, may well be indicative of ruderalization and agriculture.

Since badgers usually forage within a few kilometers of their setts, pollen assemblages from badger droppings could be biased in favour of plants growing in the vicinity, and perhaps towards those whose flowering times overlap peaks of stationary phases of badgers. Dietary biases cannot be discounted. However, in this case, the influence of vegetation is evident because the main vegetation types are represented in the pollen spectra (Table 3). This can be best appreciated if the relative pollen frequencies for each taxon are averaged for all the samples (Fig. 7).

Airborne pollen from similar areas of the Sistema Central Mountain region, dominated by *Pinus*, *Juniperus*, *Quercus*, and Poaceae, and characteristically including minor occurrences of Ericaceae, *Betula*, *Alnus*, *Salix*, *Fraxinus*, *Viburnum*, and *Olea* (Vázquez and Peinado, 1993; Andrade et al., 1994a,b), do not differ much from the coprolite pollen spectra described here. The main differences are better representation of *Juniperus* and entomophilous types in the coprolites (although they are still under-represented). Thus, while *Pinus*, Poaceae, *Plantago*, Ericaceae, and *Quercus* are well-represented in the pollen rain, other taxa like Asteraceae, Cistaceae, Lamiaceae, and Genisteae are clearly under-represented in the airborne content (Vázquez and Peinado, 1993). Thus, the coprolite pollen spectra could partly correct biases in wind-pollinated species that are customarily prominent in conventional pollen spectra from lacustrine and peaty basins. In addition, the relatively higher representation of juniper pollen in the coprolites

Table 3
Main similarities between present-day vegetation in the Torrejones Cave area, eastern Central System, and pollen assemblages of badger coprolites in this study

Modern vegetation	Coprolite pollen spectra
Arboreal cover: dominance of *Pinus halepensis*, *Quercus pyrenaica*, *Q. faginea*, *Q. ilex* subsp. *ballota*, and *Juniperus thurifera*. Extralocal abundance of *Pinus sylvestris* and *P. pinaster*	AP dominated by *Pinus* and *Quercus* (but low amounts of Cupressaceae)
Regional growing of *Acer monspessulanum*, *Alnus glutinosa*, *Betula pendula*, *Fraxinus angustifolia*, *Salix atrocinerea*, *Cedrus atlantica* (planted), *Juglans regia*, *Olea europaea*	Minor occurrences of *Alnus*, *Betula*, *Fraxinus*, *Salix*, *Cedrus*, and *Juglans* (but absence of *Acer* pollen)
Understorey: abundance of *Erica arborea*, *E. umbellata*, *Cistus ladanifer*, *C. laurifolius*, *Helichrysum stoechas*, *Santolina rosmarinifolia*, *Jasione montana*, *Carlina corymbosa*, *Genista cinerea*, *G. scorpius*, *Cytisus scoparius*, *Adenocarpus complicatus*, *Artemisia glutinosa*, *Lavandula stoechas*, *Thymus mastichina*, and *Phlomis lychnitis*	Relatively high values of Ericaceae, *Cistus*, Asteraceae, and Genisteae. Frequent *Artemisia*, and Lamiaceae
Other eventually abundant shrubs: *Prunus spinosa*, *Phyllirea angustigolia*, *Sambucus nigra*, *Rhamnus lycioides*, *Daphne gnidium*, *Pistacia terebinthus*	Presence of *Prunus*, *Sambucus*, *Phyllirea*, *Rhamnus*, Thymelaeaceae, *Pistacia*
Herbaceous stratum: dominance of grasses (largely *Stipa*, *Festuca*, *Arrhenatherum*, *Agrostis*, *Dactylis*, *Vulpia*, and *Bromus* species), *Carex hallerana*, presence of *Plantago radicans*, *P. sempervirens*, *P. lanceolata*, *Muscari neglectum*, *Rubia peregrina*	NAP diversity. Abundant Poaceae. Occurrences of *Plantago*, Cyperaceae, Liliaceae, Rubiaceae, etc

could be related to the abundance of *J. thurifera* in the surroundings of the cave.

The uppermost pollen spectra of Holocene records in the Ayllón Massif are also similar to those in the badger coprolites, notwithstanding they are all situated at higher altitudes. These spectra

include 20–40% of pine pollen, 5–30% of oak pollen, and 1–10% of juniper pollen, and include *Salix*, *Juglans*, *Fraxinus*, *Alnus*, *Olea*, *Tilia*, *Viburnum*, *Sambucus*, *Genista*, Ericaceae, *Ephedra*, *Cornus*, *Pistacia*, *Rhamnus*, and *Phillyrea*, among others. This is the case with Galve de Sorbe (Hernández Vera and Ruiz Zapata, 1984), Hayedo de Montejo (Gil García et al., 1993), Puerto de la Tejera (Gil García et al., 1995), Riaza (Ruiz del Castillo, 1993), and Pelagallinas (Franco et al., 2001). In comparison with the westernmost Sistema Central Guadarrama and Gredos mountains (Andrade, 1994; Andrade et al., 1992, 1994a,b; Vázquez and Ruiz-Zapata, 1992; Franco et al., 1997, 1998), these pollen diagrams show higher values of Ericaceae and lesser frequencies of *Pinus*, both features being shared by the badger coprolite pollen spectra studied here.

6. Final remarks

We have shown (i) that badger coprolites display good pollen preservation, acceptable pollen concentration, and a diversity of both arboreal and herbaceous types, together with a number of non-pollen palynomorph types, especially fungal spores, and (ii) that they can reflect local vegetation of the environments surrounding the cavities where badger colonies reside.

The coprolite pollen record presented here has been dated through the last three centuries, and depicts a mosaic, anthropogenic landscape very similar to the present-day, comprising pine forests, *Quercus*-dominated formations, woodland patches with *J. thurifera*, and a *Cistaceae*-dominated understorey with heliophytes and nitrophilous assemblages. The establishment of a palynological sequence was not possible since not all the coprolites studied for pollen were submitted for radiocarbon dating. Quantitative comparison with vegetation records of the last three centuries in the region is also not possible because available pollen records lack sufficient chronological control for this exercise.

In common with hyena coprolites (Carrión et al., 2001a), and bat guano (Carrión et al., in press) from similar regions, dietary input seems not to substantially bias the pollen records studied here. This does not exclude the influence of the behavior of badgers on coprolite pollen spectra. There are surely many uncertainties in our interpretation, because very little is known about how pollen is incorporated into and preserved within badger droppings and coprolites.

More research is necessary to understand how badger behaviour may affect badger dung pollen assemblages as proxies for past vegetation cover. For taphonomic research in particular, it is crucial to bear in mind that all badger species are very opportunistic, and will take whatever is available. This dietary range requires the development of experimental models that consider a broad range of habitats. It will also be informative to combine pollen with plant macrorremain analysis. Dietary biases may prove to be more important than vegetation contribution in some circumstances. In our case study, it is possible however that consumption of pollenivorous insects by badgers helped to provide a more representative assemblage from the surrounding vegetation than conventional pollen studies.

Hypothetically, like with other dung materials (Carrión, 2002), the pollen-analytical potential would be of particular value for regions where suitable basins for conventional pollen analysis are scarce, or where entomophilous species are important components of the total cover and play a crucial role in the characterization of vegetation types. However, we have no information on other sites where badger coprolites have been reported. This is in contrast with the numerous finds of hyena coprolites across Iberia (Arribas and Jordá, 1999). This can be due to problems with preservation or identification. Hyena coprolites are more solid than badger dung, which is relatively soft and breakable. However, badger remains do appear in fossil bone assemblages in a number of sites over the last two million years.

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