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Review of Palaeobotany and Palynology 140 (2006) 175–186

Review of Palaeobotany & Palynology

www.elsevier.com/locate/revpalbo

Environmental implications of pollen spectra in bat droppings from southeastern Spain and potential for palaeoenvironmental reconstructions

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Received 8 December 2005; received in revised form 23 March 2006; accepted 30 March 2006
Available online 23 May 2006

Abstract

Pollen was analysed from bat guano from nine caves in southeastern Spain and surface soils in their immediate surroundings. We compare the pollen spectra of 34 modern dung samples from the nine caves with one modern surface pollen sample from each cave. The contents suggest reasonable pollen diversity and richness, including anemophilous and zoophilous pollen types. Since the latter is usually under-represented in atmospheric pollen, the guano spectra therefore appear to reflect the vegetation more effectively than normal surface soil samples. Despite health hazards such as histoplasmosis, the difficulties of obtaining bat guano in deep caves and possible interpretational concerns relating to behaviour and feeding habits of different bat species, this material can be very useful in palaeoecological research provided that the dung was fossilized under favourable environmental conditions that allowed the preservation of pollen.

Keywords: pollen; bats; guano; fossil dung; cave sediments; climate reconstruction

1. Introduction

Bat dung may not be as easy to find as other faecal materials like rodent, hyrax and other tetrapod dung-middens and coprolites in arid areas (Davis and Anderson, 1987; Scott, 1987, 1996; Alcover et al., 1999; Carrión et al., 2000, 2001; Pearson and Betancourt, 2002) but it has recently attracted the attention of palynologists. Several recent papers have consequently suggested that pollen analysis of dung from insectivorous bats has potential in palaeoecology (Bui-Thi-Mai and Girard, 2000; Leroy and Simms, in press; Maher, 1992, in press).

Because of its high organic content, bat guano is a suitable material for radiocarbon dating, with deposits sometimes dating back several millennia (Carbonnel et al., 1996, 1999; Bui-Thi-Mai and Girard, 2000) or to the last interglacial (Jegla and Hall, 1962). Preliminary reports show that pollen concentration and preservation is reasonable (Navarro et al., 2000), probably because exines are generally resistant to degradation by digestive enzymes (Herrera and Martínez Del Río, 1998), and pH of the digestive system is relatively low (4–6) (Leroy

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doi:10.1016/j.revpalbo.2006.03.007

and Simms, in press). However, pollen may not always be preserved in bat dung under local environmental conditions in caves (Maher, in press; E. Marais & L. Scott, unpublished data).

Leroy and Simms (in press) have described the mechanisms for the incorporation of pollen into bat guano as:

(1) Direct ingestion of insects that are themselves covered by pollen, or whose digestive system contains pollen (Pendleton et al., 1996),
(2) Pollen in fragments of bat skin and hair lost during grooming (Darnton et al., 1999), and
(3) Dust brought onto guano by air currents (Coles and Gilbertson, 1994).

Although bats can migrate hundreds of kilometres, they rarely forage further than a few kilometres from shelter (Leroy and Simms, in press). We can therefore expect that pollen assemblages from bat guano are mainly representative of plants growing in the vicinity, especially those with flowering times that coincide with bat activity (Leroy and Simms, in press). The dung therefore promise to provide reasonable palynological representations of the vegetation but the behaviour of different bat species, especially their feeding strategies, influences pollen spectra that accumulate in their dung deposits (Maher, in press; E. Marais & L. Scott, unpublished data).

In view of these constrains, and the possible pollen destruction in some bat deposits, we present a palynological comparison of bat guano and surface samples from several localities in southeastern Spain with the aim of determining whether guano samples can provide a reliable picture of the vegetation surrounding the collection sites and we discuss the use of pollen from bat guano deposits as an environmental indicator.

2. Material and methods

Nine localities were selected that represent distinctive regional vegetation types in southeastern Spain (Fig. 1 and Table 1). The sampling localities, although associated with caves, mines and tunnels, appear not to be simply hibernacula, but also represent maternity colonies. According to local inhabitants and amateur speleologists, it seems they are mostly all-year sites. In each of the study site, we observed fresh droppings and active resident bats. Although there are twenty-five species of bats in the Iberian Peninsula, several species are the most likely producers of the studied guano. According to several unpublished reports and local and regional studies (Romero, 1990; Guardiola et al., 1991; Blanco and González, 1993; Franco and Rodríguez de los Santos, 2001; Monsalve et al., 2003), these would be *Miniopterus schreibersii*, *Pipistrellus pipistrellus*, *Myotis myotis*, *Myotis lythii*, *Rhinolophus ferrumequinum*, *Rhinolophus euryale*, *Rhinolophus mehelyi*, *Myotis capaccinii* and *Hypsugo savii*.

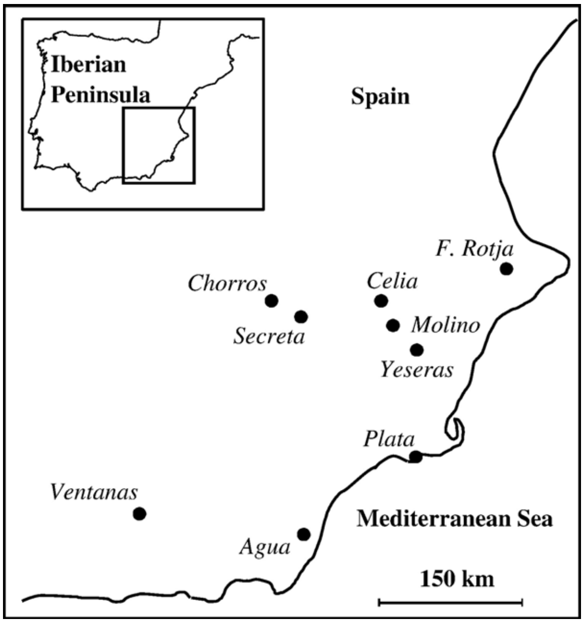

Fig. 1. Location of sampling sites in southeastern Spain.

Thirty-four bat guano samples were collected from the different caverns as well as one surface dust sample from outside each of the nine caverns ($N=34$). Two to five bat guano samples per site were collected, each comprising a mixture of several fresh and dry pellets, and therefore likely to represent more than a single season or year. Within the cavities, we avoided pellets from areas affected by dripping or superficial water flow. Surface control samples consisted of a collection of 5–10 sub-samples, which, as for dung samples, were placed in polythene bags and mixed to provide a homogenised sample. Sub-samples were located as far as possible from each other, and away from concentrations of plants within about 1000–1500 m^2. This surface sample type is minerogenic surface sediment that, supposedly, records airborne pollen. Sub-samples were mainly a loose, yellow-buff to brownish, fine-grained dust from a depth of about 0–1 cm. We discarded sands, coarser clasts, and cemented rocks, and did not sample spring deposits, evaporites, and areas with nearby signs of bioturbation (e.g., earthworm or rat mixing, burrowing, etc.) and/or wind deflation. We also avoided blackish sediments, because although they usually contain pollen grains, they may also contain considerable quantities of

Table 1
Characteristics of sampled sites in southeastern Spain

Site	Site type	Location	Sample no.	Collection date	Local vegetation (references for detailed description)
Cueva de la Plata	Karstic cave	Mazarrón, Murcia (37°35′N, 1°12′W)	1–6	25-07-1998	Ibero-Maghrebian *Mayteno-Periplocetum* scrub (Navarro et al., 2002)
Cueva del Agua	Gypsum karstic chasm	Sorbas, Almería (37°10′N, 2°05′W)	7–9	2-05-1999	Endemic communities dominated by legumes, grasses, chenopods, composites and labiates (Mota et al., 1997)
Cueva de las Ventanas	Karstic cave with archaeological remains	Píñar, Granada (37°24′N, 3°25′W)	10–14	13-04-2000	Cultivated (cereals, olive) landscape with sparse pine and oak stands (Carrión et al., 2001)
Minas de la Celia	Abandoned mine	Jumilla, Murcia (38°27′N, 1°28′W)	15–20	17-04-2000	Open pine forests patched with shrubby grasslands (*Stipa tenacissima*) on limestones
Mina del Agua del Molino	Abandoned mine	Ricote, Murcia (38°9′N, 1°26′W)	21–24	18-04-2000	Open pine (*Pinus halepensis*) forests with evergreen oaks (*Quercus rotundifolia* and *Quercus coccifera*) (Peinado et al., 1992)
Cueva de las Yeseras	Tunnel	Santomera, Murcia (38°4′N, 1°5′W)	25–28	23-04-2000	Ruderal formations with *Artemisia* and Chenopodiaceae-dominated communities. Planted exotic trees (Peinado et al., 1992)
Cueva Secreta	Chasm on limestones	El Sabinar, Murcia (38°13′N, 2°13′W)	29–31	12-05-1999	Open juniper (*Juniperus thurifera*, *Juniperus phoenicea*) woodlands with sparse pines (*Pinus nigra*, *Pinus pinaster*, *Pinus halepensis*) and oaks (mainly *Quercus rotundifolia*) (Sánchez-Gómez and Alcaraz, 1993)
Cueva de los Chorros	Cave with active karst	Riopar, Albacete (38°27′N, 2°25′W)	32–37	14-05-1999	Mixed pine–oak forest and riverine gallery forest (López Vélez, 1996)
Tunel Font Rotja	Tunnel	Alcoi, Alicante (38°44′N, 0°27′W)	38–43	19-07-2001	Oak forests (*Quercus rotundifolia* and *Quercus faginea*) with deciduous trees (Costa et al., 1982)

organic substances, which may be difficult to get rid of during the extraction processes.

The laboratory preparation techniques included HCl, HF, and KOH digestion followed by mineral separation with a heavy liquid ($ZnCl_2$). Two *Lycopodium clavatum* L. 1753 spore tablets (ca. 12,542 spores per tablet, Batch Number 938934) were added to each sample order to facilitate concentration calculations (grains/g dry weight) (Stockmarr, 1971). In the laboratory, we treated ten and two grams respectively, of dry surface material and guano samples. All slides mounts are in glycerine jelly and stained with safranine.

We used light microscopy for identification and counting. Non-vascular cryptogam spores (*Alternaria*, Sordariales and other fungal types, mosses, ferns) and other microremains (hairs, insect fragments, acari and other microarthropoda, eggs of intestinal nematodes, etc.) were not considered in this study. Reference pollen collections from the University of Murcia aided the pollen identifications. The original slides, residues and raw data are curated in the Laboratory of Palynology, University of Murcia.

Percentage pollen diagrams of selected taxa were produced using TILIA and TILIAGRAPH programs (Fig. 2). Pollen sums between 337 and 1135 pollen grains, excluding spores, are the basis for pollen percentages. *Quercus* pollen types were identified following the criteria in Planchais (1962). Detrended correspondence analyses (DCA) was performed using the PAST program written by Oyvind Hammer (http://folk.uio.no/ohammer/past/index.html) on pollen percentages of surface and guano samples of a selected taxa set, excluding rare pollen types unless they are of environmental indicator value. After performing DCA on the whole set of samples, we repeated it firstly using only bat guano samples and again using only surface control samples in order to see if patterns recurred.

3. Pollen assemblages in bat dung

When interpreting factors influencing pollen composition, we are restricted to the palynological comparison of two kinds of material, bat guano and surface dust. We have no models of regional pollen rain-vegetation relationships for southeastern Spain to help us refine these interpretations. Specific information about which bat species produced the droppings we analyzed and their diets is also not available. The typical diet of southern Spanish insectivorous bats comprises Diptera (mainly midges), Trichoptera, Lepidoptera, Coleoptera, Orthoptera, and Arachnida (Romero, 1990; Benzal and Paz, 1991). It is likely that several

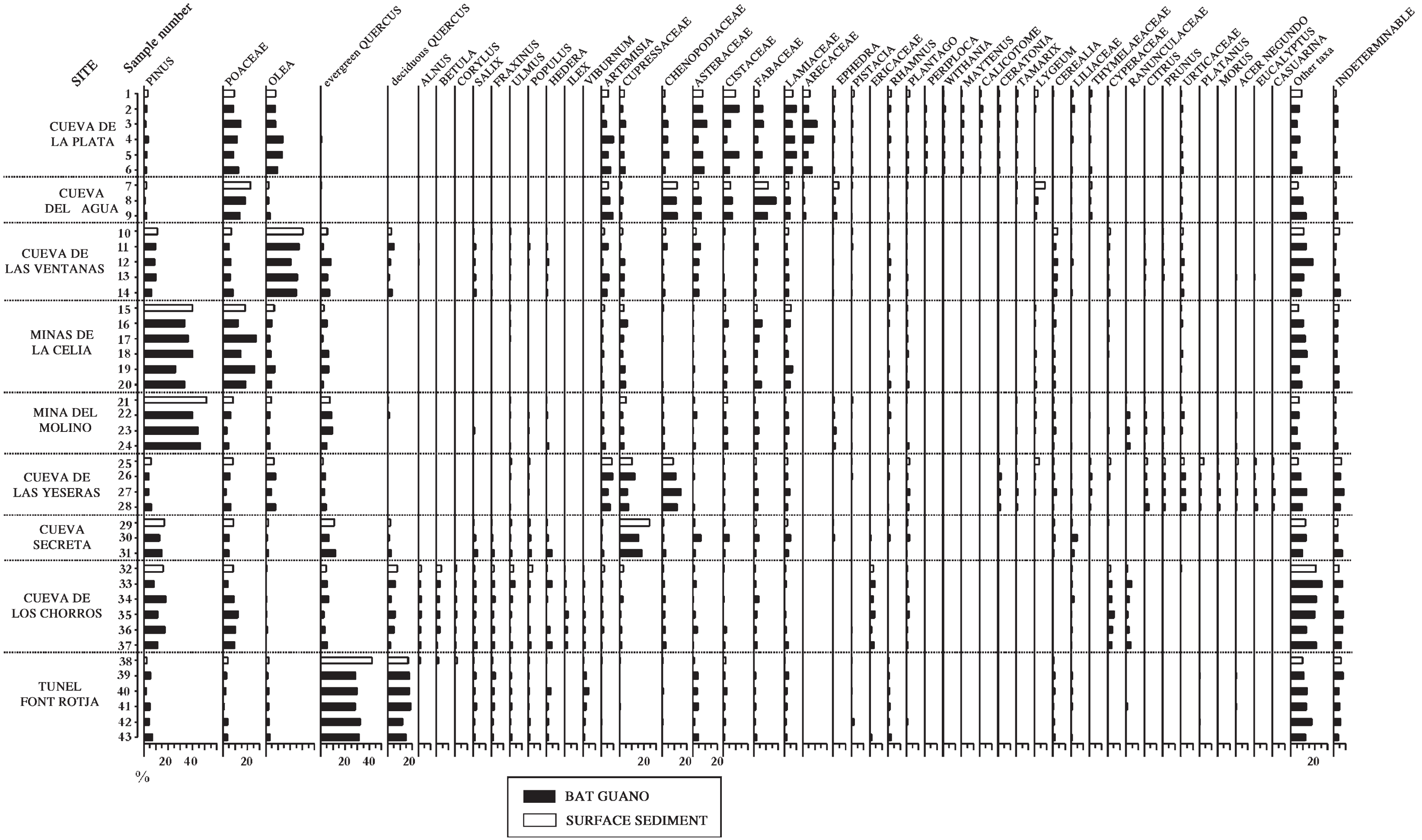

Fig. 2. Pollen percentage diagram of surface and bat guano samples from southeastern Spain.

bat species are occupying the same cavities in southern Spain, especially in the big caverns of Cueva de las Ventanas and Cueva de los Chorros. Up to five different species may share a cave site and in the case of high bat numbers they may share the habitat throughout the year (Schober and Grimmberger, 1996). Discussions on the pollen assemblages in bat guano, relevant to the data presented here, are also presented in Maher (1992, in press), Bui-Thi-Mai and Girard (2000), and Leroy and Simms (in press).

Some observations in connection with the feeding habits of bats may be of relevance for the interpretation of pollen spectra in their guano. Insectivorous bats, Microchiroptera, dominate the bat faunas of southeastern Spain (Schober and Grimmberger, 1996). All the cavernicolous bat species in Spain are insectivorous. The microchiropteran bat populations in caves of tropical and warm temperate regions are generally resident and active throughout the year (Findley, 1993), although short and medium-distance migrations may take place between suitable roosting sites because reproduction, occurrence and abundance of bats at particular sites are related to prey abundance and thus subject to seasonal fluctuations. Moreover, prey preferences of bats, and therefore the pollen incorporated in bat droppings below roosting sites, are related to the foraging strategy (Korine and Pinshow, 2004) and diet of permanent or seasonal resident bat populations. Most insectivorous bats will only feed on between one and four prey species during any given night, usually within a range of around 5 km of the roosting site (Whitaker, 1988). This does not imply year-round specialization on a limited number of prey species because seasonal changes in prey selection and foraging range (Fenton et al., 1993) occur concurrently with changes in environmental conditions, the abundance of particular flying insects, the suitability of habitats for foraging, and the foraging preferences and requirements of bats (Fenton, 1985). For example, lactating females forage more often because they require larger amounts of food while low prey densities may result in longer and more wide-ranging hunting sorties in winter. Because the size and morphology of bats determine their trophic preferences (Aldridge and Rautenbach, 1987), the composition and diversity of cavern-inhabiting bat populations will also influence pollen present in bat guano.

Most cave-inhabiting species in Spain consists of broad-winged, long-eared gleaners, which capture prey through sallying and aerial hawking, and slow-flying hawkers, which typically forage in a variety of cluttered and open habitats. Both bat types typically have low wing-loadings, low aspect ratios, relatively low flight speeds, significant manoeuvrability, and clutter-resistant echolocation calls (Aldridge and Rautenbach, 1987). Such morphological characteristics allow bats to roost in caves and to detect and capture prey among vegetation. Gleaner diets include a wide range of volant and non-volant prey, particularly Lepidoptera and Coleoptera, but also Orthoptera, Arachnida, and small vertebrates, while typical hawking diets include Lepidoptera, Diptera, Trichoptera, Ephemeroptera and some Coleoptera. The implication is that the composition of pollen assemblages of bat guano in caves is a function of the trophic preferences and composition of the resident bat fauna, with specific reference to foraging ranges (Korine and Pinshow, 2004). Droppings below roosts of insectivorous bats are likely to reflect ingested pollen derived from the annual availability, composition and activity of prey insects, particularly seasonal mass emergences and concentrations of preferred prey species. In addition, pollen accumulated on the bats themselves during foraging sorties within vegetation, and clutter and aerial pollen ingested or accumulated during their nightly flights to and from preferred hunting habitats, build up below roosts because of grooming (Maher, in press) and natural mortalities. The diversity of bats, in particular their size and ecomorphology, determines if the pollen spectra are likely to be weighed in favour of particular plant species. We suggest that the cavernicolous bat species in southern Spain are sufficiently diverse to allow deposition of a pollen assemblage broadly representative of the vegetation in the surrounding area.

4. Results and discussion

4.1. Description of pollen assemblages in fresh bat guano from Spain

We consider that both sediment and guano samples from each site (Fig. 2) give a reasonable reflection of local vegetation. The Cueva de la Plata pollen assemblages are dominated by Poaceae, *Olea*, Asteraceae, Cistaceae, Lamiaceae, Fabaceae, Arecaceae (cf. *Chamaerops* and *Phoenix*), and *Artemisia*, and to a lesser extent by Cupressaceae and Chenopodiaceae. Several taxa, including *Pistacia* and *Ephedra fragilis*, and most significantly, *Periploca*, *Withania*, *Maytenus*, and *Calicotome*, occur in most samples. These taxa are characteristic of the Ibero-Maghrebian xerothermic scrub communities of coastal southeastern Spain (Sánchez-Gómez et al., 2003). *Ceratonia siliqua* cultivars and stands of several species of *Tamarix* along watercourses are also very typical components of this predominantly treeless landscape. Pine pollen is mostly a long-distance contribution (Carrión, 2002). Other taxa not included in the pollen diagram (Fig. 2) are recorded sporadically such as *Asphodelus*, *Ziziphus*, *Bupleurum*, *Lycium*, *Osyris*, *Dorycnium*, *Myrtus*, *Oxalis*, *Ruta*, *Smilax*, *Zygophyllum*, *Mercurialis*, and *Cedrus*, among others. These results are consistent with previous studies of pollen rain in surface sediments of the cave and cave exterior (Prieto and Carrión, 1999; Navarro et al., 2001, 2002; Carrión, 2002).

Pollen spectra at Cueva del Agua are also dominated by non-arboreal taxa such as Poaceae, Fabaceae (mainly *Genista*, *Ononis*, and *Retama*), Chenopodiaceae, Asteraceae, *Artemisia*, and Cistaceae. Marked maxima for *Ephedra* (*Ephedra fragilis*) and *Lygeum* (*Lygeum spartum*), two common species of the "Sorbas" gypsophilous scrub (Mota et al., 1997), occur. Among the minor types not included in the pollen diagram are *Agave*, *Capparis*, *Coris*, and *Verbascum*.

Samples collected in Cueva de las Ventanas show more arboreal pollen, principally *Olea* (cultivars), but also *Pinus* and *Quercus*, with smaller numbers of pollen grains from *Salix*, *Populus*, *Ulmus*, and *Alnus*. This probably reflects the proximity of riparian vegetation along the adjacent Píñar River (Carrión, 1992). Because of widespread regional cereal production, Cerealia pollen in these samples reaches the highest values among the studied sites. *Pinus* and Poaceae are the prevailing pollen taxa in the Minas de la Celia surface and guano samples, reflecting relatively lower phytodiversity in this area (Sánchez-Gómez et al., 2003) in comparison with Cueva de las Ventanas. *Pinus* also dominates the pollen spectra at Mina del Molino (Fig. 2). Deciduous trees are scarce at both sites as is indicated in the pollen assemblages (Fig. 2).

Pollen assemblages in Cueva de las Yeseras, near the town of Santomera, are characterized by taxa that indicate ruderal landscapes, including Chenopodiaceae, *Artemisia* and Cupressaceae, but also Urticaceae, *Citrus*, *Prunus*, and *Plantago*. Pollen grains of planted exotic trees, which are often associated with urban areas (*Casuarina*, *Eucalyptus*, *Acer negundo*, *Platanus hispanica* Tenore 1845, *Morus*, *Cupressus*, *Chamaecyparis*, etc.), are also present (Munuera et al., 2001). In contrast to Cueva de las Yeseras, dominant Cupressaceae pollen in Cueva Secreta must correspond to local juniper species (*Juniperus phoenicea* L., *Juniperus thurifera*) as no other Cupressaceae occur in the area (Sánchez-Gómez and Alcaraz, 1993). Other important pollen contributors at this site are *Pinus*, Poaceae, and evergreen *Quercus*, with minor values for deciduous *Quercus*.

Although dominated by *Pinus* (including abundant *Pinus pinaster*) and Poaceae, the pollen spectra from Cueva de los Chorros are quite distinctive in showing higher diversity of woody taxa, including evergreen (*Quercus rotundifolia*) and deciduous *Quercus* (*Quercus faginea* and *Quercus pyrenaica*), *Alnus*, *Betula*, *Corylus*, *Salix*, *Fraxinus*, *Ulmus*, *Populus*, *Ilex*, and *Viburnum*. Several herbaceous and shrubby indicators of humid biotopes, such as Ranunculaceae, Cyperaceae and Ericaceae, occur, probably derived from vegetation along the nearby Mundo River margins (López Vélez, 1996). "Other taxa" for this site consist of *Taxus*, *Paeonia*, *Scrophularia*, *Berberis*, and *Crataegus* (Fig. 2). Corresponding with the existence of local dense oak forests (Costa et al., 1982), *Quercus* pollen dominates the spectra from Font Rotja. Pollen from other trees, such as *Salix*, *Fraxinus*, *Ulmus*, and *Populus*, occurs in lower frequencies. The diversity of non-arboreal pollen types is low.

4.2. Pollen-analytic potential of fresh bat guano inferred from the Spanish samples

Bat guano samples display good pollen-analytic potential in terms of relatively low frequencies of indeterminable palynomorphs, high total pollen concentrations (Fig. 4) and high pollen diversity (Fig. 3) that includes rare types, which may be important environmental indicators. Indeterminable palynomorphs in all samples do not exceed 10% of the total pollen sum (Fig. 2), which is reasonable even in pollen analysis of modern materials. We can assume that degradation of pollen in dung, in the short term at least, is not a primary factor in shaping pollen assemblages because highly degradable pollen types, such as *Populus*, Arecaceae, and Fabaceae, are present.

In the nine study cases, guano samples exhibit higher pollen diversity (41–91 taxa, mean of 62.9) than their surface counterparts (39–66 taxa, mean of 48.7), with the only exception being samples 35 and 41 (Fig. 3). In agreement with local specific phytodiversity (Sánchez-Gómez et al., 2003), the sites of La Plata, Secreta, Los Chorros and Font Rotja show the highest values.

Total pollen concentration (number of pollen grains per gram of dry sediment) is consistently higher in bat guano (29 351–427 933, mean of 138 450) than in the surface sediment (5910–33 893, mean of 15 840), irrespective of the study sites (Fig. 4). Pollen concentration varies greatly between sites, with the highest values reached in bat guano recovered from La

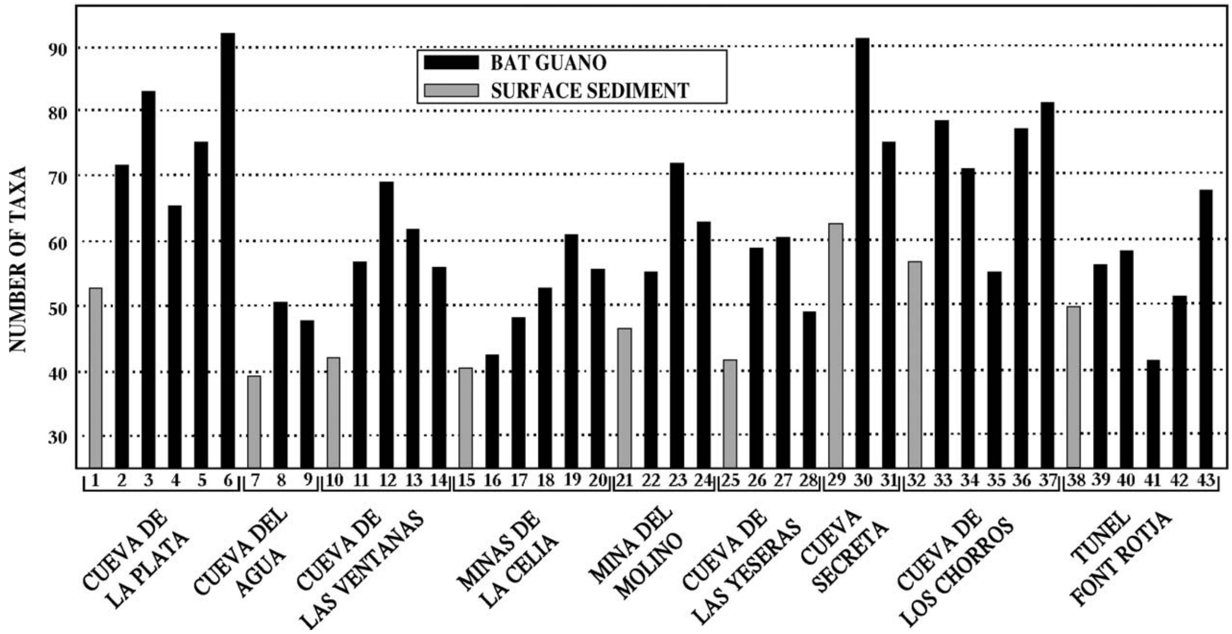

Fig. 3. Number of pollen taxa identified in surface and bat guano samples from southeastern Spain. Except for samples 35 and 41, bat guano samples show higher values of pollen diversity with respect to their surface reference samples.

Plata and Agua caves, and the lowest in guano from Font Rotja (Fig. 4). Assuming that selective post-depositional pollen decay is unimportant, this between-site variation might be the result of factors like differences in the bat species' feeding habits, bat occupation periods, and local conditions, all of which

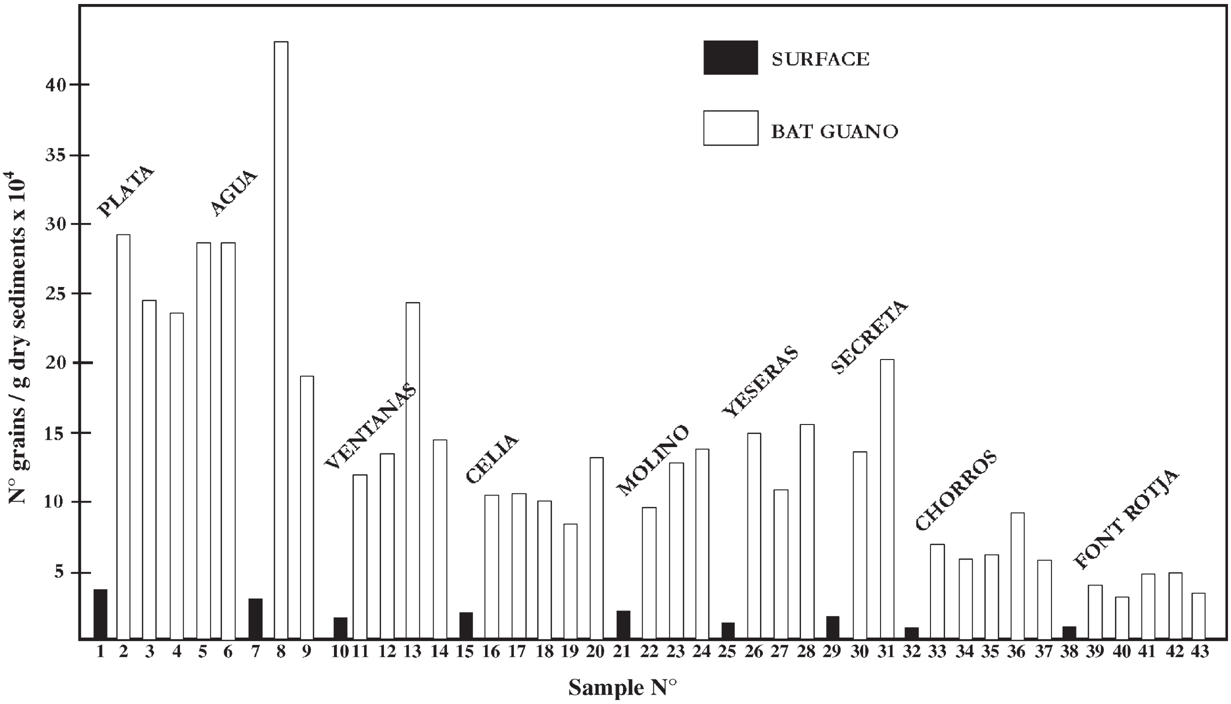

Fig. 4. Total pollen concentration of surface and bat guano samples from southeastern Spain. The latter type of sample shows considerably higher values in the nine sites studied.

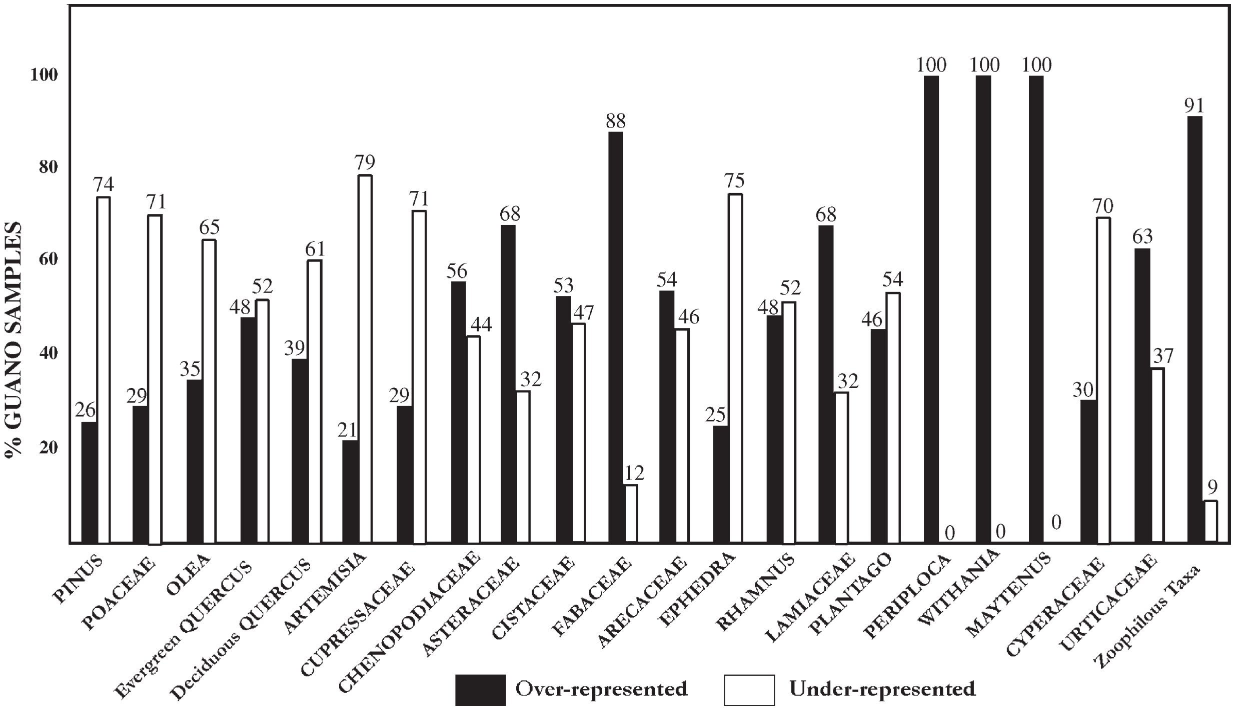

Fig. 5. Percentage over- and under-representation of selected pollen taxa in Spanish bat guano samples.

can be tested at this stage. La Plata and Agua are from areas with the fewest trees and correspond to the hottest climate (Mota et al., 1997), whereas Los Chorros and Font Rotja although not occurring in extremely cold parts, correspond with the densest tree cover (Costa et al., 1982; López Vélez, 1996).

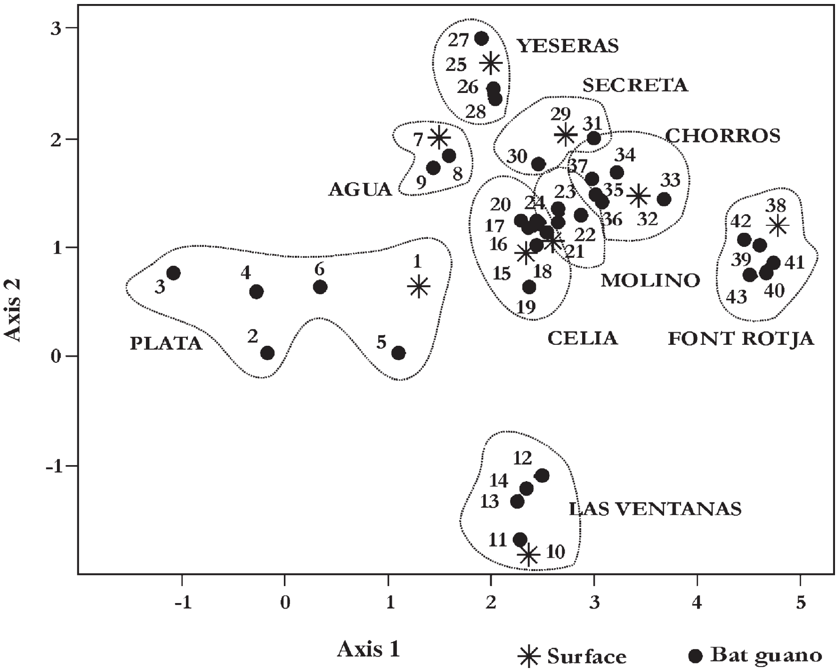

Fig. 6. DCA plot for Spanish localities. Clustering suggests that bat guano samples are representative of local vegetation.

A possible factor in determining pollen composition is the relative abundance of pollenivorous insects and coleopterophilous angiosperms. The vegetation of the first two localities includes the highest abundance of entomophilous plant species (Sánchez-Gómez et al., 2003), but there are no entomological records available to shed light on this issue. On the other hand, insects in bat diets are often not strict pollinators, although they may trap pollen for other reasons (Maher, in press).

Bat guano provides a record of zoophilous plant taxa (Navarro et al., 2000, 2001; Carrión, 2002) which are under-represented in surface pollen spectra. This is shown by the occurrence of pollen from Ericaceae in Cueva Secreta and Font Rotja; Liliaceae in Las Ventanas, Mina del Molino, Las Yeseras and Font Rotja; Ranunculaceae in Mina del Molino and Font Rotja; *Morus* in La Plata and Las Ventanas, and *Eucalyptus* in Las Ventanas.

In considering the palynological possibilities of bat guano in both types of samples, we note that minerogenic surface sediments may be biased to an unknown degree by wind-pollinated taxa due to transport distance and under-representation of local zoophilous taxa. Samples collected from depressions and conventional sources for fossil pollen studies may be particularly susceptible. This is pertinent to the La Plata and Agua sites, where, given the predominance of entomophilous species, Carrión (2002) showed that dung samples from grazing animals, such as goat, sheep, rabbit, hare, and wild boar, are often more suitable for depicting local vegetation.

In the present study, bat guano apparently partially corrects several of these biases. The prominence of several zoophilous taxa allows a more balanced interpretation of pollen spectra in terms of vegetation. The average percentage ratio of anemophilous to zoophilous taxa is 63.3/16 in guano samples and 73.2/14.3 in surface samples. Pollen from most anemophilous plant taxa is probably under-represented in guano

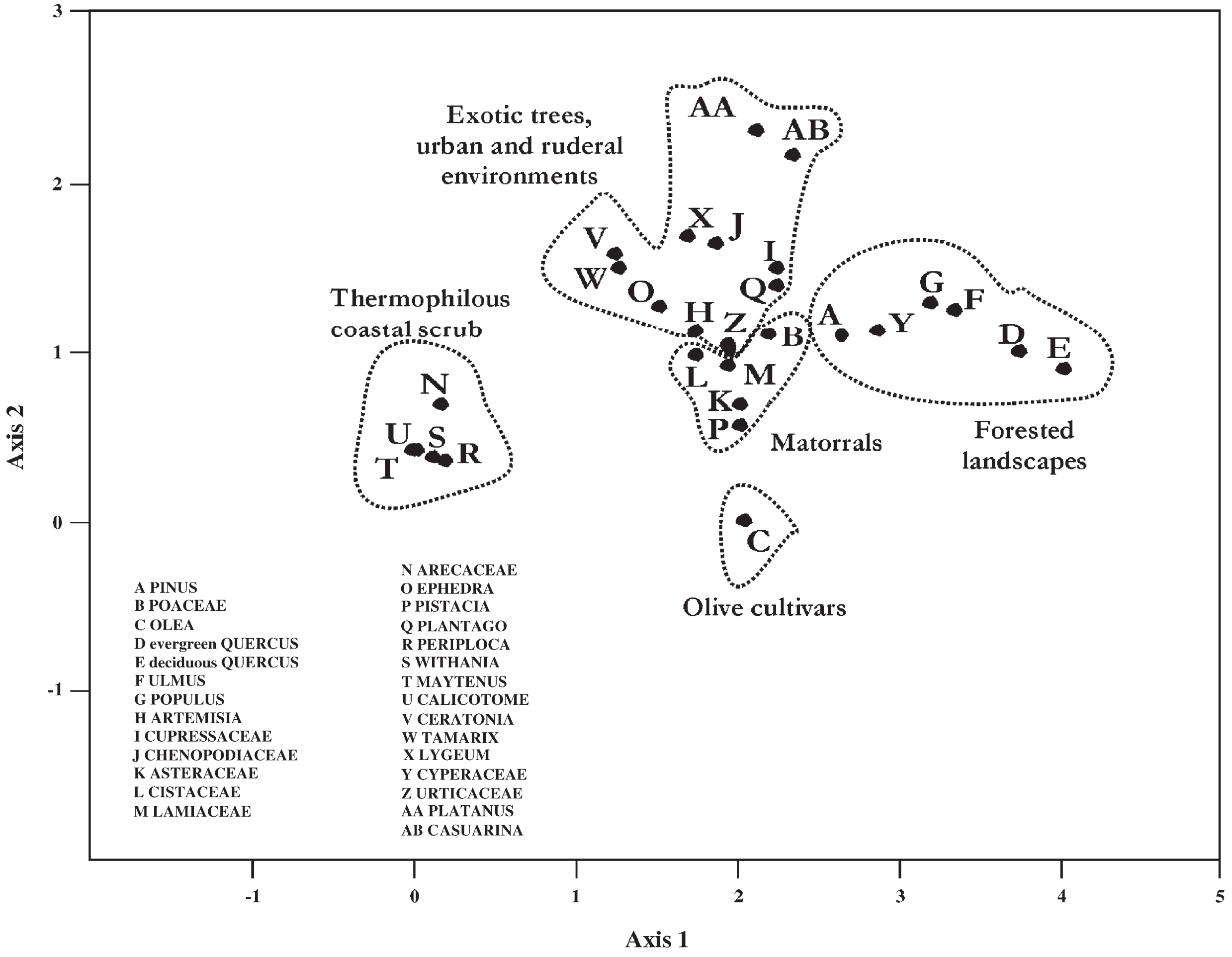

Fig. 7. DCA plots for Spanish pollen taxa of surface sediment and bat guano data combined.

samples when compared to associated surface samples, while most zoophilous taxa are most likely over-represented (Fig. 5). For instance, *Pinus*, Poaceae, Cupressaceae, *Artemisia*, *Ephedra* and Cyperaceae are thought to be under-represented in the majority of guano samples. Fabaceae and Lamiaceae dominate in 88% and 68% of guano samples, respectively, *Periploca*, *Withania*, and *Maytenus* in all samples, and zoophilous taxa combined in 91% of the samples (Fig. 5). Pollen of several taxa (Cistaceae, Arecaceae, *Rhamnus*, *Plantago* and wind-pollinated Chenopodiaceae and Urticaceae) shows low variation between guano and surface samples. Accounting for these latter two exceptions is not easy, although Urticaceae pollen is buoyant (Munuera et al., 2001). This may favour ingestion by bats. Post-depositional input through dust within the cave (Leroy and Simms, in press) may further have influenced our results, though cavern geography and the distance from the entrance will influence the contribution of dust-borne pollen.

DCA plots were generated through the PAST program to look for ecological trends in the data distribution as reflected by clustering patterns of indicator taxa. The DCA plots may also reflect ecological differences between the different sites. The results of clustering of samples show the distribution along two axes (Axes 1 and 2), which have eigenvalues of 0.4083 and 0.1213, respectively (Fig. 6). We interpret the clusters as a reflection of locality in the pollen assemblages rather than sample type because bat guano samples groups formed for each different cave are closely associated with its local surface sediment sample (Fig. 6). Even in La Plata, where the vegetation is very patchy (Carrión, 2002), the cluster is formed although not as tightly. However, even here, locality grouping is clear-cut. This seems to show that the bat guano samples give accurate reflections of the local vegetation at each site rather being excessively biased by bat activity.

DCA grouping according to selected taxa in Fig. 7 gives clusters of ecological indicators and may illustrate a potential use for bat guano in palaeoecological reconstruction. Axis 1 seems to reflect humidity change between forest taxa (*Quercus*, *Populus*, *Ulmus*, and *Pinus*) and Cyperaceae on the right and xeric *Maytenus*, *Withania*, *Calicotome*, *Periploca*, Arecaceae, *Lygeum*, *Ceratonia*, *Ephedra*, and *Tamarix* on the left. Axis 2 may be somewhat influenced by temperatures because extreme positions are occupied by thermophytes *Maytenus*, *Periploca*, *Withania*, *Calicotome*, *Olea*, *Pistacia*, Cistaceae, Lamiaceae (lower values) and *Platanus* (higher values). However, the clustering of *Platanus*, *Casuarina*, Chenopodiaceae, and Urticaceae (cf. *Parietaria*) may reflect anthropogenic influences and association of ruderal plants (Fig. 7) because these plants are all associated with disturbed habitats, and urban or agricultural areas.

5. Conclusion

In the analyses of bat dung from Spain, pollen spectra in modern surface samples are compared with those in bat guano. The results confirm that guano accumulations in caves have great potential as source for palaeoenvironmental reconstruction (Leroy and Simms, in press; Maher, 1992, in press; Bui-Thi-Mai and Girard, 2000). To test this assumption it is necessary to investigate fossil guano accumulations from appropriate caves to evaluate pollen preservation and to compare with regional palynological results. Fossil bat guano accumulations from Spain are currently unavailable, but an example from Namibia confirm that entire sequences do not always preserve pollen (E. Marais & L. Scott, unpublished data), but when available the pollen in the dung appears to give a reasonable reflection of environmental changes.

Palynologists have insufficiently exploited bat guano as source material for palaeo-landscape reconstruction. This is partly due to poor background knowledge and experimental information on bat guano and pollen–rain relationships. Fossil bat dung deposits are rare and difficult to locate without the help of chiropterologists and speleologists, due to inaccessible cavern localities. Besides the problems of access to many caves, researchers may be hesitant to undertake research in bat-inhabited caves because of concerns about the serious health problems associated with these localities, especially the potential for histoplasmosis. Bat guano deposits in more accessible places in Spain and elsewhere, e.g. southern Africa (E. Marais & L. Scott, unpublished data), have in many cases disappeared through mining for fertilizer. Although pollen in fossil guano may not always be preserved, where available it promises relatively reliable environmental reconstructions. This paper has addressed one of the primary interpretational issues, i.e., how does pollen in bat guano relate to vegetation. We have shown that pollen analysis of fresh bat guano can reflect local vegetation of the environments surrounding the cavities where bat colonies reside. These results are consistent with the palaeoecological interpretations by Bui-Thi-Mai and Girard (2000), Maher (in press), and especially Leroy and Simms (in press). Moreover, as was stressed by Leroy and Simms (in press), bat guano may be a good tool for obtaining information on entomophilous plants otherwise under-represented in more traditional pollen sampling sites such as peat bogs and lake sediments. However, more research is necessary to understand how bat behaviour and habitat interactions may affect bat dung pollen assemblages as proxies for past vegetation cover. It is possible that preservation depends on local post-depositional events in cave sites (Scott, 2003), but these taphonomic processes, including ignition of the organic material, should be examined to obtain optimal information from bat-derived pollen assemblages.

Acknowledgements

Funding for the investigation in Spain came from projects PI-17/00739/FS/01 and REN2003-02499-GLO. In South Africa, the National Research Foundation (GUN 2053236) funded research. Oyvind Hammer of the University of Oslo and co-workers are thanked for the statistical program PAST. We thank critical reviewers Suzanne Leroy and Alwynne B. Beaudoin for many meaningful suggestions to improve the manuscript.

References

Alcover, J.A., Pérez-Obiol, R., Yll, E.I., Bover, P., 1999. The diet of *Myotragus balearicus* Bate 1909 (Artiodactyla: Caprinae), an extinct bovid from the Balearic Islands: evidence from coprolites. Biol. J. Linn. Soc. 66, 57–74.

Aldridge, H.D.J.N, Rautenbach, I.L., 1987. Morphology, echolocation and resource partitioning in insectivorous bats. J. Anim. Ecol. 56, 763–778.

Benzal, J., Paz, O., 1991. Los Murciélagos de España y Portugal. Icona. Colección Técnica, Madrid.

Blanco, J.C., González, J.L., 1993. Libro Rojo de los Vertebrados de España. Icona, Madrid.

Bui-Thi-Mai, Girard, M., 2000. Les guanos de chauve-souris d'âge médiéval de la Grande Grotte d'Arcy-sur-Cure (Yonne). Analyse pollinique et implications paléobotaniques. Géol. Alp., Mém 31, 83–95.

Carbonnel, J.-P., Decu, V., Olive, P., Povara, I., Gheorghiu, V., 1996. Première datation par ^{14}C du remplissage de guano d'une grotte des Carpates méridionales: Pestera lui Adam (Roumanie). Trav. Inst. Spéol. "Emile Racovitza" 35, 143–152.

Carbonnel, J.-P., Olive, P., Decu, V., Klein, D., 1999. Datations d'un dépôt de guano Holocène dans les Carpates méridionales (Roumanie). Implications tectoniques. C. R. Acad. Sci. Paris 328, 367–370.

Carrión, J.S., 1992. Late Quaternary pollen sequence from Carihuela Cave, southeastern Spain. Rev. Palaeobot. Palynol. 71, 37–77.

Carrión, J.S., 2002. A taphonomic study of modern pollen assemblages from dung and surface sediments in arid environments of Spain. Rev. Palaeobot. Palynol. 120, 217–232.

Carrión, J.S., Brink, J., Scott, L., Binneman, J., 2000. Palynology of hyena coprolites from Oyster Bay, southeastern Cape coast, South Africa: the palaeo-environment of an open-air Howieson's Poort occurrence. S. Afr. J. Sci. 96, 449–453.

Carrión, J.S., Riquelme, J.A, Navarro, C., Munuera, M., 2001. Pollen in hyaena coprolites reflects late glacial landscape in southern Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 176, 193–205.

Coles, G.M., Gilbertson, D.D., 1994. The airfall–pollen budget of archaeologically important caves: Creswell Crags, England. J. Archaeol. sci. 21, 735–755.

Costa, M., Peris, J.B., Figuerola, R., 1982. Sobre los carrascales termomediterráneos valencianos. Lazaroa 4, 37–52.

Darnton, B., Parmentier, J., Van Egmond, W. 1999. Making a study of bat droppings. http:www.microscopy-uk.org.uk/mag/artapr99/bdbat.html.

Davis, O.K., Anderson, R.S., 1987. Pollen in packrat (*Neotoma*) middens: pollen transport and the relationship of pollen to vegetation. Palynology 11, 185–198.

Fenton, M.B., 1985. The feeding behaviour of insectivorous bats: echolocation, foraging strategies, and resource partitioning. Transvaal Mus. Bull. 21, 5–16.

Fenton, M.B., Rautenbach, I.L., Chipese, D., Cumming, M.B., Musgrave, M.K., Taylor, J.S., Volpers, T., 1993. Variation in foraging behaviour, habitat use, and diet of large slit-faced bats (*Nycteris grandis*). Z. Säugetierkd. 58, 65–74.

Findley, J.S., 1993. Bats: A Community Perspective. Cambridge University Press, Cambridge.

Franco, A., Rodríguez de los Santos, M., 2001. Libro Rojo de los Vertebrados Amenazados de Andalucía. Consejería de Medio Ambiente, Junta de Andalucía.

Guardiola, A., Fernández, M.P., González, G. 1991 (unpublished report). Los quirópteros de la Región de Murcia. Estatus, distribución y conservación. Agencia Regional para el Medio Ambiente y la Naturaleza. Comunidad Autónoma de Murcia.

Herrera, L.G., Martínez Del Río, C., 1998. Pollen digestion by New World bats: effects of processing time and feeding habits. Ecology 79, 2828–2838.

Jegla, T.C., Hall, J.S., 1962. A Pleistocene deposit of the free-tailed bat in Mammoth Cave, Kentucky. J. Mammology 43, 477–481.

Korine, C., Pinshow, B., 2004. Guild structure, foraging space use, and distribution in a community of insectivorous bats in the Negev Desert. J. Zool. 262, 187–196.

Leroy, S.A.G., Simms, M.J., in press. Iron Age to Medieval entomogamous vegetation and Rhinolophus hipposideros roost in south-eastern Wales (UK). Palaeogeogr. Palaeoclimatol. Palaeoecol.

López Vélez, G., 1996. Flora y Vegetación del Macizo del Calar del Mundo y Sierras Adyacentes del sur de Albacete. Instituto de Estudios Albacetenses, Albacete.

Maher, L.J., 1992. Palynology of bat guano may provide a useful climate record. 8th International Palynological Congress, Aix-en-Provence, France, Programs and Abstracts, p. 96.

Maher, L.J., in press. Environmental information from guano palynology of insectivorous bats of the central part of the United States of America. Palaeogeogr. Palaeoclimatol. Palaeoecol.

Monsalve, M.A., Almendar, D., Alcover, A., Monsoriu, A., 2003. Los murciélagos de la Comunidad Valenciana. Bol. Soc. Esp. Espeleol. Cienc. Karst 4, 22–33.

Mota, J., Cabello, J., Cueto, M., Gómez, F., Giménez, E., Peñas, J., 1997. Datos sobre la vegetación del sureste de Almería (Desiertos de Tabernas, Karst en Yesos de Sorbas y Cabo de Gata). Servicio de Publicaciones, Universidad de Almería, Almería.

Munuera, M., Carrión, J.S., Navarro, C., Orts, L., Espín, A., Sáez, F., García Sellés, J., 2001. Polen y alergias. Guía de las plantas de polen alergógeno de la Región de Murcia y España. Diego Marín Eds, Murcia.

Navarro, C., Carrión, J.S., Navarro, J., Munuera, M., Prieto, A.R., 2000. An experimental approach to the palynology of cave deposits. J. Quat. Sci. 15, 603–619.

Navarro, C., Carrión, J.S., Munuera, M., Prieto, A.R., 2001. Cave surface pollen and the palynological potential of karstic cave sediments in palaeoecology. Rev. Palaeobot. Palynol. 117, 245–265.

Navarro, C., Carrión, J.S., Prieto, A.R., Munuera, M., 2002. Modern cave pollen in an arid environment and its application to describe paleorecords. Complutum 13, 7–18.

Pearson, S., Betancourt, J.L., 2002. Understanding arid environments using fossil rodent middens. Journal of Arid Environments 50, 499–511.

Peinado, M., Alcaraz, F., Martínez-Parras, J.M., 1992. Vegetation of southeastern Spain. J. Cramer, Berlin.

Pendleton, M.W., Bryant, V.M., Pendleton, B.B., 1996. Entomopalynology. In: Jansonius, J., McGregor, D.C. (Eds.), Palynology: Principles and Applications. American Association of Stratigraphic Palynologists Series, vol. 3. Foundation, Dallas, pp. 939–943.

Planchais, N., 1962. Le pollen de quelques chênes de domaine méditerranéen occidental. Pollen Spores 4, 87–93.

Prieto, A.R., Carrión, J.S., 1999. Tafonomía polínica: sesgos abióticos y bióticos del registro polínico en cuevas. Publ. Espec.-Asoc. Paleontol. Argent. 6, 59–64.

Romero, P. 1990. Quirópteros de Andalucía y Marruecos. Ph.D. dissertation, University of Sevilla, Spain (unpublished).

Sánchez-Gómez, P., Alcaraz, F., 1993. Flora, Vegetación y Paisaje Vegetal de las Sierras de Segura Orientales. Instituto de Estudios Albacetenses, Albacete.

Sánchez-Gómez, P., Carrión, M.A., Hernández, A., Guerra, J., 2003. Libro Rojo de la flora silvestre protegida de la Región de Murcia. Consejería de Agricultura, Agua y Medio Ambiente, Murcia.

Schober, W., Grimmberger, E., 1996. Los Murciélagos de España y Europa. Omega, Barcelona.

Scott, L., 1987. Pollen analysis of hyena coprolites and sediments from Equus Cave, Taung, Southern Kalahari (South Africa). Quat. Res. 28, 144–156.

Scott, L., 1996. Palynology of hyrax middens: 2000 years of palaeoenvironmental history in Namibia. Quat. Int. 33, 73–79.

Scott, L., 2003. The Holocene of middle latitude arid areas. In: Mackay, A., Battarbee, R., Birks, J., Oldfield, F. (Eds.), Global Change in the Holocene. Edward Arnold, London, pp. 396–405.

Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. Pollen Spores 13, 615–621.

Whitaker, J.O., 1988. Food habits analysis of insectivorous bats. In: Kunz, T.H. (Ed.), Ecological and Behavioral Methods for the Study of Bats. Smithsonian Institution Press, Washington, pp. 171–189.