Review of Palaeobotany and Palynology 120 (2002) 217–232

Review of
Palaeobotany
& Palynology

www.elsevier.com/locate/revpalbo

A taphonomic study of modern pollen assemblages from dung and surface sediments in arid environments of Spain

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Received 12 June 2001; accepted 11 December 2001

Abstract

Coastal plant communities in arid southeastern Spain are characterized by insect-pollinated scrub species, which fail to occur in Quaternary pollen sequences from valleys, marshlands and marine cores. We investigate pollen–vegetation relationships in samples from soil surfaces, animal dung, and sediments in depressions or basins that, in theory, should have pollen spectra that are comparable to those from sedimentary basins elsewhere. Pollen spectra from basins or depressions are very susceptible to long-distance wind and water transport. This can mask representation of pollen from the surrounding insect-pollinated vegetation, as can over-representation of basin-margin halophilous and hydrophilous pollen. Pollen spectra from biogenic materials of animal origin are the best analogues of local and regional vegetation, and show the best analytical potential in terms of pollen concentration and taxon diversity. Pollination properties of the species studied indicate they will rarely be found in most conventional pollen records. It cannot be stressed too strongly that insight into Quaternary vegetation of arid regions demands complementary pollen analysis of coprolites, urine-cemented deposits, and cave sediments with preserved biotic remains, in addition to water-lain sediments.

Keywords: palynology; paleoecology; pollen–vegetation relationships; Spain; Quaternary

1. Introduction

While pollen analysis is a well-grounded tool for paleoecological studies in temperate regions, it poses several problems in arid environments, foremost among which are poor preservation, scarcity of suitable depositional basins, and relatively high rates of sedimentary accumulation (Horowitz, 1992). Pollen analyses in arid areas of southeastern Spain have tended to concentrate on those sequences that were available rather than on the more desirable ones. Those include adjacent marine sediments (Parra, 1994; Targarona, 1997); small peaty deposits in sub-coastal mountains (Riera et al., 1995); playa lakes (Burjachs et al., 1997); valley-bottom fills in badland areas (Nogueras et al., 2000); paleo-lagoons and coastal marshes (Yll et al., 1994; Pantaleón-Cano, 1997); and prehistoric sites (Mariscal, 1992; Davis and Mariscal, 1994; Carrión et al., 1995, 1999a).

The resulting paleoenvironmental picture is fragmentary (Carrión et al., 2000a). Worse, there is a striking lack of the pollen of the most abundant and characteristic species of the coastal veg-

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PII: S0034-6667(02)00073-8

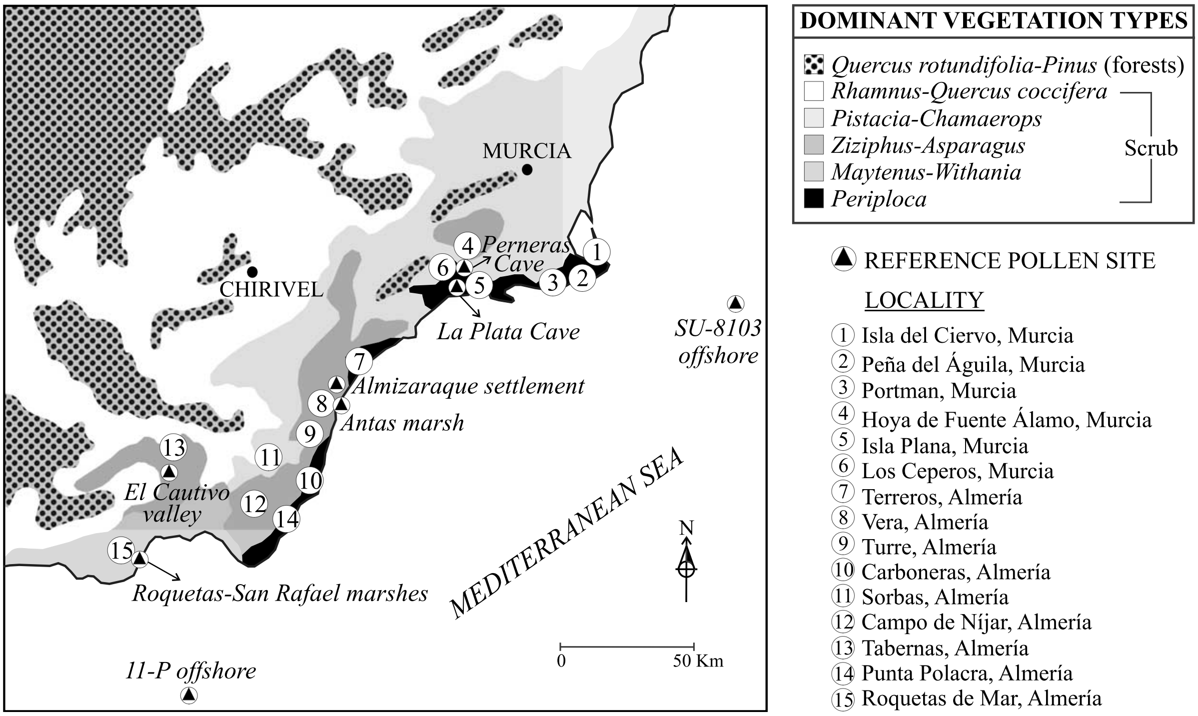

Fig. 1. Study area, location of sampling and reference pollen sites, and dominant vegetation types.

etation today, if we except minor records from the archeological sites of Perneras (Carrión et al., 1995) and Almizaraque (Davis and Mariscal, 1994). However it is unlikely that such species as *Maytenus senegalensis* subsp. *europaea* (Arto, Celastraceae), *Periploca angustifolia* (Cornical, Periplocaceae), *Withania frutescens* (Solanaceae), *Ziziphus lotus* (Azufaifo, Rhamnaceae), and *Calicotome intermedia* (Fabaceae), among others, are recent arrivals to the region, or disappeared from it during the Quaternary. These species today form structurally and floristically well-defined communities and they point to an Ibero–North African disjunction, linked to late-Miocene reopening of the Strait of Gibraltar (Mota et al., 1997).

This work was designed to test the hypothesis that the reason why these species fail to occur in the Quaternary pollen record of the region is largely taphonomical. Like other aridity-adapted plants, most of them are zoophilous (in particular, insect-pollinated), and their pollen should be rare in the deposits most often used for pollen analyses such as water-lain sediments. Studies of modern pollen samples of different kinds may shed light onto this issue. It bears emphasis that, if the working hypothesis were to be confirmed, we should revise our notions about Quaternary vegetation of the region.

2. Suitability of the study area for addressing the issue

The southeastern Iberian Peninsula, or Murcian–Almerian phytogeographical province, extends over ca. 13 000 km^2, and represents one of the richest areas of European flora, with important bioclimatic gradients and geological diversity (Sánchez-Gómez et al., 1998) (Fig. 1). Climate is Mediterranean and slightly continental, with annual values of 16–17°C in the lower bioclimatic belts. Extreme summer temperatures are common, with daily maxima of up to 46°C. The territory is limited by the Mediterranean Sea and surrounded by mountain ranges acting as a natural shield against precipitation. Yearly rainfall ranges from 250 to 330 mm, though in mountainous areas it may exceed 400 mm and in some coastal areas it falls below 190 mm. Precipitation is irregular and often causes devastating floods of great erosive power. Evapotranspiration is greater than anywhere else in the Iberian Peninsula.

More than half of the ca. 7500 Iberian vascular plants occur in the small territory of this province. There is a majority of Mediterranean contingent species (65%), including Iberian, Murcian–Almerian, Ibero–North African and Ibero–Irano–Turanian endemics (Peinado et al., 1992). Coastal mountains and littoral depressions of this province are patchily occupied by sclerophyllous brushwoods dominated by one or more of the following species: *Maytenus senegalensis* subsp. *europaea*, *Periploca angustifolia*, *Withania frutescens*, *Ziziphus lotus*, *Calicotome intermedia*, *Launaea arborescens*, and several species of *Genista*. Other abundant species include *Lycium intricatum*, *Rhamnus oleoides* subsp. *angustifolia*, *Pistacia lentiscus*, *Olea europaea* var. *sylvestris*, *Stipa tenacissima*, *Ephedra fragilis*, *Asparagus albus*, *Lavandula dentata*, *Rosmarinus officinalis*, *Euzomodendron bourgaeanum*, as well as a diversity of Cistaceae, Lamiaceae, and Asteraceae species.

Brushwoods are sometimes accompanied by sparse stands of *Pinus halepensis* and *Tetraclinis articulata*. Open forests with *P. halepensis* and *Quercus rotundifolia*, and *Quercus coccifera* scrub occur in the more continental depressions and less dry conditions of the mountainous hinterland (Fig. 1). Saline depressions or basins and intermittent water-courses, very common throughout the province, are colonized by *Artemisia*, *Nerium oleander*, Chenopodiaceae, *Tamarix*, *Limonium*, and Poaceae species.

The Murcian–Almerian bioprovince represents an excellent model system to address a variety of environmental issues because of its plant-species diversity, its varied physiography with abundance of ecotonal territories, its great risk of desertification, and the antiquity of human pressure on the landscape.

A big problem with palynology in other arid regions has been the difficulty of attaining specific and generic identifications (Horowitz, 1992). Specific identification is possible for *Maytenus*, *Periploca*, *Withania*, *Ziziphus*, *Lycium*, *Calicotome*, *Osyris*, *Nerium*, *Arisarum*, *Olea*, *Pistacia*, *Ephedra*, and *Chamaerops* (Table 1), which are monospecific in southern Spain, thereby enabling separation of regional and local sources. This makes our area suitable for studies of poorly known pollen–vegetation relationships in arid environments.

3. Materials and methods

3.1. Localities selected

Fifteen localities were selected that embody the main vegetation types with predominance of entomophilous species (Fig. 1). Localities 1, 3, 7, 10, and 14 fall within the area characterized by *Periploca angustifolia* communities, often including *Withania frutescens* and *Maytenus europaeus*, with *Lycium intricatum* and *Asparagus albus* in coastal bluffs subjected to salt spray. Locality 2 was selected because of the abundance of *Genista cinerea* subsp. *murcica* and *Calicotome intermedia*. Locality 5 is dominated by *Launaea arborescens*, *Lavandula dentata*, *Chamaerops humilis*, and several species of *Helianthemum* and *Fumana*. Localities 4, 8, and 12 are characterized by *Ziziphus lotus* and *A. albus*. Localities 6 and 9 were selected because of the respective abundance of *Launaea arborescens* and *Genista spartioides* subsp. *retamoides*. Locality 11 is situated in the Sorbas gypsum karstic area dominated by the endemic community of *Genista ramosissima*, *Ononis tridentata*, and *Retama sphaerocarpa*. Locality 13 is situated in the Tabernas desert community of *Euzomodendron bourgaeanum* and *Genista umbellata*. Locality 15 falls within the area dominated by communities of *Maytenus senegalensis* and *W. frutescens*, with abundant *Z. lotus* and *Phlomis purpurea* subsp. *almeriensis*.

3.2. Sampling

Three categories of samples were studied palynologically. Each sample consisted of a collection of 10–25 subsamples which were placed in polythene bags and mixed before proceeding with maceration. Subsamples were located as far as possible from each other, and away from concentrations of plants within about 2000 m^2. In order to minimize seasonal over-representation, sampling was made in early winter-time, when most flowers were not yet in blossom. Formaldehyde was added to the samples before the bags were sealed in order to deter bacterial activity.

The first sample type is the 'surface' type. This is minerogenic surface sediment that, supposedly, records airborne pollen. Subsamples were mainly a loose, yellow-buff to brownish, fine-grain dust from a depth of about 0–1 cm. We discarded sands and coarser clasts, cemented rocks, 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 indeed usually containing pollen grains, they may also contain considerable quantities of organic

Table 1
Taxonomic definition of the main pollen types within the study area

Pollen type	Taxa
Maytenus	*Maytenus senegalensis* subsp. *europaea*
Periploca	*Periploca angustifolia*
Withania	*Withania frutescens*
Ziziphus	*Ziziphus lotus*
Cichorioideae	*Launaea arborescens*, *Sonchus tenerrimus* (12), *L. lanifera* (10, 13)
Lamiaceae	*Rosmarinus officinalis*, *Thymus hyemalis*, *Satureja obovata*, *Sideritis pusilla*, *S. osteoxyla* (14), *Lavandula multifida*, *L. dentata*, *Ballota hirsuta*, *Teucrium freynii* (5), *T. lanigerum* (7), *T. turredanum* (11), *T. eriocephalum* (15), *Phlomis purpurea* subsp. *almeriensis* (9, 10)
Cistaceae	*Helianthemum almeriense*, *H. syriacum*, *H. alypoides* (11), *H. squamatum* (11), *H. scopulorum* (12), *H. leptophyllum* (15), *Fumana ericoides*, *F. thymifolia*, *F. laevipes*, *F. hispidula* (9), *Cistus monspeliensis* (5)
Asparagus	*Asparagus albus*, *A. horridus*
Lycium	*Lycium intricatum*
Rhamnus	*Rhamnus oleoides* subsp. *angustifolia*, *R. alaternus*, *R. lycioides* (4, 9)
Genista–Retama	*Genista cinerea* subsp. *murcica* (2), *G. umbellata* (5, 15), *G. spartioides* subsp. *retamoides* (9), *G. ramosissima* (11), *Retama sphaerocarpa* (11), *Ulex parviflorus* (15)
Calicotome	*Calicotome intermedia*
Osyris	*Osyris quadripartita*
Asteroideae	*Carthamus arborescens*, *Asteriscus maritimus* (1, 2, 15), *Phagnalon saxatile* (10), *Santolina viscosa* (8, 11),
Nerium	*Nerium oleander*
Tamarix	*Tamarix canariensis*, *T. boveana* (13)
Euzomodendron	Mainly *Euzomodendron bourgeanum*
Limonium	*Limonium cossonianum*, *L. insigne*, *L. caesium*
Arisarum	*Arisarum simorrhinum*
Artemisia	*A. barrelieri*, *A. herba-alba*, *A. campestris*
Poaceae+*Lygeum*	*Stipa tenacissima*, *Brachypodium retusum*, *Lygeum spartum*, *Dactylis glomerata*, *Saccharum ravennae* (4, 8), *Arundo donax* (4), *Phragmites australis*
Olea	*Olea europaea*
Pistacia	*Pistacia lentiscus*
Chamaerops	*Chamaerops humilis*
Pinus	*Pinus halepensis*, *P. pinea*
Chenopodiaceae	Species of *Salsola*, *Suaeda*, *Atriplex*, *Hammada*, *Anabasis*, *Salicornia*, *Arthrocnemum*, *Sarcornia*
Ephedra	*Ephedra fragilis*
Cupressaceae	*Tetraclinis articulata*, *Cupressus sempervirens*, *Juniperus turbinata* (15)
Quercus	*Quercus coccifera*, *Q. rotundifolia*
Cyperaceae	Mainly *Scirpus holoschoenus*

Numbers in brackets refer to localities in which a particular species is the most likely pollen producer (Fig. 1).

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

The second sample type is the 'dung' type. This is a mixture of pellets/feces from different animals, mainly goat, sheep, rabbit, hare, and less commonly wild boar. Both fresh and thoroughly dry excrements were collected in order to ensure they had acted long enough as pollen traps to record the whole set of flowering seasons. 'Dung' samples largely represent the pollen consumed and transported by herbivores, especially by ingestion of flowers, leaves, and other plant materials.

The third sample type is the 'depression' type. This is sediment from depressions or basins associated with marshes, wadis and arroyos. We often used the characteristic soft mud cakes deposited at the end of the last flood. This sediment type seems to correspond to pollen deposition in lagoons, marshes, salt-pans, and playa-lake systems (Horowitz, 1992), which have been a good source of long continuous sequences in the area (e.g. Pantaleón-Cano, 1997). In addition, all samples included one or several subsamples obtained by dredging the top layer of underwater sediments in bodies of perennial water. This was done in order to overcome possible biasses attributable to differential pollen preservation in samples of dry mud cakes which are exposed to temporary drying out. We avoided coarse clasts, and calcretes.

3.3. Laboratory methods

Maceration was undertaken within 2 months after sample collection. A weight of 12–42 g of dry sediment per surface sample was processed in the laboratory. This amount is thus greater than in samples from forested territories of the region, where 1 or 2 g of sediment can be enough (Navarro et al., 2000). For dung samples, we processed 2–8 g of dry material. Smaller samples may contain enough pollen to give an acceptable spectrum, but they may be inadequate for drawing firm conclusions. This increased sample size results from mixing dung fragments from different animals and is intended to overcome most of the variability that might reflect a single pellet or a single animal source. Finally, in the case of depression samples, we macerated a weight of 28–60 g of dry sediment.

The laboratory preparation techniques follow conventional methods in palynology using HCl, HF, KOH and mineral separation with a heavy liquid ($ZnCl_2$). At the beginning of the pollen processing, five *Lycopodium clavatum* spore tablets (ca. 12 542 spores per tablet) were added to each sample in order to facilitate concentration calculations (grains per gram dry weight). All slides were mounted in glycerin jelly and stained with safranin.

3.4. Pollen identification and counting

Identification and counting were performed using the pollen reference collection of Murcia University's Palynology Laboratory. Non-vascular cryptogam spores (mainly *Riccia*, *Glomus* chlamydospores, and Zygnemataceae zygospores and aplanospores), and other non-pollen microfossils (mainly *Pseudoschizaea*) were not considered in this study. No reworked palynomorphs from underlying Paleozoic and Mesozoic strata were observed.

Several pollen identifications merit explanation. *Lycium* pollen was separated from other Solanaceae types based on its characteristically small apocolpium and striate apertural membrane. *Withania* pollen shows a peculiar foveolate pattern, striate markings being seldom visible across the mesocolpium. *Ziziphus* was discriminated from *Rhamnus* on the basis of its less clearly marked reticulum and less pronounced differences in lumina-width towards the center of the mesocolpium. *Calicotome* pollen is clearly different from *Genista* type, displaying thicker reticulum muri, a rectangular shape in equatorial view, and more flattened mesocolpia. *Asparagus* pollen is relatively small when contrasted against the commonest size-pattern for the Liliaceae, and is characteristically elliptical in polar view. *Chamaerops*, being the only natural palm species in our area (where it is abundant nowadays), was distinguished from *Phoenix* by its larger and less isodiametric pollen. Considering local vegetation, *Launaea arborescens* and *Carthamus arborescens*

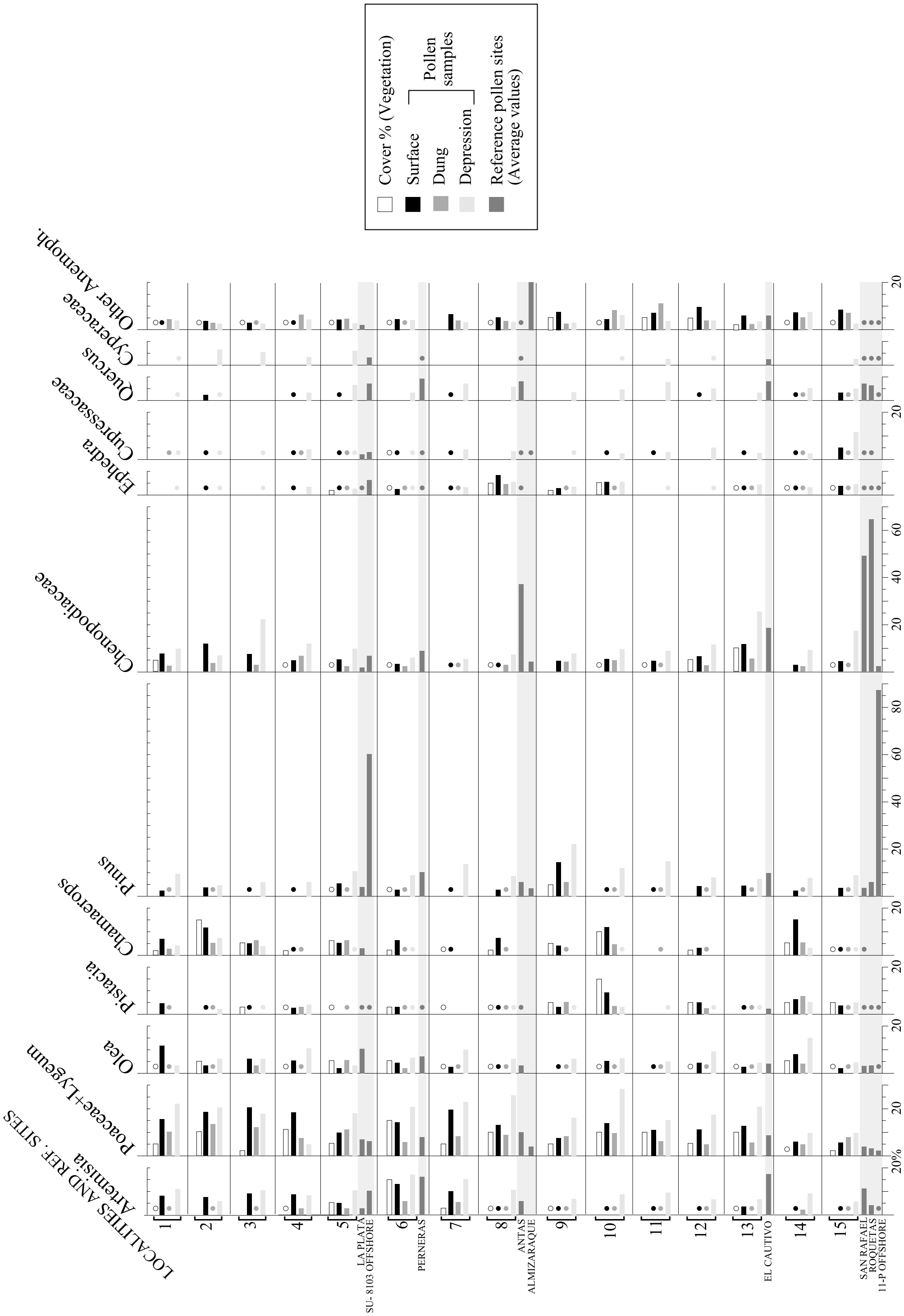

Fig. 2. Percentage pollen diagram and average cover values of anemophilous taxa.

must be the main pollen contributors to the Cichorioideae and Asteroideae groups (Table 1). The Lamiaceae type includes undifferentiated hexa- and tricolpate grains as well as pollen of *Teucrium* and *Sideritis*. Brassicaceae pollen is only abundant in locality 13 so it must belong mainly to *Euzomodendron bourgaeanum*. Pollen types relative to 'other anemophilous' (Fig. 2), and 'other zoophilous' forms (Fig. 3) are included in Table 2. Nomenclature of plant taxa follows Sánchez-Gómez et al. (1998) and Mota et al. (1997).

3.5. *Pollen diagrams*

Three pollen spectra per locality are displayed in pollen percentage diagrams of anemophilous (Fig. 2) and zoophilous taxa (Fig. 3). Pollen percentages are based on pollen sums of at least 200 pollen grains, excluding aquatic pollen and spores. Mean pollen percentages of surface, dung, and depression samples are expressed as graphs in Fig. 4. Pollen taxa with relative frequencies steadily below 2% have been excluded from pollen diagrams (Table 2).

Table 2

Pollen and spore types with percentages steadily below 2%, which form the basis for the sums of 'other zoophilous' and 'other anemophilous' taxa in the pollen diagrams (Figs. 2–4)

Zoophilous		Anemophilous and ferns
Agave	*Lotus*	*Alnus* (DP)
Anchusa	Malvaceae	*Asplenium* (SU)
Anthyllis	*Messembryanthemum* (DP)	*Betula* (DP)
Aristolochia (DU)	*Myosotis* (DU)	*Castanea* (DP)
Asphodelus	*Myrtus*	*Casuarina*
Boraginaceae	*Neatostema* (DU)	*Cedrus* (DP)
Bupleurum	*Nicotiana*	*Corylus* (DP)
Campanula	*Ononis*	*Cosentinia* (SU)
Capparis	*Opuntia*	*Equisetum* (DP)
Caryophyllaceae	*Oxalis*	*Eucalyptus*
Centaurea	*Papaver*	*Fraxinus* (DP)
Centaurium (DP)	*Paronychia*	*Juncus* (DP)
Ceratonia (DU)	*Polygala* (DU)	*Mercurialis*
Chaenorrhinum (DU)	*Polygonum* (DP)	*Phoenix*
Convolvulus	Primulaceae	*Plantago*
Coris	*Prunus*	*Populus* (DP)
Coronilla	*Psoralea*	*Rumex*
Cynoglossum	Ranunculaceae	*Sanguisorba*
Dorycnium (DU)	*Reseda* (DU)	*Schinus*
Ecballium	Rubiaceae	*Selaginella*
Echium (DU)	*Rubus*	*Thalictrum*
Ericaceae	*Ruta*	*Typha* (DP)
Erodium	*Salix*	*Ulmus* (DP)
Euphorbia	*Sarcocapnos*	Urticaceae
Fagonia (DU)	*Scrophularia*	
Ficus	*Sedum*	
Fumaria	*Smilax*	
Gladiolus	*Solanum*	
Hedera	*Thymelaea*	
Lathyrus (DU)	*Verbascum* (DU)	
Linum	*Viola* (DU)	
Lithodora	*Zygophyllum*	
Lonicera		

Types exclusively found in surface samples (SU), dung samples (DU), and depression samples (DP).

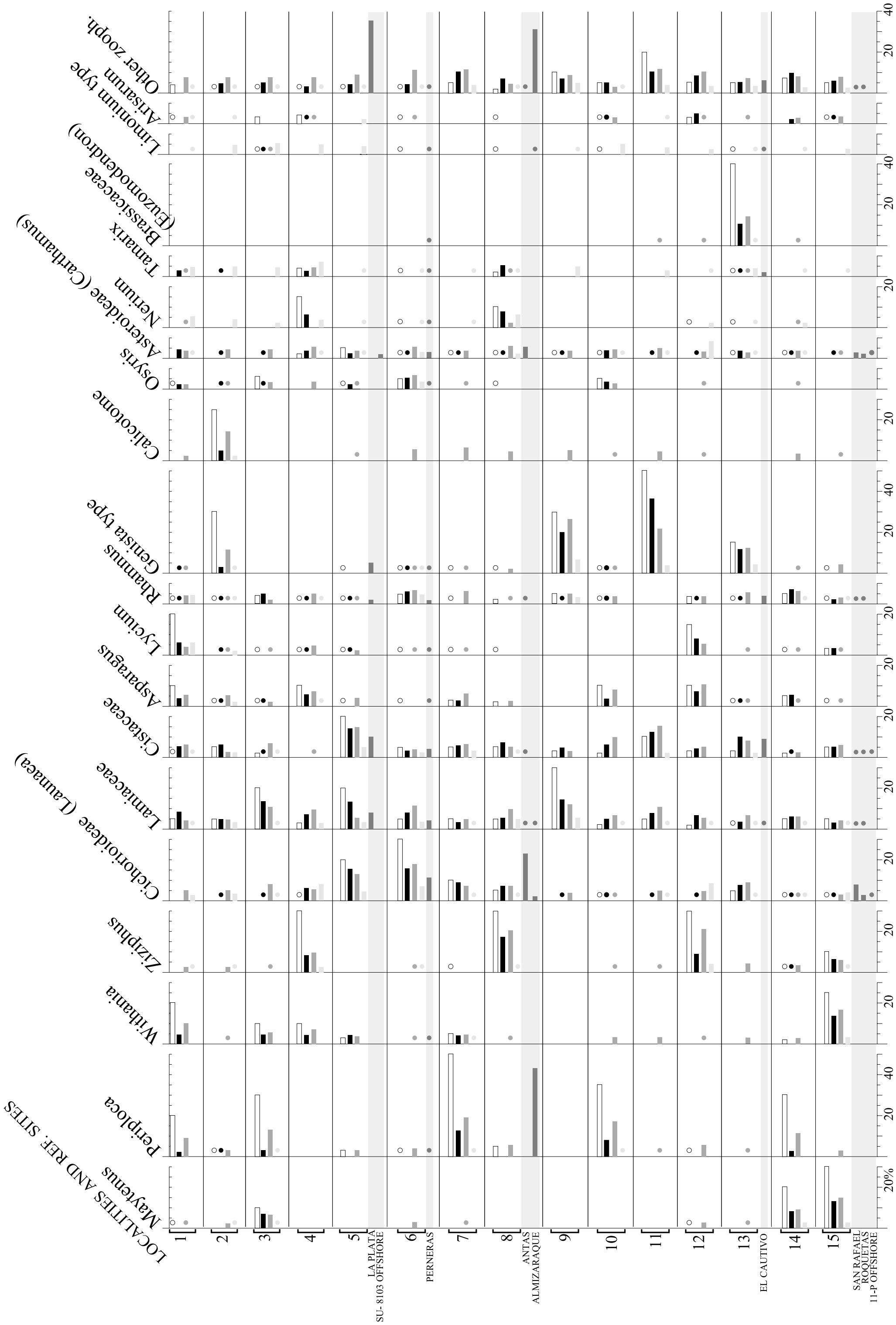

Fig. 3. Percentage pollen diagram and average cover values of zoophilous taxa.

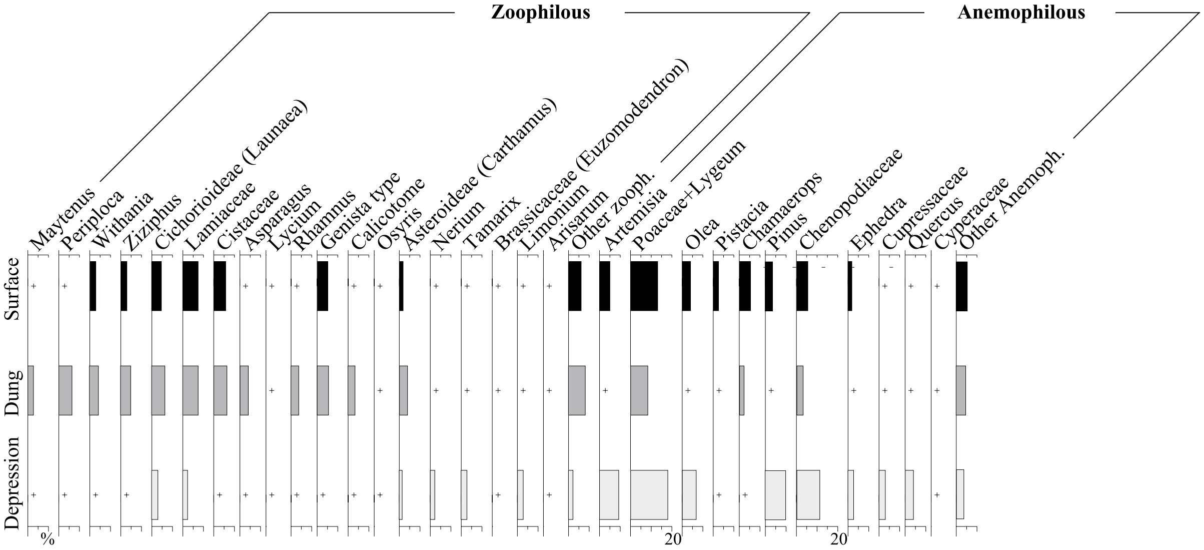

Fig. 4. Synthetic diagram representing mean pollen percentages of selected taxa in surface, dung, and depression samples.

3.6. Estimates of plant-species abundance

To estimate local taxon cover, average values that sum to 100% are used for the abundance-coverage index (Braun-Blanquet, 1964) in phytosociological studies carried out over broadly similar areas of about 2000 m^2 at localities selected here (Alcaraz et al., 1989; Peinado et al., 1992; Mota et al., 1997). In order to make them comparable with pollen taxa percentages, vegetation data of higher taxonomic ranks were eventually used instead of the original species information at the phytosociological tables. We are aware, of course, that sampling methodology here is hardly the best that could be wished for, but there are no other ecological studies that provide more reliable estimates of plant-species abundance for the area. In any case, we consider that, since this phytosociological approach permits using percentages as units of coverage index, gives weight to characteristic species that are not particularly abundant, and establishes, albeit roughly, the plant-species abundance over relatively large areas, it serves quite well our overall purpose. In order to facilitate pollen–vegetation comparison, cover values for species and species groups are graphed within the pollen diagrams (Figs. 2 and 3).

3.7. Reference pollen sites

Mean pollen percentages of selected taxa from the following pollen records (Fig. 1) have been represented in the pollen diagrams (Figs. 2 and 3):

(i) La Plata Cave (Mazarrón, Murcia), a karstic cave 1 km from locality 5 of this study. Average values derive from 10 pollen samples of floor-surface sediment (Prieto and Carrión, 1999; Navarro, 2000);

(ii) SU-8103, a late glacial to early Holocene pollen sequence from an offshore marine core beside the Murcian coast (Parra, 1994);

(iii) Perneras Cave (Lorca, Murcia), a pollen sequence from calcreted Middle Paleolithic beds (Carrión et al., 1995). The site is near Los Ceperos (locality 6);

(iv) Antas (Almería), a Holocene pollen sequence obtained in the lower course of the River Antas, Vera Basin (Pantaleón-Cano, 1997), very close to locality 8;

(v) Almizaraque (Almería), average values of pollen samples from five open sections in Chalcolithic settlement areas along major streams and near estuaries associated to the Vera Basin, within 10 km of the coast (Mariscal, 1992; Davis and Mariscal, 1994);

(vi) El Cautivo (Tabernas, Almería), a Holocene pollen sequence from a valley-bottom deposit in the Tabernas badland area (Nogueras et al., 2000), relatively near locality 13;

(vii) San Rafael (Campo de Dalías, Almería), a late Pleistocene and Holocene pollen record from a coastal marshland system in the vicinities of locality 15 (Pantaleón-Cano, 1997);

(viii) Roquetas de Mar (Campo de Dalías, Almería), a Holocene pollen record recovered from nearby San Rafael (Yll et al., 1994; Pantaleón-Cano, 1997);

(ix) 11-P, a Holocene pollen sequence from an offshore marine core of the Alborán sea at Almería (Targarona, 1997).

3.8. Detrended correspondence analysis (DCA)

DCA was carried out on a matrix of a database including cover values, pollen percentages of surface, dung, and depression samples, and average pollen percentages of selected taxa in regional reference pollen sequences (Fig. 7). DCA options (STATISTICA version 3.05) included downweighting of rare species, weights applied to columns in sequential order, and axis rescaling.

4. Results

Anemophilous pollen taxa (*Artemisia*, Poaceae, *Olea*, *Pinus*, Chenopodiaceae, *Ephedra*, Cupressaceae, *Quercus*, Cyperaceae) are over-represented in surface and especially depression samples (Fig. 2), plausibly due to to the fact that their pollen is produced in large quantities, and dispersed over large distances by wind. In particular, *Quercus* and *Pinus* occur relatively abundantly in the absence of local producers. Minor anemophilous types such as *Alnus*, *Betula*, *Castanea*, *Cedrus*, *Corylus*, and *Fraxinus*, not present in the regional flora, were only recorded in depression samples (Table 2).

Dung pollen spectra give the best reflection of coastal vegetation in terms of occurrence of minor pollen taxa that are crucial for characterizing local floristic assemblages. This would be the case with *Maytenus* at localities 1 and 12, *Periploca* in localities 2, 5, 6, and 12, *Withania* and *Ziziphus* at locality 14, and *Osyris* at locality 3 (Fig. 3). Dung samples record sometimes zoophilous pollen types where the producing species is absent locally. Thus, *Calicotome* pollen occur at localities 1, 5–12, 14, and 15, *Maytenus* at localities 6, 7, and 13, *Periploca* at localities 13 and 15, *Ziziphus* at localities 3, 10, 11, and 13, and *Osyris* at localities 4, 7, 12, and 14 (Fig. 3).

When zoophilous vs. anemophilous pollen percentages are considered together, dung samples offer the most abundant records for the first group (Figs. 4–6). Likewise, they display the best pollen-analytical potential in terms of high number of taxa, relatively high total pollen concentration, and low frequencies of indeterminable palynomorphs (Fig. 5). Finally, dung pollen spectra alone contain pollen of minor zoophilous taxa such as *Aristolochia*, *Ceratonia*, *Chaenorrhinum*, *Dorycnium*, *Echium*, *Fagonia*, *Lathyrus*, *Myosotis*, *Neatostema*, *Polygala*, *Reseda*, *Verbascum* and *Viola* (Table 2).

Surface samples, excluding those from depressions, may show relatively high amounts of particular zoophilous pollen types, but only at localities where the producing species show high cover. Thus, *Periploca* pollen is only relatively abundant at localities 7 and 10, *Maytenus* at localities 3, 14, and 15, *Withania* at locality 15, *Ziziphus* at localities 4, 8, and 12, *Asparagus* at localities 4 and 12, *Genista* at localities 9, 11, and 13, *Calicotome* at locality 2, *Osyris* at localities 6 and 10, *Euzomodendron* at locality 13, and *Arisarum* at locality 12 (Fig. 3). Clearly, pollen of zoophilous scrub is shed almost directly into the ground and shows scant lateral travel. Since it is not dispersed by wind over large distances, this pollen is poorly represented in the regional airborne pollen deposition.

Zoophilous scrub species characteristic of the present-day coastal vegetation are poorly represented or totally absent in depression pollen samples (Fig. 3). Not a single pollen grain was found of *Periploca* at localities 1, 2, 5, 6, 8, 12, and 14, of *Withania* at localities 1, 3, 4, 5, and 14, of *Asparagus* at localities 1, 10, 12, and 14, of *Lycium* at locality 12, of *Rhamnus* at localities 3 and

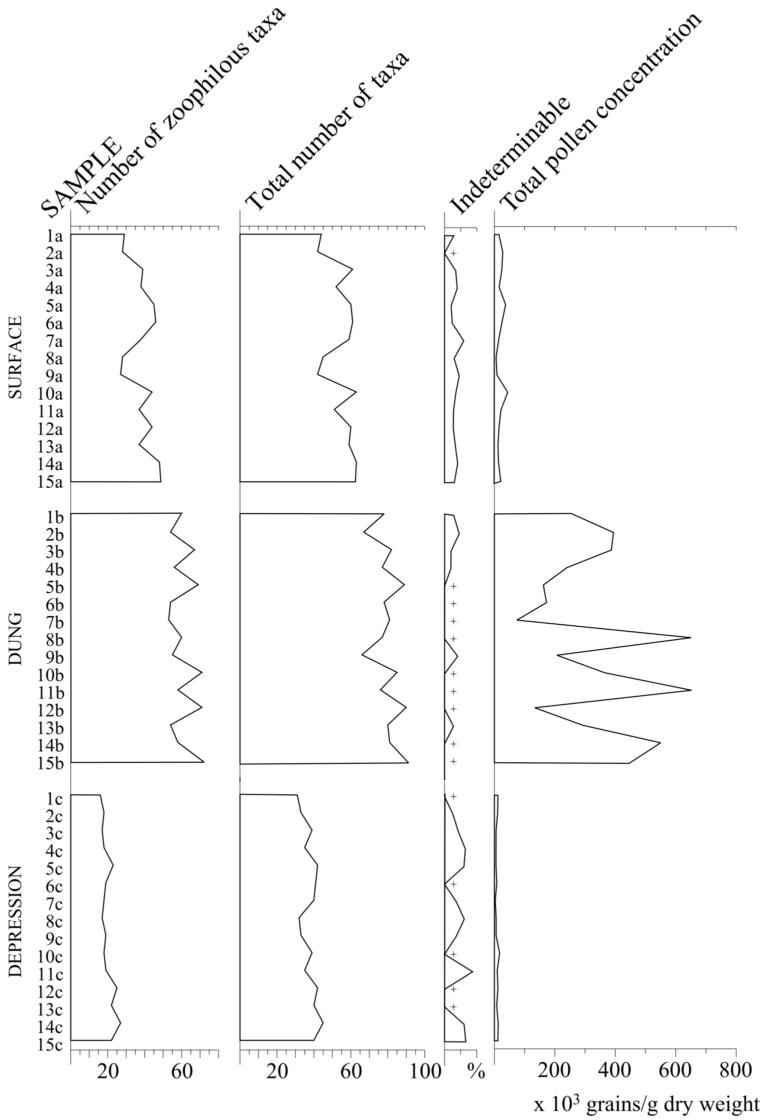

Fig. 5. Curves of variation of the number of zoophilous taxa, total number of taxa, indeterminable percentages, and total pollen concentration.

12, or of *Osyris* at locality 10. Very low amounts were found of *Euzomodendron* pollen at locality 13, *Maytenus* at localities 13 and 15, *Periploca* at localities 3, 7, and 10, *Withania* at locality 15, *Genista* at localities 9 and 11, and *Calicotome* at locality 2. The abundance of *Nerium*, *Tamarix*, and *Limonium* (Fig. 3), and exclusive occurrence of *Centaurium*, *Ulmus*, *Populus*, *Typha*, *Juncus*, *Polygonum*, *Messembryanthemum*, and *Equisetum* in depression samples (Table 2), may be related to local presence and/or water transport from other beds of the same depositional system.

DCA shows the distribution of the samples along the first two axes, A×1 and A×2, which account for 49% and 26% of the total variation (Fig. 7). It is suggested that this distribution results rather from sample type than influenced from locality. Dung samples are relatively closely located to cover samples, while depression samples group rather with continental pollen sequen-

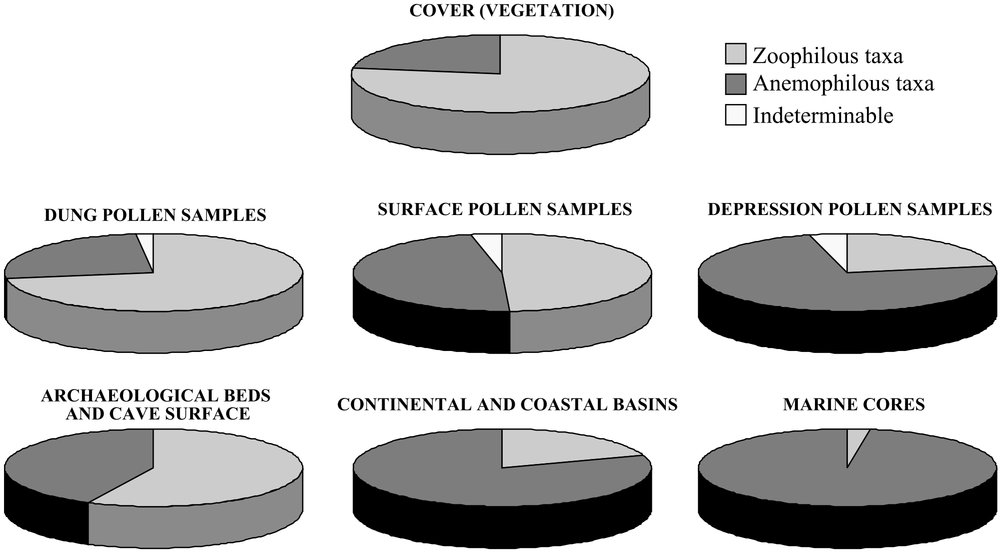

Fig. 6. Relative abundance of zoophilous and anemophilous taxa in regional vegetation, and pollen samples from recent and fossil sites.

ces of Antas, San Rafael, Roquetas de Mar, and El Cautivo. Surface samples occupy intermediate coordinates, although several of them fall close to their respective cover samples (e.g. 5, 6, 9, 13). Marine sequences SU-8103 and 11-P display isolatedly the highest values of A×1. Archeological and cave pollen records were not grouped. Perneras falls within a group made up of depression samples. La Plata falls close to the surface samples that show highest values of A×2. Almizaraque falls relatively close to cover samples 7, 3, 10, and 14. According the first DCA axis, dung and surface samples are separated from the coverage and depression samples. It is confirmed that even dung samples do better reflect local vegetation than depression samples in which anemophilous taxa can result in a biassed representation of the vegetation.

5. Discussion

5.1. *Conventional pollen spectra are influenced by long-distance transport*

Pollen spectra of the category ‘depression sample’ contain very little pollen produced by the surrounding zoophilous vegetation. Rather, they are dominated by *Pinus*, *Quercus*, deciduous trees, *Artemisia*, and Chenopodiaceae, with minor occurrences of pollen from hydrophilous and halophilous communities (*Nerium*, *Tamarix*, and *Limonium*) (Figs. 2–4, Table 2). A major problem is that most of the analyzed localities have at least some connection with water-courses and intermittent floods, thus a distinction should be made between the different contributions of pollen brought by water and wind. Establishing pollen sources for these taxa and other like Poaceae, *Lygeum*, *Olea*, Lamiaceae, Cichorioideae, Asteroideae, and *Ephedra* is difficult because these taxa are widely represented in both local and regional environments.

The category ‘surface samples’ gives a better picture of the surrounding vegetation, with significant pollen amounts of *Withania*, *Ziziphus*, Lamiaceae, Cistaceae, *Genista* type, and other zoophilous taxa (Fig. 4), but they are still biassed towards anemophilous pollen taxa (Fig. 6).

Other palynological investigations in arid areas coincide with this study in finding that pollen spectra may be greatly prone to over-representation of extra-local pollen. Long-distance transport of pollen by winds, rivers, and even sea currents, which only has a subordinate effect on pollen spectra from richly vegetated regions, is of prime importance in arid areas (Horowitz, 1992). Pollen-rain studies in the Sahara have shown that large populations of anemophilous plants (Chenopodiaceae, Poaceae, *Artemisia*, *Olea*, Cyperaceae), even distant ones, are the principal components of pollen spectra, while trees and shrubs of tropical and equatorial regions (e.g. Combretaceae, *Acacia*, *Maerua*, *Lannea*, *Ziziphus*, *Celtis*) release little pollen into the air and thus are under-represented (Van Campo, 1975; Schulz, 1980; Ritchie, 1987). On the other hand, pollen originating nowadays in the Sahara Desert and Nile Delta, very common in silt in Israel due to dust storms, can make up 20–30% of recent spectra near Jerusalem (Horowitz et al., 1975). Modern lowland pollen spectra from the Sudanian Sahel (El Ghazali and Moore, 1998) is principally made up of the anemophilous taxa Poaceae, *Aerva* and *Typha*, and although numbers of anemophilous elements are far less than zoophilous ones (eight out of 26 taxa), their total pollen percentage is considerably greater. Modern surface samples from the arid southwestern USA generally record less than 40 pollen types of which only five, namely *Pinus*, *Juniperus*, Poaceae, Chenopodiaceae, and Asteraceae, may account for 90% of the pollen counts. In contrast, Cactaceae, and the dominant Sonoran desert species *Larrea tridentata*, are under-represented in surface pollen samples (Hall, 1985).

Offshore and delta sediments are also prone to pollen brought from great distances by rivers and sea currents, which can mask dry vegetation of the nearby coastal territories. In modern sediments of the Dead Sea, desert plant pollen was considerably outnumbered by pollen of Mediterranean vegetation and carried via the River Jordan (Rossignol, 1969). In the Bay of Elat in southern Israel, modern pollen spectra contained up to 80% of pollen derived from sea-bottom muds off Lebanon and northern Israel, not to mention pollen carried by sea currents flowing across 25–30° of latitude (Horowitz, 1992). In the central Negev, wadi sediments contained up to 77% Chenopodiaceae, and 19% Poaceae–Cyperaceae, while dust collected from the surface on nearby highlands showed Poaceae–Cyperaceae 91%, Chenopodiaceae 6%, and Fabaceae 2% (Horowitz, 1979).

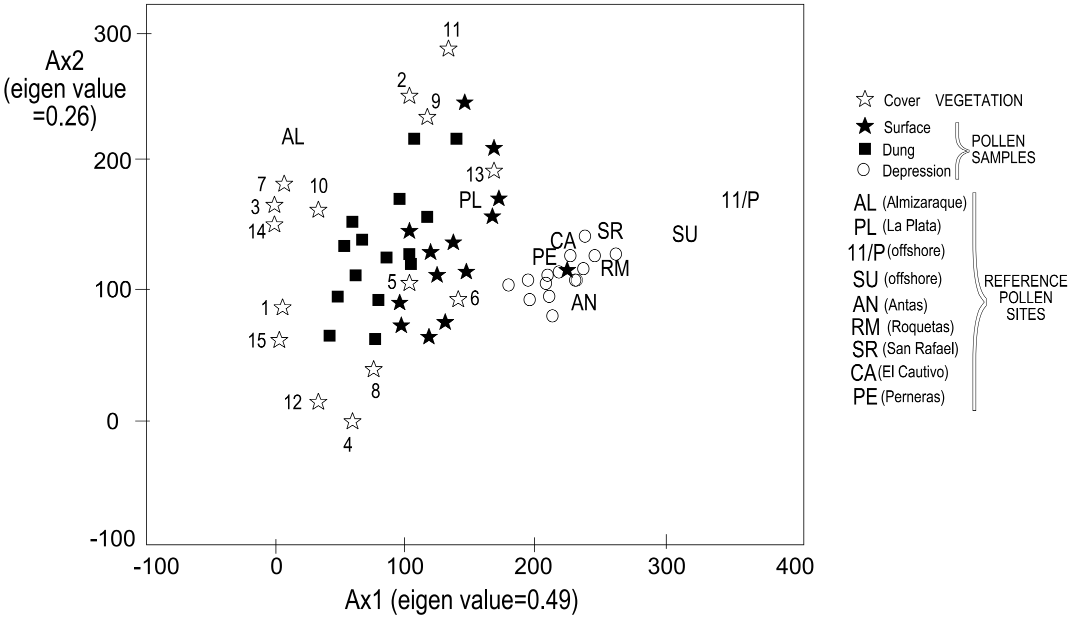

Fig. 7. DCA including cover values, pollen percentages of surface, dung, and depression samples, and average pollen percentages of selected taxa in regional reference pollen sequences.

5.2. Zoophilous pollen types are absent in marsh and offshore regional pollen sequences

It is hardly surprising that pollen of *Maytenus*, *Periploca*, *Withania*, *Ziziphus*, *Lycium*, *Calicotome*, and *Osyris* was absent from Antas, San Rafael, El Cautivo, and Roquetas de Mar, and SU-8103 and 11-P offshore cores (Fig. 3), that pine pollen dominates marine pollen spectra, and Chenopodiaceae prevail in marsh pollen sequences (Figs. 2, 6 and 7). Like depression samples, these sediments have connection with water-courses and intermittent floods. Yet it is worth wondering whether several of these studies could have paid insufficient attention to the less numerous pollen grains such as *Ziziphus*, which, albeit with low representation, occur in North African pollen diagrams of Ait Blal, Ksabi, Moulouya (Ballouche, 1986), and Tizi n-Inouzane in the Central Atlas (Reille, 1976), and several southern African sites (Scott, 1982). Minor zoophilous types carefully identified in marine cores have provided insight into past vegetation characteristics along continental northwestern Africa (Agwu and Beug, 1982). Furthermore, surface samples in our study show that these pollen grains do occur in sediment, even though, for whatever reason, they only travel very short distances and comprise but trivial shares of pollen spectra recovered from depression deposits.

5.3. The value of biogenic deposits of animal origin in paleo-vegetation studies

Dung pollen spectra represent the vegetation composition of the local area, and also carry important information about regional vegetation. Dung producers may have ingested plant material over a large part of the study area. It must also be regarded that each leaf surface eaten by a herbivore may contain regional pollen rain. For success of dung pollen spectra to represent surrounding vegetation, the mixing of fecal material from different animals may have been crucial. Moe (1983) studied pollen contained within sheep's feces in Norway and concluded that pollen analysis of feces provide virtually no information about the quantitative composition of the vegetation of the sheep's environment, but do provide valuable information about their diet.

Other studies support a different viewpoint. Thompson et al. (1980) analyzed pollen from coprolites of the Shasta ground sloth and compared it with plant remains in the same material. They concluded that the animal diet was not influential in the dung pollen spectra. Scott and Cooremans (1992) compared pollen spectra in recent bird guano, hyrax (*Procavia*) and dassie-rat (*Petromus*) midden samples with those at surface samples from various parts of South Africa. Dung samples were not strongly influenced by dietary preferences and reflected local vegetation, including relatively high values for Aizoaceae, Liliaceae, Acanthaceae, Asteraceae, *Acacia*, and *Euphorbia*. Similarly to these studies, packrat (*Neotoma*) midden pollen has been shown to represent both local and regional desert vegetation in the southwestern USA, recording under-represented and/or rare types such as *Cereus*, *Ferocactus*, *Mammilaria*, *Opuntia*, *Larrea*, *Yucca*, *Ceanothus*, etc. (e.g. Davis and Anderson, 1987). Pollen assemblages from fresh cow dung samples are in good agreement with composition of the present-day vegetation in the neighborhood of sampling sites, thus substantiating a paleoecological interpretation of pollen spectra obtained from Iron Age consolidated cow dung in Zimbabwe, Botswana, and South Africa (Carrión et al., 2001).

Deposits of faunal origin often accumulate in archeological and prehistoric sites in caves or under rockshelters. Under dry sedimentation conditions, pollen and other biogenic materials may preserve well, thus enhancing the value of paleobotanical analyses in these environments (Davis, 1990; Navarro et al., 2000). Thus, pollen assemblages of Pleistocene beds in Perneras Cave and La Plata Cave (Figs. 2 and 3) include minor occurrences of *Periploca*, *Withania*, *Lycium*, *Asparagus*, *Genista*, *Osyris*, *Nerium*, *Tamarix*, and other zoophilous taxa, and abundant pollen of Lamiaceae, Brassicaceae, Asteraceae, and Cistaceae (Carrión et al., 1995; Prieto and Carrión, 1999; Navarro, 2000).

It can be concluded that dung accumulations may represent relatively unbiassed pollen traps. Admittedly, pollen sequences obtained from conventional continental and marine deposits should be combined with studies of coprolites and other biogenic accumulations in order to achieve a more realistic picture of past vegetation characteristics of this and other arid territories.

Acknowledgements

This research was funded by the Spanish projects ARDACHO (Ref. BOS2000-0149) and PI-17/00739/FS/01 of the Ministerio de Ciencia y Tecnología and Fundación Séneca of the Murcia regional government respectively. Fernando Ojeda provided help with multivariate analysis. Michael Walker, Paleo-Anthropology Laboratory at Murcia University, kindly re-wrote the English text. Toñi Andrade and Cristina Navarro helped with respectively laboratory and statistical essays at the beginning of this work. Bas van Geel, Joost Duivenvoorden, and an anonymous referee provided constructive comments on an earlier version of this paper.

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