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An experimental approach to the palynology of cave deposits

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ABSTRACT: Surface sediment, speleothems, and bat guano from two adjacent, topographically different cave sites in eastern Spain have been studied palynologically to elucidate the potential of cave sediments for palaeoenvironmental reconstruction. A cave opening with a large entrance and constant width presented far fewer problems of alteration in the pollen assemblages than a sac-like cave opening with a constricted entrance. Pollen concentration is linked primarily to the amount of pollen input rather than to the result of post-depositional alteration. Sampling should be undertaken away from parietal and rear areas and avoiding moisture zones. Lateral differences in the pollen spectra indicate that sampling should be on the basis of a multiple-profile approach and selection of dry rather than wet sediments. If these procedures are followed, within-cave sediments can realistically reflect not only local but also regional vegetation of the site. Copyright © 2000 John Wiley & Sons, Ltd.

KEYWORDS: palaeoecology; palynology; caves; taphonomy; Spain.

Introduction

The palaeoecological potential of pollen records in caves is severely limited by the lack of an insufficient, experimentally based, conceptual framework. It is not surprising that, for the last few decades, archaeopalynology has been the subject of criticism owing to a plethora of pitfalls (Coûteaux, 1977; Turner, 1985; Campy, 1985; Turner and Hannon, 1988; Sánchez-Goñi, 1991, 1994, 1996).

It is our view that the principal effort in archaeopalynology should involve the establishment of distributional patterns of palynomorph deposition throughout cave surfaces and, in order to achieve that, emphasis should be placed on unconsolidated materials that form the most common sediment in archaeological profiles. In addition, it is vital to know how well pollen in cave sediments reflects the external vegetation. Experimentally, this problem has been addressed through research based on the airfall pollen budget collected with Cour filters (Burjachs, 1988), UFH filters (Loublier, 1974), modified Tauber traps (Burney and Burney, 1993), petri dishes (Bui-Thi-Mai, 1974; Burjachs, 1988), and microscope slides coated in petroleum jelly (Van Campo and Leroi-Gourhan, 1956; Burjachs, 1988; Coles and Gilbertson, 1994). Because of the existence of animal and water transport (Davis, 1990; Davis and Buchmann, 1994), there is a need for pollen-analytical examination of surface sediments; these hitherto have not been used as an important data source but only as a minor part of more general studies (Burjachs, 1988; Davis and Anderson 1987; Diot, 1991; Burney and Burney, 1993). With this objective in mind, we present results of pollen analyses carried out on surface sediments of two caves from eastern Spain.

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Physical setting and cave description

The Moro I and Moro II caves (38°46′28″N, 0°31′7″W) are located in the Sierra de Mariola mountains, at 843 m a.s.l. within the municipality of Agres, Alicante Province, eastern Spain (Fig. 1), an area characterised by abundant palaeolithic and neolithic settlements (Dupré, 1988). Mean annual temperature and precipitation is ca. 16°C and 479 mm respectively, according to data from the nearby meteorological

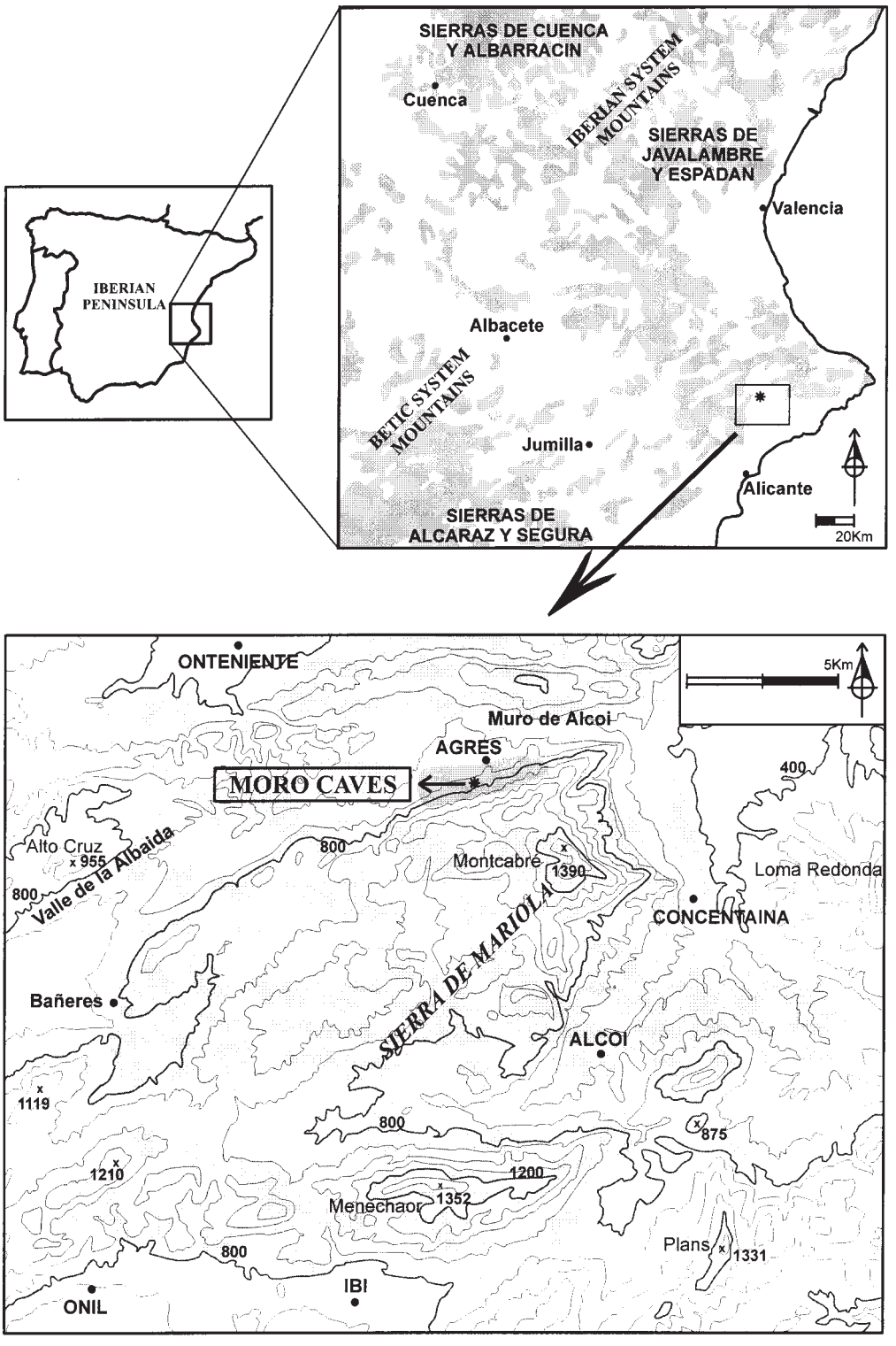

Figure 1 Location of the Moro caves in Agres Valley (Alicante, eastern Spain) with local and regional cover (local = dark grey; regional = light grey).

station of Alcoi. The area today has a dry, meso-Mediterranean bioclimate (Costa, 1982; Rivas-Martínez, 1982).

In part, because of the mountainous character of the region, present-day vegetation is patchy. The main forest species is *Pinus halepensis*. Its degradation stages are characterized by a dense scrub-matorral of the spiny legume *Ulex parviflorus* together with several Lamiaceae and Cistaceae species. Forests of the evergreen oak *Quercus rotundifolia*, often mixed with semi-deciduous oaks (*Quercus faginea*) are also common. Apart from oaks, these forests include *Fraxinus ornus*, *Acer opalus* ssp. *granatensis*, and a dense understorey of high shrubs and lianas. Natural vegetation has been replaced extensively by cultivars, among which the olive tree (*Olea europaea* var. *europaea*) is predominant. The vegetation of the valley adjacent to the caves is a *Pinus halepensis* forest with *Ulex parviflorus, Juniperus oxycedrus, Juniperus phoenicea, Rhamnus alaternus, Cistus albidus, Rosmarinus officinalis, Ruta angustifolia*, and other small shrubs. The evergreen oak is almost absent in the vicinity of the caves.

Both caves belong to the same karstic system, which is developed in Cretaceous limestones. They connect at ca.

60 m depth and have their mouths separated by ca. 15 m. Moro I is west-facing, 60 m deep, two-entranced (0.2 × 0.5 m and 6.3 × 3.8 m) and three-chambered with sac-like cavities (0.5 × 4.5 × 30 m; 3.5 × 4 × 31 m; 1.5 × 5.5 × 24 m) (Fig. 2). Moro II is west-facing, 20 m deep, single-entranced (5 × 10.6 m) and has two chambers connected by three narrow passages (2.8 × 2.3 m; 2.5 × 1.3 m; 2.9 × 1.7 m) (Fig. 3). The principal chamber lies beyond these passages (4.6 × 10.5 × 15.6 m). Karstic activity is nowadays almost absent in Moro II but still perceptible in Moro I, where parts of the floor are moistened and encrusted by dripping water, owing to the porosity of the limestone ceiling. In general, however, floor sediment is dry and uncompacted.

Material and methods

Twenty-nine samples of floor sediment were studied initially, 13 from Moro I and 16 from Moro II (Table 1). A sediment volume of ca. 2 cc was sampled from the surface using a spatula and avoiding footprint areas. Between 5 and 15 g of dry sediment were treated in the laboratory. At Moro I, samples 20, 21, 23, 28, 29, 31, 33, 34 and 36 correspond to dry uncompacted sediment, and samples 37, 38, 39 and 42 to wet, somewhat encrusted floor sediment beneath water trickles. At Moro II, all samples were taken from dry sediment. In addition to these samples, another 11 samples of a different nature were analysed for comparative purposes, including tips of small active speleothems on the ceiling, spider webs on the walls and bat guano on the floor (Table 1). As a control for the local vegetation, a mixture of moss polsters and surface sediment from the vicinity of each cavity was analysed. As for the regional vegetation, similar samples from the Agres Valley and nearby mountains were analysed. Pollen analyses of moss polsters and surface sediment in similar areas has proven to represent surrounding vegetation with reliability (Burjachs, 1986). The adopted local and regional 'pollen catchments' are represented in Figure 1.

The laboratory preparation techniques follow Dimbleby (1961), as modified by Girard and Renault-Miskovsky (1969) and are set out in full in Carrión (1992). Speleothem pollen samples were first extracted from the calcite matrix using

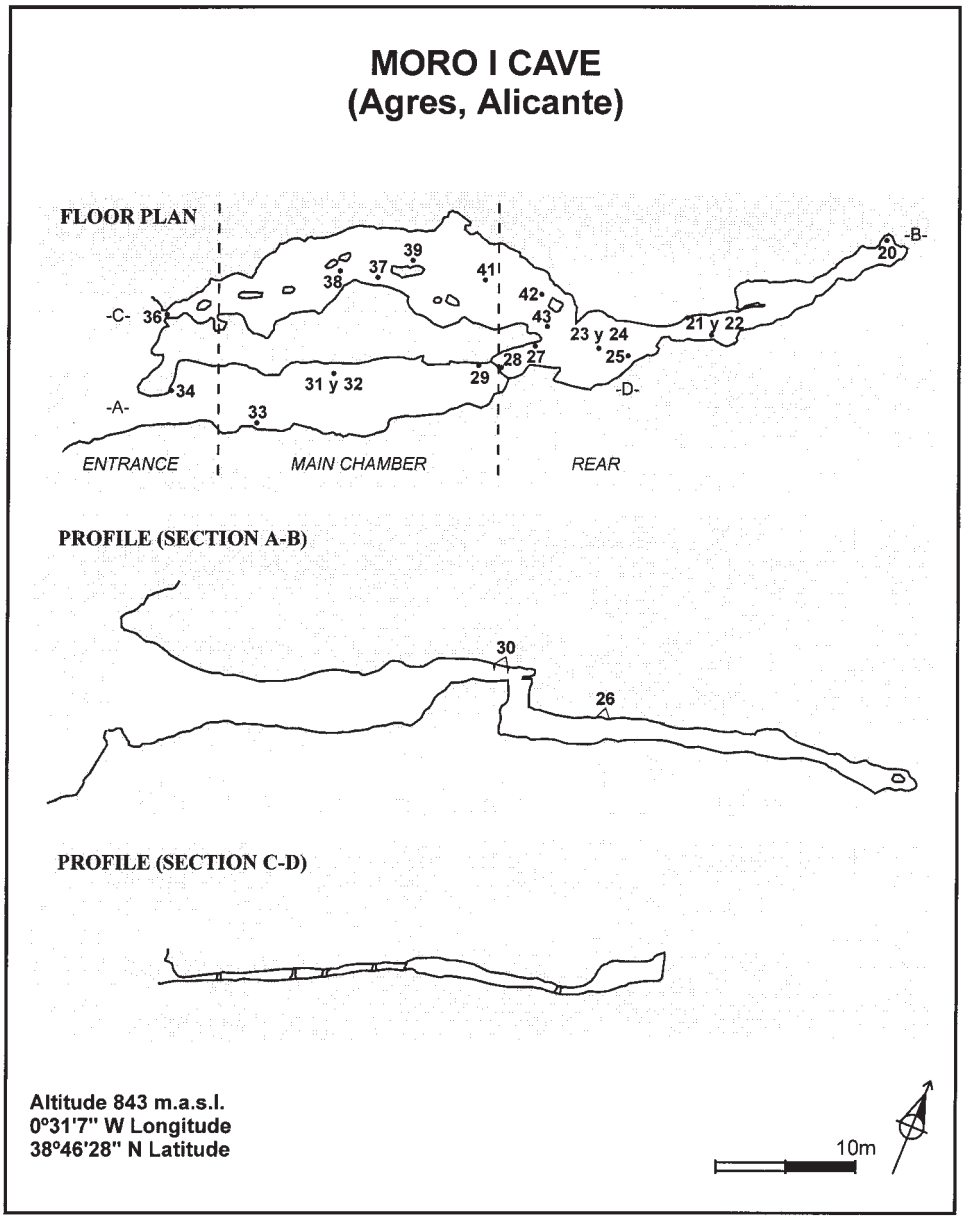

Figure 2 Longitudinal and vertical sections of Moro I cave and location of pollen samples.

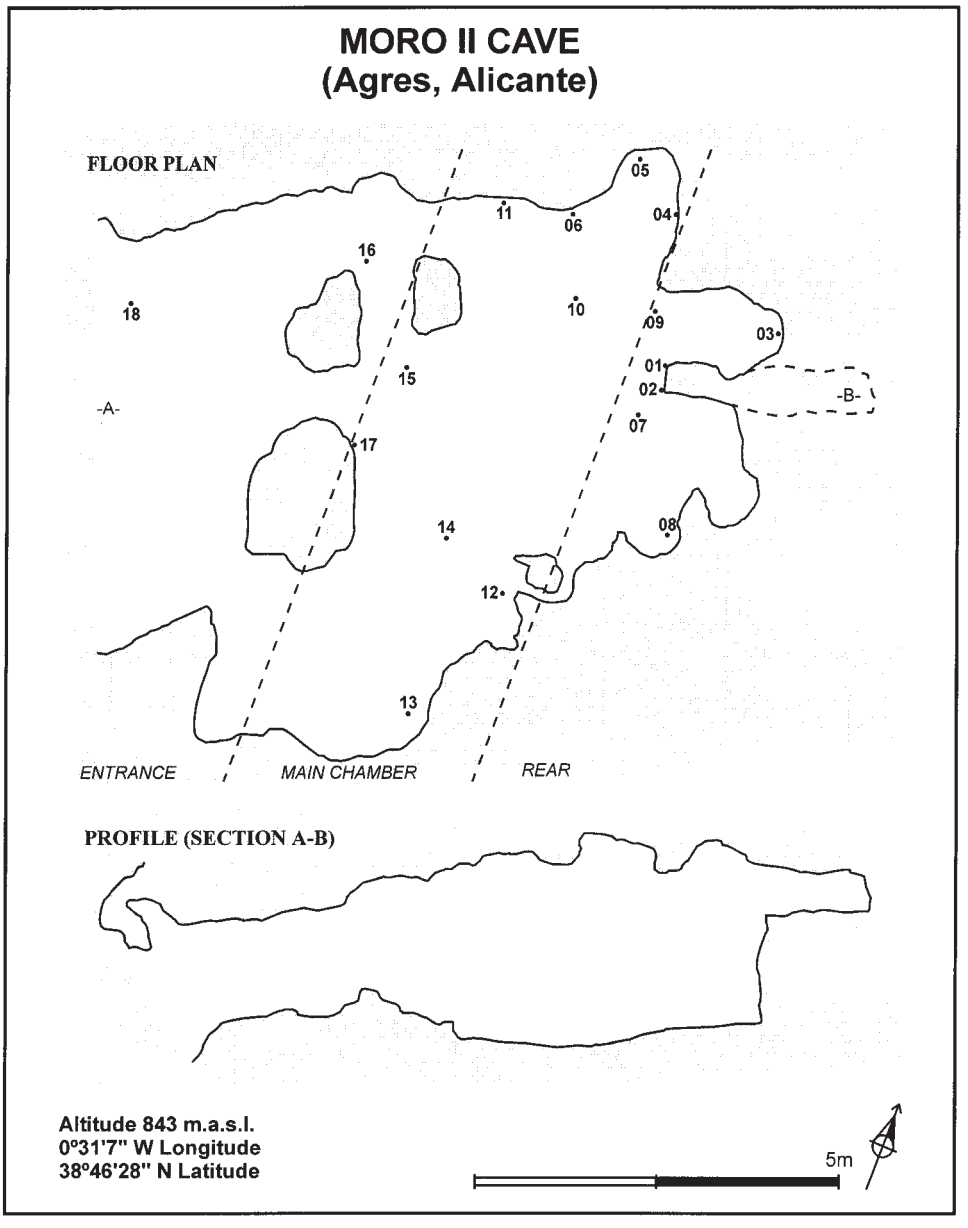

Figure 3 Longitudinal and vertical sections of Moro II cave and location of pollen samples.

35% HCl. Pollen from moss polsters was extracted by washing down with deionized water as described in Prentice (1986). At the beginning of the pollen processing, five *Lycopodium* spore tablets (12 100 spores tablet^{-1}, batch No. 124961) were added to each sample in order to facilitate concentration calculations (Stockmarr, 1972).

Identification and counting were performed using the pollen reference collection of the Laboratory of Palynology, Murcia University. Type 128a and other non-pollen palynomorphs (Fig. 4) follow descriptions and illustrations by Pals *et al.* (1980) and van Geel *et al.* (1989). Both pollen and non-pollen palynomorphs were included in the pollen sum. Pollen diagrams were plotted using Tilia 1.12 and TiliaGraph 1.18 programs (Grimm, 1987, 1991).

Results and discussion

Pollen-transport pathways

There is evidence for three types of pollen transport. Wind and animal transport seems to be ubiquitous, as suggested by a number of wind- and insect-pollinated pollen taxa, although some wind-pollinated taxa such as Poaceae may have been introduced into the cave sediment through herbivorous dung, and insect-pollinated taxa such as Cichorioideae could have been redeposited from external dust.

Irrespective of the exact place of incorporation, dung has been an important source of sediment. This is demonstrated by the presence of eggs of the parasite *Trichuris* in samples 1 and 24, the abundance of Sordariaceae ascospores in samples 1, 7, 8, 15, 27, 37, 38 and 39, and particularly *Sporormiella* in sample 4. *Tilletia* and *Thecaphora*, often parasiting grass ovaries (Ainsworth *et al.*, 1973), also could have been introduced through dung, especially the former as it co-varies with Sordariaceae (see Fig. 7). The coupled appearance of *Thecaphora* and Sordariaceae has been found in samples of Iron Age cow dung from Zimbabwe and South Africa (Carrión and Scott, 1998). It must be stressed that, in the present study, Sordariaceae spores (Fig. 4) are mostly abundant in samples of wet floor sediment (see Fig. 7), which suggests that the limiting factor for their occurrence in floor sediment may not be dung content but rather humidity and its consequent *in situ* fungal activity. The presence and occasional abundance of Zygnemataceae and Type 128a

Table 1 Samples from Moro caves

Site	Sample number	Sample type
MORO I cave	20, 21, 23, 28, 29, 31, 33, 34, 36	Dry floor sediment
	37, 38, 39, 42	Wet floor sediment
	22, 24, 26, 27, 30, 32, 41, 43	Speleothem
	25	Bat guano
MORO II cave	1, 2, 3, 4, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 18	Dry floor sediment
	5	Speleothem
	17	Spider's web
Exterior, close to the Moro I cave (Local, Fig. 2)	35, 44	Moss polsters
Exterior, close to the Moro II cave (Local, Fig. 2)	19	Moss polsters
Exterior, Agres valley and adjacent mountains (Regional, Fig. 2)	45, 46, 47, 48	Moss polsters

spores, *Gloeotrichia* sheats, and *Arcella* thecae (Fig. 4) suggests water transport through infiltration. Indeed, these palynomorphs are most frequent in speleothem and wet sediment samples (see Fig. 7). Chlamydospores of the fungus *Glomus* (Fig. 4) have been shown to be dispersed both by wind and animals, although wind seems to be more important in arid landscapes (Wilkinson, 1998). In Moro I, *Glomus* becomes abundant only in wet sediment samples, which suggests that the spores have been introduced into the cave by dripping water. A palynomorph association of *Glomus* with Sordariaceae (such as shown later in Fig. 7) has been reported recently from aerated sections of hyrax dung middens from central South Africa (Carrión *et al.*, 1999).

The quality of pollen analysis

Most samples of dry sediment yielded sufficient well-preserved grains to carry out pollen analysis, although a number of samples of wet sediment and speleothem provided counts that did not exceed 150 grains (Tables 2 and 3). The statistical reliability of these pollen spectra must be considered with caution.

The number of palynomorph types, ranging from 13 to 40 in Moro I and 27 to 54 in Moro II, is relatively high when compared with fossil assemblages from cave deposits. Normally these do not exceed 25 pollen taxa (Carrión *et al.*, 1999), although some caves show higher numbers (Carrión *et al.*, 1998).

Pollen concentration varies greatly, from 106 to 792 039 grains g^{-1} in Moro I (Table 2), and from 1514 to 1 154 630 grains g^{-1} in Moro II (Table 3), with the lowest values registered in speleothem and wet sediment samples (Tables 2 and 3). Mean concentration values for the Moro caves (64,361 grains g^{-1} in Moro I and 461,682 grains g^{-1} in Moro II), however, are higher than shown generally by fossil pollen assemblages from cave deposits: e.g. 10 000–290 000 grains g^{-1} in Cowboy Cave (Spaulding and Petersen, 1980); 2000–140 000 in four caves from the central Grand Canyon, USA (O'Rourke, 1985); and 510–7100 in Beneito Cave, Spain (Carrión and Munuera, 1997).

Indeterminable pollen frequencies are relatively high in samples 2, 7, 8, 20, 21, 39 and 42 (see Figs 8 and 13), but deterioration was not present everywhere, and taxonomic precision was good enough to discriminate more than 15 palynomorph types in most samples. Frequencies of indeterminable pollen grains normally have not been presented in the pollen diagrams from archaeological sites, but when available, they are generally high and reflect the importance of post-depositional processes in pollen decay (Carrión *et al.*, 1995).

Values of pollen concentration, number of palynological taxa, and frequency of indeterminable pollen are often considered to be good indicators of pollen analytical potential (Dimbleby, 1985). The Spearman coefficient shows a significant negative correlation between pollen concentration and indeterminable frequency in the case of Moro II, but not in Moro I (Table 4). It seems plausible that pollen concentration is linked primarily to the weight of pollen input rather than to post-depositional alteration. This is supported by the existence of a negative correlation between pollen concentration and distance to the entrance (Table 4). The number of taxa does not show significant correlation with any of the factors considered.

Distributional patterns: Moro I (Figs 5–9)

Despite their closeness to each other, the entrance samples 34 and 36 show different pollen spectra, with the former dominated by *Pinus* (76%) and the latter by several taxa (*Pinus* 27%, Poaceae 15%, Cistaceae 12%, Asteraceae 11%, *Olea* 8%). Pollen concentration varies along the entrance (71 240 grains g^{-1} in sample 36 to 126 413 grains g^{-1} in sample 34) and, with the exception of samples 31 and 33, remains below 100 000 grains g^{-1} throughout the cavity (Table 2).

Inside-cave pollen assemblages vary, in part, relative to the type of sediment. Spectra from wet sediment are dominated by Asteraceae (11–74%), moss spores, fungal spores such as *Tilletia* (36%, sample 38), Sordariaceae (24%, sample 38), *Glomus* (22%, sample 37), and indeterminable pollen (10–112% as excluded from the pollen sum). Pollen spectra from dry sediment show a higher diversity, a relatively constant pattern of Poaceae (4–33%) and Asteraceae (1–75%) dominance, with important contributions from Cistaceae, *Quercus* and *Pinus*. Although they become abundant in some samples, zoophilous taxa never exceed 60% (Fig. 9). Indeterminable pollen increase from the entrance (29%, sample 36) to inner areas (61%, sample 25). In fact, the Spearman coefficient shows a significant positive correlation between indeterminable percentage values and sample distance from the entrance (Table 4), which suggests that degradation processes are more effective towards the rear of the cavity, probably resulting from the occurrence of wetness–dryness cycles (Davis, 1990).

The high incidence of indeterminable pollen, together with moss and fungal spores, in samples of wet sediment supports the suggestion that the appearance of these cryptogam spores should be largely connected to post-depositional processes of biological degradation. Fossil sediment pollen data from Perneras Cave, southeastern Spain, supports this view (Carrión *et al.*, 1995). At this

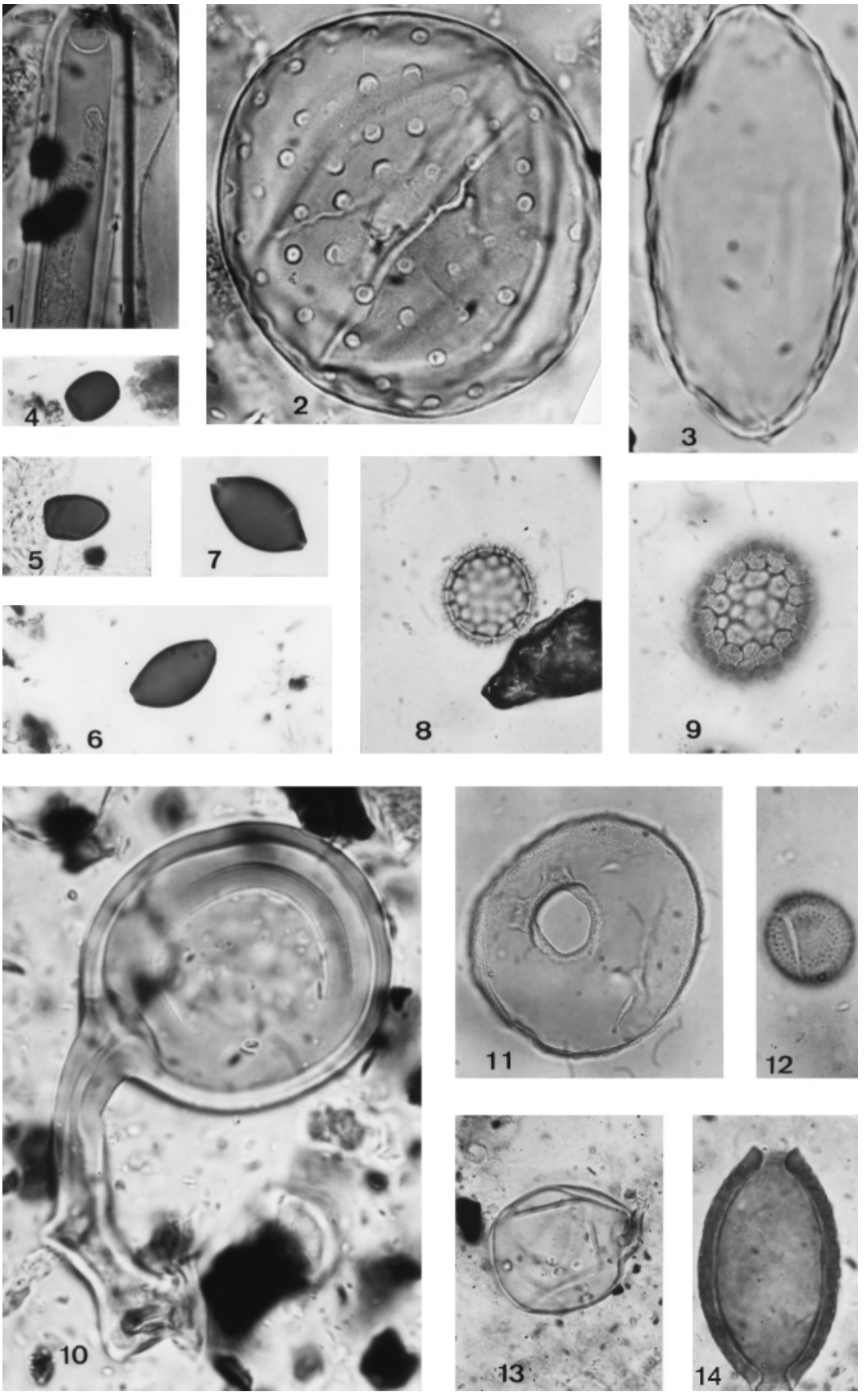

Figure 4 Light microscope micrographs of non-pollen microfossils in the surface sediment of Moro caves: 1, *Gloetrichia*, ×704; 2, *Zygnema*, ×704; 3, *Spirogyra*, ×704; 4–7, Sordariaceae, ×1760; 8 and 9, *Tilletia*, ×1760; 10, *Glomus*, ×704; 11, *Arcella*, ×704; 12, Type 128, ×1760; 13, *Glomus*, ×704; 14, *Trichuris*, ×704.

Table 2 Pollen sums and concentrations at Moro I cave according to sample type. Indeterminable pollen is not included in the total

Sample type	Sample number	Pollen sum	Concentration (grains g^{-1})
Dry floor sediment	20	215	15 367
	21	232	6767
	23	441	40 359
	28	444	14 206
	29	487	5314
	31	425	792 039
	33	441	249 066
	34	581	126 413
	36	476	71 240
Wet floor sediment	37	104	14 472
	38	118	14 904
	39	65	11 532
	42	101	15 398
Speleothem	22	46	223
	24	177	5805
	26	99	761
	27	103	679
	30	277	542
	32	442	3571
	41	59	106
	43	85	260
Bat guano	25	417	26 905
Exterior	35	455	1 076 927
	44	434	443 507

Table 3 Pollen sums and concentrations at Moro II cave according to sample type. Indeterminable pollen is not included in the total

Sample type	Sample number	Pollen sum	Concentration (grains g^{-1})
Dry floor sediment	1	439	95 780
	2	387	43 806
	3	682	206 384
	4	502	1 554 630
	6	585	341 523
	7	497	24 772
	8	438	28 108
	9	429	262 428
	10	585	805 902
	11	475	506 172
	12	551	495 300
	13	546	1 008 333
	14	631	750 499
	15	605	861 787
	16	583	147 220
	18	568	381 830
Speleothem	5	110	1514
Spider's web	17	585	794 287
Exterior	19	606	774 307

rock shelter, upper Palaeolithic infillings contain abundant *Glomus* assemblages, coinciding with low pollen concentration and abundance of degraded and reworked grains.

Speleothem samples show variable pollen percentages with, in some cases, high Cichorioideae (49%, sample 24), *Olea* (25%, sample 27; 20%, sample 30), and Asteroideae (20%, sample 41). Total pollen concentration (106–5805 grains g^{-1}) is much lower than in floor sediment samples (5314–792 039 grains g^{-1}) (Table 2). Bat guano (sample 25) is dominated by *Olea* (22%), Asteraceae (21%) and Poaceae (14%), among 32 other minor pollen taxa represented in the regional vegetation. Pollen concentration is 26 905 grains g^{-1} (Table 2).

Table 4 Spearman correlation coefficients for a set of variables (LE* = 0.05; LE** = 0.01; dist = distance to the entrance; anem = anemophilous taxa; zooph = zoophilous taxa; conc = pollen concentration; ast = Asteraceae; indet = indeterminable pollen, fung = fungal spores; lam = Lamiaceae)

Variables	Moro I	Moro II
Dist-Anem	–0.4012*	–0.4255*
Dist-Zooph	0.5213**	0.4176*
Dist-Ast	0.5113**	
Dist-Lam	0.5613**	
Dist-Conc	–0.5209**	–0.5134*
Dist-Indet	0.6593**	
Indet-Conc		–0.4667*
Indet-Fung	0.4558*	
Indet-Ast	0.6174**	0.5368**
Ast-Conc		–0.4439*
Ast-Fung	0.5970**	

The Spearman correlation coefficient (Table 4) provides evidence that anemophilous taxa are more abundant in the entrance areas, whereas zoophilous taxa, especially Asteraceae and Lamiaceae, increase towards the rear. This agrees with preliminary conclusions in pioneer work by van Campo and Leroi-Gourhan (1956), Loublier (1974), Bui-Thi-Mai (1974), Bottema (1975) and Leroi-Gourhan and Renault-Miskovsky (1977), and recent studies by Coles and Gilbertson (1994), although the issue needs more experimentation because of the complexity of pollen taphonomy in caves (Coles *et al.*, 1989; Davis, 1990).

The component Y1 of the principal component analysis (see Fig. 15a later, and Table 5) displays large positive loadings for anemophilous taxa and pollen concentration, and large negative loadings for the distance to the entrance, indeterminable, zoophilous and Asteraceae pollen percentages. This confirms most Spearman correlations (Table 4) and confirms the existence of an entrance to rear gradient, through which degradation processes increase, pollen input diminishes and pollen spectra are progressively biased by the influence of animal transport. This pattern of variation is also observed when samples are plotted instead of variables (see Fig. 15b). Thus, for instance, samples 34, 44 and 35, which are located in the entrance of the cave, show the lowest Y1 values, whereas sample 20, in the very rear, has the highest. The component Y2, fungal spores versus number of taxa (see Fig. 15a), could plausibly be identified with sediment wetness. When plotting samples (see Fig. 15b), the highest Y2 values correspond to the wet sediment samples 42, 39, 37 and 38. The first two principal components accounted for 44.4% and 23.7% of the total variance, 68.1% in total (Table 5).

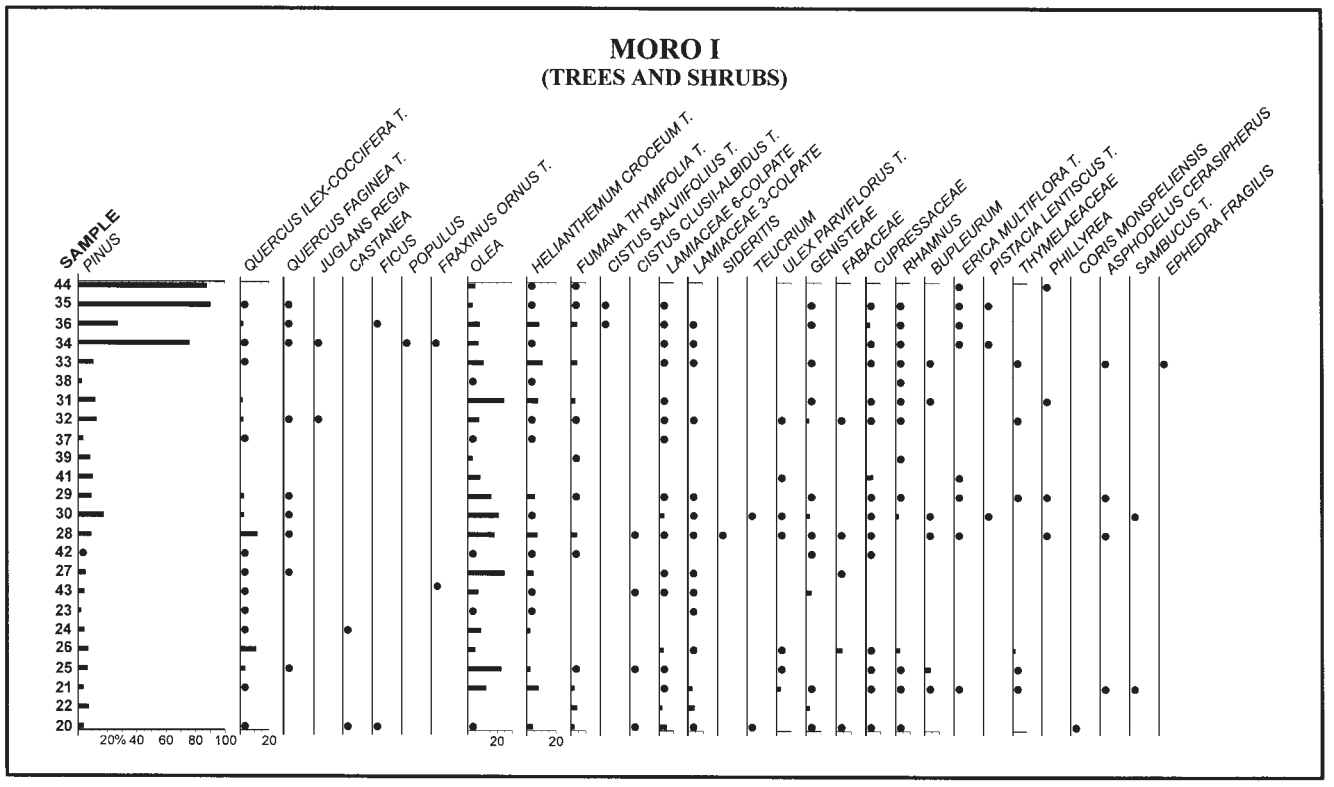

Figure 5 Pollen diagram of arboreal taxa at Moro I. Samples ordered according to distance from the entrance.

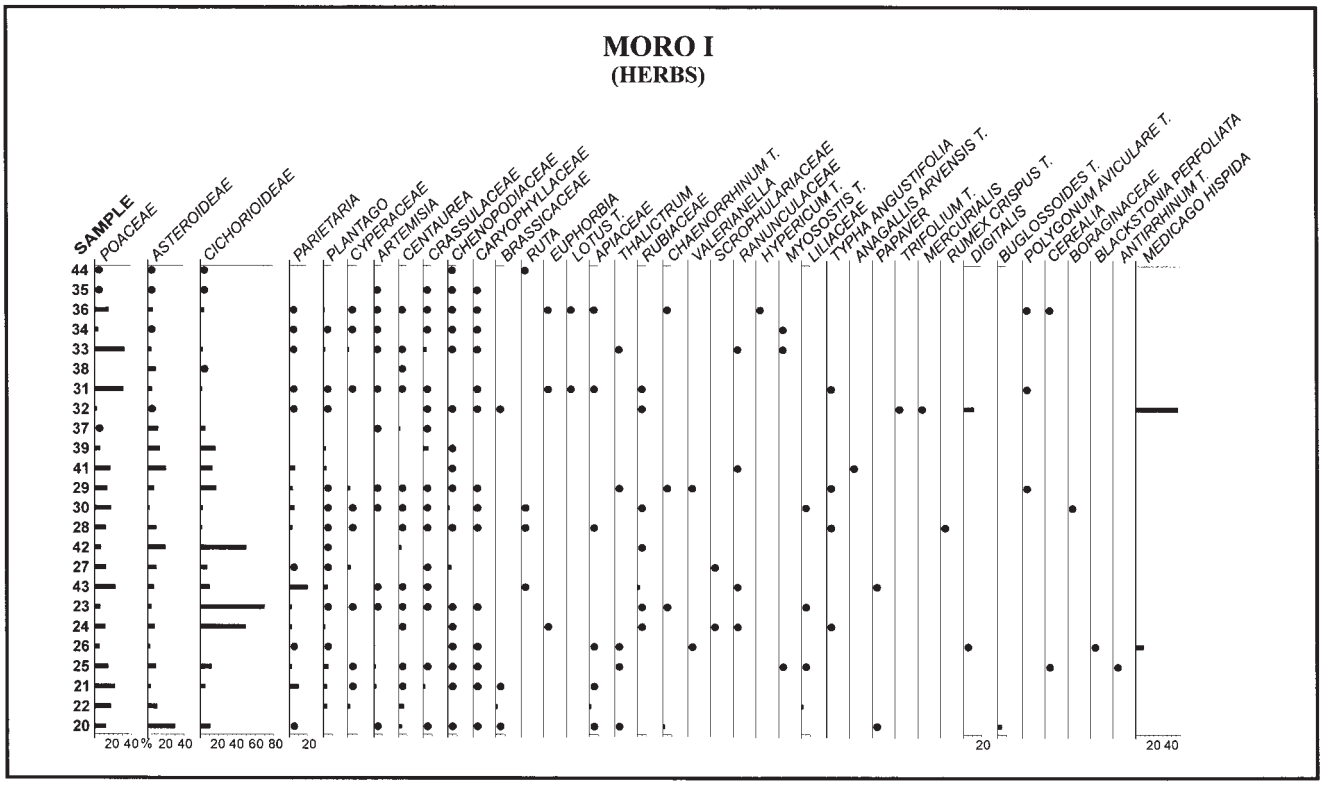

Figure 6 Pollen diagram of herbaceous taxa at Moro I. Samples ordered according to distance from the entrance.

Distributional patterns: Moro II (Figs 10–14)

The entrance samples 16 and 18 show similar pollen spectra in terms of composition and pollen dominants (*Pinus* 55% and 59% respectively). Taxa occurring at lower values are *Olea* (8% and 6%), Cistaceae (5% and 6%), Asteraceae (4% and 7%) and Poaceae (10% and 5%). These samples resemble the exterior surface sample 19 (see below). They also are similar to the spider's web sample 17, although this has a higher pollen concentration (794 287 grains g^{-1}) (Table 3). Pollen concentration values decrease from the exterior sample 19 (774 307 grains g^{-1}) to samples 16 and 18 at

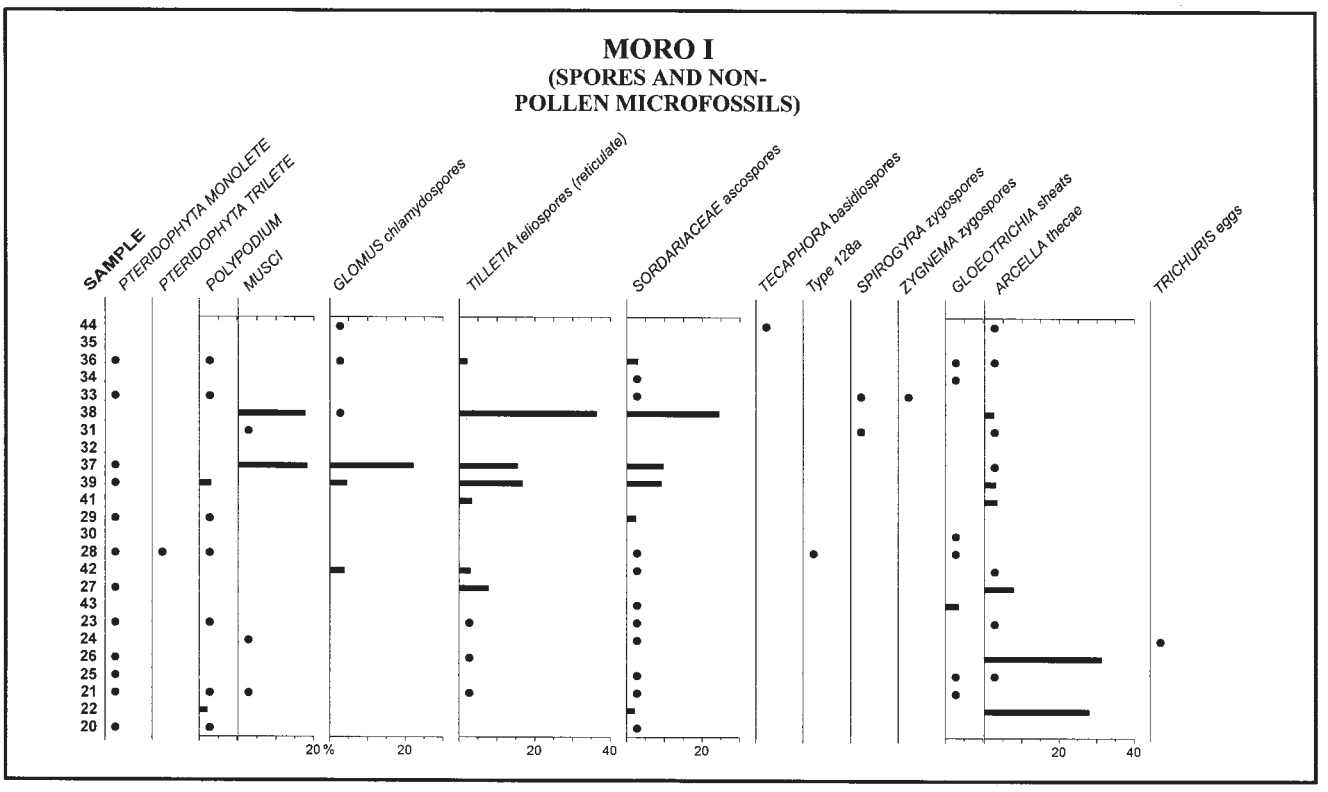

Figure 7 Pollen diagram of spores and non-pollen microfossils at Moro I. Samples ordered according to distance from the entrance.

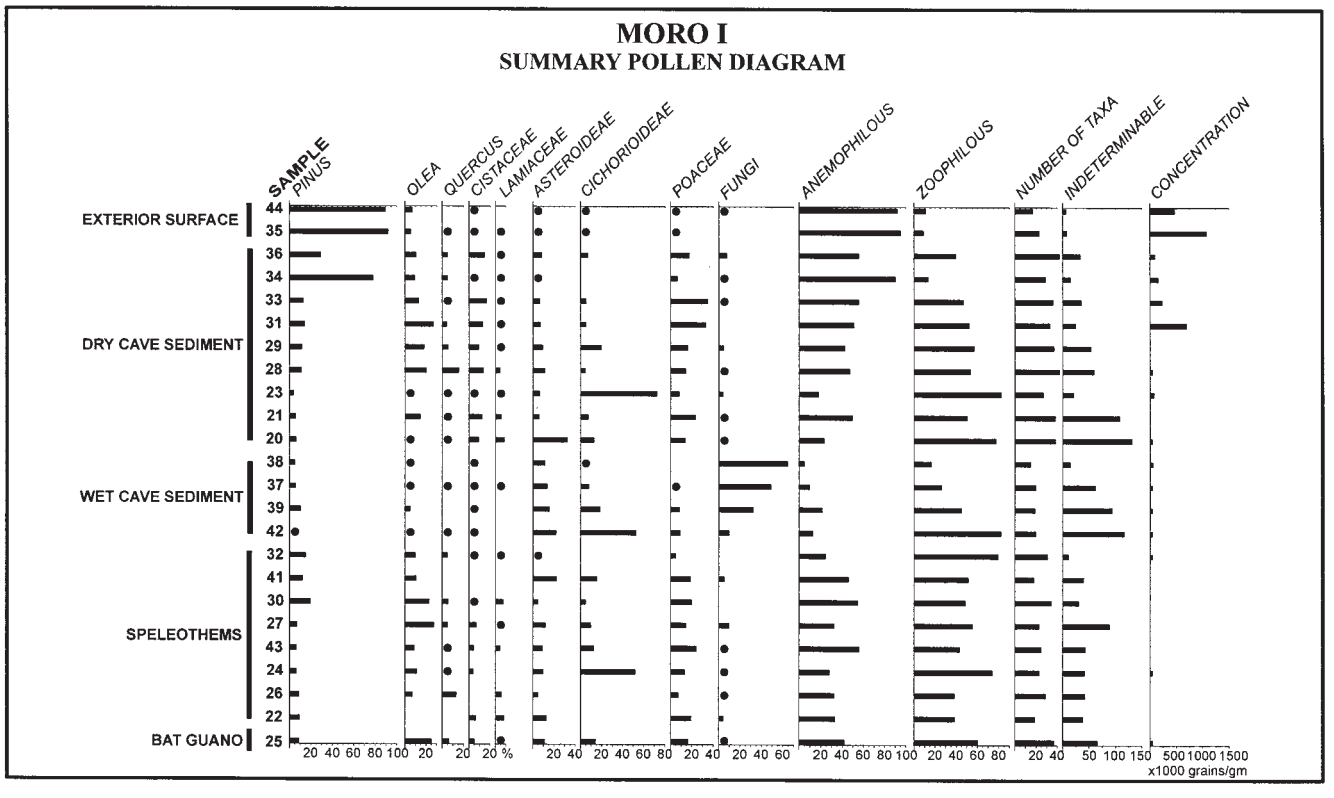

Figure 8 Summary pollen diagram of selected taxa at Moro I. Samples grouped according to sediment types and distance from the entrance.

the entrance (147 220 grains g^{-1} and 381 830 grains g^{-1} respectively). In contrast to Moro I, however, this pattern does not continue into the cave, where pollen concentration values surpass exterior ones (i.e. 1 008 333 grains g^{-1} in sample 13 861 787 grains g^{-1} in sample 15, 805 902 grains g^{-1} in sample 10 and 1 554 630 grains g^{-1} in sample 4) (Table 3).

Inside-cave pollen assemblages are evenly dominated by Poaceae (5–29%), *Pinus* (3–59%), *Quercus* (1–31%), *Olea* (2–12%), Cistaceae (3–18%), and Lamiaceae (0–3%), and

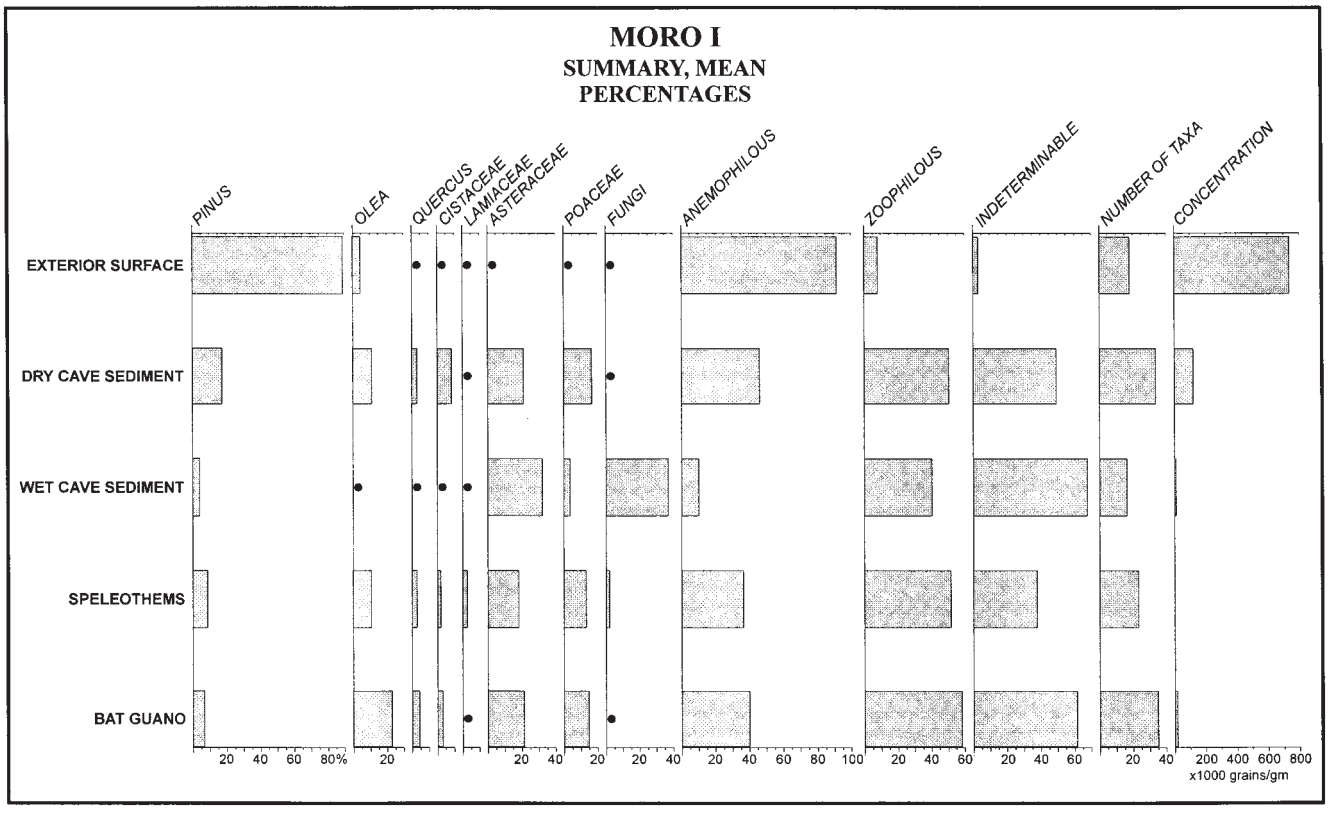

Figure 9 Summary pollen diagram of mean percentages of each sediment type at Moro I.

Table 5 Principal component loadings and percentages of variance explained by the first two principal components for surface pollen samples from Moro I cave sediments

Variable	CP1	CP2
Distance to the entrance (dist)	–0.436	–0.151
Indeterminable (indet)	–0.389	–0.062
Anemophilous (anem)	0.419	–0.352
Zoophilous (zooph)	–0.436	–0.258
Asteraceae (ast)	–0.387	0.069
Fungal spores (fung)	–0.022	0.666
Number of taxa (taxa)	–0.055	–0.566
Pollen concentration (conc)	0.374	–0.121
Variance (eigenvalues)	3.5546	1.8934
Per cent of total variance	44.4	23.7
Cumulative per cent of total variance	44.4	68.1

similar to the samples of dry floor sediment in Moro I. Pollen concentration varies from 24 772 (sample 7) to 1 554 630 g^{-1} (sample 4) (Table 3). The pollen spectrum of speleothem, sample 5, resembles those found in floor samples. It is dominated by Poaceae (22%), *Pinus* (16%), *Olea* (16%), *Quercus* (8%), Lamiaceae (2%) and Cistaceae (1%). As in Moro I, the speleothem shows the lowest total pollen concentration (1514 grains g^{-1}) (Table 3).

By comparison, Moro II shows pollen spectra with lower percentages of Sordariaceae (0–7%) than Moro I (0–24%) (Fig. 12), a higher number of taxa (27–54 in Moro II, 13–40 in Moro I) (Fig. 13), and higher pollen concentrations (Table 3). There is no significant correlation in Moro I between indeterminable values and sample distance to the entrance (Table 4).

In the principal components analysis, the component Y1 (Fig. 15c, Table 6) shows strong positive loadings for distance to the entrance, indeterminable, zoophilous taxa, Asteraceae and fungal spores, although grouping is not so tight as for Moro I. Pollen concentration and anemophilous taxa show negative loadings. The analysis of samples (Fig. 15d) suggests Y1 is correlated with the distance to the entrance. Thus, for instance, the innermost samples, 1, 7 and 8, correspond to the highest Y1 values. The second principal component Y2, the interpretation of which remains uncertain, shows the largest positive loadings for indeterminable and anemophilous taxa, and the largest negative loadings for zoophilous taxa, number of taxa and pollen concentration. The first two principal components accounted for 49% and 21.8% respectively of the total variance, 70.8% in all (Table 6).

External vegetation and pollen spectra from Moro caves

The most abundant pollen types recorded from both caves' surfaces represent the most prominent plant taxa forming the thermo-Mediterranean vegetation of eastern Spain, namely *Pinus*, *Quercus*, *Olea*, Cistaceae, Lamiaceae, Cupressaceae, *Rhamnus*, *Pistacia*, Fabaceae, Poaceae and Asteraceae (Figs 5–14). Presumably, a part of the *Olea* records comes from cultivars. In addition, there are pollen records of plant taxa that define regional communities and chorological sectors. These are *Fraxinus ornus*, *Quercus faginea*, *Acer granatense*, *Ulex parviflorus*, *Erica multiflora*, *Viburnum tinus*, *Arctostaphyllos uva-ursi* and *Coris monspeliensis* (Costa, 1982). In addition, high frequencies of *Parietaria*, *Rhamnus* and Lamiaceae 3-colpate pollen are best explained by *in situ* pollen deposition from, respectively, *Parietaria judaica*, *Rhamnus lycioides* and *Ballota hirsuta*, with individual plants growing on the cave entrance walls

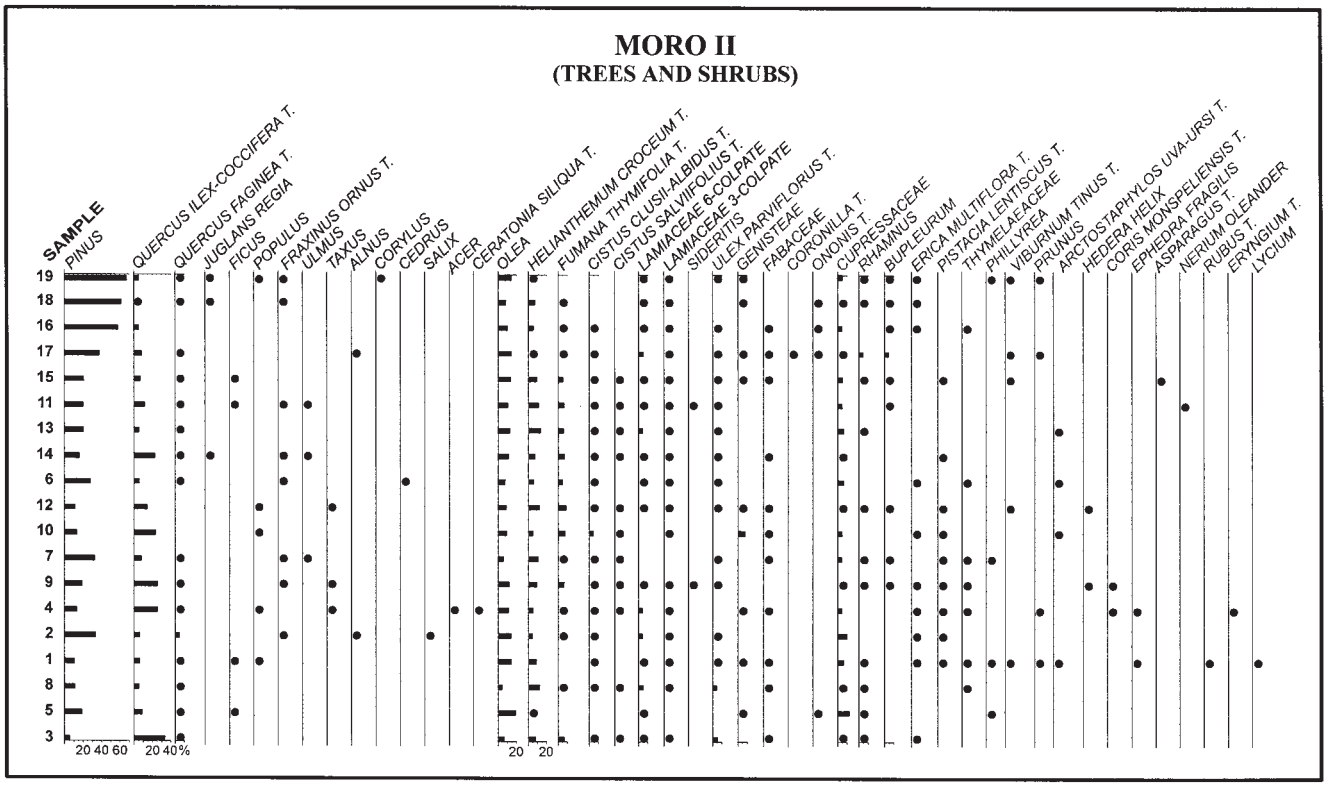

Figure 10 Pollen diagram of arboreal taxa at Moro II. Samples ordered according to distance from the entrance.

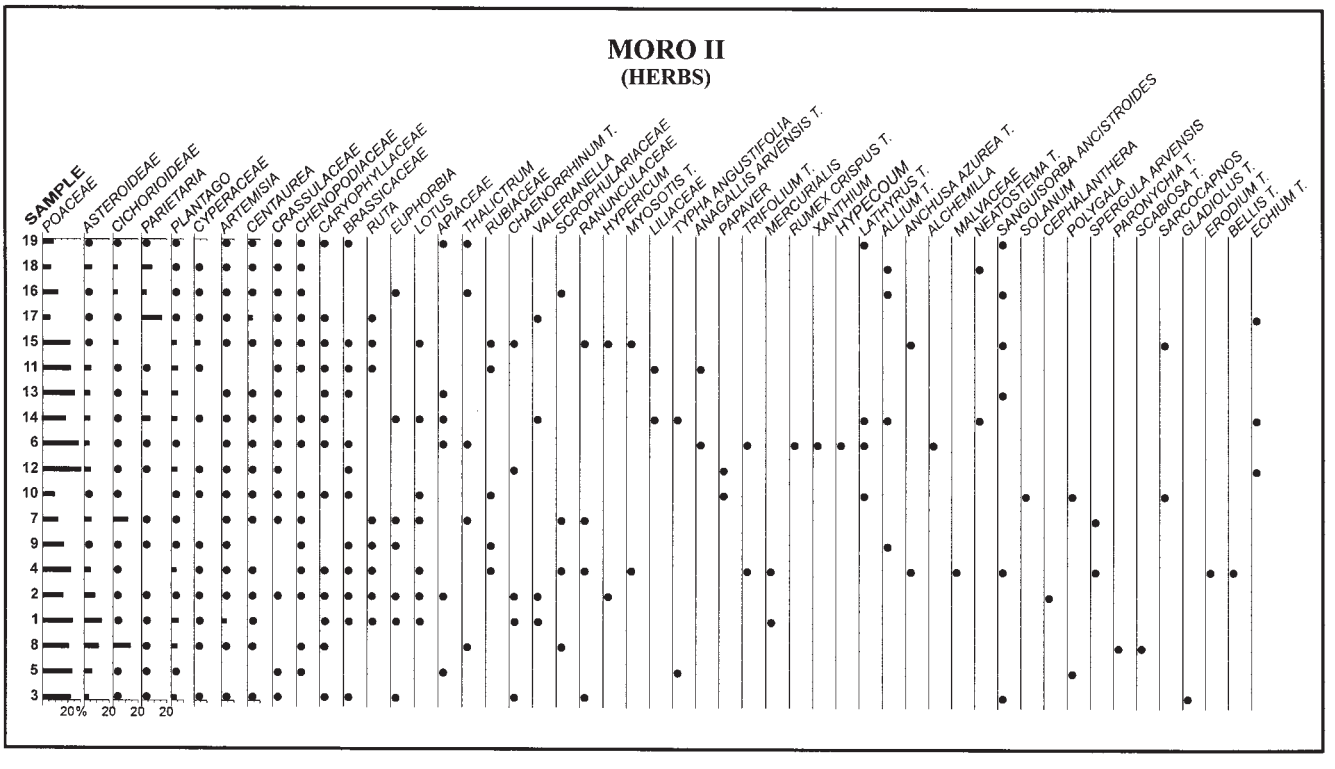

Figure 11 Pollen diagram of herbaceous taxa at Moro II. Samples ordered according to distance from the entrance.

and overhangs. This also may account for the occasional presence of *Ficus*, *Sedum*, *Euphorbia*, *Hypericum* and *Mercurialis*. Other taxa occurring above 2% (*Plantago*, *Artemisia*, *Centaurea*, Chenopodiaceae), and some minor contributors (*Lotus* type, *Myosotis* type, *Anagallis arvensis*, *Cerealia*, *Polygonum aviculare* type, *Buglossoides* type, *Bellis* type, *Malvaceae*, *Lathyrus* type, *Neatostema* type, *Xanthium*, *Solanum*, *Medicago hispida* type) are indicators of ruderalisation. The results of *Castanea*, *Cedrus* and *Corylus* are presumably a consequence of long-distance pollen transport, although they may grow in isolated locations in the Agres valley.

The exterior samples, 19, 44 and 35, used to define a 'local pollen rain', are dominated by *Pinus* (65, 88 and 90% respectively) and, to a lesser extent, *Olea* (12, 5 and 3%

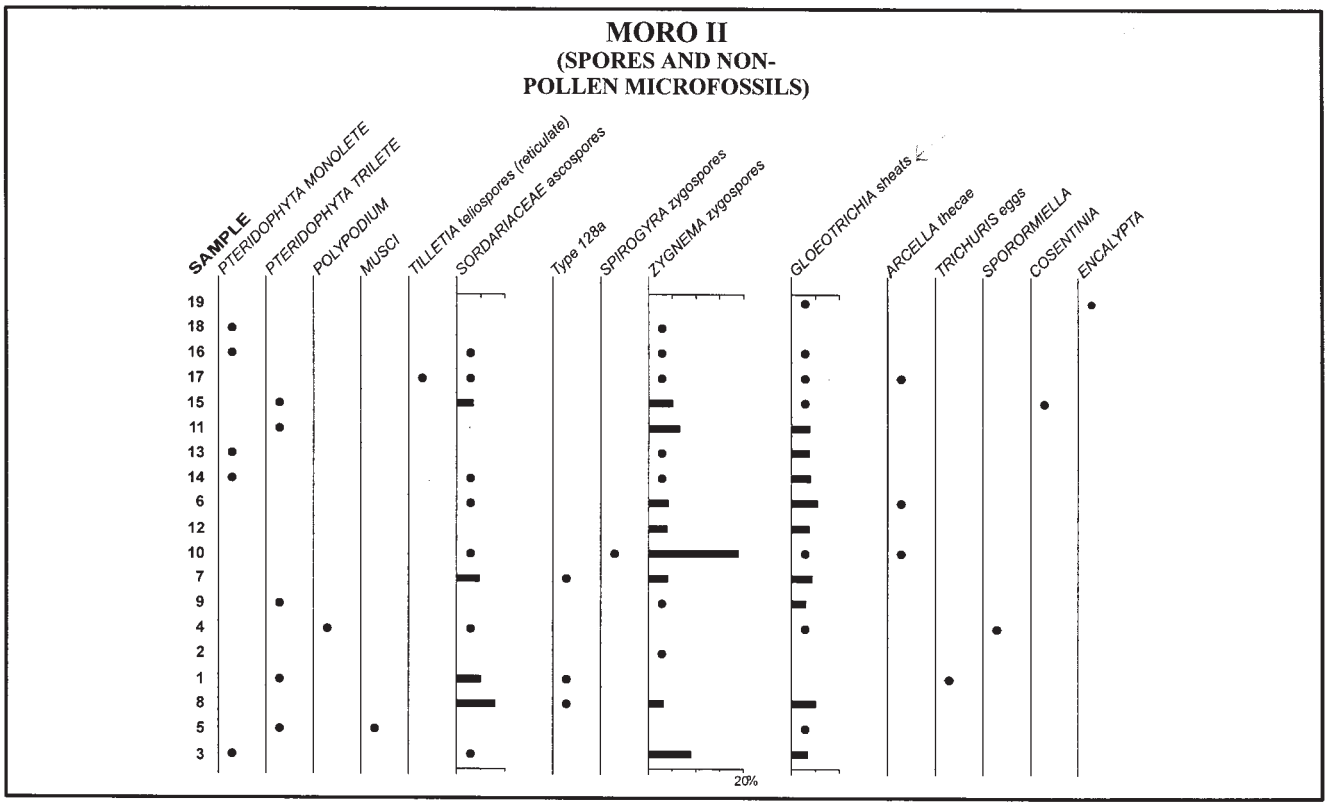

Figure 12 Pollen diagram of spores and non-pollen microfossils at Moro II. Samples ordered according to distance from the entrance.

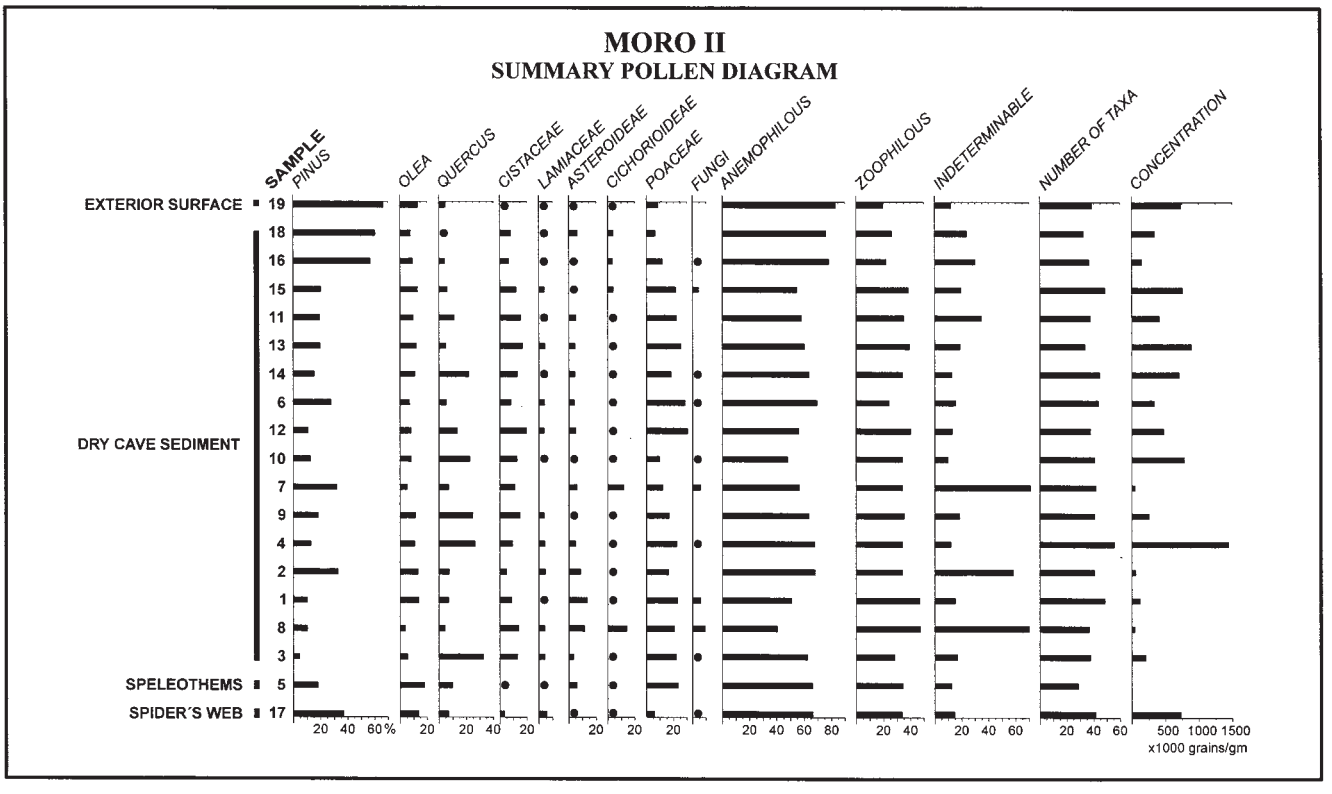

Figure 13 Summary pollen diagram of selected taxa at Moro II. Samples grouped according to sediment types and distance from the entrance.

respectively). Poaceae does not exceed 5%, with the exception of sample 19 (7%). Many taxa do not exceed 3%, such as Cistaceae, *Quercus*, *Erica*, *Phyllirea*, Asteraceae, Chenopodiaceae and *Ruta*. Pollen concentration is relatively high (443 507 grains g^{-1} in sample 44, 1 076 927 grains g^{-1} in sample 35). The exterior samples 45, 46, 47 and 48, defining the 'regional pollen rain', are also dominated by *Pinus*, but with lower percentages (22–83%). The second most important pollen component of the regional pollen rain is *Quercus* (2–69%), and there are minor values for *Olea*

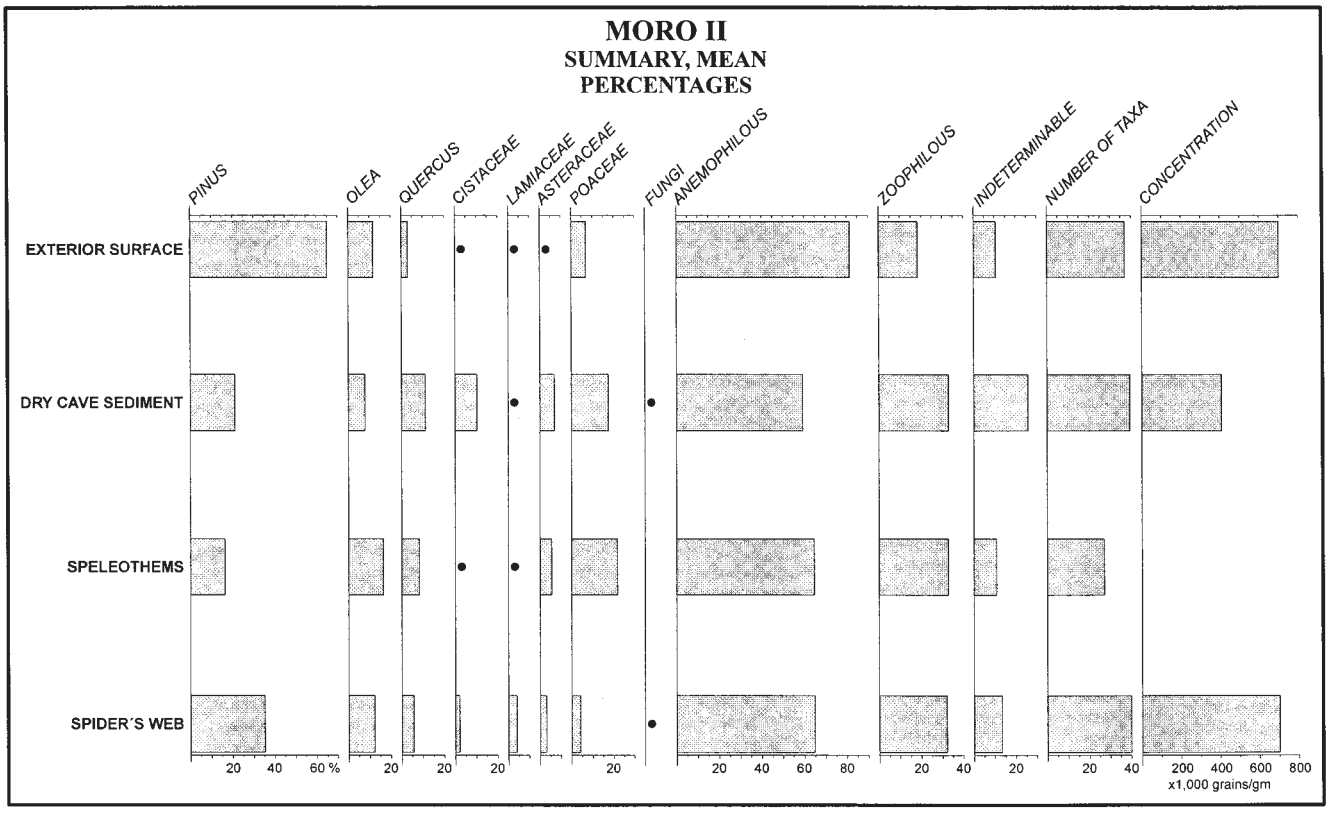

Figure 14 Summary pollen diagram of mean percentages of each sediment type at Moro II.

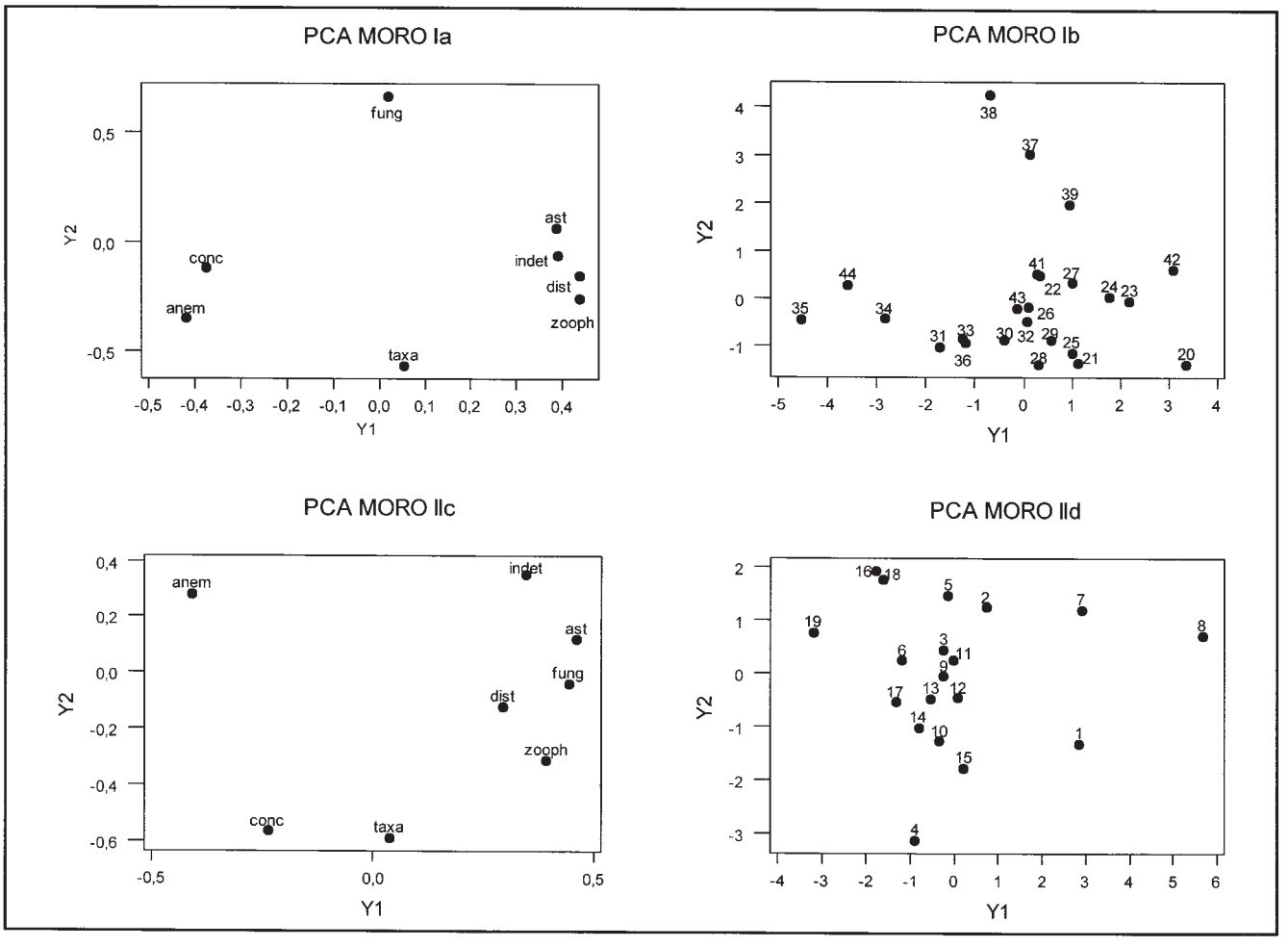

Figure 15 Principal components analysis, factor scores for variables and pollen samples at Moro caves.

Table 6 Principal component loadings and percentages of variance explained by the first two principal components for surface pollen samples from Moro II cave sediments

Variable	CP1	CP2
Distance to the entrance (dist)	0.297	–0.120
Indeterminable (indet)	0.347	0.351
Anemophilous (anem)	–0.41	0.279
Zoophilous (zooph)	0.394	–0.313
Asteraceae (ast)	0.462	0.122
Fungal spores (fung)	0.445	–0.041
Number of taxa (taxa)	0.036	–0.591
Pollen concentration (conc)	–0.237	–0.567
Variance (eigenvalues)	3.9193	1.7447
Per cent of total variance	49.0	21.8
Cumulative per cent of total variance	49.0	70.8

(1–2%), Poaceae (1–4%), Asteraceae and Cistaceae (0–1%). Mean pollen concentration is 1 300 558 grains g^{-1}.

Figure 16 illustrates a percentage comparison of the main pollen taxa in floor dry sediment, local and regional pollen inputs. There are significant differences both between each cave and the whole set of cave samples. These differences are particularly marked for *Pinus* and *Quercus*, and only for *Olea* is there a similarity between cave and local pollen input (Figure 16). With the exception of Poaceae, wind-pollinated taxa are underrepresented in the cave pollen spectra and insect-pollinated taxa are overrepresented (Figure 16), particularly in Moro I. However, it must be kept in mind that the external pollen rain is, on its own, a biased representation of vegetation (Janssen, 1972). Thus, for instance, when considering vegetation-cover values from phyto-sociological tables from the area (Costa *et al.*, 1982; Peris, 1983; De la Torre, 1991), *Pinus* does not exceed a 50% cover in the vicinity (whereas it surpasses 80% in local pollen rain) and never reaches a 30% cover within the regional area (although it surpasses 55% in regional pollen rain). *Quercus*, at around 20% cover in phyto-sociological tables, would also be overrepresented in the regional pollen rain. It is worth mentioning that the mean pollen spectra from Moro caves appears to offer a better reflection of vegetation cover than the exterior pollen rain. This could be merely a chance occurrence, or the result of a complex of methodological constraints (i.e. different number of samples considered for cave and external sediment, different number of taxa to share an equal 100% of total frequency). Given the tendency of cave sediment to overrecord entomophilous taxa, it might seem logical to assume that this sediment can correct, at least in part, the bias produced by the very abundant production and almost universal dispersal of pollen of wind-pollinated taxa. We now need, however, to determine to what degree this effect could affect individual taxa.

In order to determine the most suitable samples for pollen analysis from cave sediments, a linear model has been developed that statistically contrasts internal and external pollen input at the sample level. This model establishes the amount of external-sample variability explained by internal-sample values, i.e. it quantifies the representativity of internal samples with respect to the external pollen rain. The model establishes a relationship between pollen percentages of each internal sample with external percentages (local and regional in each case).

The model can be represented as follows:

$$P_{ext} = c + a_1 p_1 + a_2 p_2 + \ldots \quad (1)$$

where c, a_1, a_2, ... are constant values, p_1, p_2, ... are internal relative pollen percentages, and P_{ext} represents external pollen percentages. The parameters c, a_1, a_2, ... are estimated automatically by this model (equation 1) from the relationships between external and internal pollen percentages. From these estimations, and using this model (equation 1), both local and regional pollen percentages (P_{ext}) are calculated from the internal pollen percentages (p_1, p_2, ...) in different sample points (Arnold, 1981). The goodness of the model is measured using the squared correlation coefficient (ExpVar%) which gives the variability of external pollen percentages explained by the model (equation 1).

It must be concluded from the explained variability percentages (ExpVar%) obtained for Moro I and Moro II that dry floor sediment is, beyond doubt, the most reliable for pollen analysis (Table 7a). This occurs for both local and regional data, and contrasts with the assumption that pollen spectra from caves are strongly biased by local input (Bui-Thi-Mai, 1974; Burjachs, 1986; Weinstein-Evron, 1983, 1994). Speleothem is potentially interesting, but wet sediment contains too many altered pollen spectra.

When the samples of dry sediment are grouped according to the distance from the entrance (cave areas of Figures 2 and 3), both caves behave differently (Table 7b). In accordance with correlation and principal component analysis data described above, the sac-like Moro I cave shows a distance–decay pattern towards the main chamber, which begins abruptly once the entrance area is passed. The inner increase in ExpVar% (Table 7b) could be due to the effect of increased entomophilous pollen-taxa frequencies. It is important to note that only certain samples close to the entrance appear suitable for reliable pollen analysis, a point that agrees with data from pollen influx studies carried out by Burney and Burney (1993) in several caves from New York State. These authors showed that influx rates declined rapidly at greater distances from an entrance. The more isodiametric Moro II cavity offers a better potential, especially in the main chamber, but it is still also acceptable in the entrance and rear areas.

Finally, samples close to the cave walls (up to 50 cm from the wall, parietal samples) display lower values of ExpVar% (Table7c) than samples more distant from the walls (non-parietal samples). This phenomenon is apparent in both Moro I and Moro II cavities but in Moro I is crucial because parietal samples show very low values of ExpVar% and are, therefore, very far from representing the external pollen input. In Moro II, parietal samples can still be significant. This confirms the importance of the morphology of caves for pollen studies and the fact that better results are obtained from samples from the centre of the cavity (O'Rourke, 1985; Davis, 1990; Burney and Burney, 1993).

Final remarks

It is clear that cave palynology still needs much experimentally based work before we can make reliable inferences in terms of palaeoecology and palaeoclimatology. Recent advances, however, confirm its potential. First, long pollen sequences have been reported from cave sediments with acceptable palynomorph preservation and concentration, ecological coherence of the pollen assemblages, chronological control, and suitable correlation with reference to lacus-

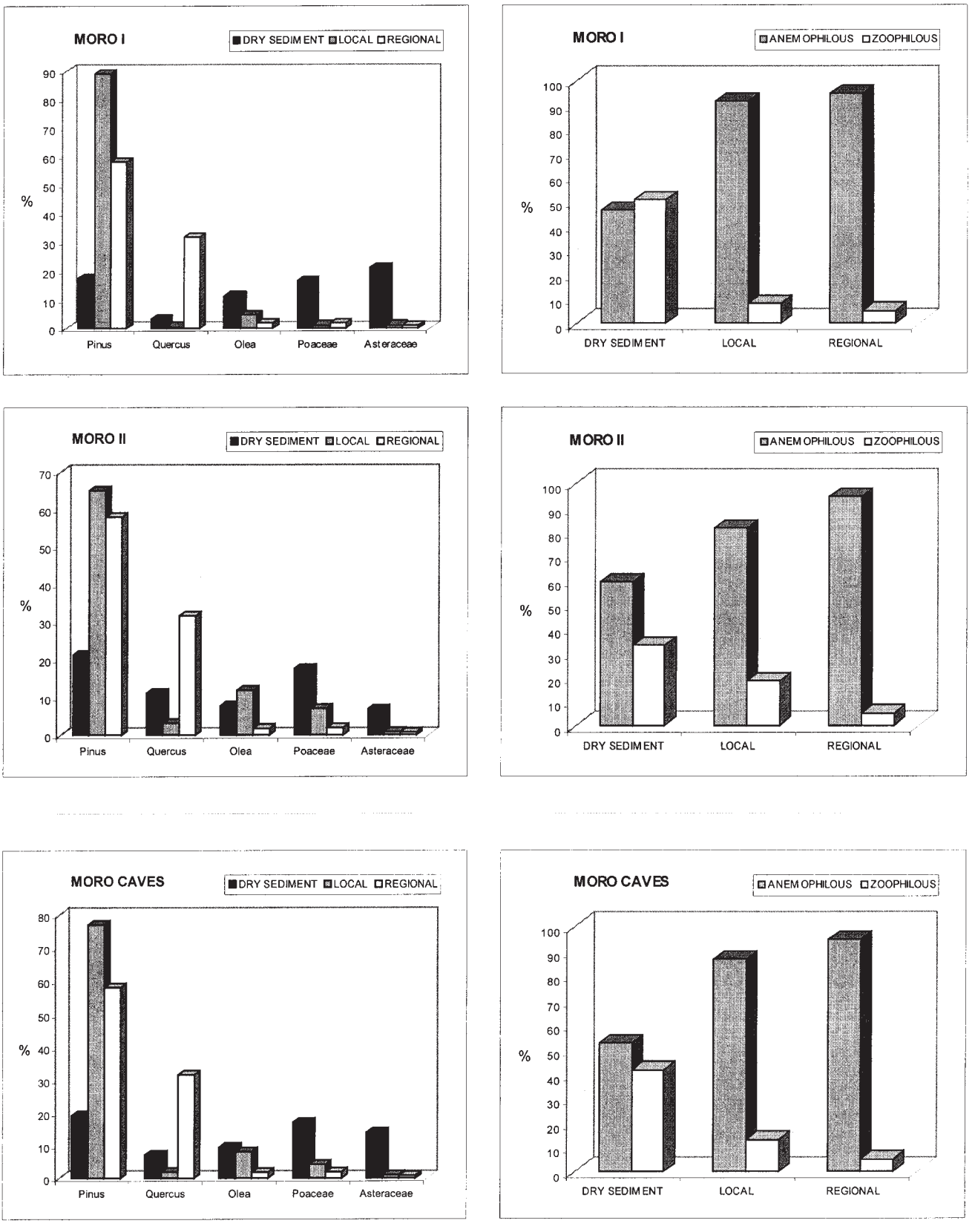

Figure 16 Comparision of mean regional and local cover with dry cave sediment pollen spectra and comparison of anemophilous–zoophilous taxa at local and regional cover with the mean of dry cave sediment.

trine sequences (see Carrión *et al.*, 1999). Second, caves are often sites of archaeological excavation and hence the sediments provide palaeoecological data in a multidisciplinary context. Third, caves frequently lie in physiographically different environments from lake and mire sites, and add valuable information, for example, on montane palaeovegetation and on location of the glacial refugia of thermophilous plant taxa. Finally, entomophilous taxa, often dominating the vegetation of dry lands, are poorly represented in lacustrine or marine palynology and, therefore, biotic transport into cave sites can be more of a help than a hindrance in reconstructing palaeoenvironments.

Table 7 Regression analyses (a) Between samples of Moro caves according to sediment type and local and regional samples

Sediment type		ExpVar (%)	
		Local	Regional
Moro I	Dry, surface	99.9	95.1
	Wet, surface	5.4	15.6
	Speleothem	48.7	50.3
	Bat guano	1.0	15.6
Moro II	Dry, surface	99.7	99.5
	Speleothem	31.9	25.0
	Spider's web	81.7	70.8

(b) Between dry floor sediment samples of Moro caves according to distance from the entrance and local and regional samples

Cave area		ExpVar (%)	
		Local	Regional
Moro I	Entrance	99.6	78.5
	Main chamber	7.2	19.4
	Rear	12.0	39.8
Moro II	Entrance	93.0	80.1
	Main chamber	92.5	92.4
	Rear	76.3	77.3

(c) Between dry floor sediment samples of Moro caves according to nearness to the cavity wall and local and regional samples

Sample type		ExpVar (%)	
		Local	Regional
Moro I	Parietal	17.2	39.5
	Non-parietal	99.7	79.4
Moro II	Parietal	91.1	87.0
	Non-parietal	99.3	97.7

This paper stresses that neither problems with concentration nor post-depositional alteration of pollen assemblages seem to be as general and important to suggest that cave sediments should be ignored as a source of palaeoecological information. What cannot yet be produced is a categorical set of empirical indicators of analytical success, in part because pollen deposition in caves is complex and subject to stochastic elements (Burney and Burney, 1993). From our results and other published studies, however, we are aware that caves with large entrances and isodiametric chambers present fewer problems of alteration in the pollen assemblages. Normally sampling should be undertaken on the basis of a multiple-profile approach, if possible not very close to parietal and rear areas and avoiding zones of actual moisture, or areas where old cycles of hydratation–dessication can be detected from sedimentological features.

It is of vital importance to use all the information available (pollen percentages, concentration, diversity and preservation) to establish a robust taphonomic model. This then facilitates the isolation of abnormal inputs, e.g. overrepresentation of entomophilous taxa, allowing a more reliable ecological interpretation of the data (Carrión, 1992a). Furthermore, in arid lands where the entomophilous component of the vegetation reaches high values (Horowitz, 1992), this can partially correct the bias produced by the universal prevalence of airborne transport and deposition.

Speleothems from the Moro caves and from other sites (Carrión and Scott, 1999) have been demonstrated not to be suitable for pollen analysis. However, in other cases, especially when situated close to the entrances of caves from arid regions, analyses have been more successful (Brook *et al.*, 1990).

Although in a rather uneven form throughout the caves, sediments from the Moro caves contain pollen assemblages that reflect the vegetation of the local and regional catchment areas. Whether this relationship can be established for other cave systems can be determined only from further studies.

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