Cryptogam spores and other non-pollen microfossils as sources of palaeoecological information: Case-studies from Spain

Article *in* Annales Botanici Fennici · January 2002

2 authors:

José Carrión
University of Murcia

Cadine Navarro
Massachusetts Institute of Technology

Ann. Bot. Fennici 39: 1–14 ISSN 0003-455X
Helsinki 8 March 2002

Cryptogam spores and other non-pollen microfossils as sources of palaeoecological information: case-studies from Spain

José S. Carrión & Cristina Navarro

Carrión, J. S. &, Navarro, C., Departamento de Biología Vegetal (Botánica), Facultad de Biología, Universidad de Murcia, 30100 Murcia, Spain (e-mail: carrion@um.es)

Received 17 May 2001, accepted 10 August 2001

Carrión, J. S. & Navarro, C. 2002: Cryptogam spores and other non-pollen microfossils as sources of palaeoecological information: case-studies from Spain. — *Ann. Bot. Fennici* 39: 1–14.

Four examples from Mediterranean Spain are used to show that records of non-pollen palynomorphs (algal and fungal spores and cysts, charophytes and other microfossils of unknown biological origin) are worthwhile in addition to pollen analysis for studies of palaeoecological reconstruction. In the lacustrine sequence of Cañada de la Cruz, the stratigraphy of palaeolimnological indicators is compatible with climatic control of vegetation stages at the response scales of decades to centuries. The sequence of Navarrés provides evidence of millennial-scale change in the trophic conditions of a peat-forming basin, which parallels local and vegetation changes since the last glacial to the Holocene under the influence of fire events, climate change and human activity. The sequence of Villaverde shows out-of-phase relationships of vegetational and limnological developments. The sequence of San Rafael offers an example of synchronous variation of xerophytic pollen and microfossils indicative of temporary marsh desiccation, in concordance with regional evidence of aridification since the mid-Holocene.

Key words: algal cysts, fungi, Holocene, palaeobotany, palaeoecology, palaeolimnology, Quaternary, Spain, spores

Introduction

The combination of pollen analysis with the records of cryptogam spores and other non-pollen palynomorphs has shown to be valuable for detailed reconstructions of the changing local environment of Quaternary sites from northern Europe (e.g., Van Geel *et al.* 1989). In lake

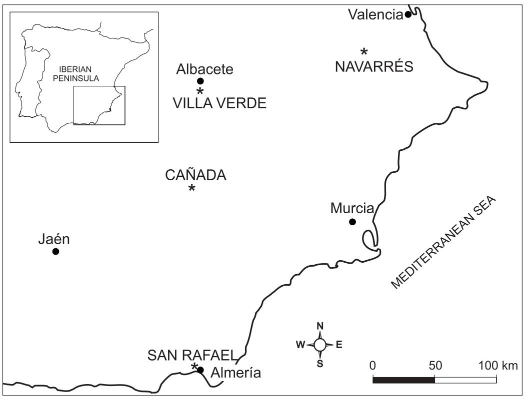

Fig. 1. Location of the studied sites.

sediments, for instance, long-term rapid changes in the microfossil record may be limnological responses via variations in the flux of water, nutrients and particulate material to the site from its drainage basin (Moore 1986). In studies of palaeoclimatic reconstruction, it is of paramount importance to elucidate whether limnological changes correlate to events of vegetation change. To judge from the published record, however, research on non-pollen palynomorphs has formed little or no part of studies of the majority of Quaternary palynologists from southern Europe. Moreover, the synchronous history of vegetation types and "extra" palynomorphs is still a rather unexplored field of study in the Mediterranean area. This paper offers examples of the valuable use of this approach in deposits from southern Spain.

Methods

The selected case studies correspond to the late Quaternary palaeoecological sequences of Cañada de la Cruz (Jaén), Navarrés (Valencia), Villaverde (Albacete), and San Rafael (Almería) in the Mediterranean region of Spain (Fig. 1). The section of Navarrés was obtained by means of metal boxes, the sharp edges of which were pushed into an exposed profile and subsequently cut out. The three remaining basins were sampled with piston corers. Extraction of pollen and spores from the sediment matrix followed the standard procedure described in Moore *et al.* (1991), which, by using hydrofluoric acid, precludes the preservation of microfossils possessing silicified walls such as diatoms. Mineral separation with zinc chloride density 2.0 was used for all the samples. Exotic *Lycopodium* tablets of a known concentration were added to calculate pollen concentrations.

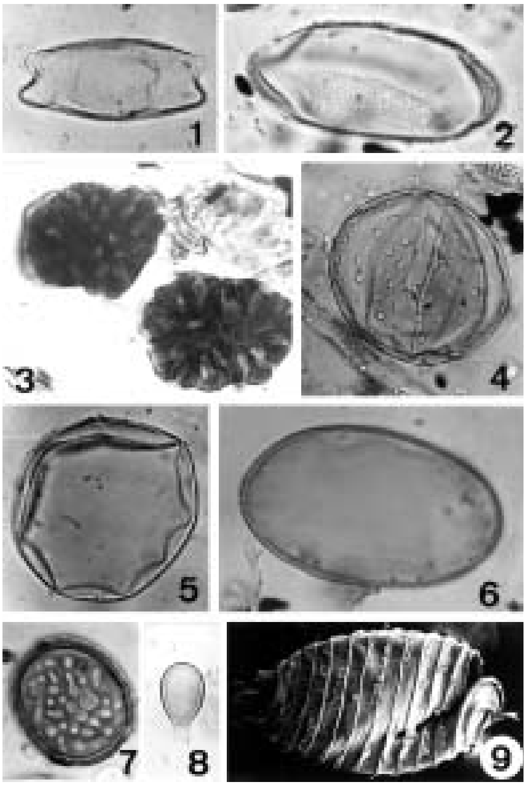

Fig. 2. LM and SEM micrographs of palynomorphs. — **1** and **2**: *Closterium*, ×1600. — **3**: *Botryococcus*, ×704. — **4**, **5**, **7**: *Zygnema*-type, ×1760. — **6**: *Spirogyra*-type, ×1600. — **8**: *Rivularia*-type heterocyst, ×1950. — **9**: *Chara hispida* gyrogonite, ×110 (SEM)

Identification of palynomorphs was aided by the use of the reference collections at Universidad de Murcia and Universiteit van Amsterdam. For the nomenclature of non-pollen microfossils of unknown or controversial biological origin, we have followed the sequence established by van Geel *et al.* (1989), in which the types indicated by a number can be considered as provisionally, but not formally, named form-taxa (Figs. 2–4). Relevant information on these types can be found in references listed in Table 1. Identification criteria for Characeae gyrogonites followed Haas (1994).

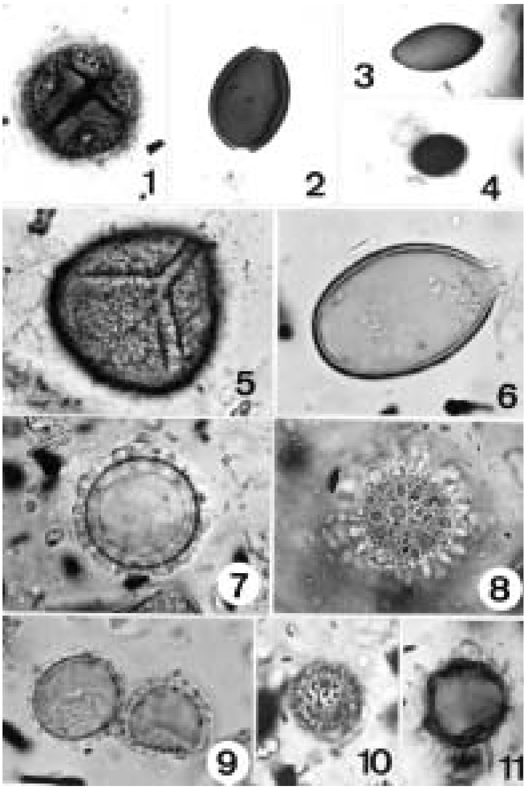

Fig. 3. LM micrographs of palynomorphs. — **1**: *Thecaphora*, ×1760. — **2** and **3**: Sordariaceae, ×1760. — **4**: *Gelasinospora*, ×1760. — **5**: Pteridophyta trilete, ×1600. — **6**: Type 179, ×1760. — **7** and **8**: Type 984, ×1760. — **9** and **10**: Type 983, ×1760. — **11**: Type 985, ×1760

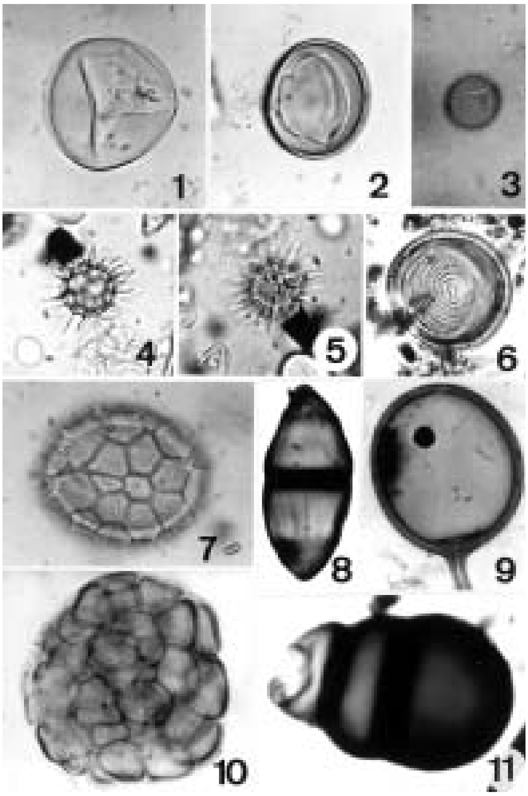

Fig. 4. LM micrographs of palynomorphs. — **1** and **2**: Type 119, ×1760. — **3**: Type 128, ×1760. — **4** and **5**: Type 182, ×1760. — **6**: *Pseudoschizaea*, ×960. — **7**: *Tilletia,* ×1800. — **8**: *Fusiformisporites*, ×1300. — **9**: *Glomus*, ×704. — **10**: *Polyadosporites*, ×704. — **11**: Type 359, ×704

Percentage pollen diagrams of selected taxa were elaborated using Tilia 1.12 and TiliaGraph 1.18 programs (Grimm 1992). Between ca. 400 and 1500 total palynomorphs were counted for each sample. Hydro- and hygrophytic pollen, and non-pollen microfossils were excluded from the pollen sum. In Navarrés and Villaverde, these diagrams also include concentrations of charcoal particles and Characeae gyrogonites. The total number of charcoal particles in the microscope slides can be taken as an indication of regional fire occurrence, while macrocharcoal peaks can be rather indicative of local events of fire (Mehringer *et al.* 1977). The delimitation of percentage zone boundaries was aided by stratigraphically constrained incremental sum-of-squares analysis (CONISS analysis, Grimm 1992) using a square-root transformation and chord-distance dissimilarity measure for all pollen and spores taxa. In Villaverde, a distinction was made between "pollen" (VP) and "microfossil" (VM) zones, the latter including the stratigraphic variation of non-pollen microfossils and basin-associated pollen. The number of zones was finally determined using the method of Bennett (1996) and the delimitation of VP and VM assemblage zone boundaries was obtained from an optimal division of the sequence using the information content criterion, after exploration of four other methods (binary splitting by sums-of-squares, binary splitting by information content, optimal splitting by sum-of-squares, and constrained cluster analysis). All chronologies were established on the basis of radiocarbon dates obtained from bulk organic sediment, dated by the AMS method where necessary

Table 1. Non-pollen microfossils selected for this study. Ecological indication, biological and taxonomic affinities and reference literature.

Microfossil type	Indication	Taxonomic/biological affinities	Literature
Glomus (T. 207)	Colonisation of lake margins, root activity	Glomaceae chlamydospores	Van Geel *et al.* (1989), Carrión *et al.* (1995, 1999)
Fusiformisporites	Organic matter decomposition	Unknown. Ascospores of e.g. *Nectria, Herpotrichia, Parodiella, Ceriophora*?	Elsik (1980, 1983), Carrión & van Geel (1999)
Polyadosporites (T. 367)	Organic matter decomposition	Colonies of thin-walled fungal cells?	Jarzen & Elsik (1986), Van Geel *et al*. 1981)
Tilletia (T. 27)	Fungal activity	*Tilletia* spores	Van Geel (1972), Navarro *et al.* (2000)
Thecaphora (T. 364)	Fungal activity, agricultural practices?	*Thecaphora* basidiospores	Van Geel *et al.* (1981)
Gelasinospora (T.1)	Decomposing activity	*Gelasinospora* ascospores	Lundqvist (1972), Van Geel (1978)
Type 359	Fungal activity	Septate conidia	Van Geel *et al.* (1981)
Sordariaceae (T.55)	Eutrophic conditions, dung input	Sordariaceae ascospores	Van Geel (1978), Van Geel *et al*. (1989), Carrión *et al*. (1999, 2000b), Navarro *et al.* (2000)
Zygnemataceae (*Spirogyra, Zygnema, Mougeotia*-types)	Shallow stagnant, oxygen-rich waters, lake margins	Zygospores and aplanospores of Zygnemataceae	Van Geel *et al.* (1989)
Rivularia-type (T.170)	Increased alkalinisation and concentration of oxidizable organics in water bodies	Cyanophyta heterocysts	Van Geel *et al.* (1983)
Closterium idiosporum type (T. 60)	Oligo-mesotrophic, temperate to cold water	Zygospores of several species of *Closterium*	Van Geel *et al.* (1981)
Botryococcus	Open water	Colonies of *Botryococcus*	Mateus (1992)
Pseudoschizaea	Relatively warm climate with local seasonal drying	Unknown, Resting structure of any of a wide variety of organisms	Scott (1992)
Type 128	Mesotrophic, cold to temperate open water	Unknown, Algal cyst or spore?, Similar to *Sigmopollis hispidus* (Hedlund 1965)	Krutzsch (1970), Pals *et al.* (1980), Van Geel *et al*. (1983)
Type 119	Lacustrine environment with aquatic angiosperms	Unknown	Pals *et al.* (1980)
Type 179	Stagnant open water, eutrophic conditions	Unknown, Phoretic cysts of epibiontic or parasitic Copepoda, Euglenophyta?	Van Geel *et al.* (1989), Wolowski (1998)
Type 182	Stagnant shallow open water	Unknown, Algal origin?	van Geel *et al.* (1983)
Type 983	Shallow freshwater	Unknown, Encystment phase of algae (e.g. desmids)?	Strother (1996), Carrión & van Geel (1999)
Type 984	Shallow freshwater	Unknown, *Euastrum* zygospores?	Carrión & van Geel (1999)
Type 985	Shallow freshwater	Unknown, Algal origin?	Carrión & van Geel (1999)

because of low carbon content in the organic extracts.

Palaeoecological sequences

Cañada de la Cruz (Fig. 5)

The Cañada de la Cruz (38°04´N, 2°42´W, 1595 m a.s.l.) is a shallow lake situated in a high-altitude mountain valley within the Sierra de Segura, Betic Cordillera (Fig. 1). It extends up to ca. 0.25 × 2.7 km during high-rainfall years, but normally dries up for 6 to 8 months per year, being fed by direct precipitation and surface runoff from the catchment. Pollen and spores were only found in the uppermost 128 cm of a sediment core raised from a central point in the dry lake. The depositional context is a compact bed of brown calcareous clays overlying a small-scale river deposit of calcreted conglomerates. The pollen sequence has provided insights into the vegetation history of the region since ca. 8320 yr BP. Abrupt changes in abundance of the pollen dominants are shown at about 7770 yr BP, 3370 yr BP, 2630 yr BP, 1525 yr BP, and 790 yr BP (Fig. 5). This sequence has been crucial to demonstrate that pollen may be a sensitive indicator of Holocene climate changes at the multi-decadal to century scale in Mediterranean context (Carrión *et al.* 2001b).

Pollen curves generally correlate to patterns of non-pollen palynomorphs. Several facts support the view that the stratigraphy of palaeolimnological indicators is compatible with climatic control of vegetation stages. Firstly, the ecotone between pine forest and xerophytic grassland-scrub is known to be sensitive to thermal lapse rate, wind intensity, summer length, and rainfall distribution (Valle *et al.* 1989). Secondly, the correlation between Poaceae, *Artemisia*, Chenopodiaceae, *Juniperus*, and *Ephedra nebrodensis* suggests cold arid conditions for the stages in which pollen of these taxa increase in value, namely at ca. 8320–7770 yr BP, 3370–2630 yr BP, and to a lesser extent, 1525–790 yr BP. Declines of these herbaceous assemblages correspond with increases in value of pollen of mesophilous (*Quercus*, *Pinus pinaster*, *Fraxinus*, *Acer*, *Erica arborea*, *Alnus*, *Betula*, *Corylus*, *Arbutus*, *Ulmus*) and thermophilous (*Pistacia*, *Cistus*, *Phillyrea*, *Ephedra fragilis*, *Olea*) taxa. Thus, the montane climate must have been relatively warmer and wetter during the periods of ca. 7770–3370 yr BP, 2630–1525 yr BP, and 790 yr BP to present. During these stages, invasion of high-elevation grassland-scrub by pines is consistent with upward displacement of deciduous forests, and expansion of evergreen forest and scrub (Carrión *et al.* 2001b). Thirdly, zones C1, C3, and, to a lesser extent, C5, characterized by *Closterium* and Type 128, and increased minerogenic influx, may represent stages with comparatively poor-nutrient water in the context of low temperatures, and short summers leading to treeless catchment vegetation. In contrast, zones C2, C4, and C6, with characteristic Zygnemataceae-dominated assemblages, decomposing fungi, and hygrophyte pollen would represent moderate eutrophication and temporary colonisation of the lake by marginal vegetation within a more forested landscape and milder climate. Finally, *Polygonum dumetorum* type may also indicate shifts to longer snow-free periods and mesic summer conditions. The absence of both peaty layers and preserved macroremains suggests, however, that prolonged dessication of the basin, organic matter decomposition and mineralization occurred throughout the sequence. The highest values of the pelagic *Botryococcus* suggest that water levels may have reached their maxima during C2, in concordance with spread of deciduous oaks. However, water levels would have diminished soon thereafter, as the subsequent peak of Zygnemataceae suggests.

Navarrés (Fig. 6)

The Canal de Navarrés is a tectonic, endorheic valley (39°06´N, 0°41´W, 225 m a.s.l.), 1 to 2 km wide, running NW–SE in the limits of the Iberian Cordillera, province of Valencia, eastern Spain (Fig. 1). A sedimentary sequence of 25 m depth was preliminarily reported (Dupré *et al.* 1998) describing 10 lithostratigraphic units in the valley deposit, of which only the topmost layer (above 250 cm depth) was peaty and

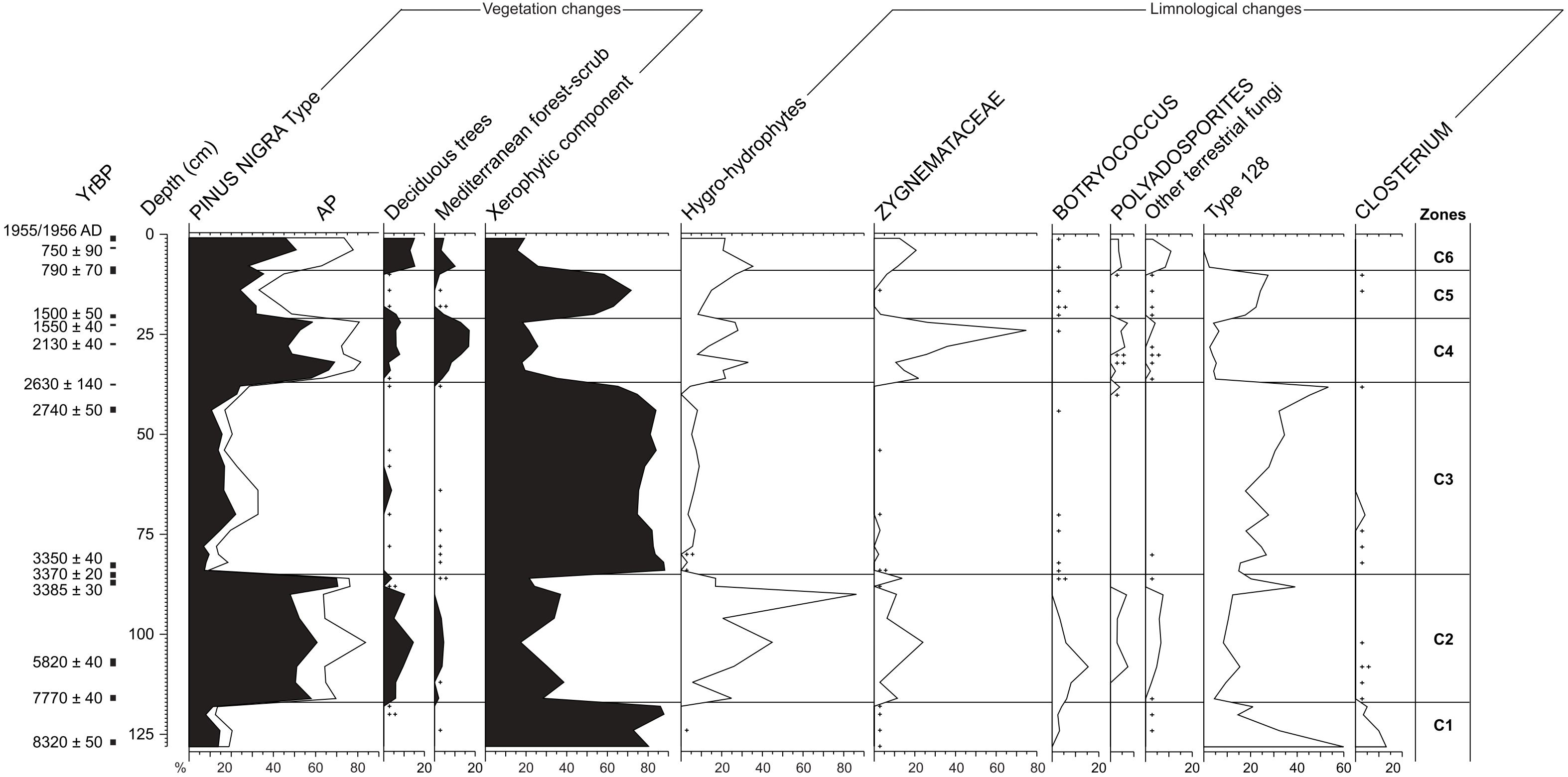

Fig. 5. Palaeoecological sequence of Cañada de la Cruz (Jaén). AP: sum of arboreal pollen. “Deciduous trees”: deciduous *Quercus, Fraxinus, Acer, Alnus, Betula, Corylus, Ulmus, Salix.* “Mediterranean forest-scrub”: *Pinus pinaster*, evergreen *Quercus, Erica arborea, Arbutus, Ephedra fragilis, Pistacia, Cistus, Phillyrea*. “Xerophytes”: Poaceae, *Juniperus, Artemisia, Ephedra nebrodensis,* Chenopodiaceae, Asteraceae. Hydro-hygrophytes: *Polygonum dumetorum* type, Cyperaceae, *Typha.* Crosses indicate palynomorph frequencies below 2%. Ages in uncalibrated radiocarbon years BP. Hygrophyte pollen and non-pollen palynomorphs excluded from pollen sum. Zonation follows Grimm (1992)

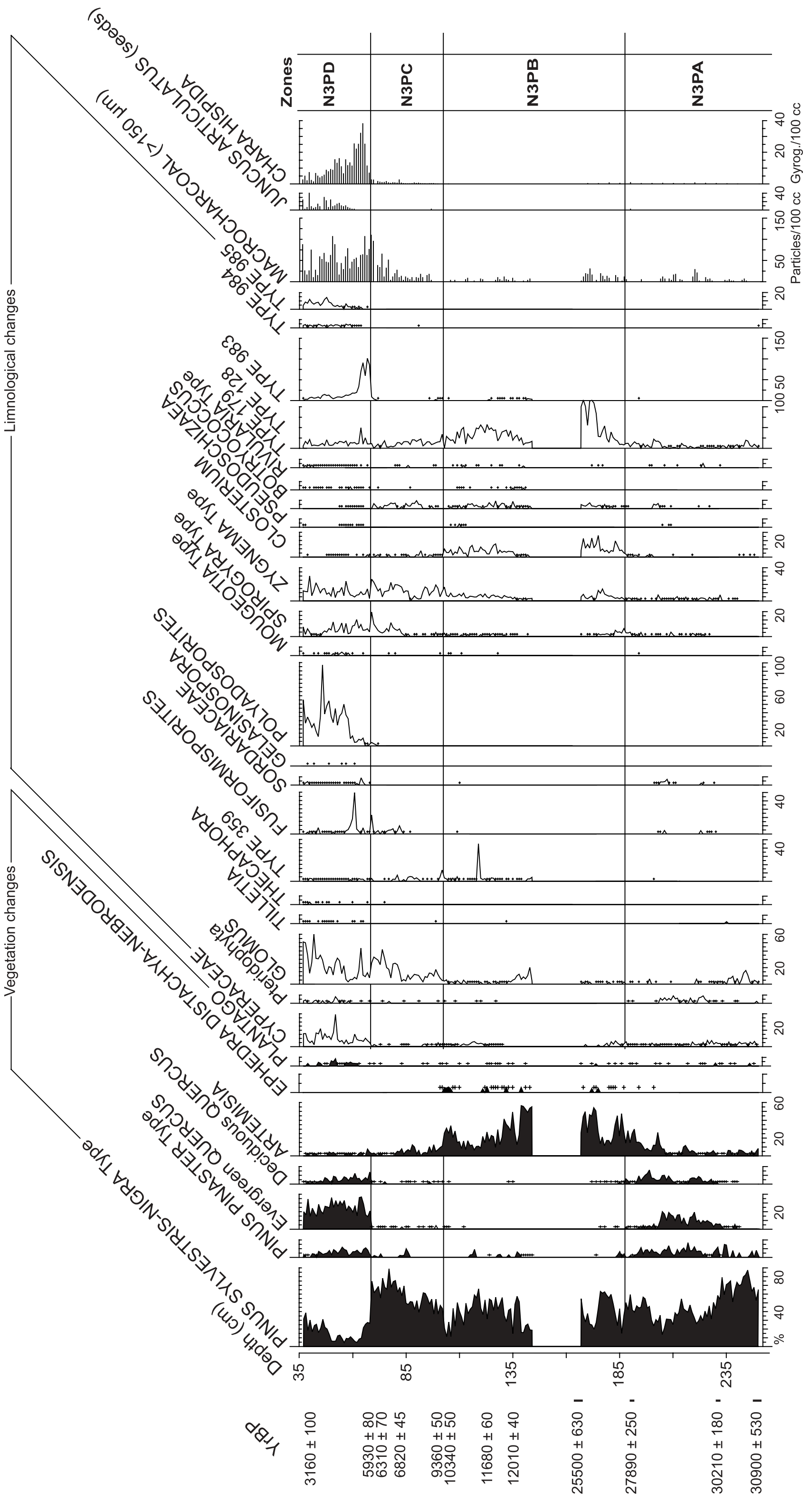

Fig. 6. Palaeoecological sequence of Navarrés (Valencia). Crosses indicate palynomorph frequencies below 2%. Ages in uncalibrated radiocarbon years. Zonation follows Grimm (1992)

polliniferous. This upper unit was formed under continuous sedimentation processes in a shallow lacustrine environment. Several pollen phases have been reported from the study of this section (Carrión & Dupré 1997, Dupré *et al.* 1998), the last one covering the period from ca. 30 900 to 3160 yr BP (Carrión & van Geel 1999).

The last glacial vegetation (N3PA-N3PB) is characterized by *Pinus–Artemisia–Ephedra* assemblages (Fig. 6). This dominance is interrupted between ca. 30 260 and 27 890 uncalibrated ^{14}C yr BP by the development of *Quercus, Pinus pinaster*, deciduous trees and Mediterranean shrubs, suggesting the proximity of glacial refugia and an expansion of their vegetation under influence of a milder climate. The palynological sequence of N3PB is interrupted between 166 and 145 cm. This hiatus seems to correspond with the last glacial maximum, during which conditions were not favourable for biotic preservation in wide parts of the basin. A Younger Dryas signal is indicated by increases of *Artemisia* and *Ephedra* around 10 340 BP. There is no immediate response of *Quercus* to the lateglacial and Holocene climatic ameliorations and *Pinus* continues to dominate the landscape until drastic drop at ca. 5930 BP, presumably by severe fire events, which may be linked with the installation of Neolithic settlement in the vicinities (Carrión & van Geel 1999). The suggestion of fire derives from the sharp increase of charcoal particles prior to the vegetation change, especially at 69 cm (dated at ca. 6310 BP).

Above 145 cm, there is evidence of a change in the trophic conditions, shallow water and plant advancement into the lake, as shown by the curves of Cyperaceae, some fungal types (Type 359 and *Glomus*) and *Zygnema* type. Still, the occurrence of *Rivularia* and the continuous curves of *Closterium* type and *Botryococcus* along zone N3PB indicate the presence of open water. Type 128 also occurs continuously. During N3PC, Type 128 and *Closterium* diminish and *Botryococcus* and zygnemataceous zygospores (*Zygnema* first and *Spirogyra* afterwards) increase. During N3PD, there are indicators of increased colonization of the lake margins and peat decomposition (e.g. pollen of Cyperaceae, *Typha, Apium*, spores of terrestrial ferns, fungal types like *Gelasinospora*, *Fusiformisporites, Polyadosporites, Glomus)*. Human influence in the landscape is suggested by the curve of *Plantago*. Since it frequently parasites grasses, *Thecaphora*, might also be related with agricultural practices. In addition, there are indicators of dung input such as spores of Sordariaceae.

The algal succession observed since the Lateglacial is remarkable, and is characterized by the following assemblages: (N3PB) Types 128–*Closterium–Botryococcus*, (N3PC) *Zygnema–Spirogyra–Botryococcus*, (N3PD) *Zygnema–Spirogyra–Mougeotia–Rivularia–Chara*. This succession may be certainly related with a trophic change to increased alkalinization and concentration of oxidizable organic compounds in relatively warm water. Types 179, 983, 984, and 985 parallel this distribution, with the very abundant Type 983 showing a peak just when maxima for *Quercus* and *Chara hispida* are recorded. This Type must be related with a shallow freshwater lake environment. Finally there is an important increase of angiosperm seeds, notably *Juncus articulatus*, which suggests partial infilling.

Villaverde (Fig. 7)

The site (2°22´W, 38°48´N, 870 m a.s.l.) is a tuffaceous peat deposit developed on an old lake-bed adjacent to the Cubillo River, 57 km west of the city of Albacete (Fig. 1). A sediment core (total depth 550 cm) was obtained with a piston corer at the eastern part of the fan. The pollen stratigraphy at Villaverde has been used to infer past vegetation changes from ca. 8700 to 1230 uncalibrated ^{14}C yr BP within a well-defined catchment area that represents boundary conditions for semi-arid, plateau and mountain vegetation (Carrión *et al.* 2001a). At the millennial scale, climate appears to have been a major control of the species pool. The picture is of a generally wet mid Holocene stage (VP3–VP5) characterized by spread of mesophilous vegetation, anteceded and followed by drier conditions, which are inferred from a higher abundance of xerophytes, pines, evergreen oaks, and Mediterranean scrub (Fig. 7).

The lithology comprises pale-brown organic marls (VM1, VM3, VM5) and black organic

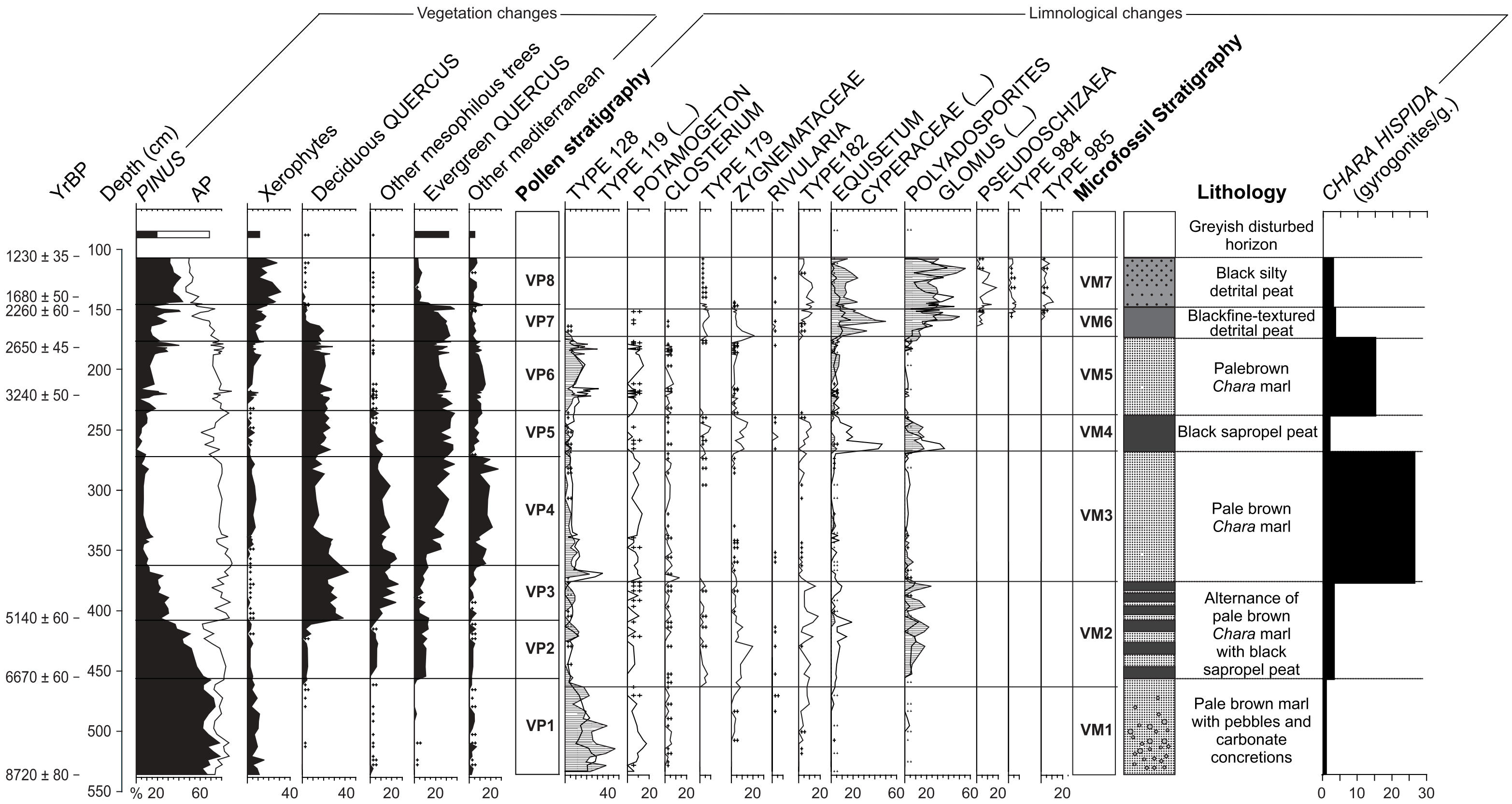

Fig. 7. Palaeoecological sequence of Villaverde. VP: pollen stratigraphy, VM: stratigraphy of other microfossils. VP and VM zones are out-of-phase below c. 350 cm depth. AP: sum of arboreal pollen. "Xerophytes'': *Artemisia*, Chenopodiaceae, *Ephedra fragilis*, and Asteraceae. "Other mesophilous trees'': *Betula*, *Fraxinus*, *Salix*, *Corylus*, *Alnus*, *Ulmus*, *Acer*, and *Sorbus*. "Other Mediterranean'': *Pistacia*, *Phillyrea*, *Erica arborea*, *Olea*, *Cistus*, *Rhamnus*, and *Myrtus.* Crosses indicate palynomorph frequencies below 2%. Ages in uncalibrated radiocarbon years. Delimitation of VP and VM zone boundaries follows Bennett (1996)

sediments of varying states of humification (“peats”: VM6, VM7) or decomposition (“sapropels”: VM2, VM4) (Fig. 7). Characeae mineral detritus is the main component of plant macrofossils throughout the core from VM2 upwards, although the detritus component is better preserved in marl layers. This detritus consists of branchlets, fragments of axial internodes with the typical diplostichous-anisostichous cortex, clusters of spine cells attached to axial fragments, and gyrogonites. The variations of the lithology suggest fluctuating water levels with the deposition of marls during periods of higher lake levels and the deposition of peats associated with advances of littoral emergent vegetation during lower lake levels. Overall, charophyte-rich facies throughout the core confirms the presence of permanent, albeit relatively shallow, water conditions. The abundance of *Chara hispida* gyrogonites in VM3 and VM5 indicates *in situ* deposition as well as submersion for at least three months, which is the time required for the plant to complete a full cycle of growth including calcification of the reproductive organs (Soulié-Märsche 1993). Associated microfossil assemblages (VM3, VM5) fit into this picture. Similarly to Navarrés (Fig. 6), the association *Closterium*–Type 128 may be characteristic of mesotrophic stages in lake hydroseres of the region. Type 119 and pollen of aquatic angiosperms (e.g., *Potamogeton*, *Myriophyllum*) correlate to this association. Physico-chemical precipitation, in addition to biogenic, must have taken place during the initial VM1 stage because those lime marls are not associated with charophyte-rich facies, and gyrogonites are almost absent. Higher flow velocities would have prevented biofilm colonisation and *Chara* growth.

During short periods in VM2, and stages VM4, VM6, and VM7, there must have been increased organic input associated with lowered water levels. Increased turbidity would have diminished the reproductive capability of aquatic angiosperms and charophytes carpeting the bottom of the lake. Characteristic microfossil assemblages include Zygnematales, *Rivularia*, Types 182, 179, *Glomus*, and *Polyadosporites*. Together these palynomorphs suggest advances of peat- and sapropel-producing marsh environments, areas of temporary stagnant water and lake eutrophication. In comparison with the sapropelic VM2 and VM4 zones, the peats VM6 and VM7 appear to be formed under more terrestrial conditions, as is further indicated by the occurrence of *Equisetum* spores, Cyperaceae, *Pseudoschizaea* cysts, *Polyadosporites*, *Glomus*, and spore Types 984 and 985.

While remaining clear that these biological and geological changes must be coupled with water level variation, it is difficult to pinpoint the prime source of the hydrological events since there must have been alterations in local drainage patterns caused by karst dynamics and groundwater input. Similar karstic lake systems show heavily fissured bedrock and concentrated flows of groundwater. These landscapes may indeed show great sensitivity to disturbance, and small-scale events can result in basin-wide change in regime (Goudie *et al.* 1993). This would explain why there is no good correlation between limnological and pollen events (Fig. 7), and suggests that this basin is not a suitable model for multi-proxy palaeoclimate reconstruction studies. In any case, there might be a relationship between the last millennia peat humification and infilling, and the climate change suggested by the pollen record through the increase of xerophytes.

San Rafael (Fig. 8)

A sediment core (depth 1900 cm) composed of organic clays and silts was obtained from the eastern edge of a marshland (36°20´N, 2°12´W, 10 m a.s.l.) in the Campo de Dalías, Almería province, the most arid region of Spain (Fig. 1). The pollen record covers the last ca. 17 000 years (Fig. 8). It demonstrates that temperate trees (e.g. deciduous *Quercus*, *Betula*, *Corylus*, *Alnus*, *Fraxinus*, *Acer*, *Abies*) and Mediterranean scrub (e.g. evergreen *Quercus*, *Pistacia*, *Phillyrea*, *Myrtus*, *Chamaerops*, *Buxus*) persisted in small quantities in the southeastern littoral ranges during full glacial times (SRA-SRB), with no palynological evidence of xerophytization of vegetation (Pantaleón-Cano 1997). In contrast, *Artemisia* reaches a first maximum from lateglacial to early Holocene (SRC-SRD). As in the former sequences, the optimum of deciduous

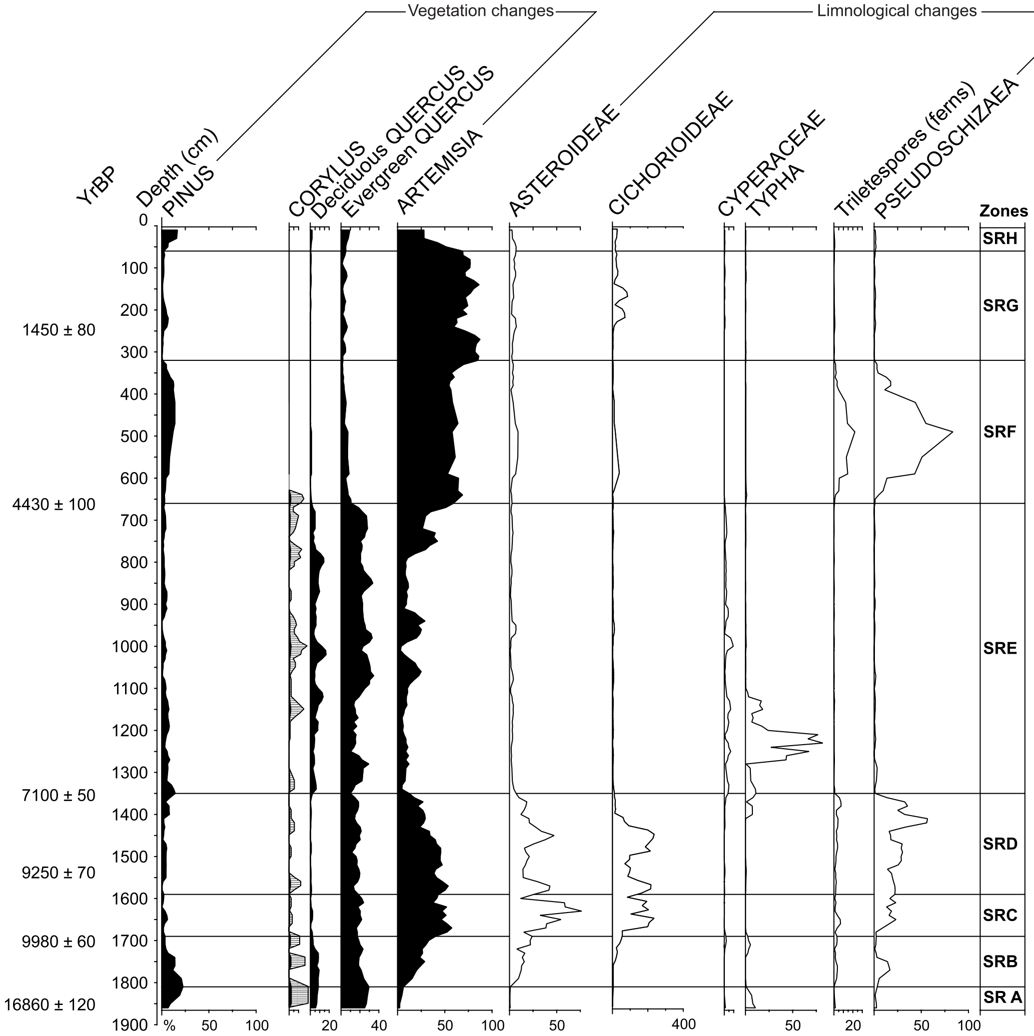

Fig. 8. Palaeoecological sequence of San Rafael (Almería) (Pantaleón-Cano 1997). Ages in uncalibrated radiocarbon years. Zonation follows Grimm (1992).

trees and Mediterranean scrub (ca. 7500–4500 yr BP, SRE) occurs later than mesocratic early-Holocene phase of forest development in north-west Europe (Birks 1986), and coincides with the highest percentage values of basin-associated hygrophytes (Cyperaceae, *Typha*).

Percentage curves of Asteraceae, *Pseudoschizaea* and trilete spores (mainly ferns) mark the boundaries of the mesophytic phase, thus coinciding with important changes in the plant cover (Fig. 8). *Pseudoschizaea* increases have been shown to correlate with decreased pollen concentrations and increased minerogenic input within this and other regional sequences obtained from alluvial sediments (Pantaleón-Cano *et al.* 1996). In concordance with the highly resistant trilete spores and composite pollen, the abundance of *Pseudoschizaea* cysts may be related with increased oxydization and average desiccation of the basin, the alternation of wet-dry phases, or the prolongation of summer drought (Scott 1992). The synchronous increases of *Artemisia* and *Pseudoschizaea* together with mesophyte depletion after ca. 4500 yr BP can be viewed as the consequence of enhanced regional aridity, which would have been critically manifested in the pollen record of Villaverde at 4500, 3240, 2200, and 1700 yr BP (Fig. 5), in Cañada de la Cruz after 3370 yr BP and 1525 yr BP (Fig. 3), and Navarrés after 3160 yr BP, when peatbog formation ceased (Fig. 6). Other palynological data from Mediterranean Spain coincide to suggest sub-humid forest declines after ca. 4500 yr BP (Dupré 1988, Riera 1993, Burjachs *et al.* 1997, Yll *et al.* 1997, Carrión *et al.* 1999, 2000a). Several pollen records from elsewhere in the Mediterranean show progressive matorralization during the last four millennia at the expense of sub-humid forests (Bottema & van Zeist 1991, Willis 1994). The arid tendency is also supported by palaeoanthracological information relative to species composition (Badal *et al.* 1994), and wood anatomy (Terral & Arnold-Simard 1996), geomorphological evidence of badlands (Wise *et al.* 1982), and sedimentological evidence of changes in the hydrological regimes of lakes of tropical and Mediterranean north Africa (Lamb *et al.* 1995, Gasse 2000).

Concluding remarks

The occurrence of characteristic microfossil assemblages of the Late Quaternary in lacustrine systems of Mediterranean Spain has been shown. Regarding the water level, water temperature, and trophic stage, the alternation of stages dominated by *Zygnemataceae* zygospores and *Closterium*–Type 128 spores can be particularly meaningful. Fungal types such as *Polyadosporites*, *Fusiformisporites*, *Glomus*, and *Gelasinospora* are often abundant during the advances in marginal vegetation and formation of peaty layers. *Pseudoschizaea* cysts occur in parallel with desiccation phases or enhanced summer drought.

The correlation of these palynofacies with events of vegetation change as reflected in the pollen record is a reliable indicator of broad-scale environmental change. The most striking example derives from the sequence of Cañada de la Cruz, where a sensitive response of Holocene vegetation correlates to palaeolimnological indicators. The sequence of Navarrés provides evidence of millennial-scale change in both vegetation and the trophic conditions of a peat-forming basin since the last glacial to the Holocene under the influence of fire events, climate change and human activity. The sequence of Villaverde shows certain discordance between vegetational and limnological developments, but there are palynomorphs whose variation fits into the overall scheme of climate control for both systems. The sequence of San Rafael offers an example of synchronous variation of xerophytic pollen and microfossils indicative of temporary marsh desiccation, which agrees with broader evidence of aridification since the mid Holocene.

Acknowledgements

This research was funded by the Spanish Ministerio de Educación y Ciencia through the project ARDACHO (Ref. BOS2000-0149). A DGICYT fellowship (PR95-214) awarded to J. S. Carrión for research at the Hugo de Vries Laboratorium during 1996 under the supervision of Dr. Bas van Geel was equally crucial. J. Pantaleón kindly provided the database relative to the site of San Rafael.

References

Badal, E., Bernabeu, J. & Vernet, J. L. 1994: Vegetation changes and human action from the Neolithic to the Bronze Age (7000–4000 B.P.) in Alicante, Spain, based on charcoal analysis. — *Veg. Hist. Arch.* 3: 155–166.

Bennett, K. D. 1996: Determination of the number of zones in biostratigraphical sequence. — *New Phytol.* 132: 155–170.

Birks, J. H. B. 1986: Late Quaternary biotic changes in terrestrial and lacustrine environments, with particular reference to north-west Europe. — In: Berglund, B. E. (ed.), *Handbook of Holocene palaeoecology and palaeohydrology*: 3–65. Chichester, Wiley.

Bottema, S. & van Zeist, W. 1991: Late Quaternary vegetation of the Near East. — *Beih. Tübinger Atlas Des Vorderen Orients,* Reihe A (Naturwissenchschaften) 18: 1–156.

Burjachs, F., Giralt, S., Roca, J. R., Seret, G. & Julià, R. 1997: Palinología holocénica y desertización en el Mediterráneo occidental. — In: Ibáñez, J. J., Valero, B. L. & Machado, C. (eds.), *El paisaje mediterráneo a través del espacio y del tiempo. Implicaciones en la desertificación*: 379–394. Logroño, Geoforma Editores.

Carrión, J. S. & Dupré, M. 1997: Late Quaternary vegetational history at Navarrés, eastern Spain. A two-core approach. — *New Phytol.* 134: 177–191.

Carrión, J. S., Scott, L. & Vogel, J. 1999: Twentieth century changes in montane vegetation in the eastern Free State, South Africa, derived from palynology of hyrax dung middens. — *J. Quat. Sci.* 14: 1–16.

Carrión, J. S. & van Geel, B. 1999: Fine-resolution Upper Weichselian and Holocene palynological record from Navarrés (Valencia, Spain) and a discussion about factors of Mediterranean forest succession. — *Rev. Palaeobot. Palynol.* 106: 209–236.

Carrión, J. S., Andrade, A., Bennett, K. D., Munuera, M. & Navarro, C. 2001a: Crossing forest thresholds: inertia and collapse in a Holocene pollen sequence from south-central Spain. — *Holocene*11: 635–653.

Carrión, J. S., Dupré, M., Fumanal, M. P. & Montes, R. 1995: A palaeoenvironmental study in semi-arid southeastern Spain: the palynological and sedimentological sequence at Perneras Cave (Lorca, Murcia). — *J. Arch. Sci.* 22: 355–367.

Carrión, J. S., Munuera, M., Dupré, M. & Andrade, A. 2001b: Abrupt vegetation changes in the Segura Mountains of southern Spain throughout the Holocene. — *J. Ecol.* 89: 783–797.

Carrión, J. S., Munuera, M., Navarro, C. & Sáez, F. 2000a: Paleoclimas e historia de la vegetación cuaternaria en España a través del análisis polínico. Viejas falacias y nuevos paradigmas. — *Complutum* 11: 115–142.

Carrión, J. S., Scott, L., Huffman, T. & Dreyer, C. 2000b: Pollen analysis of Iron Age cow dung in southern Africa. — *Veg. Hist. Arch.* 9: 239–249.

Dupré, M. 1988: *Palinología y paleoambiente. Nuevos datos polínicos. Referencias.* — Servicio de Investigación Prehistórica, Valencia. 188 pp.

Dupré, M., Carrión, J. S., Fumanal, M. P., La Roca, N., Martínez-Gallego, J. & Usera, J. 1998: Evolution and palaeoenvironmental study of a semiendorheic area in eastern Spain (Navarrés, Valencia). — *Il Quaternario* 11: 95–105.

Elsik, W. C. 1980: The utility of fungal spores in marginal marine strata of the late Cenozoic, northern Gulf of Mexico. — *IV Internat. Palynol. Conference, Lucknow* 2: 436–443.

Elsik, W. C. 1983: Annotated glossary of fungal palynomorphs. — *AASP Contr. Series* 11: 1–36.

Gasse, F. 2000: Hydrological changes in the African tropics since the last glacial maximum. — *Quat. Sci. Rev.* 19: 189–211.

Goudie, A. S., Viles, H. A. & Pentecost, A. 1993: The late-Holocene tufa decline in Europe. — *Holocene* 3: 181–186.

Grimm, E. 1992: *Tilia version 1.12.* — Illinois State Mus., Res. Coll. Center, Springfield, USA.

Haas, J. N. 1994: First identification key for charophyte oospores from central Europe. — *Europ. J. Phycol.* 29: 227–235.

Jarzen, D. M. & Elsik, W. C. 1986: Fungal palynomorphs recovered from recent river deposits, Luangwa Valley, Zambia. — *Palynology* 10: 35–60.

Krutzsch, W. 1970: *Atlas der mittel und jungtertiären dispersen Sporen und Pollen sowie der Mikroplanktonformen des nördlichen Mitteleuropas*. — Fischer, Jena. 149 pp.

Lamb, H. F., Gasse, F., Benkaddour, A., El Hamouti, N., van der Kaars, S., Perkins, W. T., Pearce, N. J. & Roberts, C. N. 1995: Relation between century-scale Holocene arid intervals in tropical and temperate zones. — *Nature* 373: 134–137.

Lundqvist, N. 1972: Nordic Sordariaceae *s. lat*. — *Symb. Bot.* 20: 332–335.

Mateus, J. E. 1992: *Holocene and present-day ecosystems of the Carvalhal Region, southwest Portugal*. — Ph.D. thesis, Univ. Utrecht. 184 pp.

Mehringer, P. J., Arno, S. F. & Petersen, K. L. 1977: Postglacial history of Lost Trail Pass Bog, Bitterroot Mountains, Montana. — *Arctic Alp. Res.* 9: 345–368.

Moore, P. D. 1986: Hydrological changes in mires. — In: Berglund, B. E. (ed.), *Handbook of Holocene palaeoecology and palaeohydrology*: 91–107. Chichester, Wiley.

Moore, P. D., Webb, J. A. & Collinson, M. E. 1991: *Pollen analysis*. 2nd ed. — Blackwell Sci. Publ., Oxford. 216 pp.

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.

Pals, J. P., van Geel, B. & Delfos, A. 1980: Paleoecological studies in the Klokkeweel Bog near Hoogkarspel (Prov. of Noord-Holland). — *Rev. Palaeobot. Palynol.* 30: 371–418.

Pantaleón-Cano, J. 1997: *Estudi palinològic de sediments litorals de la provincia d´Almería. Transformacions del paisatge vegetal dins un territori semiàrid*. — Ph.D. thesis, Universidad Autónoma de Barcelona. 189 pp.

Pantaleón-Cano, J., Yll, E., Pérez-Obiol, R. & Roure, J. M. 1996: Las concentraciones polínicas en medios semiáridos. Su importancia en la interpretación de la evolución del paisaje. — In: Ramil-Rego, P., Fernández, C. & Rodríguez, R. (eds.), *Biogeografía pleistocena-holocena de la Península Ibérica*: 215–226. Xunta de Galicia.

Riera, S. 1993: Changements de la composition forestière dans la plaine de Barcelone pendant l'Holocene (littoral méditerranéen de la Péninsule Iberique). — *Palynosciences* 2: 133–146.

Scott, L. 1992: Environmental implications and origin of microscopic *Pseudoschizaea* Thiergart and Franz ex R. Potonié emend. in sediments. — *J. Biogeogr.* 19: 349–354.

Soulié-Märsche, I. 1993: Diversity of Quaternary aquatic environments in Africa as shown by fossil charophytes. — In: Thorweine, U. & Schandelmeier, H. (eds.), *Geoscientific research in northeast Africa*: 575–579. Balkema, Rotterdam.

Strother, P. K. 1996: Acritarchs. — In: Jansonius, J. & McGregor, D. C. (eds.), *Palynology: principles and applications 1*: 81–106. Amer. Ass. Stratigr. Palynologists Found., Texas.

Terral, J. F. & Arnold-Simard, G. 1996: Beginnings of olive cultivation in eastern Spain in relation to Holocene bioclimatic changes. — *Quat. Res.* 46: 176–85.

Valle, F., Gómez-Mercado, F., Mota, J. F. & Díaz de la Guardia, C. 1989: *Parque Natural de Cazorla, Segura y Las Villas. Guía botánico-ecológica*. — Rueda, Madrid. 354 pp.

Van Geel, B. 1972: Palynology of a section from the raised peat bog “Wietmarscher Moor” with special reference to fungal remains. — *Acta Bot. Neerl.* 21: 261–284.

Van Geel, B. 1978: A palaeoecological study of Holocene peat bog sections in Germany and The Netherlands, based on the analysis of pollen, spores and macro- and microscopic remains of fungi, algae, cormophytes and animals. — *Rev. Palaeobot. Palynol.* 25: 1–120.

Van Geel, B., Bohncke, S. J. P. & Dee, H. 1981: A palaeoecological study of an Upper Late Glacial and Holocene sequence from “De Borchert”, The Netherlands. — *Rev. Palaeobot. Palynol.* 31: 367–448.

Van Geel, B., Hallewas, D. P. & Pals, J. P. 1983: A Late Holocene deposit under the Westfriese Zeedijk near Enkhuizen (Prov. of Noord-Holland, The Netherlands): Palaeoecological and archaeological aspects. — *Rev. Palaeobot. Palynol.* 38: 269–335.

Van Geel, B., Coope, G. R. & Van der Hammen, T. 1989: Palaeoecology and stratigraphy of the Lateglacial type section at Usselo (The Netherlands). — *Rev. Palaeobot. Palynol.* 60: 25–129.

Willis, K. J. 1994: The vegetational history of the Balkans. — *Quat. Sci. Rev.* 13: 769–788.

Wise, S. M., Thornes, J. B. & Gilman, A. 1982: How old are the badlands? A case-study from south-east Spain. — In: Bryan, R. & Yair, A. (eds.), *Badland geomorphology and piping*: 259–278. Geobooks, Norwich.

Wolowski, K. 1998: Taxonomic and environmental studies on euglenophytes of the Kraków–Czestochowa upland (southern Poland). — *Fragm. Flor. Geobot.* 6: 1–192.

Yll, E. I., Pérez-Obiol, R., Pantaleón-Cano, J. & Roure, J. M. 1997: Palynological evidence for climatic change and human activity during the Holocene on Minorca (Balearic Islands). — *Quat. Res.* 48: 339–347.