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)

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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
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, pre-
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.

<table>
<thead>
<tr>
<th>Microfossil type</th>
<th>Indication</th>
<th>Taxonomic/biological affinities</th>
<th>Literature</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Tilletia</em> (T. 27)</td>
<td>Fungal activity</td>
<td><em>Tilletia</em> spores</td>
<td>Van Geel (1972), Navarro et al. (2000)</td>
</tr>
<tr>
<td>Type 359</td>
<td>Decomposing activity</td>
<td><em>Gelasinospora</em> ascospores</td>
<td>Lundqvist (1972), Van Geel (1978)</td>
</tr>
<tr>
<td><em>Zygnemataceae</em></td>
<td>Shallow stagnant, oxygen-rich waters, lake margins</td>
<td>Zygospores and aplanospores of <em>Zygnemataceae</em></td>
<td>Van Geel et al. (1989)</td>
</tr>
<tr>
<td>(Spirogyra, Zygnema, Mougeotia-types)</td>
<td>Increased alkalisation and concentration of oxidizable organics in water bodies</td>
<td>Cyanophyta heterocysts</td>
<td>Van Geel et al. (1983)</td>
</tr>
<tr>
<td><em>Rivularia</em>-type (T. 170)</td>
<td>Open water</td>
<td>Zygospores of several species of <em>Closterium</em></td>
<td>Van Geel et al. (1981)</td>
</tr>
<tr>
<td><em>Botryococcus</em> (idiosporum type) (T. 60)</td>
<td>Relatively warm climate with local seasonal drying</td>
<td>Colonies of <em>Botryococcus</em></td>
<td>Mateus (1992)</td>
</tr>
<tr>
<td><em>Pseudoschizaea</em></td>
<td>Mesotrophic, cold to temperate open water</td>
<td>Unknown, Resting structure of any of a wide variety of organisms</td>
<td>Scott (1992)</td>
</tr>
<tr>
<td>Type 128</td>
<td>Lacustrine environment with aquatic angiosperms</td>
<td>Unknown, Algal cyst or spore?, Similar to <em>Sigmopollis hispidus</em> (Hedlund 1965)</td>
<td>Krutzsch (1970), Pals et al. (1980), Van Geel et al. (1983)</td>
</tr>
<tr>
<td>Type 119</td>
<td>Stagnant open water, eutrophic conditions</td>
<td>Unknown, Encystment phase of algae (e.g. desmids)?</td>
<td>Pals et al. (1980)</td>
</tr>
<tr>
<td>Type 179</td>
<td>Stagnant shallow open water</td>
<td>Unknown, Phoretic cysts of epibiontic or parasitic Copepoda, Euglenophyta?</td>
<td>Van Geel et al. (1989), Wolowski (1998)</td>
</tr>
<tr>
<td>Type 182</td>
<td>Shallow freshwater</td>
<td>Unknown, Algal origin?</td>
<td>van Geel et al. (1983)</td>
</tr>
<tr>
<td>Type 983</td>
<td>Shallow freshwater</td>
<td>Unknown, Encystment phase of algae (e.g. desmids)?</td>
<td>Strother (1996), Carrión &amp; van Geel (1999)</td>
</tr>
<tr>
<td>Type 985</td>
<td>Shallow freshwater</td>
<td>Unknown, Algal origin?</td>
<td>Carrión &amp; van Geel (1999)</td>
</tr>
</tbody>
</table>
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 palaeoecological 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. 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 14C 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 late glacial and Holocene climatic ameliorations and Pinus continues to dominate the landscape until a 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 zygnematoceous zygosporites (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, Fusi-

formisporites, 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 Late-glacial 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 14C 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, antecedent 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 is 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, Pseudoschizacea 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
trees and Mediterranean scrub (ca. 7500–4500 yr BP, SRE) occurs later than mesocratic early-Holoce

e} 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 oxidation 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 critical-

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

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References


