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Fine-resolution Upper Weichselian and Holocene palynological record from Navarrés (Valencia, Spain) and a discussion about factors of Mediterranean forest succession

J.S. Carrión [a,*], B. Van Geel [b]

[a] *Departamento de Biología Vegetal (Botánica), Facultad de Biología, Universidad de Murcia, Campus de Espinardo, 30100 Murcia, Spain*

[b] *The Netherlands Centre for Geo-ecological Research, Universiteit van Amsterdam, Kruislaan 318, 1098 SM Amsterdam, Netherlands*

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Abstract

A detailed study is presented of the Upper Pleistocene and Holocene pollen sequence of the Navarrés peat deposit (Valencia, eastern Spain) including non-pollen palynomorphs, Characeae gyrogonites, seeds and charcoal abundance. The study covers the period from ca. 30,900 to 3160 yr B.P. The last glacial vegetation is characterised by *Pinus–Artemisia–Ephedra* assemblages. This dominance is interrupted between ca. 30,260 and 27,890 yr B.P. 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. A Younger Dryas signal is noticed by increases of *Artemisia* and *Ephedra* around 10,380 yr B.P. There is no immediate response of *Quercus* to the Late Glacial and Holocene climatic ameliorations and *Pinus* continues to dominate the landscape until removed at ca. 5930 yr B.P., presumably by severe fire events whose causes are discussed in the light of palynological, anthracological and paleoclimatical data.

Keywords: paleoecology; pollen; Younger Dryas; Quaternary; Holocene; vegetation history; Spain; Navarrés

1. Introduction

The Canal de Navarrés peat deposit, eastern Spain (Fig. 1), has been subject of paleoenvironmental research during the last few decads (Menéndez-Amor and Florschütz, 1961; Dupré et al., 1985; Dupré, 1988). Recently, a two-core palynological study was published (Carrión and Dupré, 1996) showing the late Quaternary vegetational history of the area from ca. 20,700 to 3075 yr B.P. The most remarkable feature of that study was the absence of disruptive vegetation patterns following the commencement of the Holocene, and the fact that a *Pinus* forest continued to be dominant up to ca. 5500–6000 yr B.P., when it was replaced almost completely by *Quercus*-dominated assemblages. Two major issues arose from that study. First, there was a not clearly discernible Younger Dryas signal in the pollen record. Second, we failed to explain the particular *Pinus–Quercus* dynamics. A new study was aimed to solve both questions and, in order to facilitate that effort,

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* Corresponding author. Tel.: +34-968-307100; Fax: +34-968-363963; E-mail: carrion@fcu.um.es

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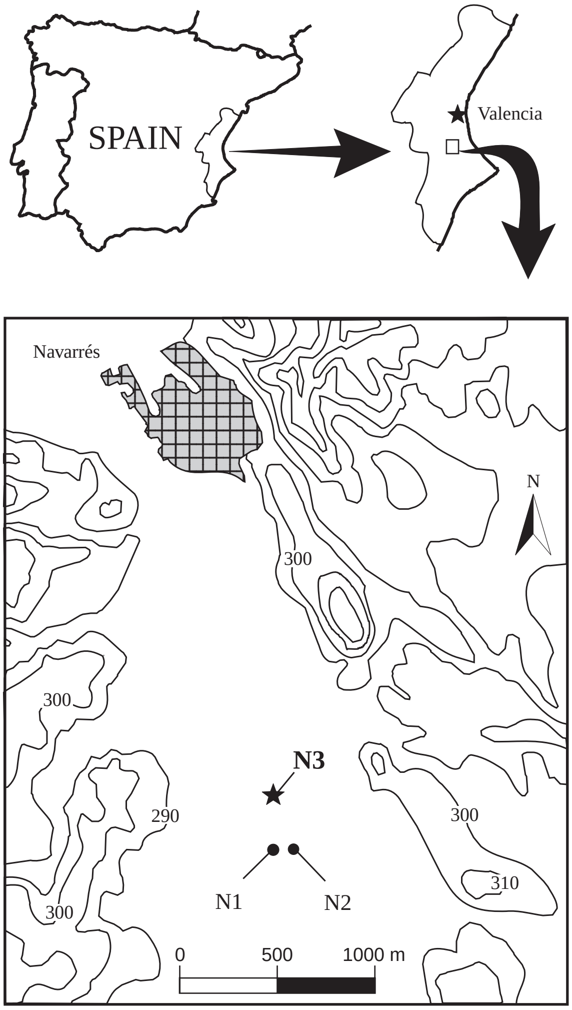


Fig. 1. The site of Navarrés and location of previously studied cores (*N1* and *N2*) and section at this study (*N3*). The Ereta del Pedregal Neolithic population was occupying the same site as the present-day village of Navarrés.

we increased the taxonomic and temporal resolution. Thus, a new paleoecological record is presented here, including not only records of pollen grains and spores but also of other microfossils, seeds, and microscopic and macroscopic charcoal. While our goal was to provide a more detailed work, we were able to find a thicker peat section, starting ten thousand years before the above-mentioned sites, and thus covering a time span of ca. 30,900 to 3160 yr B.P.

2. The site

The Canal de Navarrés is a tectonic, flat-bottom valley (39º06′N, 0º41′W), 1 to 2 km wide, situated at 225 m a.s.l. and running northwest–southeast in the limits of the Iberian Cordillera, province of Valencia, eastern Spain (Fig. 1). The valley is flanked by flattened mountains, actively eroded by the River Xúquer tributary courses. The endorheic character of the site is reflected in the quantity of water which gave rise to significant formations of travertine and peat. The nearby Neolithic and Bronze Age settlement of Ereta del Pedregal (Pla et al., 1983) was situated in the valley on an elevation between the former fenlands.

A sedimentary sequence of 25 m depth has been recently reported (Dupré et al., 1999) describing 10 lithostratigraphic units in the valley deposit, of which only the topmost layer (above 250 cm depth) is peaty and polliniferous. This upper unit, a sandy peat, was formed under continuous sedimentation processes in a shallow lacustrine environment. The rest of the Quaternary sequence, dated since ca. 178,000 yr B.P., is dominated by fluvial facies alternating with phases of sedimentation of fine sediments.

The present climate of the area is characterised by mean annual temperatures of 15–16ºC and an average annual precipitation of around 550 mm, with a typical Mediterranean summer drought regime. Rainfall is extremely variable throughout the adjacent mountains owing to the sharp topographical differences. The vegetation edging the valley is largely a garrigue in which *Quercus coccifera* and *Pistacia lentiscus* are dominant, while the endorheic areas support a variety of cultivars.

We have no pollen rain studies available in the area. However, taking into account the location of the basin and its altitude and geographical extent, as well as the dispersal mechanisms of individual species (Markgraf, 1980), the expected pollen source area should include not only the 1–2 km wide valley, mostly dominated by cultivars and garrigue, but also the surrounding 10–15 km of low mountains including present-day patches of *Q. rotundifolia* forests, and the vegetation of the high altitude Iberian and Baetic ranges, including today *P. sylvestris* and *P. nigra* relict forests.

3. Methods

Sampling was done by means of metal boxes with dimensions 100 × 20 × 15 cm, open at one side. The sharp edges of the boxes were pushed into the exposed profile and subsequently cut out. At the laboratory, subsamples for the analysis of microfossils were taken at every 1 cm from the contents of the metal boxes. Subsequently, they were treated with KOH and acetolysed. *Lycopodium clavatum* spores were introduced (ca. 12,542 spores per tablet) to calculate pollen concentration. For the separation of organic material from sand and clay, a bromoform–alcohol mixture (specific gravity 2) was used. The material was embedded in glycerine and sealed with paraffin wax. The uppermost 36 cm were part of an agricultural soil and they were not treated in the laboratory. Samples between 145 and 166 cm depth were palynologically sterile. All the remaining samples were analysed for pollen, algae, fungi and other palynomorphs. Pollen percentage diagrams (Figs. 3–8) and pollen concentration diagram (Fig. 9) were constructed and their zonation was made using the Tilia 1.12 and TiliaGraph 1.18 programs. Distinctive 'new' types of palynomorphs were photographed and described (Figs. 8, 11 and 12; Plates I and II).

The subsamples for macrofossil analysis were boiled in 5% KOH for 5–10 min and strained through a sieve with 140 × 140 μm meshes. Only some seed types and *Chara* gyrogonites were recorded, mainly in the uppermost part of the profile (Fig. 10).

Charcoal counts were made for the whole section (Fig. 10). Samples were diluted with water in a cross-ruled petri dish and analysed for macroscopic charcoal fragments larger than 150 μm using a stereo microscope with low magnification. In the microscopic pollen slides, two classes of charcoal (larger and smaller than 25 μm) were distinguished (Mehringer et al., 1977).

A chronology was established on the basis of 14 radiocarbon dates. Samples consisted of bulk peaty sediment, some of them were AMS dated or conventionally dated through extended counting because of the poor carbon content (Table 1). A time–depth curve is shown in Fig. 2.

Identification criteria for pollen and macrofossil types (Appendix A), and descriptions of new non-

Table 1
Radiocarbon age determinations for the Navarrés 3 sedimentary sequence. The dates at 61 and 197 cm depth are excluded from the calculation of the age–depth model

Lab. No.	Depth (cm)	Conventional ^{14}C age (yr B.P.)	Analysis
Beta-102170	40	3160 ± 100	extended counting
Beta-105203	61	6290 ± 90	extended counting
Beta-102171	68	5930 ± 80	standard
Pta-7438	69	6310 ± 70	standard
Pta-7204	82	6820 ± 45	standard
Beta-1052021	103	9360 ± 50	AMS
Beta-102172	106	10,340 ± 50	AMS
GrA-9008	123	11,680 ± 60	AMS
Beta-105205	135	12,010 ± 40	AMS
Pta-7442	166	25,500 ± 630	standard
Beta-102173	193	27,890 ± 250	standard
Pta-7205	197	26,600 ± 350	standard
Beta-102174	230	30,210 ± 180	AMS
Pta-7207	249	30,900 ± 530	standard

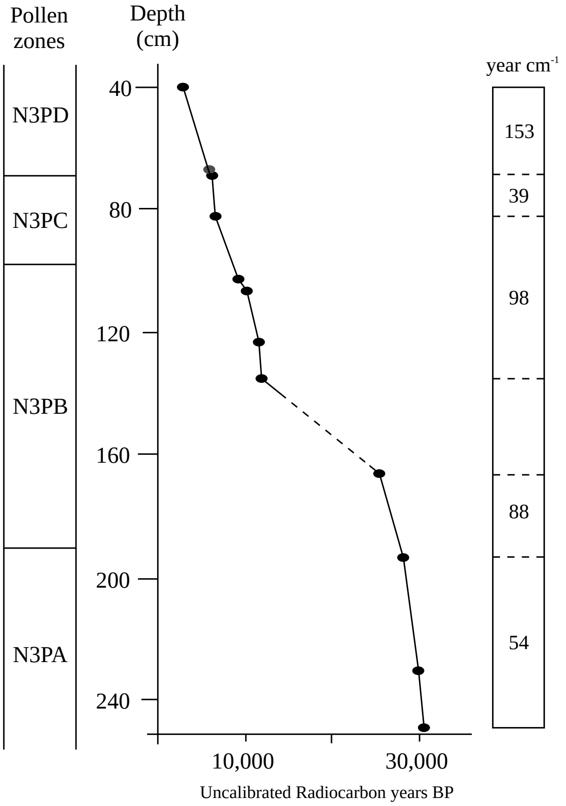
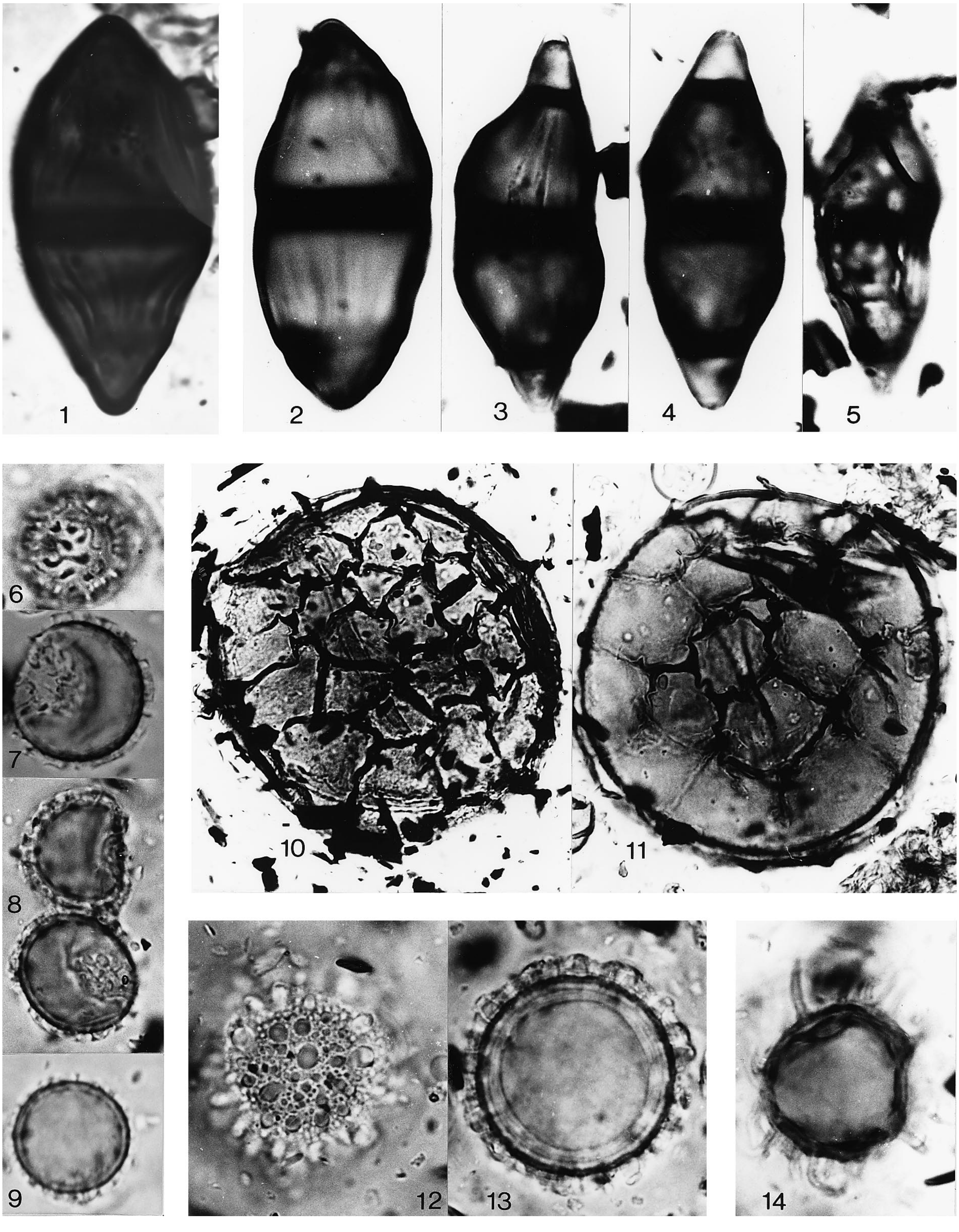


Fig. 2. Sediment depth and pollen stratigraphy to radiocarbon age relationships from the Navarrés-3 section. Lines connecting each plotted point are interpolated sediment accumulation rates.

PLATE I



pollen palynomorphs (Appendix B) are presented at the end of the paper.

4. Paleoecological sequence

The Navarrés-3 study is based on the analysis of 192 samples, including 188 palynological types, 2 types of Characeae gyrogonites, 19 seed types and 3 size classes of charcoal particles. The pollen diagrams are subdivided in 4 pollen zones and show the records of trees (Fig. 3), shrubs (Fig. 4), herbs, including some small shrubs (Figs. 5 and 6), local hygrophytes, hydrophytes, pteridophytes and bryophytes (Fig. 7), non-pollen palynomorphs (Fig. 8), macroscopic and microscopic charcoal, gyrogonites and seeds (Fig. 10). In addition there are two synthetic diagrams (Figs. 11 and 12), the last one covering the uppermost meter of the sequence. The pollen concentration curves for selected taxa (Fig. 9) show similar trends to the percentage curves and support their paleoecological reliability.

Basal zone N3PA (ca. 31,000–27,000 yr B.P.) is an interpleniglacial phase, characterised by the dominance of *Pinus* but showing high percentages of evergreen (around 15%) and deciduous *Quercus* (around 10%) between ca. 30,210 and 27,890 yr B.P. At the onset of this zone *Pinus* surpasses 80%. The almost continuous presence of *Q. suber* and a conspicuous curve for *Pinus pinaster* and *Erica arborea* are worth mentioning, the last species even shows its maximum values. Altogether these records suggest the presence of woodlands dominated by pines and oaks. Additional indicators of a Mediterranean forested landscape are *Arbutus*, *Pistacia terebinthus*, *Myrtus communis*, and *Viburnum tinus*, while *Olea*, *Phillyrea*, *Pistacia lentiscus*, *Cistus*, *Helianthemum*, *Asphodelus fistulosus*, *Sideritis*, *Teucrium* and other Lamiaceae are suggestive of open spaces under a summer-drought rainfall regime. Some pollen inputs may well be due to long-distance transport, especially in the case of *Cedrus*, whose present-day distribution does not point to a late Quaternary presence in Europe (Parra, 1994). A regional presence of *Abies*, *Taxus*, *Alnus*, *Betula*, and *Corylus* appears to be more easily explained in view of the present and past botanical evidence in eastern Spain. Some parts of the basin during zone N3PA were colonised by *Apium*, *Typha angustifolia*, ferns, and Cyperaceae, which is confirmed with the presence of *Carex* and *Cyperus* seeds. Some hydrophytes suggesting water bodies are also present: *Myriophyllum spicatum*, *Potamogeton*, *Alisma* and *Nuphar*.

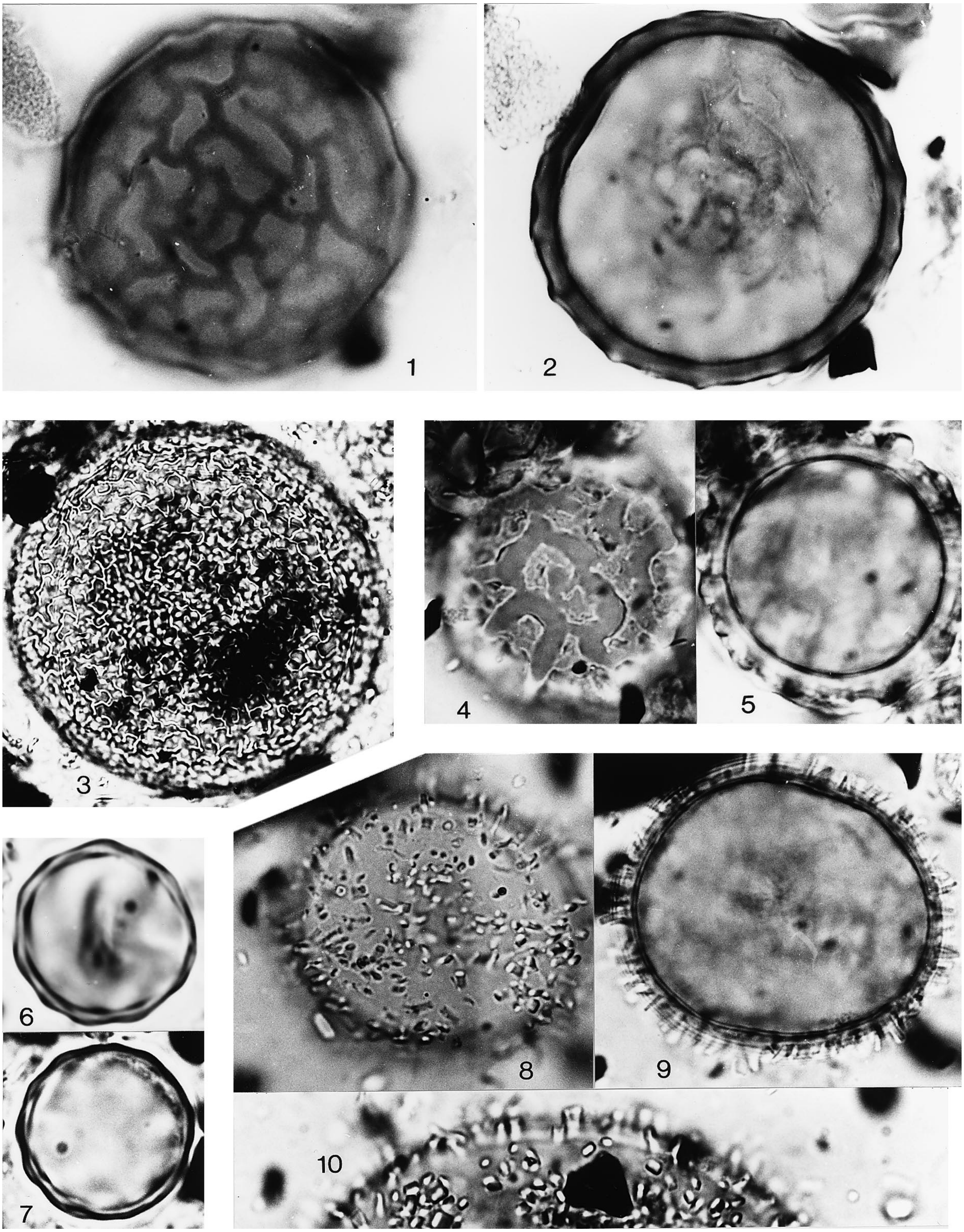
Zone N3PB (ca. 27,000–10,000 yr B.P.) evidently shows the glacial conditions already suggested in the uppermost samples of the preceding phase, namely high percentages of *Artemisia* (which surpass 50% in some samples), a notable increase in Chenopodiaceae and the constant presence of *Ephedra distachya–nebrodensis*. However, *Pinus* continues to be abundant, and eventually reaches high proportions. It is worth mentioning that when *Pinus* increases, *Artemisia* decreases and vice versa. *Quercus* and other mesothermophilous and Mediterranean trees and shrubs disappear from the pollen record. The pollen of Asteroideae and Cichorioideae is abundant, but this could be due to strictly local occurrence, especially in the case of Cichorioideae, for which pollen clumps have been recorded both in this zone and the following.

The palynological and macrofossil sequence of N3PB is interrupted between 145 and 166 cm. This hiatus seems to correspond to the last glacial maximum, during which conditions were not favourable for biotic preservation in wide parts of the basin. The sediment is sandy, suggesting increased processes of erosion and denudation of the surroundings, without vegetation cover. Chronological extrapolation from the limiting dates of ca. 12,010 yr B.P. at 135 cm and ca. 25,500 yr B.P. at 166 cm provides a critical date of ca. 18,000 yr B.P. at 150 cm. Thus, it is not casual that the previously studied cores (Carrión and Dupré, 1996) were also palynologically sterile just before ca. 16,000 yr B.P. What makes a difference is that no equivalent zone to N3PA was reported in

PLATE I

1, 2.	*Fusiformisporites*. ×1760.
3–5.	Type 981. ×1760.
6–9.	Type 983. ×1760.
10, 11.	Type 982. ×704.
12, 13.	Type 984. ×1760.
12.	High focus.
13.	Low focus.
14.	Type 985. ×1760.

PLATE II



those sequences, possibly as a consequence of later erosional processes. As a matter of fact, the high occurrence of *Artemisia*–Chenopodiaceae–*Ephedra* assemblages between ca. 130 and 180 cm suggests extraordinary aridity, which is a general feature of the Mediterranean vegetation during the Weichselian late Pleniglacial (Tzedakis et al., 1997; Carrión et al., 1998).

Above 145 cm, *Artemisia* shows a decline and *Pinus* increases again, with some occurrence of *P. pinaster*. 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, *Typha*, 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 (A and B) also occurs continuously and attains its maxima. Van Geel et al. (1983a,b) have reported these types associated with eu- to mesotrophic open water, which agrees with our records from Navarrés.

According to the high pollen percentages of *Artemisia* recorded from 143 to 130 cm depth, the Older Dryas event could be represented in the Navarrés sequence around ca. 12,010 yr B.P. (zones N3PBiv or N3PBvi). This climatic deterioration has been shown from botanical proxy records of northern Europe by ca. 12,200–11,800 yr B.P. (Van Geel et al., 1989; Walker, 1995), The Older Dryas event is relatively rarely shown in southern Europe (Guiot, 1987; Pérez-Obiol, 1988; Van der Knaap and Van Leeuwen, 1997). In any case, there are four peaks of *Artemisia* in Navarrés around 12,000 yr B.P. and this may well be a consequence of the several short-lived climatic events occurring through the last-glacial interglacial transition in the region, the Older Dryas being only one of them. Other regional pollen records such as Carihuela (Carrión et al., 1998) show similarly abrupt changes in the pollen curves of the Late Glacial. This agrees with the paleoclimatical picture portrayed from marine records (Lowe and NASP Members, 1995) and general circulation model simulations (Kutzbach et al., 1993) suggesting that the North Atlantic remained very unstable for this period. A fine-resolution, well-dated pollen stratigraphy in the Serra da Estrela, Portugal (Van der Knaap and Van Leeuwen, 1997) shows a particularly complex vegetational and climatic history for the peninsular Late Glacial, including phases correlated with the Bølling and Allerød interstades and the Older Dryas and Younger Dryas cold spells. Even more, these authors describe internal variation in Bølling and Younger Dryas phases.

Navarrés is not a suitable site for assessing the regional development of *Quercus* during the Late Glacial Interstadial, such as it has been described southwards in Padul (Pons and Reille, 1988), and northwards in Delta del Ebro (Yll and Pérez-Obiol, 1992). In these sequences, oak colonisation starts at ca. 13,000 and 11,000 yr B.P., respectively. However, a Late Glacial amelioration is visible in Navarrés-1, Navarrés-2 (Carrión and Dupré, 1996), and Navarrés-3 by a concomitant decline of *Artemisia*, *Ephedra* and Chenopodiaceae together with *Pinus* increase (Figs. 11 and 12). The intra-mountainous nature of the Navarrés region could have determined pine prevalence during the Late Glacial climatic improvement such as in northernmost parts of the Iberian Cordillera (Peñalba et al., 1997).

The Younger Dryas cold spell is shown in the end of zone N3PB (Fig. 11) with a radiocarbon date of $10,340 \pm 50$ yr B.P. at 106 cm depth. This phase is characterised by the latest important peak of *Artemisia* associated to the latest appearance of *Ephedra distachya–nebrodensis*. Because no important changes are recorded in the local vegetation, we interpret those features as part of a regional signal. The pollen diagram constructed for the section of 120–35 cm (Fig. 12), offers a clear picture of the Younger Dryas (subzone N3PBviii). A more precise chronological setting of this climatic stage has not

PLATE II

1, 2. Type 986. ×1760.
1. High focus.
2. Low focus.
3. Type 987. ×1760.
4, 5. Type 989. ×1760.
4. High focus.
5. Low focus.
6, 7. Type 988. ×1760.
8, 9. Type 990. ×704.
8. High focus.
9. Low focus.
10. Type 990. ×1760.

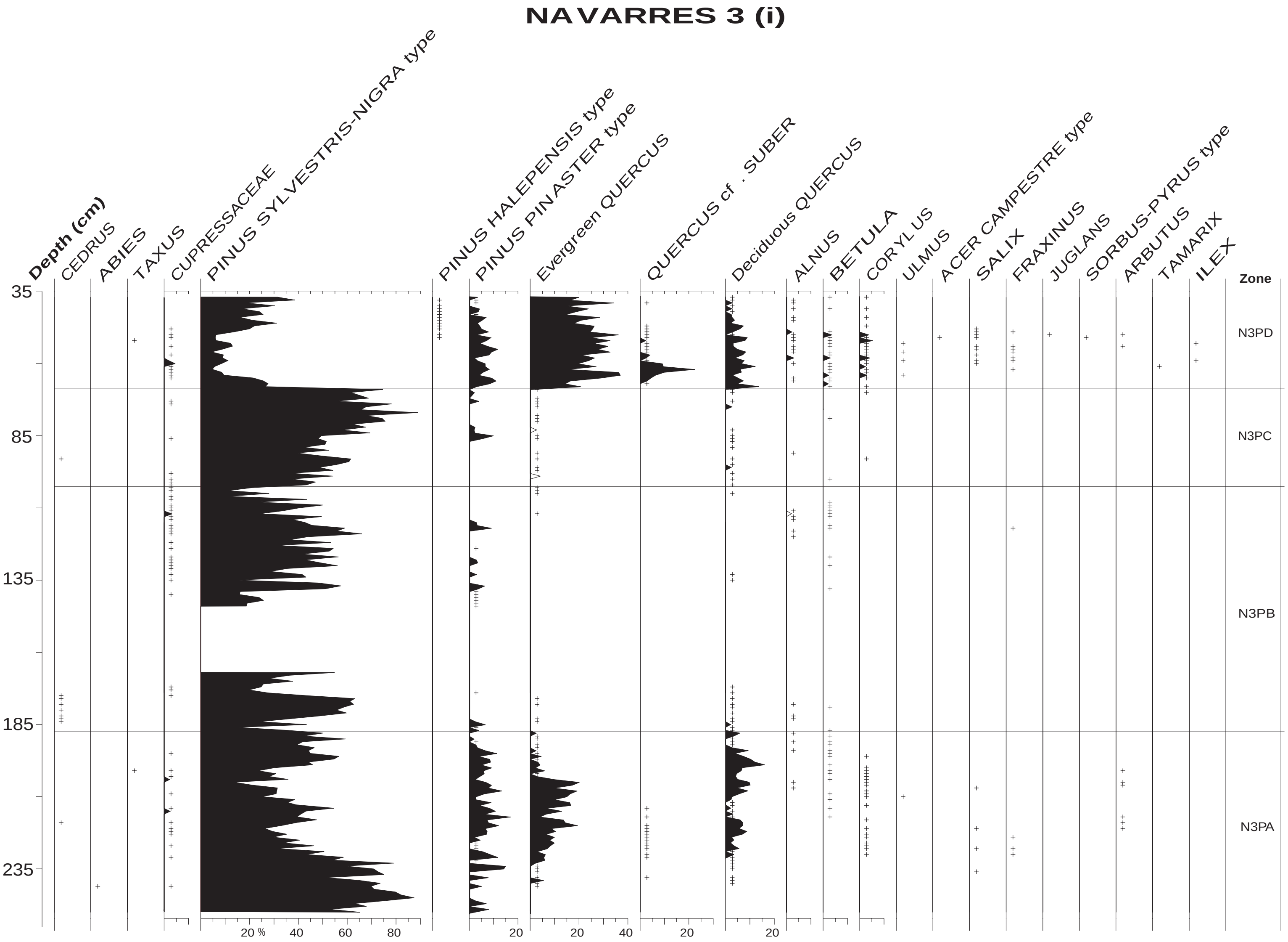


Fig. 3. Percentage pollen diagram of Navarrés-3 (trees).

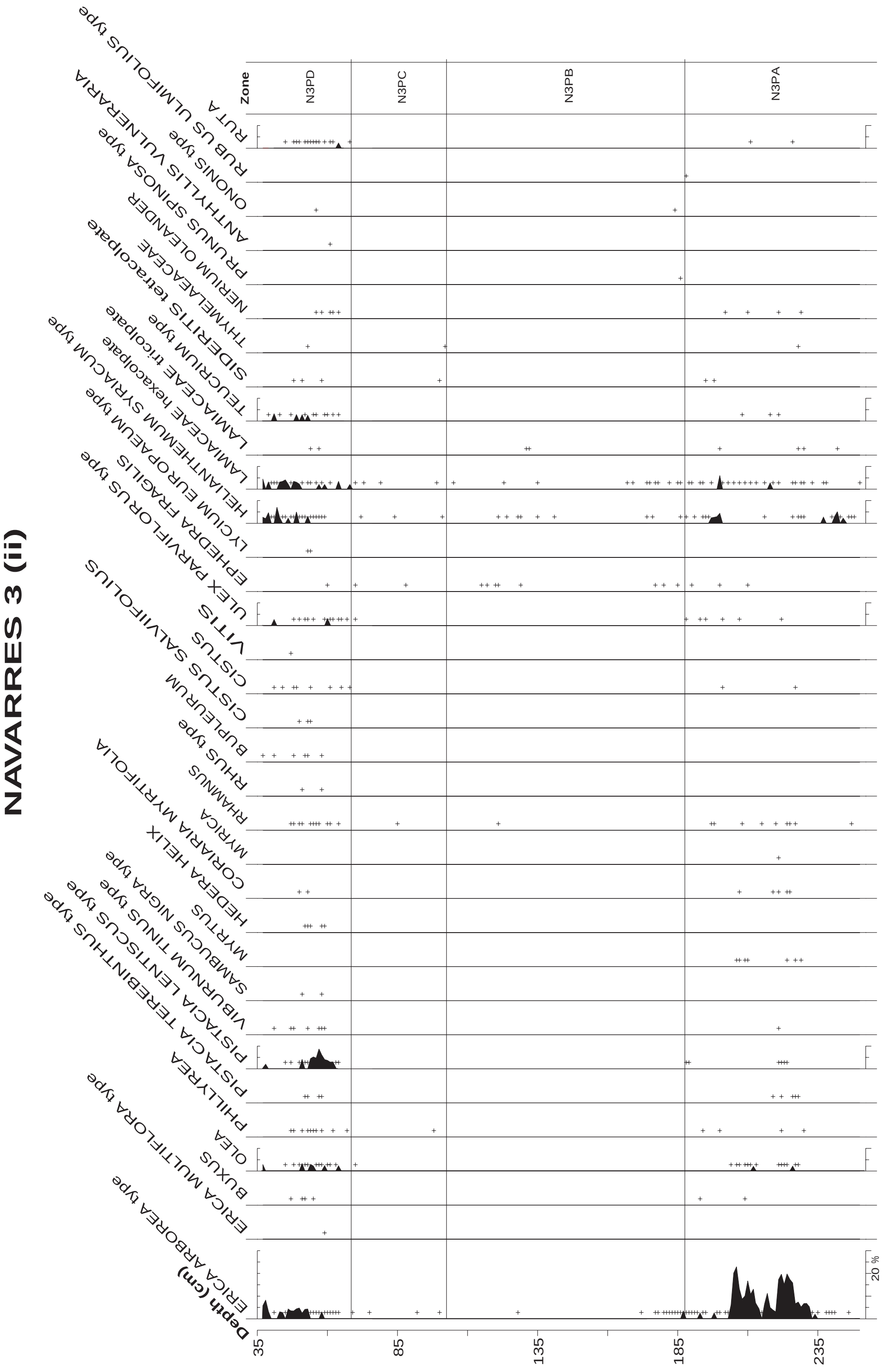


Fig. 4. Percentage pollen diagram of Navarrés-3 (shrubs).

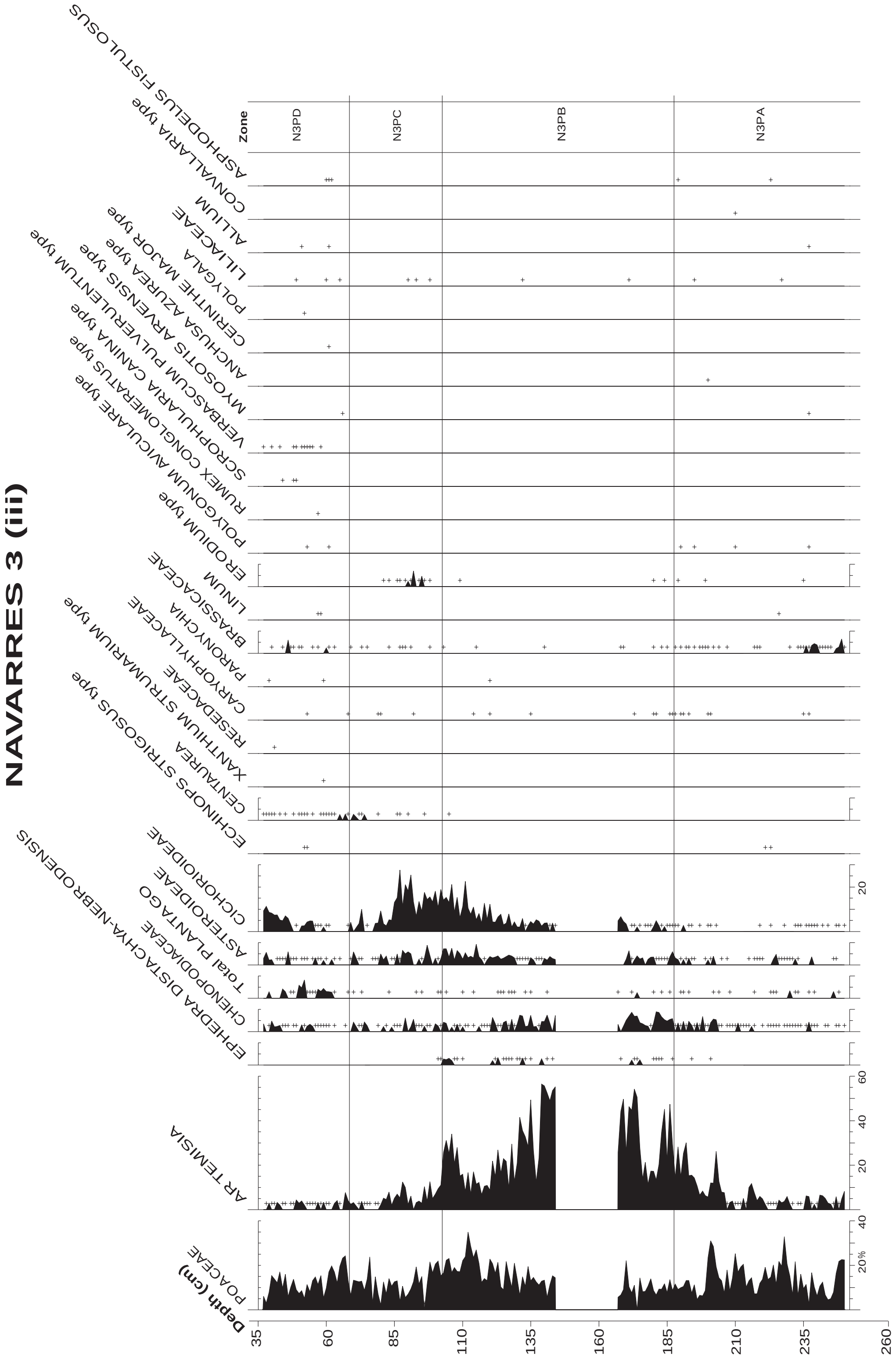


Fig. 5. Percentage pollen diagram of Navarrés-3 (herbs).

Fig. 6. Percentage pollen diagram of Navarrés-3 (herbs, cont.).

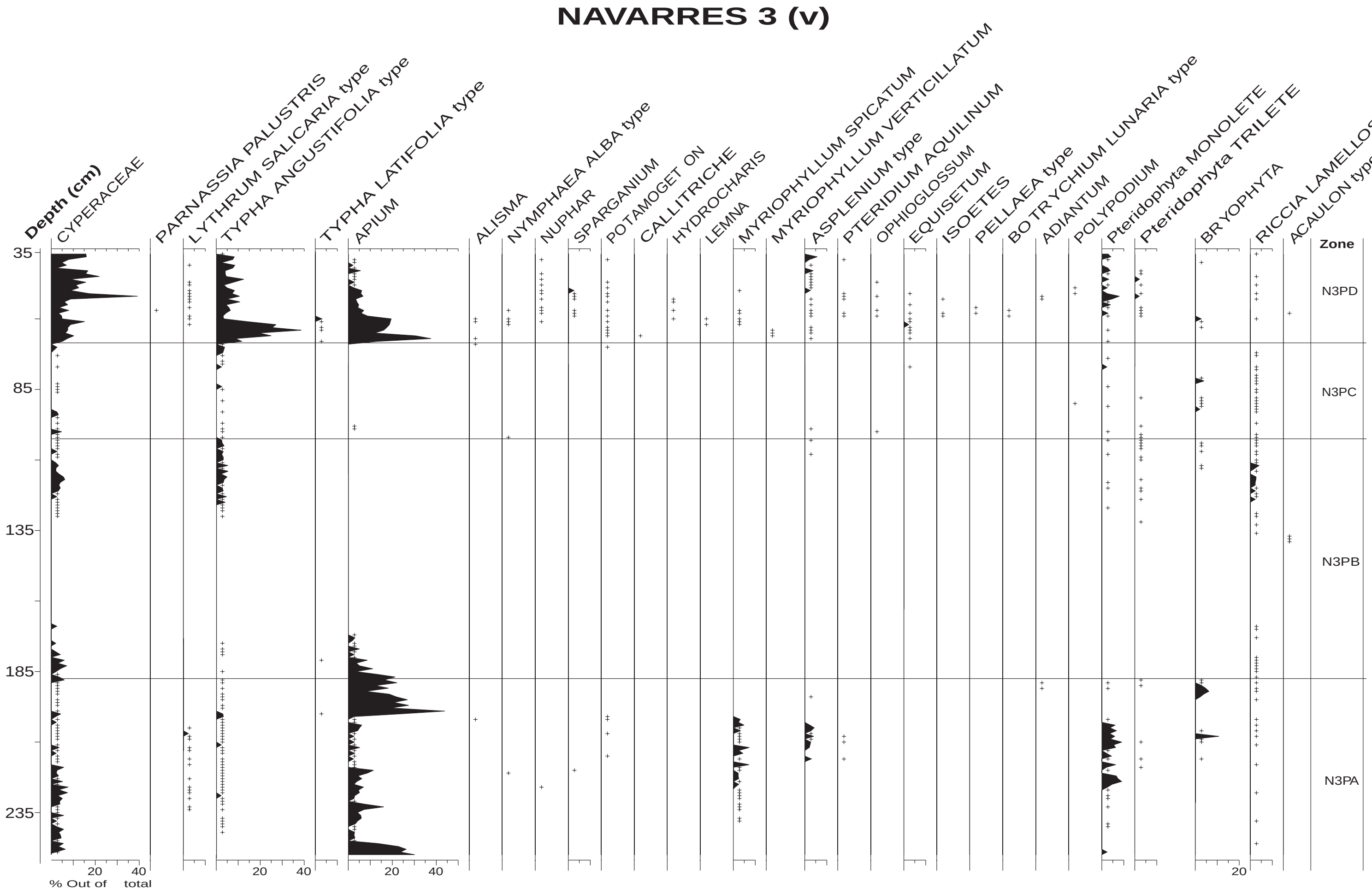


Fig. 7. Percentage pollen diagram of Navarrés-3 (local herbs, pteridophytes and bryophytes). All types excluded from pollen sum.

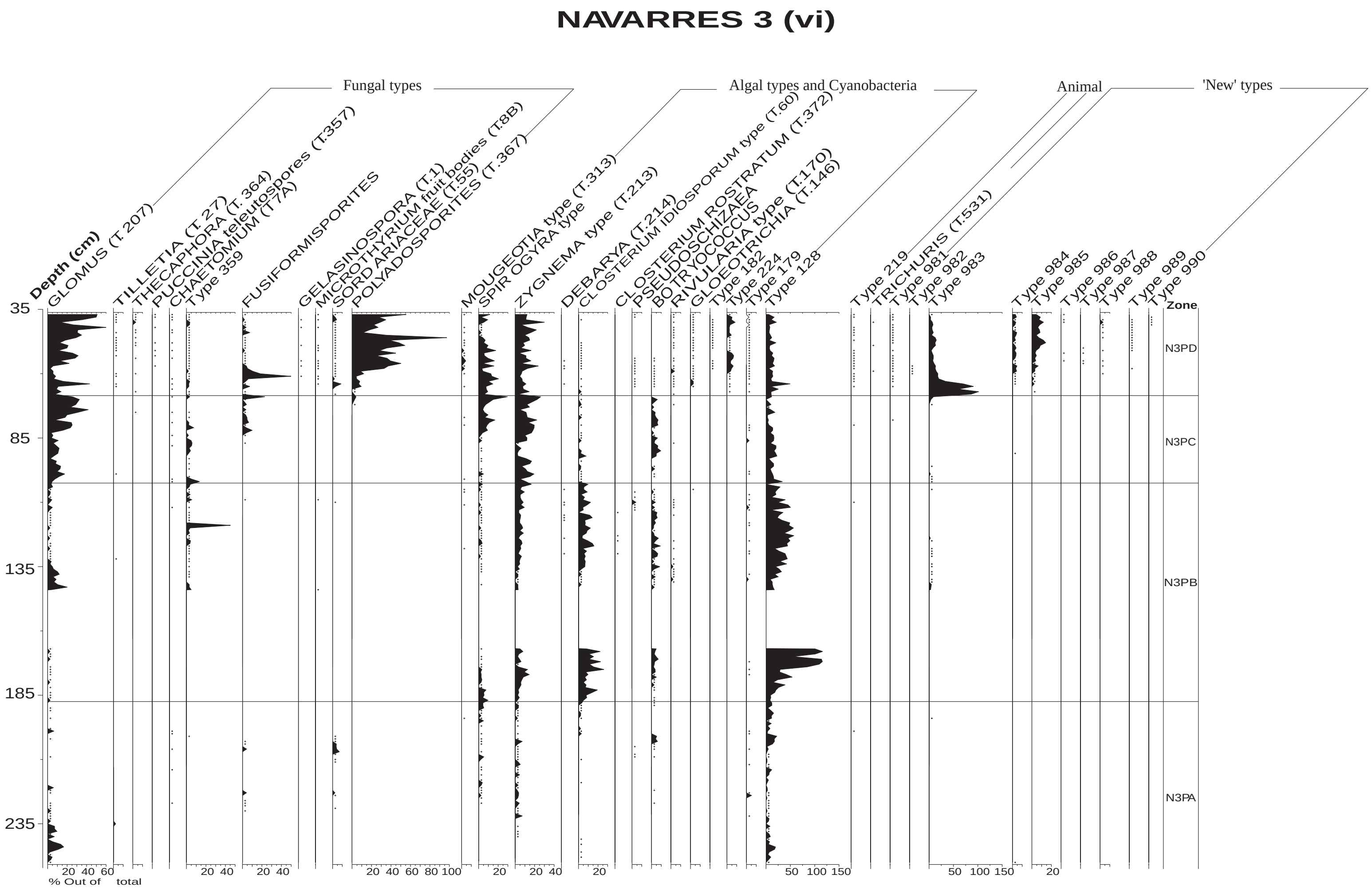


Fig. 8. Percentage pollen diagram of Navarrés-3 (non-pollen palynomorphs including ‘new’ types). All types excluded from pollen sum.

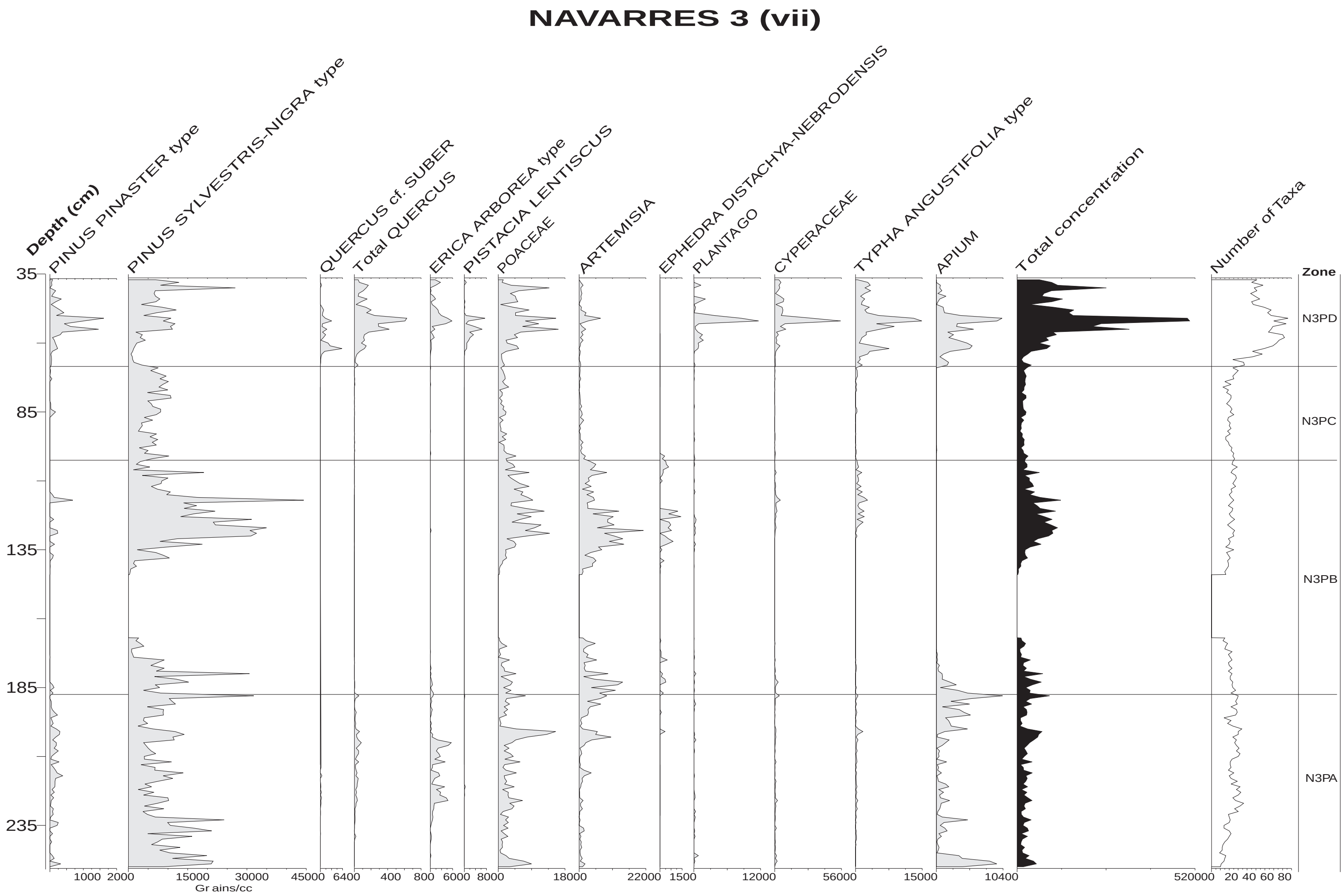


Fig. 9. Concentration pollen diagram of selected types of Navarrés-3.

been possible since no seeds or fossil leaves for AMS radiocarbon dating were available and we had to use bulk sediment. In any case, the date of 10, 340 ± 50 yr B.P. at 106 cm depth represents a relatively confident approach for the peak of the event.

Zone N3PC (ca. 10,000–6000 yr B.P.) parallels well the corresponding early Holocene zones in Navarrés-1 and Navarrés-2 (Carrión and Dupré, 1996), which means that there is no evidence of angiosperm forest colonisation and *Pinus* continues to be dominant, reaching similar values (above 80%) as in bottom zone N3PA, especially from ca. 6820 to 6320 yr B.P. *Pinus pinaster* occurs again but its presence is not continuous. There are no palynological indications for a change to a Mediterranean landscape. At the sampling site, desmids and types 128 become rare and *Botryococcus* and zygnemataceous zygospores (*Zygnema* first and *Spirogyra* afterwards) increase. The top of this zone (N3PCii, Fig. 12) shows a very important increase in charcoal particles, both microscopic and macroscopic, which strongly suggests fire events, especially at 69 cm (dated at ca. 6310 yr B.P.). Until ca. 6820 yr B.P., there are some minor increases of *Artemisia* and it remains to be established whether they could be paleoclimatically significant.

Like in the Navarrés-1 and -2 cores (Carrión and Dupré, 1996), at the start of zone N3PD (ca. 6000–3000 yr B.P.) there is an abrupt change in the pollen assemblages. *Quercus* becomes the most important arboreal taxon, *P. pinaster* occurs continuously, a number of deciduous trees (*Alnus*, *Betula*, *Corylus*, *Ulmus*, *Acer*, *Salix*, *Fraxinus*, *Juglans*), and Mediterranean shrubs appear regularly (*Erica arborea*, *Arbutus*, *Phillyrea*, *Olea*, *Viburnum tinus*), many of them indicative of summer drought rainfall regime (*Pistacia lentiscus*, *Cistus salviifolius*, *Helianthemum syriacum*, *Teucrium*, *Sideritis*, *Nerium oleander*, *Ruta*, *Bupleurum*, *Erica multiflora*, *Asphodelus fistulosus*), or suggestive of arid environments (*Tamarix*, *Lycium europaeum*, *Mesembryanthemum nodiflorum*, *Pellaea* type). All of these findings suggest a mosaic landscape with macchia and garrigues.

In the basin, there are, during this zone, indicators of water bodies such as *Nymphaea*, *Nuphar*, *Potamogeton*, *Callitriche*, *Hydrocharis*, *Lemna*, *Myriophyllum spicatum*, *M. verticillatum*, *Isoetes* (some of them providing seeds such as *Potamogeton coloratus* and *Myriophyllum verticillatum*) and others that suggest increased colonisation of the lake margins (maxima in palynomorph concentration and taxa diversity, pollen of Cyperaceae, *Typha*, *Apium*, *Lythrum salicaria*, *Equisetum*, ferns, seeds of *Alisma*, *Cyperus*, *Scirpus*, *Schoenus*, *Carex*, *Juncus*, *Mentha*, *Verbena*, etc.), and peat decomposition (fungal types like *Gelasinospora*, *Chaetomium*, *Fusiformisporites*). Human influence in the landscape is suggested by the curve of *Plantago*, the appearance of *Vitis* and *Juglans*, and supposedly, the abundance of herbaceous and shrubby assemblages with Boraginaceae, Asteraceae, Lamiaceae, Cistaceae, and Fabaceae (e.g. *Ulex parviflorus* type). It must be noticed that the curve of *Plantago* begins later than the curves of *Quercus* and Mediterranean shrubs (Fig. 12). On the other hand, since they frequently parasite grasses, *Puccinia* and to a lesser extent, *Thecaphora*, might also be related with agricultural practices. In addition, there are indicators of dung input into the sediment such as spores of Sordariaceae and eggs of the intestinal parasite *Trichuris*.

Since the Late Glacial, an algal succession at the site is shown (Fig. 11) by the following assemblages: (N3PB) types 128–*Closterium*–*Botryococcus*; (N3PC) *Zygnema*–*Spirogyra*–*Botryococcus*; and (N3PD) *Zygnema*–*Spirogyra*–*Mougeotia*–*Rivularia*–*Gloeotrichia*–*Chara*. This succession may be related with a trophic change to increased alkalinisation and concentration of oxidizable organic compounds in relatively warm water, but this needs to be confirmed by sedimentological analyses. Types 182, 224, 179, 219, and 981–990 parallel this distribution, with the very abundant Type 983 showing a peak in N3PDi, just when maxima for *Quercus*, *Apium*, *Typha angustifolia* and *Chara hispida* are recorded. This Type must be related with a shallow freshwater lake environment, considering the abundance of fossil gyrogonites which indicates submersion for at least three months. Charophyte deposits cannot be attributed to ephemeral environments created by stagnant water remaining for a short period after heavy rainfall or exceptional flooding (Soulié-Märsche, 1991, 1993). Before this change (N3PCii), there is an important increase of charcoal particles and afterwards (N3PDii), of Cyperaceae pollen and seeds (e.g. *Carex distans*) and, finally (N3PDiii), of

Juncus articulatus-type seeds (Fig. 12). This is worth mentioning because a succession with (1) *Chara*, (2) *Typha*, (3) Cyperaceae, and (4) *Juncus* has been repeatedly described for eastern Spanish lakes as a consequence of infilling (Cirujano, 1990).

Dating precisely the transition from *Pinus*- to *Quercus*-dominated assemblages is complicated. The date of Navarrés-3 at 68 cm depth is 5930 ± 80 yr B.P. At 69 cm the radiocarbon age is 6310 ± 70 yr B.P. (Figs. 11 and 12). However, a date at 61 cm depth was 6290 ± 90 yr B.P. and the transition at Navarrés-1 and Navarrés-2 was dated at around 5725 and 5150 yr B.P., respectively (Carrión and Dupré, 1996). The exact time of the transition is therefore not clearly established. It can be said, however, that it occurs relatively fast (over 1 cm, that is, within ca. 39–153 yr) and around 6000–5500 yr B.P.

5. Discussion

5.1. Comparison with a previous study

The most detailed palynological investigation of the Navarrés deposit carried out hitherto is that by Carrión and Dupré (1996), reporting two 150 cm depth cores in which sampling was done at intervals of 10 cm (Navarrés-1) and 5 cm (Navarrés-2). Both cores were taken at 5 m distance. The section studied here is located around 300 m to the north of those cores, which is closer to the village of Navarrés (Fig. 1).

The present pollen record is similar to the Navarrés-1 and Navarrés-2 records in respect to: (1) the absence of pollen below the first 150 cm of peaty sediment; (2) the importance of *Pinus*, *Artemisia*, *Ephedra* and Chenopodiaceae during late Pleniglacial and Late Glacial times; (3) the indication of a Late Glacial climatic improvement deduced from pine increases; (4) the dominance of *Pinus* forests during the first half of the Holocene; (5) the replacement of *Pinus* by *Quercus*-dominated assemblages around 6000–5500 yr B.P.; (6) the synchronous increase of pollen taxa indicative of eutrophication and lake infilling when pine forest was replaced by *Quercus*; and (7) the evidence of anthropogenic disturbance (e.g. the *Plantago* curve), following the Holocene development of *Quercus*.

The new sequence, more detailed in chronology, identification of micro- and macrofossils, and in sampling resolution, confirms all these events and, in addition, shows a stage of *Quercus* development between ca. 31,000 and 27,000 yr B.P. and provides evidences for a vegetational change related to the Younger Dryas climatic event in the region. Other Late Glacial climatic deteriorations are also suggested, one of them probably corresponding to the Older Dryas chronozone.

There are, considering the three sequences, taphonomic differences which account for the different behaviour of the total pollen concentration curves and some differences in the individual pollen curves of the main taxa. Such locational differences were widely discussed by Carrión and Dupré (1996). However, there are no differences in the main trends, neither they affect our conclusions regarding the vegetational history of the site. On the other hand, in the present study, the pollen concentration curves correspond well to the percentage variations, which did not happen in Navarrés-1 or Navarrés-2. For example, the variation of *Artemisia* and *Ephedra*, which is essential to distinguish a Younger Dryas signal, is most significant at Navarrés-3.

Because its higher taxonomic detail, Navarrés-3 provides a wider spectrum of evidence related to both the plant biogeography and the evolution of the lake basin. However, the most important contribution of this new study is to provide an explanation for the middle Holocene replacement of *Pinus* forests by *Quercus*.

5.2. N3PA: Interpleniglacial development of Mediterranean vegetation

Menéndez-Amor and Florschütz (1961) reported a presumably Late Glacial *Quercus* expansion which was not seen in Navarrés-1 and Navarrés-2 (Carrión and Dupré, 1996). If we take into account that they did not provide dating for that event, it may well correlate with zone N3PA at Navarrés-3. Unfortunately, we do not know the exact position of their study site and the section cannot be revisited or interpreted in the light of the basin evolution.

During N3PA, while the basin was experiencing some advancement of local hygrophytes, the surroundings of the site, formerly occupied by pines, were partially invaded by different species of oaks, *Pinus pinaster* and shrubs possibly benefiting from some soil change. Many different plant communities may have taken part in the advancement, while the region has a contrasting and diverse topography. Charcoal counts correspond well with the *Quercus* curve (Fig. 11) and indicate that natural fires must, at least partially, have favoured the maintenance of the *Quercus* formations. Further evidences of fire could be the high pollen percentage and concentration values of *Erica arborea*, the curves of heliophytic Cistaceae and Lamiaceae (Fig. 4), and the presence of *Pteridium aquilinum* spores (Fig. 7). It is worth mentioning that charcoal is only relatively prominent after the appearance of the *Quercus* and *Pinus pinaster* curves, which is a different situation compared with zone N3PD. Thus, it is not possible to invoke fires as responsible for a partial replacement of *Pinus* by *Quercus* at this stage.

Palynozone N3PA represents the most clear evidence for an expansion of thermophilous vegetation in Spain during glacial times. Almost similar increases of *Quercus* and other trees and shrubs are recorded in the Upper Pleistocene cave sequences of Cova Beneito, Alicante (Carrión, 1992a; Carrión and Munuera, 1997), and Abric Romaní, Barcelona (Burjachs and Julià, 1994), but these events have been dated before 35,000 and 40,000 yr B.P., respectively, and they have been obtained from different sediment sources, namely karstic infillings and breccia, for which, the significance of the pollen percentage measurements is not yet completely understood (Carrión et al., 1999). A slight signal of regional extension of a Mediterranean vegetation in southern Spain during ca. 32,000–28,000 yr B.P. comes from the Core 11P pollen sequence recovered offshore Almería (Targarona, 1997). The basal zone of that record shows the synchronous presence of *Q. ilex–coccifera*, Ericaceae, Cistaceae and *Pistacia*.

In the sequence of the lake Banyoles, Pérez-Obiol and Julià (1994) postulated the existence of a ‘clear interstadial event’ between ca. 30,000 and 27,000 yr B.P. based on slight increases (less than 5%) of *Juniperus*, *Betula* and deciduous *Quercus* over no more than 6 pollen samples. If we compare this sequence with, for instance, the Padul pollen record, it is evident that Pons and Reille (1988) do not recognise any interstadial in the middle part of the last glacial stage, even when there are higher increases in thermophytes than in Banyoles. Definitively, the concept of an interstadial may be confusing, perhaps because it is often used interchangeably as chronozone and biozone. While used as chronozone it should have clear-cut temporal boundaries, but biozones are necessarily time-transgressive and their assignment to a particular chronozone must be taken cautiously, especially from long-distance comparisons.

In the Navarrés area, from ca. 31,000 to 27,000 yr B.P., we can only assess the regional development of a Mediterranean vegetation. This appears in chronological overlap with the last part of the north European middle Pleniglacial mild phase, during which several interstadials have been described, among them the Denekamp Interstadial (32,000–28,000 yr B.P.) (Ran and Van Huissteden, 1990). It is evident from marine (Shackleton, 1987) and continental records (Lorius et al., 1990) that temperatures just before 27,000 yr B.P. were not so low as during the last glacial maximum. Thus, it is plausible a climatic cause for the oak development in Navarrés during zone N3PA, but since the phenomenon has not been described regionally hitherto, we must leave the issue open to other interpretations. A longer Upper Pleistocene pollen record of the region is needed to elucidate this problem and other related questions, because the Padul pollen sequence (Pons and Reille, 1988) lies in a physiographically very different area.

Another question arising from the pollen records of zone N3PA is about the physiognomy and spatial distribution of the plant communities. We have seen synchronous evidences for the existence of forested and open landscapes, pines and oaks, sclerophyllous and broad-leaf trees, sciophyllous and heliophyllous plants. It is likely that temperate plant associations of the region were differently shaped in terms of floristic composition and, besides, encapsulated in small pockets under environmentally favourable conditions (Willis, 1996), but plant communities could also have recurred fortuitously at ‘meeting points’ in time and space, especially during periods of relative climatic stability, when some plant migrations are slowing down, and populations of slower-moving taxa are enabled to catch up (Tallis, 1991). Such topics as glacial refugia and plant reservoirs of diversity in the Mediterranean (Magri and Parra, 1998) are open to debate since our paleoecological data set is clearly insufficient both spatially and temporarily.

5.3. On the presence of *Pinus pinaster*

The presence of *Pinus pinaster* pollen in the sequence of Navarrés poses a question related with the biogeography of the species. Although most local botanists realise that elucidating the natural area of distribution is not possible since the repeated afforestations, they do not recognise a role for *P. pinaster* in the natural vegetation succession of eastern Spain (e.g., Costa, 1987). For Portugal, the issue has been studied by Figueiral (1995) using prehistoric charcoal data. It appears that the present distribution of *P. pinaster* is the result of human activities, but there are clear anthracological evidences for the presence of this pine species in southern and central Portugal already during the Late Pleistocene.

At Navarrés, *P. pinaster* is abundant both during zones N3PA as N3PD. It also appears sporadically during other periods. Its distribution in the pollen record (e.g., Fig. 3) correlates well with the curves of *Quercus*, although *P. pinaster* starts earlier and ends later. The similarity between *P. pinaster* and the curve of deciduous *Quercus* is even better. It shows that the species behaves as a meso-thermophyte, eventually expanding together with other taxa of the Mediterranean vegetation. This agrees with present-day observations in the Betic and Iberian mountain ranges, where *P. pinaster* forms mixed forests with *Quercus faginea*, *Q. pyrenaica* and *Q. rotundifolia*, and an understorey of mainly Ericaceae and Cistaceae (Blanco et al., 1997). The first author (unpublished) has observed the species mixing with relict populations of *Q. ilex* in edaphically favourable conditions within gullies in the semi-arid region of southeastern Spain. More paleo- and autoecological research should be done on *P. pinaster* in order to place the species in a general picture of the Spanish vegetation dynamics. But, to start with, we should abandon some rigid schemes that identify stable equilibrium conditions (e.g., climax, potential vegetation; Peinado et al., 1992) on the basis of merely present-day floristically defined associations and without any consideration to the increasing amount of evidence from the past.

5.4. Pine forests of the Late Pleistocene and early Holocene

The data presented here support the view that wide parts of southern Europe were covered by pine forests during the coldest phases of the last glacial (Carrión, 1992b). Hypothetically the main species involved in the Mediterranean region of Spain were *P. sylvestris* and *P. nigra*. There are some differences in the ecological requirements of these species (Blanco et al., 1997) but both nowadays occur in an 'orophilous' position within the vegetation belts of the Iberian mountains (Rivas-Martínez, 1987). Hypothetically, these two pine species would have formed 'glacial' forests and, later, after climate change to interglacial conditions they only survived in the upper forest belts (Oro-Mediterranean belt). At Navarrés, we recorded the small palynotype (allegedly *P. sylvestris* and/or *P. nigra*) mainly during Pleniglacial times (zone N3PB), but also during the early Holocene (zone N3PC). So the evidence supports the idea that one or both species were important in the last glacial forests, however, their generalised Holocene displacement is more doubtful. Recent anthracological data (Badal et al., 1994) show that *P. nigra*, which is found today at more than 1000 m a.s.l. and more than 50 km from the current coast line, was relatively abundant around 7000 yr B.P. near the eastern Mediterranean coast. In addition, the available ethnobotanical and toponimic information suggests a much larger extension of *P. nigra* during the last centuries in the region (Sánchez-Gómez et al., 1995).

During the dry phases of the late Pleniglacial and Late Glacial, the pine forests surrounding Navarrés must have experienced notable regression in favour of xeromorphic communities of *Artemisia*, grasses, chenopods and species of *Ephedra* indicative of continentality (*E. nebrodensis*, *E. distachya*). Although pollen records for the last glacial maximum stage are lacking, the tendencies in the pollen curves suggest such dry conditions just before and after the sterile deposit.

During the first part of the Holocene (N3PC) there was a recovery of pine forests, which, like the previous phases, were relatively poor in understorey species, something in common with the present-day pine-dominated communities in Mediterranean Spain (Blanco et al., 1997).

The *Quercus* colonisation is not synchronous in the Iberian Peninsula. It occurs during the Late Glacial (Pons and Reille, 1988) or during the early Holocene (Van der Knaap and Van Leeuwen, 1994), but as yet there is no other pollen record with such a late first *Quercus* expansion as at Navarrés. In the northern part of the Mediterranean basin and in the North African mountains, there is normally a replacement of *Pinus* firstly by deciduous *Quercus* and, at around 6000 yr B.P., by *Quercus* type *ilex–coccifera* and *Q. suber* forests (Reille and Pons, 1992). It is not a novelty for southern Europe that the sharp increase in angiosperm tree pollen frequencies is recorded about 5500 yr B.P. or later, while, as in the case of Italy, the immigration of angiosperm trees already starts at about 14,000 yr B.P. (Magri, 1997).

5.5. Younger Dryas

The Younger Dryas chronozone (ca. 11,000 to 10,000 yr B.P.) has been the subject of intensified investigation for the last few years and it is generally accepted that its effects, although not necessarily in the form of important temperature drops, can be recorded in southern Europe (Rossignol-Strick et al., 1992; Reille and Andrieu, 1995; Watts et al., 1996), including Portugal (Van der Knaap and Van Leeuwen, 1997), and northern (Allen et al., 1996) and central Spain (Peñalba et al., 1997).

Based on the data obtained in the Navarrés-2 pollen sequence, Carrión and Dupré (1996) suggested evidence for a Younger Dryas signal in eastern Spain. The present study based on Navarrés-3 confirms that suggestion. Dating has to be improved but problems are inherent to bulk-sediment dating. Using the trace-element contents in lacustrine ostracod valves in Lake Banyoles (northeastern Spain), Wansard (1996) has postulated a temperature decrease of 8°C for the onset of the Younger Dryas and a duration of the event of ca. 400 years. In southern Spain we do not yet have information to compare this model but the vegetation appears to have been affected in both the disappearance and regression of thermophytes as well as in the extension of xerophytic communities (Pons and Reille, 1988; Carrión et al., 1998). Hence, the climatic change would have involved a remarkable precipitation decrease.

5.6. Quercus colonisation and fire events

In a previous paper (Carrión and Dupré, 1996), the possible causes of the middle Holocene change from *Pinus* to *Quercus* were considered, namely climatic change, successional patterns, catastrophic events and human interference. From the new data presented in this paper, we hypothesise that the replacement was a consequence of punctuated episodes of severe forest fires. Charcoal concentrations at Navarrés-3 (Figs. 10–12) indicate that minor fires may have occurred intermittently since the beginning of the sequence and with larger virulence and/or proximity to the site since ca. 7000 yr B.P. The first important micro- and macro-charcoal peak is noticed 1 cm below the first Holocene *Quercus* increase at ca. 5930 yr B.P. (Fig. 12). Thereafter, fires seems to continue, increasing at 51 cm onwards with a maximum at 40 cm, while *Pinus* is slightly increasing again. The picture appears to be one where *Quercus* is favoured after some intermittent episodes of fire and, afterwards, remain dominant, probably because its high flammability levels compared to *Pinus*. After the time of pine persistence, explained by the aforementioned ‘home-field advantage’, there was an abiotically induced change when fires opened up resources and permitted a competitively driven replacement, provoking a new ecological balance. We suppose that fires destroyed the remaining toxic humus that had accumulated during the millennia of pine forest which preceded the dominance of *Quercus* in the Navarrés region.

Our foundation for the former hypothesis is the assumption that macroscopic charcoal fragments are indicative of local fires, since such particles are not transported over long distances (Mehringer et al., 1977; Segerström et al., 1996; Whitlock and Millspaugh, 1996). While interpretation from micro-charcoal countings is problematic, particles larger than 0.06 mm indicate fires in the surroundings. In addition, the occurrence of larger fragments and charcoal peaks indicate that the area was affected by recurrent fires. A better approach to infer fire frequency and pattern should involve the study of additional lake sites in the region (Millspaugh and Whitlock, 1995).

Apart from the similarity in the micro- and macro-charcoal curves (Fig. 10), and the size and tem-

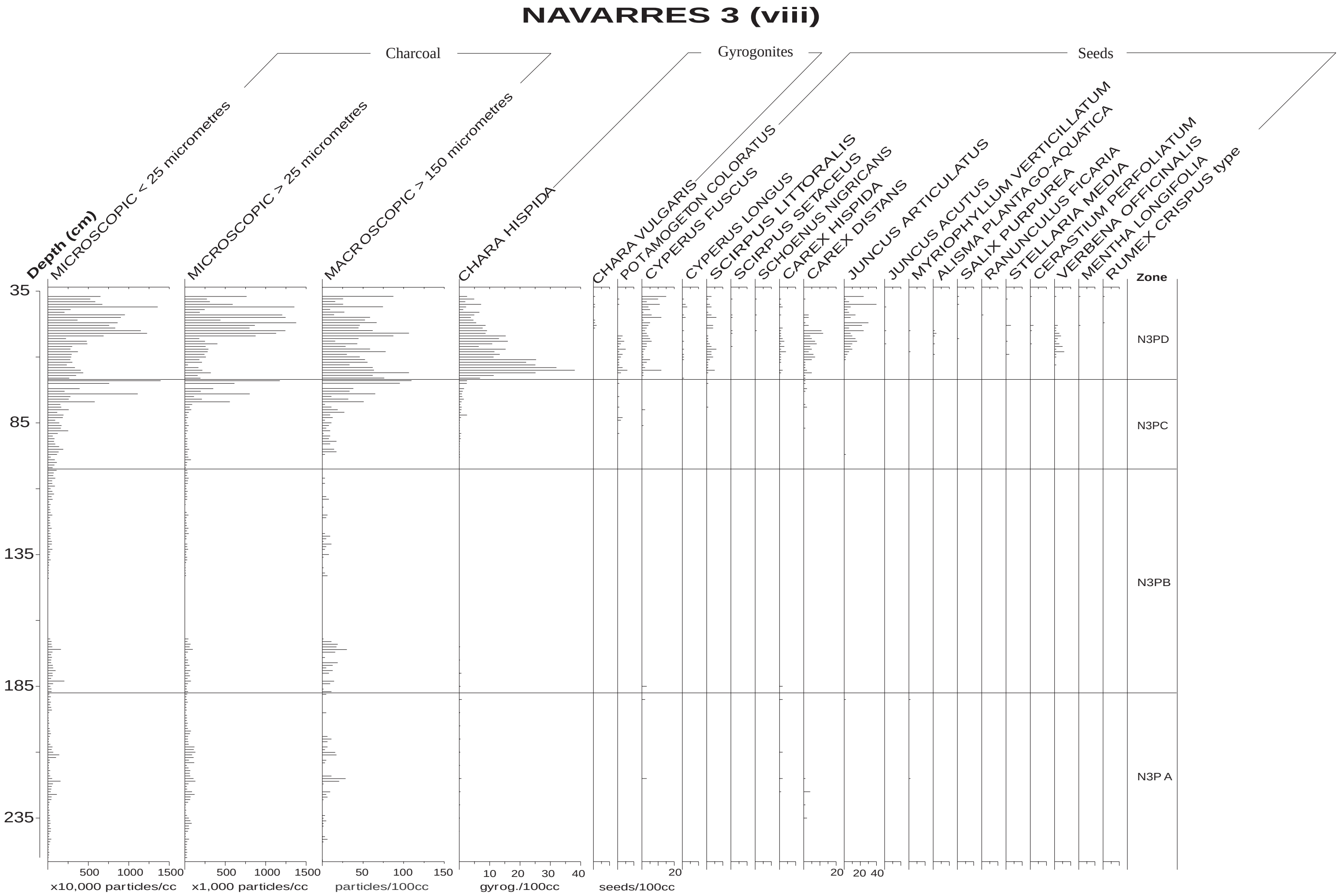


Fig. 10. Charcoal particles, Characeae gyrogonites, and seeds at Navarrés paleoecological sequence.

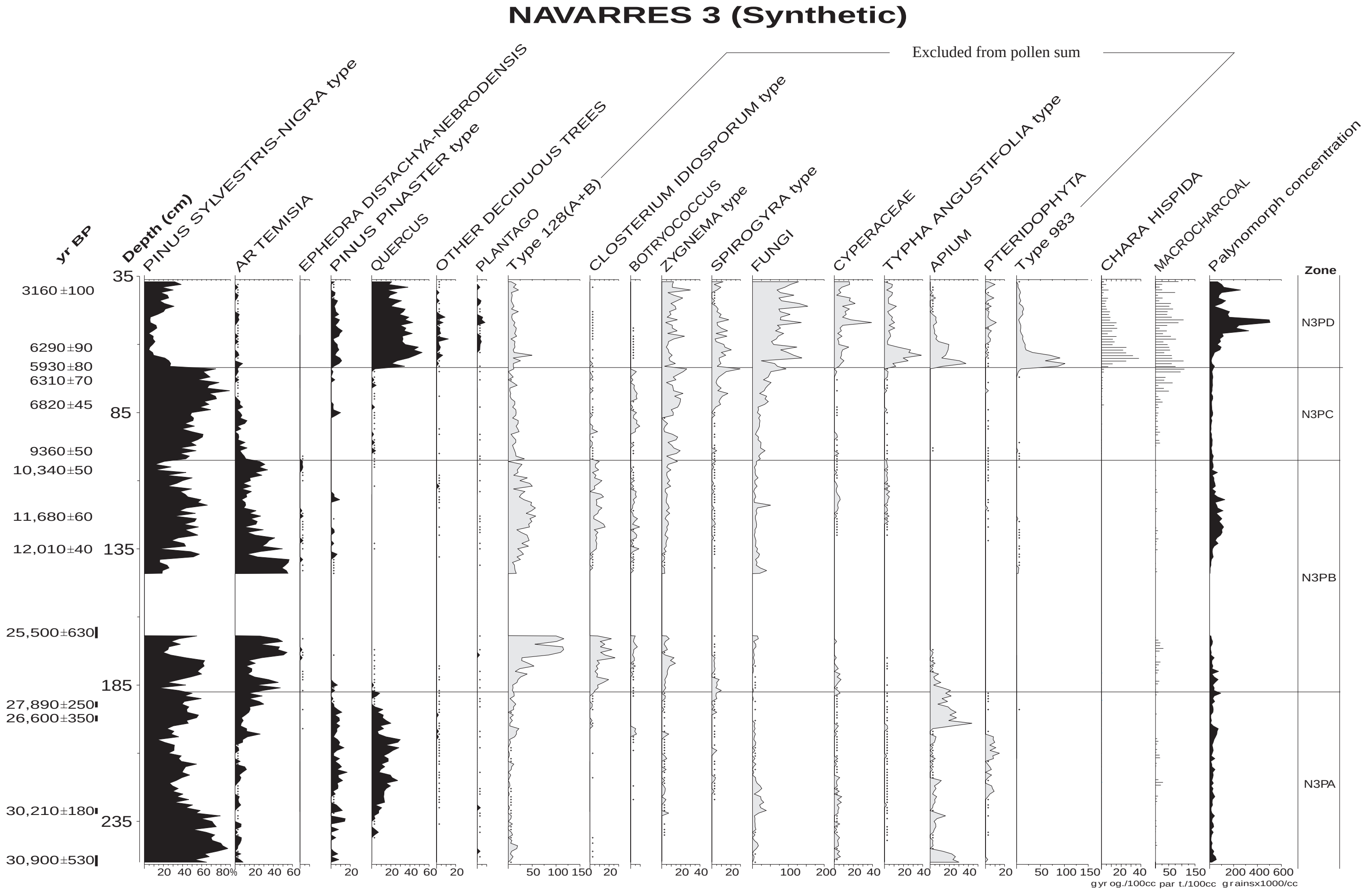


Fig. 11. Synthetic pollen diagram of Navarrés-3.

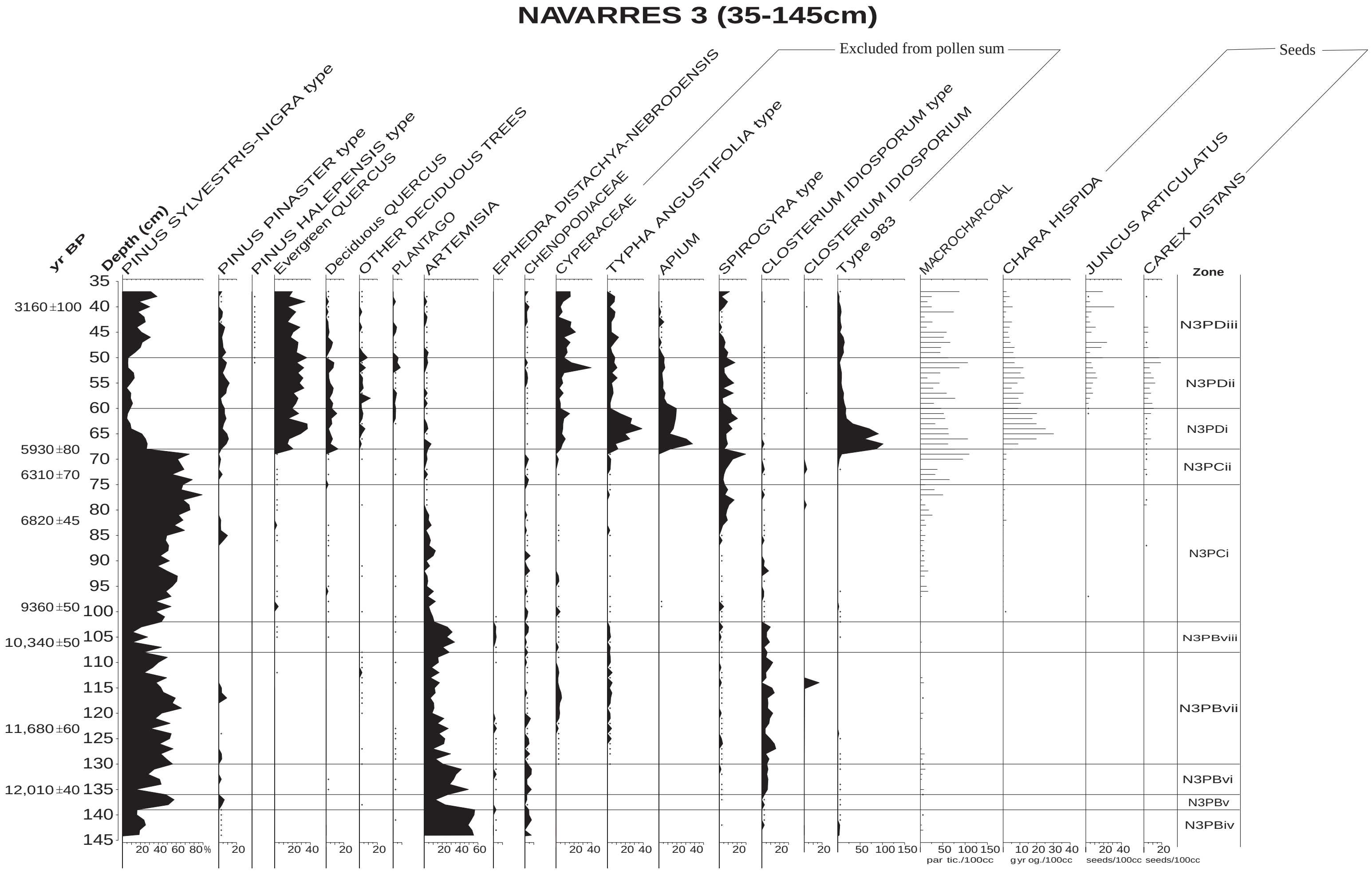

NAVARRES 3 (35-145cm)

Fig. 12. Synthetic pollen diagram of a selected 35–145 cm section from Navarrés-3.

poral distribution of the particles (Figs. 10 and 11), there are palynological data supporting the existence of fire events during the latest part of zone N3PC and during N3PD. These are the curve of *Erica arborea*, the increases of *Ulex parviflorus* type, *Pistacia lentiscus*, and *Phillyrea*, and the presence of *Anagallis arvensis*, *Cistus salviifolius* and *Pteridium aquilinum*. Many other heliophytic shrubs could also have taken advantage from burning, such as several species of Lamiaceae, Brassicaceae, Asteraceae, and *Ruta*. All these taxa become important in the natural recolonisation after fires in pine forests in the region, as has been shown in after-fire plot studies (Martínez-Sánchez, 1994; Martínez-Sánchez et al., 1996; Thanos et al., 1996). These experiments show that most Mediterranean pines cannot be considered as pyrophytes (in the meaning of Kuhnholtz-Lordat, 1958), since their regeneration is not stimulated by fire and it is therefore difficult for them to recolonise some burnt areas when there are other taxa present such as *Q. coccifera*, *Erica arborea*, *Phillyrea*, *Cistus*, and *Rosmarinus*. Most *Quercus* species rapidly create a shady environment which is unsuitable for pine seedlings (Trabaud et al., 1985). On the other hand, there are paleoecological data demonstrating that sclerophyllous shrubs can expand after fire at the expense of pine forests, like in Corsica (Reille, 1992; Carcaillet et al., 1997), Hungary (Willis et al., 1995), and southwestern Spain (Stevenson and Moore, 1988).

In this context, the presence at Navarrés of the curve of *Quercus suber* is also suggestive of post-fire dynamics. This oak increases around 5000–6000 yr B.P., just after the transition from *Pinus*- to *Quercus*-dominated assemblages (Figs. 3, 11 and 12). *Q. suber* has received relatively little attention among paleoecologists despite the fact that it is of crucial importance for understanding the forest succession on the Iberian Peninsula. Parra (1993, 1994) has reported about several Holocene pollen diagrams of the Mediterranean coast, where *Q. suber* parallels *Q. ilex–coccifera* and eventually (e.g. pollen diagram of Sobrestany, Girona) *Q. suber* is pioneer in successional phases after deciduous forests. Ecological data from present-day studies in the Parque de los Alcornocales, Cádiz (Cabezudo et al., 1995) also confirm the highly competitive character of the cork oak after fire. *Q. suber* is one of the tree species best adapted to fire (Pausas, 1997).

Burning of pine forests may have been favoured by a number of natural factors such as increased frequency of lightnings and dry spells. We cannot positively demonstrate the primary cause for the vegetation change at Navarrés, especially when taking into account that models of vegetation succession are experiencing notable revolution since the appearance of hypothesis involving a certain amount of indeterminism (Lavorel and Lebreton, 1992). Certainly, there are some data suggesting that burning could have been anthropogenically induced. The introduction of the agricultural practices in the Navarrés region has been dated at ca. 7000 yr B.P. (Martí, 1988) coincidently with the appearance of animal domestication (Martí et al., 1980). Anthracological data (Badal et al., 1994) and pollen diagrams from archaeological sites in caves (Dupré, 1988) suggest increased clearance in the regional landscape between 6000 and 4700 yr B.P., although this does not necessarily implies human action. Locally, the immigration at ca. 4700 yr B.P., of the Ereta del Pedregal Neolithic population within the basin, in clear proximity to the coring site, is worth mentioning (Fig. 1). It is therefore likely that men were responsible for fires during the last millennia in the area, but the fact that the first fires favouring *Quercus* were anthropogenically induced cannot be proven since there is no unequivocal evidence of human impact upon the landscape in the pollen diagram. The curve of *Plantago* and the large increase in the diversity of the woodland together with the increase in open ground herbaceous types can be associated with anthropogenic activity in the form of clearance by burning, but also to natural development of the landscape under increasing dryness. On the other hand, the *Quercus* curve precedes *Plantago*. A more conclusive approach might come from studies which provide confident charcoal size and distribution characteristics of either wild or human-induced fires.

Finally, a climatic change influencing the Holocene oak expansion is also plausible. Synchronous maxima in sclerophyllous oaks in other parts of southern Europe have been recorded abundantly (Magri, 1997) and the vegetation change in Navarrés parallels the onset of the warm moist phase in the Sahara around 6000 yr B.P. (Petit-Maire, 1978).

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Appendix A. Identification criteria for pollen and macrofossil types

For *Quercus*, we have largely adopted the long-standing criteria by Planchais (1962), even though her key does not completely fit into the populational variation recorded in the Spanish species, which is particularly noticeable for *Q. pubescens*. In this paper, 'Evergreen *Quercus*' include *Q. ilex*, *Q. rotundifolia* and *Q. coccifera*. 'Deciduous *Quercus*' include *Q. faginea*, *Q. pyrenaica* and *Q. pubescens*. *Q. suber* type includes pollen grains with a relatively wide polar triangle, amb circular, and slightly marked, continuous colpi in equatorial view. This type should mainly correspond to the cork oak, *Q. suber*. That the major pollen type of the Navarrés record belongs to the evergreen *Quercus ilex–coccifera* group has been confirmed under scanning microscopy. According to Sáenz (1973) and Colombo et al. (1983), this group exhibits exines characterised by dense, protruding elements in an irregular arrangement.

For *Pinus*, the criteria for identification were those described by Roure (1985) for the Iberian species. Thus, from the most abundant *Pinus sylvestris–nigra* type, we separated *P. pinaster* because of its larger pollen body, relatively short alveoli and thick proximal exine, and *P. halepensis* type (also including *P. pinea*) based on its large sac alveoli and thick proximal exine. For *Pistacia terebinthus*, *P. lentiscus*, *Rhus*, and *Acer campestre* types we also followed the criteria by Roure (1985). For the Ericaceae types we followed Díez and Fernández (1989).

The following types are within the criteria by Valdés et al. (1987): *Polygonum aviculare*, *Papaver rhoeas*, *Papaver argemone*, *Verbascum pulverulentum*, *Lythrum salicaria*, *Rubus ulmifolius*, *Scrophularia canina*, *Mesembryanthemum nodiflorum*, *Anchusa azurea*, *Cerinthe major*, *Viburnum tinus*, *Sambucus nigra*, *Prunus spinosa*, *Ranunculus peltatus*, *Ulex parviflorus*, *Echinops strigosus*, *Xanthium strumarium*, *Rumex conglomeratus*, and *Lycium europaeum*.

The following types are according to Moore et al. (1991): *Sorbus–Pyrus*, *Lythrum salicaria*, *Erodium*, *Alchemilla*, *Anthyllis vulneraria*, *Nymphaea alba*, *Iris pseudacorus*, *Gladiolus*, *Iris*, *Anagallis arvensis*, *Anagallis tenella*, *Teucrium*, *Ononis*, *Myosotis arvensis*, *Convallaria*, *Lotus*, and *Trifolium*.

Most seed types follow Beijerinck (1976) while *Potamogeton coloratus* type was identified according to Aalto (1970). The *Chara* gyrogonites were identified using Wood and Imahori (1964), Krause (1986), and Haas (1994).

Appendix B. Non-pollen palynomorphs: palynological criteria and descriptions of new types

At this section, we follow the procedure established since 1968 at the Hugo de Vries Laboratorium for the description of 'extra' palynomorphs (Van Geel et al., 1989), in which the types indicated by a number can be considered as provisionally, but not formally, named form-taxa.

No descriptions are presented for the following types since they have been described in detail: Type 1 (*Gelasinospora* ascospores), Type 7A (*Chaetomium* ascospores), Type 8B (*Microthyrium* fruit-bodies), Type 27 (*Tilletia* spores), Type 41, Type 55 (Sordariaceae ascospores), Type 60 (*Closterium idiosporum*-type zygospores), Type 146 (*Gloeotrichia*-type sheaths), Type 170 (*Rivularia*-type heterocysts), Type 179, Type 182, Type 207 (*Glomus* chlamydospores), Type 214 (zygospores of *Debarya*), Type 219 (mandibles, labia, various invertebrates), Type 224, Type 313 (*Mougeotia* zygospores), Type 314 (pitted *Zygnema*-type zygospores), Type 333, Type 357 (*Puccinia* teleutospores), Type 359 (septate conidia), Type 364 (basidiospores of *Thecaphora*), Type 372 (*Closterium rostratum*-type zygospores), and Type 531 (*Trichuris* eggs). Relevant information on these types can be found in Pals et al. (1980), Van der Wiel (1982), Van Geel (1972, 1976, 1978, 1986), Van Geel et al. (1981, 1983a,b, 1986, 1989), and Mateus (1992).

Type 367 (Van Geel et al., 1981) has been named *Polyadosporites* following Jarzen and Elsik (1986). Regarding *Fusiformisporites* (Plate I; Elsik, 1980, 1983), we have not seen any published connection of this type to an extant fungal taxon. However, although in smaller size, a similar spore morphology can be seen in *Nectria peziza* Tode, some Pleosporaceae such as *Herpotrichia lignicola* (Mout.) Bose and *Parodiella perisporioides* (Berk. et Curt.) Speg., and in Amphisphaeriaceae parasiting Bambusoideae such as *Ceriophora palustris* Berk et Broome (Müller and Von Arx, 1962).

Type 179 (Van Geel et al., 1989) is a vasiform microfossil, (24–60) × (13–38) μm, with a protruding 3–7.5 μm wide opening at one end. The origin of these structures is difficult to assess. They possibly represent phoretic cysts of epibiontic or parasitic Copepoda. Other organisms, mainly Protozoa, have been described to produce similar cysts (Trégouboff and Rose, 1957).

The following types are described and recorded for the first time in the present paper and their curves shown in Figs. 8, 11 and 12. All of them have mainly been found in zone N3PD, which, as we shall see later, is associated with shallow, stagnant water and progressive eutrophication of the basin.

Type 981 (Plate I). Ascospore dark-brown, elliptic to ventricose, (39–54) × (13–20) μm, triseptate with a major median transverse septum and two minor distal septa. Infra-reticulate spore wall. A similar spore morphology including infra-sculpture has been observed in the pyrenomycete *Gnomonia dryadis* Averswald (Diaporthaceae) (Barr, 1959). Other resembling spores occur in *Herpotrichia diffusa* Fuckel, *H. rubi* Fuckel (Sivanesan, 1984), and *Leptosphaeria discors* Sacc. et Ellis (Kohlmeyer and Kohlmeyer, 1964).

Type 982 (Plate I). Spore brown, subglobose, 85–100 μm in diameter, irregular reticulate sculpture, meshes of the reticulum variable but up to 25–30 μm in size, muri showing subtriangular thickenings. Possibly oospores of species of *Oedogonium* (Algae) such as *O. pseudo–cleveanum* Gauthier-Lièvre (Mrozinska, 1985). The same sculpture pattern occurs in other species such as *O. sphaerocephalum* Gauthier-Lièvre, *O. ibadanense* Gauthier-Lièvre, *O. subspirale* Mrozinska, and *O. henriquesii* Lacerda (Gauthier-Lièvre, 1964). Although all the *Oedogonium* species occur in fresh water environments, their ecological requirements are diverse and cannot be generalised.

Type 983 (Plate I). Microfossil hyaline to light-brown, globose, 12–16 μm in diameter. Sculpture of often anastomosing, bifurcate and seemingly palmate processes. Similar to Type 181 (Van Geel et al., 1983b). Probably the encystment phase of some algae (Strother, 1996). Some desmids, mainly of the genus *Staurastrum*, have similar zygospores (*S. polytrichum*, *S. teliferum*, *S. asperum*, *S. hirsutum*, *S. pilosum*) (West, 1971).

Type 984 (Plate I). Microfossil hyaline, globose, 26–41 μm in diameter, ornamented with numerous, densely arranged bluntly rounded processes, which are more or less circular in surface view. Size of processes variable, up to 5 μm. This type resembles zygospores of some species of the desmid genus *Euastrum* such as *E. ansatum* Ralfs and *E. oblongum* (Grev.) Ralfs (West, 1971).

Type 985 (Plate I). Microfossil hyaline to light-brown, subglobose, 20–29 μm in diameter, exclusive of the numerous up to 16 μm long spines, most of which are curved and only rarely furcated. The most similar spore type found among extant algae is the zygospore of *Euastrum bidentatum* Näg, but that spore is larger in diameter (40–42 μm) (West, 1971).

Type 986 (Plate II). Microfossil subcircular to polygonal in outline, 48–60 μm in diameter, dark-brown, infra-reticulate, lumina variable in size and shape, but up to 18 μm in diameter. Wall up to 4–5 μm thick.

Type 987 (Plate II). Microfossil globose, ca. 50–55 μm in diameter, reticulate with very thin muri. Lumina 0.2–4 μm. Probably an algal spore.

Type 988 (Plate II). Microfossil hyaline, globose, 19–25 μm in diameter, psilate, wavy to subpolygonal in outline.

Type 989 (Plate II). Microfossil hyaline, globose, 29–57 μm in diameter, ornamented with numerous, densely arranged, anastomosing processes. Similar to Type 984, apart from the anastomosis, which does not occur in Type 984.

Type 990 (Plate II). Microfossil hyaline, globose, 86–120 μm, ornamented with sparsely arranged, truncated, ca. 2–4 μm long processes. Similar to the spores of some *Euastrum* species (West, 1971).

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