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Vegetation variability in Greece during the last interglacial

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Abstract

The extent of regional variability in vegetation development in mainland Greece during the last interglacial is considered. Three pollen sequences – Ioannina (northwest Greece), Tenaghi Philippon (northeast Greece) and Kopais (central Greece) – all located in different environmental settings, extend into the last interglacial. Examination of the vegetation histories of the three sites during the last interglacial reveals the influence of local climatic conditions with closed mixed forests in the northwest, becoming progressively more open and less diverse farther to the east and south. All three sequences contain a number of similar trends, however, in the expansion of certain taxa. In addition, they also show the presence of a two-step late glacial interval, a short episode of forest reduction in the second part of the interglacial and a final small expansion of tree populations at the very end of the interglacial. Comparison with other European records shows a number of common features, but also suggests differences consistent with the particular environmental setting of the Greek sites.

Keywords: Eemian, Greece, last interglacial, palynology, regional variabiliy, vegetation

Introduction

Given its stratigraphical position, the last interglacial (equivalent to the Eemian and also broadly corresponding to marine isotope substage [MIS] 5e) has been the most extensively studied pre-Holocene stage north of the Alps. A substantial body of palynological evidence has accumulated that provides insight into the vegetational character and gradients across large parts of the continent over this time interval. By comparison, the overall density of pollen sites of this age in southern Europe is low, in part as a reflection of a historical 'northern' bias in Quaternary studies. In addition, southern records of this time form part of a continuum of long sedimentary sequences that have accumulated relatively undisturbed in volcanic crater lakes or tectonic basins. Thus, retrieval of sequences usually requires coring through substantial thickness of sediments and the palynological examination of both interglacial and glacial intervals, which also accounts for the relatively slower rate of emergence of new sites. Most of the available southern sequences, however, provide relatively complete and high-resolution records spanning multiple climatic cycles where the position of different interglacial periods within the same sequence defines their chronostratigraphical relation.

A coherent stratigraphical framework for the last 500,000 years is beginning to emerge in southern Europe (see, among others, Tzedakis et al., 1997), where, unlike the northern European situation, biostratigraphy does not have to be both the basis for correlations and the evidence for vegetation dynamics. This means that the position of the last interglacial within these long sequences can be determined with confidence, and that attention can be focused on comparisons of the vegetation character between the various sites, without circular reasoning. In addition, the continuity of the records provides an opportunity to examine not only the full interglacial sequence, but also the intervals immediately pre- and post-dating it, which may not always be represented in fragmentary records.

Greece contains several Quaternary intermontane lake basins where thick sedimentary sequences (often in the order of hundreds of metres) have accumulated under a regime of tectonic subsidence. To date, three basins (Fig. 1) have provided long pollen records extending back at least to the last interglacial: Ioannina (in north-western Greece), Tenaghi Philippon (in north-eastern Greece) and Kopais (in central-eastern Greece). The present contribution considers the vegetation development in mainland Greece during the last interglacial on the basis of these three records. First, the position of the basins in relation to the present-day climatic regimes of Greece is examined in order to determine to what extent they provide an adequate coverage of regional variability. The last interglacial pollen record from each site is presented and differences and similarities are discussed. This provides an opportunity to compare the vegetation character of each site without the influence of anthropogenic activities, which is often a complicating factor in Holocene pollen diagrams. The behaviour of certain taxa and some of the emergent features from the Greek diagrams are finally considered within a wider European context.

Environmental setting

Climatic regimes

The climate of Greece is generally considered to be of Mediterranean type with hot, dry summers and relatively mild and wet winters. This regime is controlled by the westerlies in winter and the subtropical high-pressure cell in summer (Barry & Chorley, 1982). The position of Greece – between the landmass of eastern Europe and the southern basin of the eastern Mediterranean Sea – means, however, that its climate has certain transitional characteristics: there are considerable variations from the pure Mediterranean type, with features of continental climate of central and eastern Europe present in certain areas (NID, 1944).

Physiography plays an important role in the distribution of temperature and precipitation. The northern mountain ranges provide shelter during the winter months by blocking incursions of polar and arctic air, whereas the north-northwest to south-southeast trending Pindus mountain range – running parallel to the Ionian coast – intercepts the easterly moving depressions. High levels of precipitation are therefore encountered along the western region of Greece and a rain-shadow effect is produced to the east of Pindus (Karapiperis, 1974). In general, the temperature shows an increase from north to south during all seasons. There are marked differences, however, between plains and mountains, interior and coastal areas, west and east coasts of the mainland and the various parts of the same coast, depending on their degree of shelter.

A considerable variety of climatic types thus exists, despite the limited area of Greece. According to the NID (1944), three main climatic types can be identified:

- a true Mediterranean climate that is mainly confined to lowlands of central and southern Greece (the western region of the mainland is different, with heavier winter rainfall, shorter summer drought and a lower range of temperatures);
- a modified Mediterranean climate that is encountered in the coastal and interior plains of Thessaly and northern Greece, where features continental in type are present; the seasonal range in temperature is greater than farther south, with cold winters and frequent occurrences of frost;
- a mountain climate in the Pindus region and the mountain ranges of western Macedonia and Thrace, being a variant reminiscent of the continental type of central Europe: although summer is the season of minimum rainfall, the summer drought is not complete; winter temperatures are sufficiently low for much of the precipitation to fall as snow.

Location of sites

The Kopais basin (in Boeotia, central Greece), once occupied by a seasonal lake approximately 18x11 km^2 in size and fed by the Kephissos and Melas rivers, is now all farmland following artificial drainage. Sinkholes border the northern and eastern sides of the basin, while south of the Kopais and Theban plain a narrow scarp zone rises to an upland plateau (350-400 m) that forms most of southern Boeotia. In the southwest, the Helikon massif – rising to altitudes of 1526 m – is connected through a series of outlying mountains to the massif of Parnassus (2457 m) to the northwest of the area (Rackham, 1983). Kopais is positioned within the region of true Mediterranean climate with mild winters and little rainfall during the summer months. Mean July and January temperatures on the Kopais plain are 27 °C and 9 °C, respectively. Total annual precipitation near Thebes is 472 mm, while at Levadhia, nearer to the mountains, it is 732 mm (Rackham, 1983). The vegetation of the area is characterised by low woody and herbaceous scrub vegetation. Low-elevation macchia is dominat-

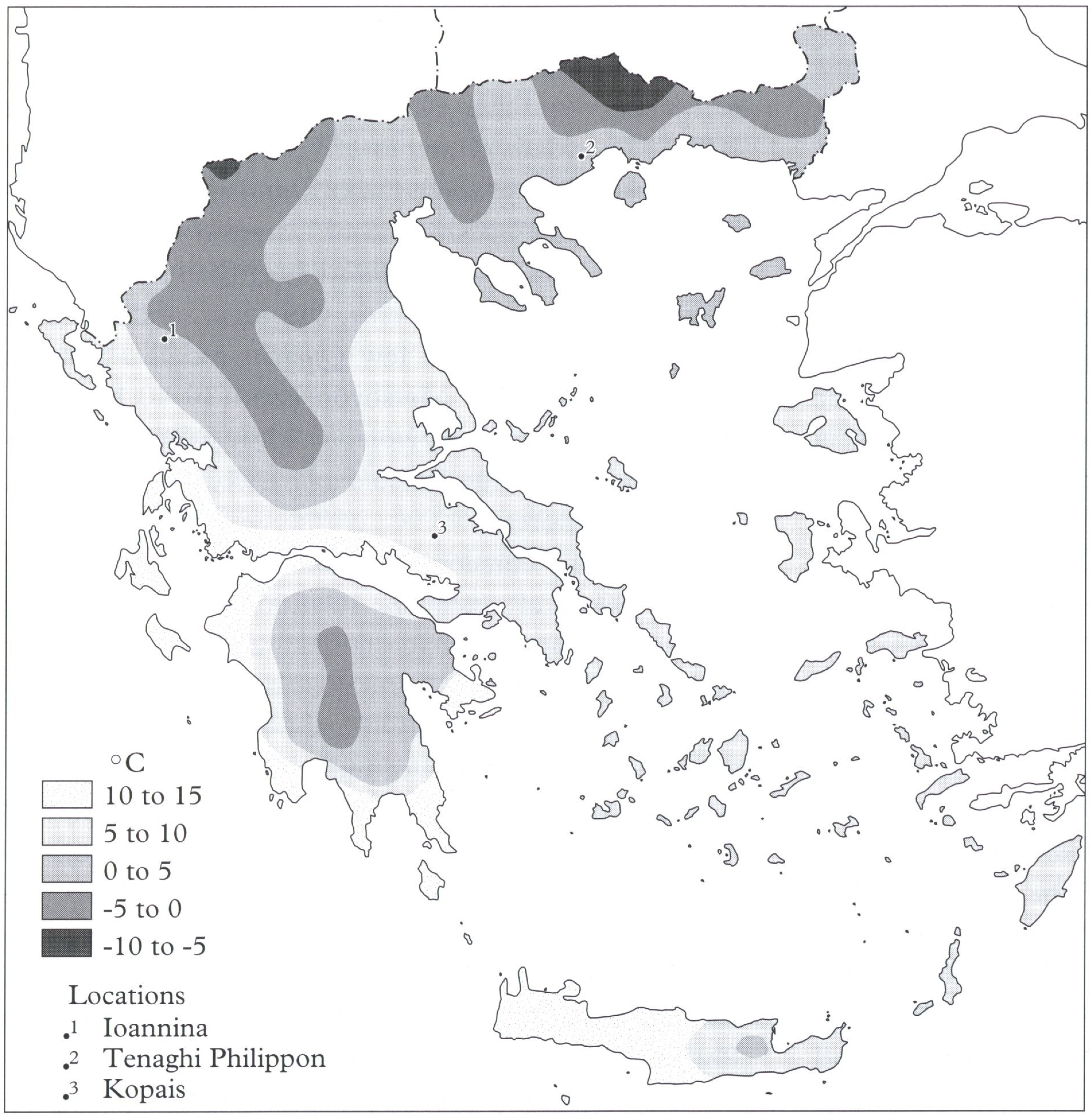

Fig. 1. Location of sites and geographical distribution of January mean temperatures. Modified after NID (1944) and Polunin (1980).

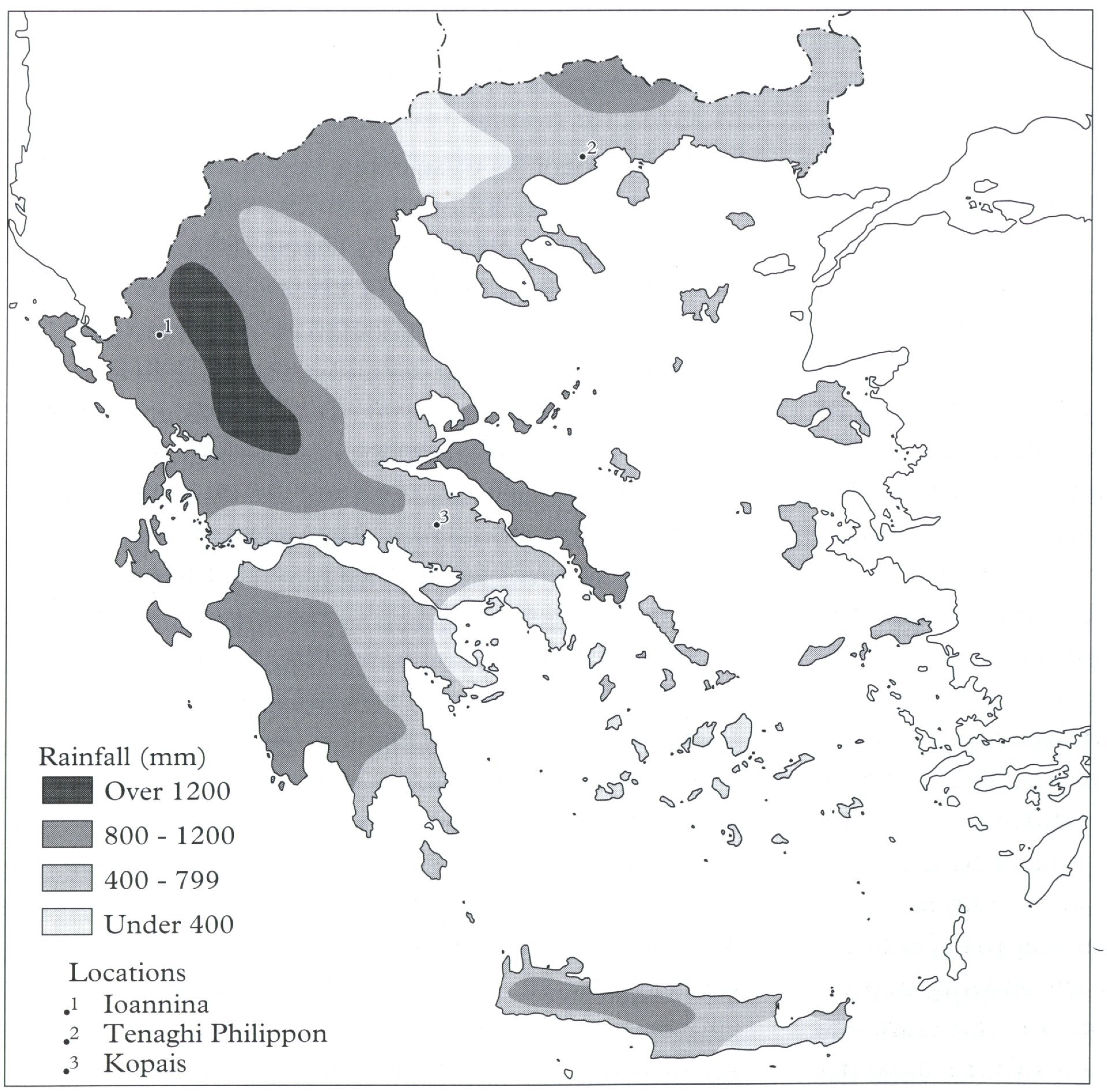

Fig. 2. Location of sites and geographical distribution of annual precipitation. Modified after NID (1944) and Polunin (1980).

ed by *Quercus coccifera* and *Pistacia lentiscus* with some *Phillyrea* and *Olea*. At higher altitudes, trees and shrubs (*Pistacia* at 400 m, *Olea* at 600 m) are replaced by *Juniperus*. Macchia with *Q. coccifera* as the most common species persists well into the *Abies cephalonica* zone (800-1500 m) of the surrounding mountains. At certain places, small woods and patches with deciduous oaks as well as *Acer*, *Tilia*, *Ostrya* and *Fraxinus* have been reported (Rackham, 1983).

The Tenaghi Philippon basin is part of the interior plain of Drama, in northeast Macedonia. The plain is bounded by the Pangaion mountain (1956 m) to the south-southwest, the Lekanis mountains (1298 m) to the northeast and mountain Falakron (1911 m) further to the north. An extensive peat deposit (areal extent 55 km^2) is found in the southwestern part of the basin (Wijmstra, 1969). The basin is located within the region of modified Mediterranean climate regime with generally colder winters and somewhat wetter summers than southern Greece. The mean annual temperature is 10.8 °C and the mean annual precipitation is 642 mm, as recorded at the nearby Kavala station (Walter et al., 1975). The once extensive marsh of Philippi consists nowadays almost completely of cultivated land, following artificial drainage and land reclamation in the 1930's. Farming and grazing have left little of the original vegetation. Wijmstra (1969) described *Quercus ilex*, *Juniperus*, *Pistacia terebinthus*, *Arbutus unedo* and *Cistus* spp. on hills and lower slopes of the surrounding mountains. Scrub vegetation of *Carpinus orientalis*, *Quercus ilex* and *Q. coccifera* occurred above 300 m, while trees of *Q. coccifera*, *Carpinus orientalis* and *Castanea* were encountered above 450 m. *Pinus nigra*, *Ostrya carpinifolia* and *Acer* were the dominant trees at higher altitudes.

Finally, the Ioannina plain is located on the west side of the Pindus mountain range, in the interior of Epirus, approx. 60 km from the Ionian coast. The plain has an elevation of 470 m and is bordered to the east by the Mitsikeli mountain (1810 m). The present surface area of Lake Pamvotis (22.8 km^2) represents only part of its extent prior to artificial drainage. The original size is not precisely known, although it is reported as having extended over a distance of 20 km (Conispoliatis et al., 1986). The climate of the area is transitional between the Mediterranean climate of the west coast (with high levels of rainfall and moderate summer drought) and the mountain climate of the Pindus. Annual precipitation levels (1200 mm) at Ioannina are amongst the highest recorded at stations in mainland Greece. The mean annual temperature is 14.4 °C, the mean temperatures for January and July being 4.9 °C and 24.9 °C, respectively. As with the other sites, natural vegetation is virtually absent from the immediate vicinity, given farming and grazing pressures. On the Mitsikeli Mountain, Bottema (1974) recorded *Juniperus* cf. *oxycedrus* shrub along with *Carpinus orientalis*, *Cornus*, and *Amygdalus*. Further east, dense brushwood of *Carpinus orientalis*, *Juniperus* cf. *oxycedrus*, *Fraxinus*, *Acer*, *Quercus cerris*, *Q. pubescens*, *Colutea arborescens*, *Craetagus*, and *Phillyrea* occurs and there are a few *Quercus coccifera* patches on the plain. In the Metsovon area (30-40 km east-northeast of Ioannina), *Abies borisii-regis* and *Pinus nigra* (Strid, 1986) and also *Fagus sylvatica* (Bottema, 1974) are reported.

In general, consideration of the position of the palaeoecological sites in relation to the climatic regimes of Greece suggests that all three represent quite distinct situations and provide a good cross-section of regional variability (Figs. 1-2). In simple terms, there is a general trend of reduced precipitation from Ioannina to the sites towards the east and south, and of increased temperature from Tenaghi Philippon towards the south. As regards potential vegetation, the Ioannina region would be characterised by a mixture of Mediterranean, East-central European deciduous and montane beech and coniferous forests, Tenaghi Philippon by Mediterranean and transitional deciduous forests, and Kopais by Mediterranean evergreen forests and macchia (Polunin, 1980).

Pollen records

Pollen frequencies of selected taxa and also the arboreal-pollen : non-arboreal quotient (AP/NAP), which is an index of changes in forest biomass (Magri, 1994), are presented for all three sites. For Ioannina and Kopais, the basic calculation sum contained all pollen of non-aquatic vascular plants. Palynological separation of the genus *Quercus* into evergreen and deciduous types was undertaken. Assignment to the evergreen type was made only if the distinction could be made unequivocally; otherwise the grain was added to the deciduous category, which also contained any semi-evergreen types (the latter were encountered very infrequently). The *Quercus* evergreen curve should therefore be treated as a minimum curve. For Tenaghi Philippon, the basic calculation sum used here follows that adopted in the original publications by Wijmstra (1969) and Wijmstra & Smit (1976) and excludes pollen from aquatic vegetation or hygroseres. There is no separation in the original data set between different types of *Quercus*, although qualitative notes on the presence of evergreen, semi-evergreen and deciduous *Quercus* are included in the publications. In addition, there has been no separation between *Olea* and *Fraxinus* types.

Vascular plant nomenclature used here follows Flora Europaea (Tutin et al., 1964-1980). The following abbreviations are used unless otherwise indicated: chenopod(s) for Chenopodiaceae/Amaranthaceae, *Ostrya* for *Ostrya carpinifolia/Carpinus orientalis* and *Carpinus* for *Carpinus betulus*.

Ioannina 284

Earlier results from a 165 m core (I-249) have provided a pollen record of the last 430,000 years (Tzedakis, 1993, 1994). A new sequence (I-284; 39°45'N, 20°51'E, 472 m above sea level) has since been cored, again by the Greek Institute of Geology and Mineral Exploration (IGME) from the same basin, extending down to 319 m. Several dating methods – including radiocarbon determinations, palaeomagnetic analyses and U-series dating – have been applied to I-284 in an attempt to derive a comprehensive age model, according to which the sequence extends back to approx. 620 ka BP (Frogley, 1997). Given correlations with the earlier sequence I-249, and the results of the palaeomagnetic analyses and U-series dating, the position of the last interglacial in I-284, locally defined as the Metsovon Interglacial (Tzedakis, 1994), is well constrained.

Here, a new last-interglacial pollen sequences from core I-284 is presented (Fig. 3). This study shows the same broad palynological features as I-249, but with a mean sampling interval of 200 years it improves the temporal resolution tenfold, thereby providing far greater detail than has hitherto been available at Ioannina, or any other Greek site indeed.

The lower part of the pollen diagram is dominated by steppe-vegetation taxa with some arboreal pollen. Deciduous *Quercus* (and also *Ulmus*) pollen frequencies then show a steady expansion to approx. 40% interrupted by a short interval where an increase in chenopods and Gramineae along with *Juniperus* suggests an opening of the vegetation. This is followed by a sharp increase in deciduous *Quercus*, signalling the beginning of the interglacial proper. Immediately after, there is an expansion of Mediterranean elements (*Pistacia, Olea, Phillyrea,* evergreen *Quercus*) and a rise in the AP/NAP ratio, suggesting a significant increase in forest biomass. The ensuing interval is characterised by high *Carpinus* values; frequencies of Mediterranean elements decrease (*Olea* virtually disappears) and the AP/NAP ratio begins to drop, pointing to a gradual decrease in forest biomass. After 90.7 m, Mediterranean elements disappear, while *Carpinus* appears to be replaced by deciduous *Quercus*; *Abies* frequencies also show an increase and noteworthy is the re-appearance of *Betula*. Within this interval, an episode of increased herbaceous pollen frequencies (from 10-15% to 22-27%) and reduced AP/NAP-ratio values is recorded between 88.0-89.0 m, suggesting a reduction in forest biomass. In the upper part of the diagram, expansion of NAP values, suggesting the progressive onset of stadial conditions, is interrupted by a brief increase in deciduous *Quercus* frequencies.

Tenaghi Philippon

Pollen investigations from Tenaghi Philippon (eastern Macedonia: 41°10'N, 24°20'E, 40 m above sea level) have been published in a series of papers over a 20-year period (Wijmstra, 1969; Wijmstra & Smit, 1976; Van der Wiel & Wijmstra, 1987a,b). Results have been obtained from two cores (TF1 and TF2) with a total length of 197 m of polleniferous organic lake deposits representing the last 1.0 million years (Wijmstra, 1969; Wijmstra & Smit, 1976; Van der Wiel & Wijmstra, 1987a,b). The chronological context was provided by radiocarbon determinations in the upper part of the sequence (Wijmstra, 1969), U-series dating (Heijnis, 1992) and magnetostratigraphy (Wijmstra & Groenhart, 1983). The position of the last interglacial, locally defined as the Pangaion Interglacial, is determined on the basis of the chronological scheme.

The pollen diagram from the interval containing the last interglacial is shown in Figure 4, redrawn from the data of Wijmstra (1969) and Wijmstra & Smit (1976). The lower part of the diagram – representing the penultimate glacial stage – is characterised by steppe-vegetation taxa with negligible presence of any arboreal pollen. The deglaciation interval shows *Quercus* (mainly semi-evergreen) frequencies expanding to 40% (with some presence of *Ulmus*). This is interrupted by a short-lived increase in Gramineae, before *Quercus* values re-expand, followed immediately by a peak in Mediterranean elements (*Pistacia, Olea/Fraxinus, Phillyrea*). An interval characterised by deciduous *Quercus, Abies* and *Carpinus* is then recorded. It was interpreted by Wijmstra & Smit (1976) as indicating the presence of *Quercus* forest with *Carpinus* on lower slopes, while *Abies* populations were present at higher altitudes. This interval is followed by an interval of increased *Pinus* values and the re-appearance of *Betula*. Towards the upper part of the diagram, herbaceous frequencies show a steady rise, while lower values of the AP/NAP ratio point to a gradual opening of the *Quercus* (including an evergreen component) – *Pinus* forest. The trend towards stadial conditions is interrupted by a brief re-increase in *Quercus* and *Pinus* frequencies.

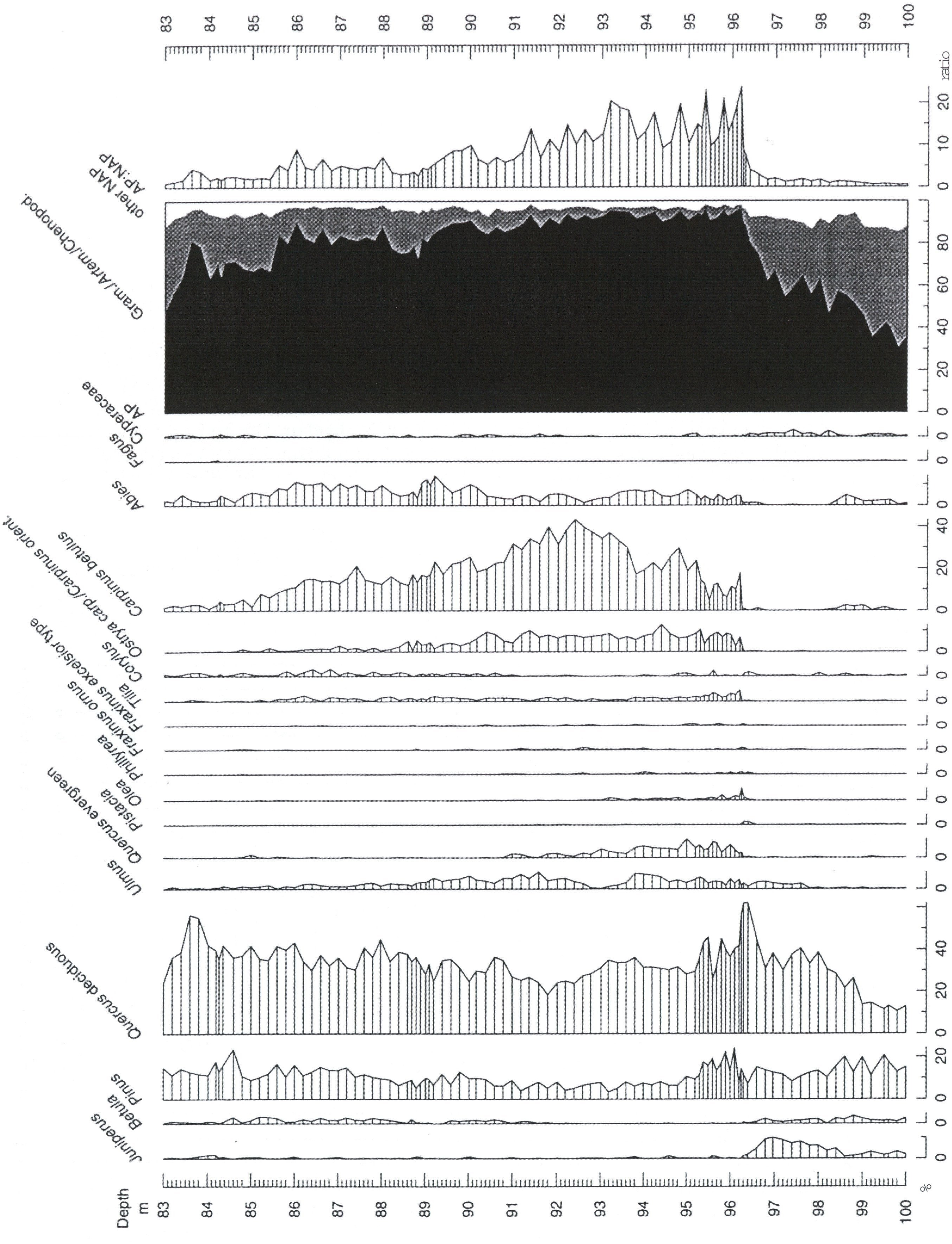

Fig. 3. Pollen diagram of selected taxa from the last interglacial in Ioannina 284.

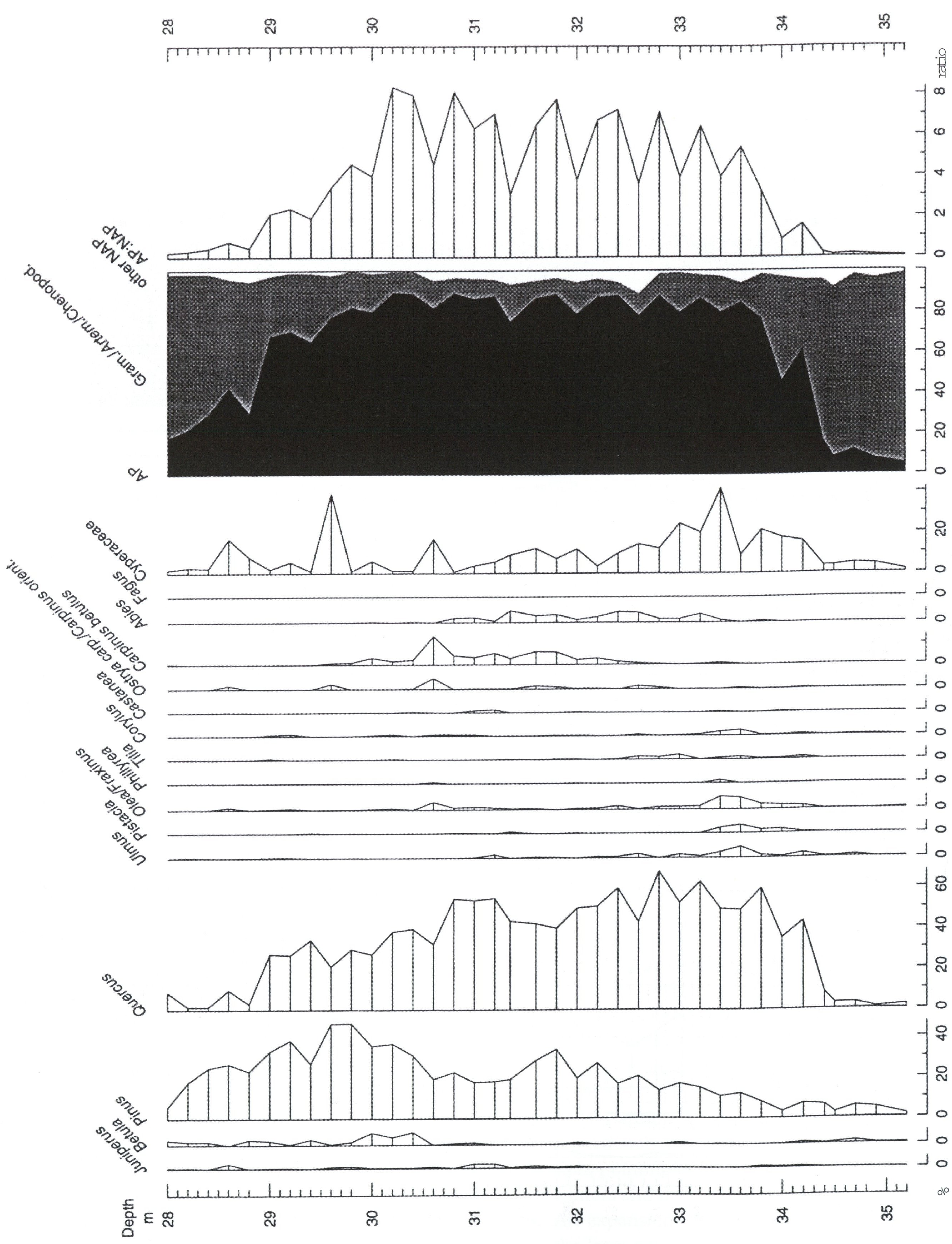

Fig. 4. Pollen diagram of selected taxa from the last interglacial in Tenaghi Philippon.

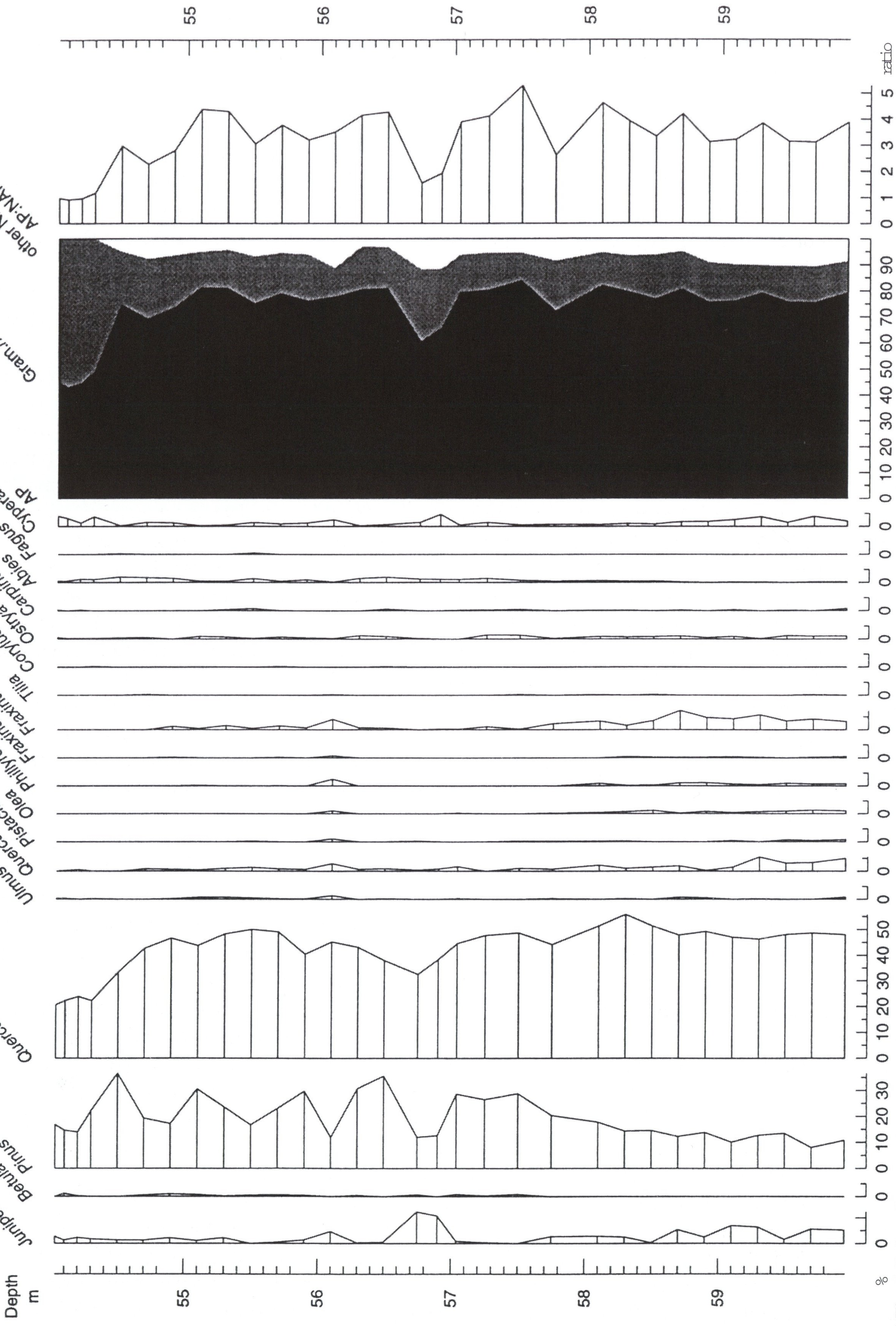

Fig. 5. Pollen diagram of selected taxa from the last interglacial in Kopais K93.

Kopais K93

Previous palynological work on Kopais was undertaken by Greig & Turner (1974), Turner & Greig (1975) covering the Late Glacial and Holocene and Allen (1986, 1990) whose cores (pollen analysis by J.C. Ritchie) extended into the last Pleniglacial. Borehole K93 (38°26′16″N, 23°03′01″E, 92.4 m above sea level) was drilled by IGME in close proximity to the earlier sites and a core of 60 m was obtained. The chronostratigraphical framework of the sequence was based on correlations with the Tenaghi Philippon and Ioannina 249 records and, by extension, with the marine isotopic record. According to this scheme, the K93 core contains a sequence extending from the early Holocene into the last interglacial (Tzedakis, 1999).

A cursory look at the K93 pollen diagram (Fig. 5) reveals that the sequence does not extend to the end of the penultimate glacial stage and does not contain a complete record of the last interglacial. Comparisons with Ioannina and Tenaghi Philippon suggested that the early transitional phase of the last interglacial is absent at K93, the base of which is placed somewhere within the ensuing expansion of Mediterranean elements (Tzedakis, 1999). Overall, the last-interglacial part contained in K93 is dominated by deciduous *Quercus* pollen. Values for evergreen *Quercus* together with those of *Olea*, *Pistacia*, *Phillyrea* and *Fraxinus* are higher during the early part of the interval, while mostly deciduous *Quercus* and *Pinus* are abundant in the later part along with some presence of *Abies* and *Betula*. Within the second part of the last interglacial, there is an interval showing a distinct reduction in forest cover suggested by an increase in herbaceous frequencies, a drop in the AP/NAP ratio, and expansion of *Juniperus* populations. Before the onset of stadial conditions, a small rise in AP (mainly *Pinus*) values is recorded.

Emerging differences and similarities

The overall impression derived from the three last-interglacial sequences presented here is one of considerable variability in terms of the nature of the vegetational sequences and the extent of the forest cover. In essence, the records form a spectrum with Ioannina and Kopais as the end members, and Tenaghi Philippon somewhere in between. Thus the I-284 diagram shows a distinct interglacial vegetation succession with *Quercus*/*Ulmus*, *Pistacia*/*Olea*/*Phillyrea*, *Carpinus*/*Abies*, and again *Quercus*. By comparison, K93 is dominated by deciduous *Quercus* with some *Pinus* and does not show any clear replacement of communities, other than an earlier part with increased frequencies of Mediterranean elements and a later part in which *Abies* values show a slight increase. The Tenaghi Philippon diagram contains evidence for a transient vegetation development with *Quercus*/*Ulmus*, *Pistacia*/*Olea*/*Phillyrea*, *Abies*/*Carpinus* and finally *Pinus*, but in general *Quercus* and *Pinus* dominate the assemblages. In terms of the extent of forest cover, the records suggest a similar pattern with the highest tree densities occurring at Ioannina (AP frequencies over 90% and a high AP/NAP ratio), followed by Tenaghi Philippon (AP frequencies mostly between 80-90% and an intermediate AP/NAP ratio), while Kopais suggests the presence of relatively open forest (AP frequencies between 70-80% and the lowest AP/NAP ratio). Thus, there is a general trend from mixed interglacial forests with high biomass to more open and less diverse forests, going from Ioannina to Tenaghi Philippon and then to Kopais.

These differences do not appear to be a result of local control of substrate, since all three sites share broadly similar geologies. Nor do they arise from differences in pollen catchment areas, as all three basins have similar sizes. Physiography may, to some extent, account for the variability of the records, as the Kopais catchment represents an overall lower lying area than the other sites. Both Ioannina and Tenaghi Philippon, however, have mountains in the immediate proximity, yet their pollen signatures differ. Instead, the factor that appears to correlate more closely with the individuality of the vegetation history of each site is the local climatic setting and in particular the relative amount of moisture availability during the course of the year.

Beyond these differences in the vegetational character of the three sites, the following features appear to be of extra-regional significance, occurring in the same part of the sequence and suggesting the general effect of regional climatic trends during the course of the interglacial.

1. Both sequences extending into the penultimate glacial stage (Tenaghi Philippon and Ioannina), show a two-step late-glacial period with an early increase in *Quercus* populations interrupted by an oscillation towards more open vegetation, before a second, more extensive expansion of *Quercus* populations.
2. An expansion of Mediterranean elements occurs immediately following the second *Quercus* expansion, pointing to increased temperatures with mild winters and drier (summer drought) conditions.
3. An expansion of *Pinus* and *Betula* is observed in the later part of the interglacial, signalling a drop in winter and summer temperatures and increased precipitation.

4. Both Ioannina and Kopais show an episode involving a reduction in forest cover during the *Pinus-Betula* phase, suggesting reductions in temperatures and precipitation. Such an event is not as clearly recorded at Tenaghi Philippon, perhaps as a result of the sampling resolution (mean sampling interval: ~600 years). Some suggestion of this event is indicated in Figure 4, between approx. 29.40-29.60 m, by a decline in AP frequencies and the AP/NAP ratio. This is also associated with an increase in Cyperaceae, pointing to an expansion in fen vegetation, possibly as a result of a fall in lake levels.
5. Finally, a small peak in AP frequencies representing a brief re-expansion of *Quercus*/*Pinus* populations is recorded at the very end of the interglacial.

Comparison with Eemian records

In the European pollen literature, the importance of *Carpinus* and virtual absence of *Fagus* have traditionally been highlighted as characteristic Eemian features (see, among others, Phillips, 1974; Turner, 1975; Watts, 1988) and have often been used as the basis for correlation and chronostratigraphical assignment of isolated deposits. As discussed earlier, long pollen sequences provide – in contrast to fragmentary records – an opportunity to examine the stage record of these taxa from the vantage point of continuous stratigraphies where the chronostratigraphical position of the last interglacial is clearly established. Inspection of last-interglacial pollen diagrams from such long sequences in France at Grande Pile (Woillard, 1978; De Beaulieu & Reille, 1992a), Les Echets (De Beaulieu & Reille, 1984), Ribains (De Beaulieu & Reille, 1992b), Bouchet (Reille et al., 1998) and Italy at Valle di Castiglione (Follieri et al., 1988) reveals a common pattern with high values of *Carpinus* characterising the middle part of the vegetation succession.

The situation in Greece, however, appears to be more complicated. Of the three last-interglacial sites, Ioannina is the one that appears to share the greatest similarities with central and western European records in terms of a substantial expansion of *Carpinus* (reaching values over 40%). The diagram from Tenaghi Philippon, on the other hand, shows a rather subdued phase of *Carpinus* (maximum values approx. 10%), whereas the diagram from Kopais has negligible presence. Indeed, the last-interglacial pattern of abundance of *Carpinus* in Greece shows a close coincidence with its present-day distribution (Strid & Tan, 1997), where it is virtually absent in central and southern parts of the country. Thus, while examination of Eemian sequences confirms the importance of *Carpinus* in European landscapes, it also underlines the modulating effects of local factors, especially near the edges of the species' ranges. Moreover, examination of earlier interglacial periods in Greece (Wijmstra & Smit, 1976), but also in Italy (Follieri et al., 1988) and France (Reille et al., 1998), suggests that high *Carpinus* values are by no means restricted to the last interglacial, but in addition show maxima during earlier temperate stages, particularly during the penultimate interglacial complex.

Fagus is the other taxon that has a common pattern on a broad scale. With the exception of occasional grains, it is virtually absent throughout the last interglacial in all long pollen sequences, except Valle di Castiglione (Follieri et al., 1988), where it persists at low abundances. The *Fagus* values at the Italian site, however, are the lowest recorded during a forest period within that sequence. Examination of the Greek diagrams reveals the same pattern of almost complete lack of *Fagus* pollen grains. The absence of *Fagus* throughout the last interglacial is also supported by the palynological record from central and western Europe (a.o. Watts, 1988) where generally, apart from sporadic occurrences in some deposits, its pollen is generally not encountered. The reasons for this are far from clear. Tzedakis (1994) speculated that particular climatic conditions and/or disease may have had an adverse effect on refugial populations during the preceding cold stage, which may have inhibited its expansion during the last interglacial. Removal of a species (through disease or otherwise) can have a substantial impact on forest composition for several millennia as other species adjust (see Bennett, 1993). If this was the case, events taking place during the preceding glacial would have influenced the character of the interglacial vegetation succession several millennia later.

An additional feature of interest, although not as geographically extensive as the above two case studies is the expansion of Mediterranean elements (*Olea, Pistacia, Phillyrea*) recorded at the Greek sites during the early part of the last interglacial. A prominent phase of increase in *Olea* pollen values, associated with evergreen *Quercus* and some *Phillyrea*, is also observed during the same part of the interglacial sequence at Valle di Castiglione (Follieri et al., 1988). The presence of *Pistacia* and *Olea* pollen during the *Corylus* acme period is also recorded at the high-altitude sites of Ribains and Bouchet in the French Massif Central, where they have been attributed to long-distance transport and are considered to indicate a significant expansion of Mediterranean-type vegetation at the southern margins of the region (De Beaulieu & Reille, 1992b; Reille et al., 1998). What is particularly interesting about the Eemian sequences of the Massif Central is that they contain features typical of central European records, but also display evidence from events in the Mediterranean region. Thus, they form a link between sites north and south of the Alps. On this basis, it appears that the last-interglacial optimum was characterised by expansion of Mediterranean vegetation elements in southern Europe, and north of the Alps by expansion of *Corylus* and also *Taxus*. The rise of the Mediterranean elements has also been registered in marine cores from the eastern Mediterranean (Cheddadi & Rossignol-Strick, 1995), where it was found to occur contemporaneously with the deposition of sapropel S5. Sapropel formation has been correlated with maxima in monsoonal activity, which is a function of precessional insolation variations (Rossignol-Strick, 1983) and the lag time between orbital forcing and initiation of sapropel deposition is in the order of 1000 years (Melières et al., 1997). On this basis, deposition of S5 began about 126,800 BP, following the maximum insolation anomaly during the last interglacial and this also provides the age for the rise in *Olea*, *Pistacia* and *Phillyrea*.

Beyond similarities in the patterns of expansion of individual taxa, a final consideration is the occurrence of brief oscillations similar to those encountered at the Greek diagrams. The first relates to a brief episode of open vegetation interrupting the first increase in tree populations during the late glacial part of the records. A similar succession of vegetation changes is also observed at Valle di Castiglione (Follieri et al., 1988) and in a recent last-interglacial marine pollen record MD952042, off the southwestern Portuguese margin (Sánchez-Goñi et al., 1999). A step-like transition to full interglacial conditions is also seen at Grande Pile (De Beaulieu & Reille, 1992a) and Les Echets (De Beaulieu & Reille, 1984), although it involves early rises in *Pinus*, *Betula* and *Juniperus*, interrupted by an increase in Gramineae and *Artemisia*. The oscillation towards drier and more open vegetation environments appears to be coeval and may be causally linked with the occurrence of Heinrich event 11 (Heinrich, 1988; Chapman & Shackleton, 1998, 1999).

The second event concerns the reduction in forest cover during the second part of the interglacial. A similar change is also recorded at Bouchet (Reille et al., 1998) and Ribains (De Beaulieu & Reille, 1992b) in the same part of the sequence. This event may be associated with a possible weakening in the North Atlantic thermohaline circulation (a.o. Cortijo et al., 1994), which may have had a downstream climate impact on Europe, but lack of detailed chronological control makes correlations difficult. Inspection of high-resolution Eemian profiles from central and northern Europe, however, shows little evidence for any changes in the extent of forest cover (see for example Zagwijn [1996] and references therein). Thus, a north/south division emerges, which can be explained in terms of either a geographically restricted climatic event or, alternatively, a difference in climatic susceptibility between northern and southern forest communities.

Finally, the third event refers to the brief increase in mainly *Quercus* and *Pinus* populations, interrupting the onset of stadial conditions. This is also observed in the marine pollen record of MD952042 (Sánchez-Goñi et al., 1999), where the re-expansion of *Quercus* populations occurs just before marine isotopic event 5.4. This increase in tree populations may be equivalent to the re-expansion of *Abies/Picea* separating a double peak of *Pinus* and may reflect a brief oscillation towards a more temperate and humid climate during the transition to stadial conditions in western and central Europe (see De Beaulieu & Reille, 1989, for a review of relevant records). Once again, however, only some sequences show this oscillation, while others with equally high sampling resolution bear no trace of it. De Beaulieu & Reille (1989) discuss this variability in terms of proximity to ecotones. It is possible that, while a climatic oscillation may have extended over large parts of Europe, its vegetational expression may have been muted in certain areas depending on the composition of vegetation and the available pool of taxa in close proximity.

Conclusions

Assessment of last-interglacial pollen diagrams from Greece has revealed the presence of considerable regional variability. In general, there is a trend from mixed interglacial forests with high biomass to more open and less diverse forests as one moves from northwest Greece to areas farther to the east and finally to the south. This variability appears to reflect closely differences in climatic regimes found in Greece today and suggests the presence of similar spatial climatic patterns during the last interglacial. Despite local differences, all sequences share certain features both in terms of the behaviour of certain taxa and also in terms of the occurrence of oscillatory events. Within a European context, the records of Greece contain features found in other long sequences from southern Europe and, indeed, sometimes from further north, but at the same time they show differences consistent with their location near the edge of the region and their particular environmental setting.

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