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QUATERNARY HISTORY OF *CEDRUS* IN SOUTHERN EUROPE

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ABSTRACT – A database of 68 pollen records of Pleistocene age was compiled from the western Mediterranean regions, with the aim of reconstructing the history of *Cedrus* in south Europe during the last 2 Ma. Marine pollen records from the Alboran Sea suggest that *Cedrus* was present in Morocco throughout the Quaternary, while it was absent from the Iberian peninsula, except a possible local presence in a coastal site of southern Spain. In France, *Cedrus* pollen was recorded in Pliocene deposits, but its Quaternary finds are always very sparse and suggest a long distance origin of cedar pollen. *Cedrus* was widespread in all the Italian sites during the Early Pleistocene, but it is sporadically found in the Middle Pleistocene deposits. Although times and modes of the disappearance of *Cedrus* from Italy are not known, it appears that the marked climate changes occurred between 0.9 and 0.7 Ma determined its local extinction. A similar trend is found in Greece, where *Cedrus* may have persisted a little longer than in the Italian Peninsula. On the whole, the history of *Cedrus* in southern Europe indicates that it is a taxon vulnerable to global climate changes and warns of a future risk of extinction also in the rest of the Mediterranean Basin.

KEYWORDS: *CEDRUS*, POLLEN, QUATERNARY, EUROPE

INTRODUCTION

The genus *Cedrus* includes three extant species native in the Mediterranean mountains (Fig. 1): *Cedrus atlantica* Manetti, in Algeria and Morocco (Linares et al., 2011), *Cedrus libani* Rich., in Asia Minor (Fady et al., 2008), *Cedrus brevifolia* (Hooker fil.) Henry, in Cyprus (Eliades et al., 2011). A further species, *Cedrus deodara* Don, lives in Afghanistan and in the southern slopes of the western Himalaya (Bou Dagher-Kharrat et al., 2007; Qiao et al., 2007).

Fossil data show that the genus *Cedrus* has a long history in Europe, being already present during the Middle Miocene (16-11 Ma) in Turkey (Yavuz-Işık, 2007), Bulgaria (Ivanov et al., 2002), and Austria (Jiménez-Moreno et al., 2008). However, in the course of the Pleistocene *Cedrus* underwent a strong reduction, disappearing from the Iberian (Postigo-Mijarra et al., 2010; Feddi et al., 2011; Magri & Palombo, 2012), Italian (Bertini, 2010) and Balkan Peninsulas (Tzedakis et al., 2006).

Currently, the distribution of *Cedrus atlantica* populations in northern Africa, occurring at elevations between ca. 1300 and 2600 m a.s.l., is severly fragmented as a result of the unfavorable climate conditions of the last glacial period (Cheddadi et al., 2009) and is still undergoing a process of reduction enhanced by increasing aridity in the region (Linares et al., 2011).

Taking advantage of the wealth of published pollen records of Early to Middle Pleistocene age, the present paper reviews the fossil data available for *Cedrus* from Quaternary deposits in southern Europe, with the aim of discussing times and modes of its disappearance.

MATERIALS AND METHODS

The high pollen productivity of *Cedrus* and the long-distance transport of its pollen make it difficult assessing the local presence of *Cedrus* in a region from fossil records. Sparse pollen grains of *Cedrus* are often found in late Quaternary sedimentary deposits from the north Mediterranean regions,

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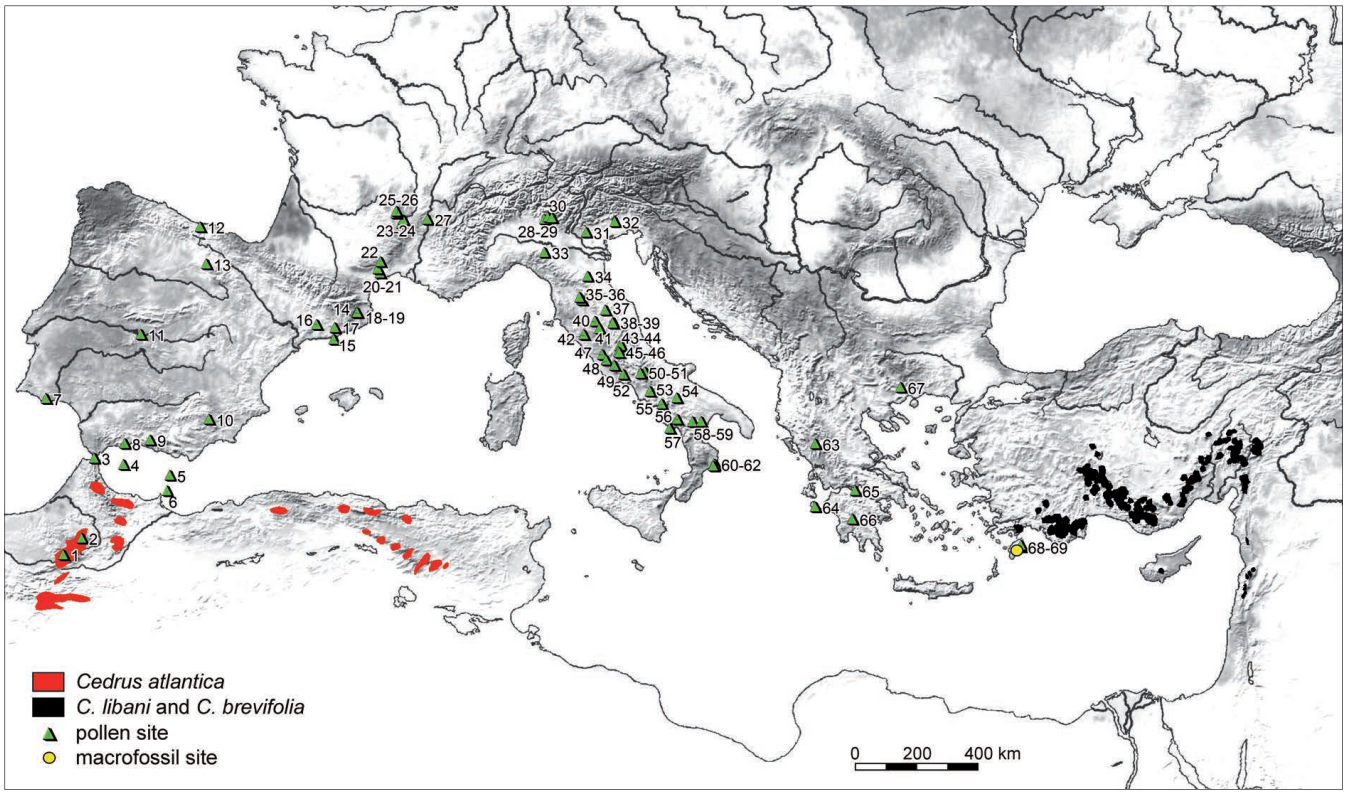

Fig. 1. Distribution of *Cedrus atlantica* Manetti, *Cedrus libani* Rich., and *Cedrus brevifolia* (Hooker fil.) Henry, and location of the Pleistocene sites mentioned in the text: 1. Tigalmamine: Lamb et al., 1989; 2. Lake Ifrah: Cheddadi et al., 2009; Rhoujjati et al., 2010; 3. Benzú: Ramos et al., 2008; 4. ODP976: Joannin et al., 2011; Combourieu-Nebout et al., 2009; 5. MD95-2043: Sánchez-Goñi et al., 2002; 6. Nador 1: Feddi et al., 2011; 7. Morgadinho: Antunes et al., 1986; 8. Cueva Bajondillo: Cortés-Sánchez et al., 2008; 9. Padul: Pons & Reille, 1988; 10. Cueva Negra: Carrión et al., 2003; 11. Puente Pino: Ruiz Zapata et al., 2009; 12. Caranceja: Alcalde Olivares et al., 2004; 13. Atapuerca: Rodríguez et al., 2010; 14. Tres Pins: Leroy, 1997; 15. Garraf: Suc & Cravatte, 1982; 16. Abric Romaní: Burjachs & Julià, 1994; 17. Cal Guardiola D2: Postigo Mijarra et al., 2007; 18. Bòbila-Ordis IV: Leroy, 2008; 19. Banyoles: Julia Bruguès & Suc, 1980; 20. Saint-Macaire: Leroy et al., 1994; 21. Nogaret: Leroy & Seret, 1997; 22. Bernasso: Leroy & Roiron, 1996; 23. Velay maars: Reille et al., 2000; 24. Ceyssac-8: Ablin, 1991; 25. Alleret: Pastre et al., 2007; 26. Senèze: Elhaï, 1969; Roger et al., 2000; 27. Montrebut, Saint-Vallier: Argant, 2004; 28. Fornaci di Ranica: Ravazzi et al., 2005; 29. Leffe: Ravazzi & Rossignol-Strick, 1995; Ravazzi, 2003; Muttoni et al., 2007; 30. Pianico Sellere: Rossi, 2003; 31. Lago di Fimon: Pini et al., 2010; 32. Azzano Decimo: Pini et al., 2009; 33. Stirone: Bertini, 2001; 34. Lamone Valley: Fusco, 2007; 35. Poggio Rosso: Bertini et al., 2010; 36. Santa Barbara: Bertini & Roiron, 1997; 37. Gubbio: Lona & Ricciardi, 1961; 38. Cesi: Bertini, 2000; 39. Colle Curti: Bertini, 2000; 40. Pietrafitta: Ricciardi, 1961; 41. Fosso Bianco: Pontini & Bertini, 2000; 42. Lagaccione: Magri, 1999; 43. Madonna della Strada: Magri et al., 2010; 44. Pagliare di Sassa: Palombo et al., 2010; 45. Borgorose: Sadori et al., 2010; 46. Marano de' Marsi: Sadori et al., 2010; 47. Valle Ricca: Urban et al., 1983; 48. Valle di Castiglione: Follieri et al., 1988; 49. Fontana Ranuccio: Corrado & Magri, 2011; 50. Sessano: Russo Ermolli et al., 2010a; 51. Isernia - La Pineta: Lebreton et al., 2002; 52. Ceprano: Manzi et al., 2010; 53. Saticula (Sant'Agata de' Goti): Russo Ermolli et al., 2010b; 54. Lago Grande di Monticchio: Allen et al., 2000; 55. Acerno: Munno et al., 2001; 56. Vallo di Diano: Russo Ermolli, 1994; 57. Camerota: Brenac, 1984; 58. Sant'Arcangelo: Sabato et al., 2005; 59. Montalbano Jonico: Joannin et al., 2008; 60. Santa Lucia: Joannin et al., 2007b; 61. Semaforo-Vrica: Coubourieu-Nebout & Vergnaud-Grazzini, 1991; Combourieu-Nebout, 1993; 62. Valle di Manche: Capraro et al., 2005; 63. Ioannina: Tzedakis, 1993, 1994; Roucoux et al., 2008; 64. Zakynthos: Subally et al., 1999; 65. Gulf of Corinth: Rohais et al., 2007; 66. Megalopolis Basin: Okuda et al., 2002; 67. Tenaghi Philippon: Tzedakis et al., 2006; 68. Tsampika Bay: Joannin et al., 2007a; 69. Kolymbia Bay: Boyd, 2009.

especially during the last glacial period (Magri & Parra, 2002), and are generally interpreted as the effect of long-distance transportation from North Africa (Reille, 1990). By contrast, the pollen records from Morocco and Algeria show high pollen percentages of *Cedrus* in the vicinity of modern cedar forests (Lamb et al., 1989; Cheddadi et al., 2009). Despite it is very difficult to determine the local presence of *Cedrus* and the exact timing of its disappearance from a region on the basis of pollen records, it is anyway possible to describe its decline to very reduced populations and to compare the behaviour of cedar populations in different regions of south west Europe.

A number of pollen records have been selected to reconstruct the history of *Cedrus* during the Quaternary in south Europe.

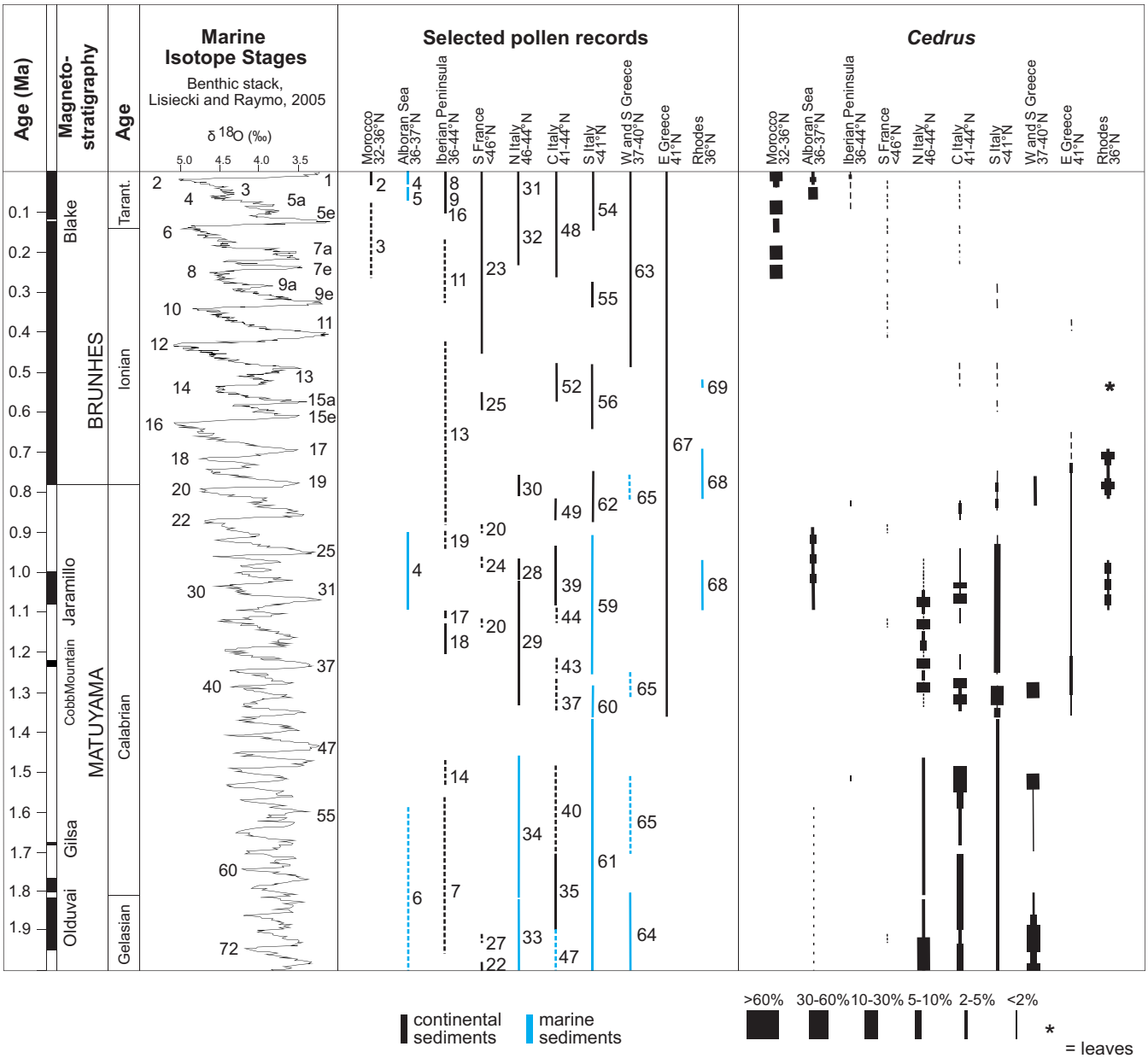

Fig. 2. Stratigraphical setting of selected Early and Middle Pleistocene pollen records from Morocco to Rhodes (dotted lines indicate uncertain cronologies) and schematic stratigraphical distribution of *Cedrus* fossils. The stratigraphic scale follows IUGS statements of 2010. Numbering of the sites follows Fig. 1.

Their geographic and stratigraphic distribution is represented in Figs 1 and 2, respectively. The chronostratigraphical setting of the selected pollen sites is based on a variety of methods, including magnetostratigraphical data (Bertini, 2000; Roger et al., 2000; Joannin et al., 2007a; Leroy, 2008; Madurell-Malapeira et al., 2010; Corrado and Magri, 2011), astronomical calibration (Okuda et al., 2002; Tzedakis et al., 2006), comparison with marine oxygen isotope stratigraphy (Fusco, 2007; Capraro et al., 2005; Joannin et al., 2007a), and radiometric dates of tephra layers (Ablin, 1991; Karner et al., 1999; Roger et al., 2000; Munno et al., 2001; Nomade et al., 2010). In a number of cases the chronology of the pollen records is not well constrained, being based on a combination of lithostratigraphical and mammalian fauna information (e.g., Lona & Ricciardi, 1961; Julia Bruguès & Suc, 1980; Leroy, 1997; Magri et al., 2010; Russo Ermolli et al., 2010b).

THE FOSSIL RECORD OF *CEDRUS*

The stratigraphical distribution of pollen records (Fig. 2) allows a reconstruction of the history of *Cedrus* in the regions of south Europe.

Various marine sediment cores from the Alboran Sea record *Cedrus* pollen: its presence was discontinuous at the end of the Pliocene and during the early Early Pleistocene (Feddi et al., 2011), while continuous and appreciable percentages of *Cedrus* pollen are found during the time intervals ca. 1.09-0.90 Ma (core ODP976: Joannin et al., 2011), 48-26 ka BP (core MD95-2043: Sánchez-Goñi et al., 2002), and the last 25 ka (core ODP976: Combourieu-Nebout et al., 2009). These records support a continuous presence of cedar throughout the Pleistocene in the regions facing the Alboran Sea, with a most likely north African origin of this anemophilous pollen type, considering the abundant distribution of *Cedrus* in Morocco during the late Middle Pleistocene (Benzú rockshelter: Ramos et al., 2008) and the Late Pleistocene (Tigalmamine: Lamb et al., 1989; Lake Ifrah: Cheddadi et al., 2009; Rhoujjati et al., 2010). The abundance of coastal cedar forests in northern Morocco and northern Algeria during the last glacial maximum was followed by postglacial local extinction of low altitude cedar populations (Cheddadi et al., 2009).

The only significant record of *Cedrus* in the Iberian Peninsula is from an Upper Paleolithic-Epipaleolithic (34-7 ka BP) coastal cave near Málaga, in the southernmost area of Spain (Cueva Bajondillo: Cortés-Sánchez et al., 2008), where local presence of *Cedrus* may be suggested by pollen values around 5% (Fig. 2). However, these occurrences are too isolated and recent to suggest that *Cedrus* may have been present in the Iberian Peninsula throughout the Quaternary, contrary to Postigo-Mijarra et al. (2010). Even in the southern site of Padul, at the eastern foot of the Sierra Nevada, *Cedrus* is found in low percentages (<1%) throughout the last 100 ka, suggesting a long distance provenance of pollen (Pons & Reille, 1988).

Cedrus was found in significant amount in northern Spain at the Pliocene/Pleistocene transition (Garraf 1: Suc & Cravatte, 1982; González-Sampériz et al., 2010), but in the pollen records south of the Pyrenees only discontinuous occurrences are documented from the Miocene to the Pleistocene (Jiménez-Moreno & Suc, 2007; Barrón et al., 2010). Only sporadic occurrences are recorded during the Pleistocene everywhere in the Iberian Peninsula except Cueva Bajondillo. Pollen of *Cedrus* was very rare or absent in the Early Pleistocene sites of Morgadinho in Algarve (Antunes et al., 1986), in the Caranceja deposit (Alcalde Olivares et al., 2004), at Tres Pins (Leroy, 1997), Banyoles (Julia Bruguès & Suc, 1980), Cal Guardiola D2 (Postigo Mijarra et al., 2007), Bòbila Ordis IV (Leroy, 2008), in the Early and Middle Pleistocene site of Atapuerca (Rodríguez et al., 2011), in the Middle Pleistocene site of Puente Pino (Ruiz Zapata et al., 2009), and in the Late Pleistocene site of Cueva Negra (Carrión et al., 2003). In the Late Pleistocene record of Abric Romaní (Burjachs & Julià, 1994) *Cedrus* is discontinuously recorded.

In southern France, *Cedrus* was found in various deposits of Pliocene age (Fauquette et al., 1999; Suc & Drivaliari, 1991). In the Early Pleistocene it was recorded in a few samples at Montrebut, Saint-Vallier (Argant, 2004), and in very low amounts at Senèze (Elhaï, 1969), Bernasso (Leroi & Roiron, 1996), Nogaret (Leroy & Seret, 1992), Saint Macaire (Leroy et al., 1994), and Ceyssac-8 (Ablin, 1991). Interpreting these low pollen frequencies of cedar pollen is a difficult task. However, a similar discontinuous presence of *Cedrus* pollen in the Middle and Late Pleistocene records from the Velay, when the persistence of *Cedrus* in France appears very unlikely (Reille et al., 2000), suggests that cedar was missing from the region already in the Early Pleistocene, as also confirmed by the absence of *Cedrus* in the Alleret maar, of Middle Pleistocene age (Pastre et al., 2007).

In northern Italy, abundant *Cedrus* pollen is documented during the Pliocene (Aulla: Bertoldi, 1988; Stirone: Bertini, 2001) and the Early Pleistocene both in the Prealps (Leffe: Ravazzi & Rossignol Strick, 1995; Ravazzi, 2003; Muttoni et al., 2007) and in the northern Apennines (Stirone: Lona & Bertoldi, 1972; Bertini, 2001; Lamone valley: Fusco, 2007). It becomes sporadic in the Prealps at the end of the Early Pleistocene (Fornaci di Ranica: Ravazzi et al., 2005), and it is absent in the Middle Pleistocene (Pianico Sellere: Rossi, 2003; Azzano Decimo: Pini et al., 2009), as well as in the Upper Pleistocene (Azzano Decimo: Pini et al., 2009; Fimon: Pini et al., 2010).

In central Italy, *Cedrus* is well represented in several sites during the Pliocene (e.g., Upper Valdarno basin: Bertini & Roiron, 1997; Bertini, 2010; Bertini & Martinetto, 2011; Borgorose and Marano de' Marsi: Sadori et al., 2010). In the Early Pleistocene it often shows high percentages (Gubbio: Lona & Ricciardi, 1961; Pietrafitta: Ricciardi, 1961; Valle Ricca: Urban et al., 1983; Fosso Bianco: Pontini & Bertini, 2000; Colle Curti: Bertini, 2000; Poggio Rosso: Bertini et al., 2010), although in some areas it was scarce (Madonna della Strada: Magri et al., 2010; Pagliare di Sassa: Palombo et al., 2010; Sant'Agata de' Goti: Russo Ermolli et al., 2010b; Fontana Ranuccio: Corrado & Magri, 2011), suggesting that during the late Early Pleistocene its distribution was already rather fragmented in the Italian Peninsula. The record of cedar in central Italy was occasional at all sites during the Middle Pleistocene (Cesi: Bertini, 2000; Ceprano: Manzi et al., 2010; Valle di Castiglione: Follieri et al., 1988), as well as during the Late Pleistocene and Holocene (Valle di Castiglione: Follieri et al., 1988; Lagaccione: Magri, 1999).

In southern Italy, *Cedrus* was already present in the Pliocene, together with other montane conifers (*Cathaya*, *Tsuga*, *Abies*,

and *Picea*) (Punta Piccola: Combourieu-Nebout et al., 2004). In the Early Pleistocene it was abundant in the marine sediments of Semaforo-Vrica (Combourieu-Nebout & Vergnaud-Grazzini, 1991; Combourieu-Nebout, 1993), Camerota (Brenac, 1984) Santa Lucia (Joannin et al., 2007b), Montalbano Ionico (Joannin et al., 2008) and Valle di Manche (Capraro et al., 2005). Towards the end of the Early Pleistocene its presence was discontinuous in the lacustrine pollen records (Sant'Arcangelo Basin: Sabato et al., 2005; Saticula: Russo Ermolli et al., 2010b). In the Middle and Late Pleistocene *Cedrus* pollen is sporadic or absent at all sites (Vallo di Diano: Russo Ermolli, 1994; Acerno: Munno et al., 2001; La Pineta: Lebreton, 2002; Sessano: Russo Ermolli et al., 2010a; Lago Grande di Monticchio: Allen et al., 2000).
The Early Pleistocene vegetation history of western and southern Greece is reconstructed from the marine records of Zakynthos dated to the Olduvai subchron (Subally et al., 1999) and the Gulf of Corinth, where sparse samples span the time interval 1.8-0.9 Ma (Rohais et al., 2007). *Cedrus* appears to be present in the region throughout the Early Pleistocene, in some phases with frequencies as high as 20%. In the Middle Pleistocene, the records from Ioannina (Tzedakis, 1993, 1994; Roucoux et al., 2008) and Megalopolis (Okuda et al., 2002) do not document presence of *Cedrus* in the region. It is also possible that the published diagrams, representing only selected taxa, do not report occasional finds of *Cedrus*, whose presence must have been negligible.
In eastern Greece, Tenaghi Philippon may be considered a key site for the reconstruction of the vegetation history since 1.4 Ma (Wijmstra, 1969; Wijmstra & Smit, 1976; Wijmstra & Groenhart, 1983; Tzedakis et al., 2006). *Cedrus* is recorded with continuity, although in low frequencies (<4%) from the base of the diagram up to approx. 0.75 Ma, then it becomes sporadic until approx. 0.35 Ma, when its last occurrence is recorded.
Marine sediments from Rhodes (Joannin et al., 2007a) show a continuous presence of *Cedrus* in the island in the time interval 1.1-0.65 Ma, with frequencies >20% in forest phases of the early Middle Pleistocene correlated to Marine Isotope Stage (MIS) 19 and MIS 17. Interestingly, fossil leaves of *Cedrus* were found in the island of Rhodes in sediments with a suggested age of about 0.5 Ma, confirming the local presence of the genus until at least the Middle Pleistocene (Boyd, 2009).

Discussion and conclusions

The pollen stratigraphy of Fig. 2 highlights significant regional differences in the distribution of cedar during the Quaternary.
Cedrus atlantica was present in North Africa throughout the Pleistocene, and it still persists in Morocco and Algeria. By contrast, the pollen records from the Iberian Peninsula indicate that *Cedrus* was absent from the region throughout the Quaternary. The modest pollen frequencies found at Cueva Bajondillo (Cortés-Sánchez et al., 2008), at the southern edge of the Peninsula facing Morocco, may either be the result of long distance transport and selective preservation in a cave environment, or the evidence of a small population immigrated from north Africa. In any case, in no other pollen diagram from Spain and Portugal there is continuous presence of *Cedrus* in significant frequencies (>1%) in the same time interval.
Cedrus was also absent from southern France throughout the Quaternary, although pollen analysis of Pliocene sediments confirmed its local presence before 2.6 Ma. Its disappearance occurred in France much earlier than in Italy, where *Cedrus* is abundant at all sites during the Early Pleistocene. During the late Early Pleistocene, the frequencies of cedar show a clear decrease, so that in the Middle Pleistocene *Cedrus* was discontinuously found in low amounts. The present state of knowledge does not allow assessing the age of the local extinction of *Cedrus* in Italy, because of both the impossibility to distinguishing local from long-distance transported pollen grains and the gaps in the stratigraphical distribution of the pollen records. Only a few sedimentary deposits in the time interval 0.9-0.6 Ma have been palynologically investigated in Italy, so that the history of *Cedrus* populations is poorly known at the time of its dramatic reduction, during the so called Mid-Pleistocene Revolution. For the same reason it is not possible to define the geographical pattern of *Cedrus* disappearance along the Italian Peninsula, although it seems that it occurred first in northern Italy, then in central Italy and finally in the southern regions (Fig. 2).
In Greece, *Cedrus* possibly persisted a little longer, but the continuous record from Tenaghi Philippon indicates that during the last 1.4 Ma it was always rather sparse and disappeared around 0.7 Ma (Fig. 2). The fossil record in Rhodes, very close to the current distribution of *Cedrus libani*, shows high percentages during the early Middle Pleistocene, when in the rest of Europe *Cedrus* was already absent or very sparse. The lack of data after 0.5 Ma does not allow fixing the age of its disappearance from the island.
On the whole, it appears that a dramatic decrease of *Cedrus* in the central Mediterranean regions took place in a relatively short time, similarly to other conifer taxa (e.g. *Tsuga*, *Cathaya*) that were extirpated from the region during the Middle Pleistocene Revolution, corresponding to a time of major changes of periodicity and amplitude of the glacial-interglacial cycles from 41 ka to approximately 100 ka (Tzedakis et al., 2006; Bertini, 2010; Magri & Palombo, 2012). We do not know whether this reduction occurred during glacial or interglacial phases, but the ongoing

consistent declines of *Cedrus atlantica* correlated to increased drought sensitivity (Linares et al., 2011) confirm that climate changes are one of the main factors determining the disappearance of tree taxa from Europe, and warn that in the long run the isolated populations of *Cedrus* in the Mediterranean mountains are destined to fatal reductions.

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