Quaternary Science Reviews
Volume 26, Issues 7-8, April 2007, Pages 1037-1054
doi:10.1016/j.quascirev.2006.12.009

Vegetation dynamics in southern France during the last 30 ky BP in the light of marine palynology

Célia Beaudouin[a, b*] Gwénaël Jouet[c, d], Jean-Pierre Suc[a], Serge Berné[d], Gilles Escarguel[a]

a UMR CNRS 5125 Laboratoire PaléoEnvironnements et PaléobioSphère, Université Claude Bernard Lyon 1, Campus La Doua, Bâtiment Géode, 2 rue Dubois, 69622 Villeurbanne Cédex, France
b Department of Earth Sciences, Sun Yat-sen University, 135 Xin Gang Xi Lu, 510275 Guangzhou, China
c UMR CNRS 6538 Domaines océaniques, Institut Universitaire Européen de la Mer, 1 Place Copernic, 29280 Plouzané, France
d Laboratoire Environnements Sédimentaires, Géosciences Marines, IFREMER, Centre de Brest, BP 70, 29280 Plouzané, France

*: Corresponding author : celia.beaudouin@hotmail.com

Abstract:

The composition of the glacial vegetation of southern French plains has been a matter of debate for several decades. Vegetation is considered as steppic according to French and Spanish lacustrine pollen records whereas cave deposits suggest the presence of mesothermophilous trees through the Last Glacial Maximum. In our paper, we display new palynological records from marine sediments of the Gulf of Lions. They indicate the presence of *Abies*, *Picea* and deciduous *Quercus* in the Gulf of Lions, certainly located in the drainage basins of the Pyreneo-Languedocian rivers. These populations that were sensitive to short climatic events during Marine Isotopic Stage 2 could have been linked to northeastern Spanish and southeastern French relicts already evidenced by phylogenetic data. These trees were absent from the Rhone drainage basin during the deglaciation and certainly also disappeared from the Pyreneo-Languedocian drainage basins from ca 17 to 15 ky cal BP. Finally, the Last Glacial Maximum does not appear as stable, cold and dry as previously thought.

Keywords: Vegetation, Climate, Pleistocene, Mediterranean Sea

1. Introduction

The composition of West-European vegetation during the Last Glacial and in particular during the Last Glacial Maximum (LGM) has been a matter of debate for several decades (e.g. Tzedakis, 2002, 2003; Stewart, 2003). Two models were developed. The first merely suggests the existence of two bioprovinces: most of European vegetation would be represented by steppe while southwards (i.e. in southern Spain, Italy and Balkan Peninsula) mesophilous trees would have survived in favourable climatic areas (e.g. Elenga et al., 2000; Taberlet and Cheddadi, 2002). This model was built on 11 long lacustrine sequences, on several well-dated macrorests and also from the Holocene expansion pathways reconstructed by phylogenetical and pollen studies (Huntley and Birks, 1983; Hewitt, 1999; Petit et al., 2002). In this model, the northern tree limit is not well-constrained. Several authors suggested that conifers could have survived out of these refugia (e.g. Bennett et al., 1991; Huntley and Birks, 1983). Tzedakis (2004) proposed a tree limit at 45-46°N. But several authors suggested there were no tree (except *Pinus*) in France during the Last Glacial Maximum (Reille and Lowe, 1993). A second model was developed in parallel and suggests the presence of mesophilous trees as well as temperate mammals out of these southern refugia. They would have survived in protected valleys benefiting from a microclimate (Stewart and Lister, 2001; Willis and Van Andel, 2004). It would explain the late-Pleistocene non-analogue mammalian assemblages (i.e. corresponding to a mixture of steppic mammals like Bison priscus, Equus sp., Mammuthus primigenius and also temperate mammals now living under a closed forest canopy like Cervus elaphus or Sus scrofa). This model is mainly supported by palynological studies made on cave sediments also containing mammals. It is often criticized using two arguments: (1) the ecology of mammals and in particular their adaptability for what concerns their ecological niches would be poorly understood (2) these occurrences (mammals, pollen or charcoals) correspond to reworking (See McGarry and Caseldine (2004) for a review). Choosing between the two models has important consequences for our understanding of the climate of Western Europe, the ecology and evolution (Davis and Shaw, 2001). The presence of mammals or plants taxa out of southern refugia would either imply a more temperate climate or their greater capacity of adaptation to the climate. In particular, the reality of non-analogue assemblages has consequences on our understanding of present-day ecosystems, their link with climate and their capacity to face climatic changes.

The composition of southern France vegetation (i.e. between ca. 42° and 45°N) during the LGM is a part of this debate. The lacustrine data suggesting the absence of mesothermophilous trees (Fig.1) are scarce and mainly situated at high altitudes (Beaudouin et al., 2005a). On the contrary, many palynological studies carried out on caves show the presence of mesothermophilous taxa at high latitudes such as deciduous *Quercus*, *Carpinus*, *Tilia* or *Juglans* during interstades of Marine Isotopic Stage 2 (MIS) (Lebreton et al., 2004). However, pollen is extracted from different sediment granulometry (from silts to coarse sands) leading to different degradation intensities and to an over-representation of some taxa like the Asteraceae. Furthermore, the chronology is supposed to be particularly discontinuous and not well-constrained. For these reasons, many palynologists often consider that pollen assemblages from caves are not suitable to reconstruct palaeovegetation. The recent discussion between d'Errico and Sánchez-Goñi (2003) and Carrión (2004) illustrates this debate.

In order to reconstruct the palaeovegetation of southern France, new sequences were

acquired in marine sediments from the Gulf of Lions. We focussed on the area where sedimentation rate was very high during the Last Glacial in order to acquire high-resolution pollen data. Preliminary records (Acherki, 1997; Beaudouin et al., 2005a) displayed high amounts of pollen of *Picea*, *Abies* and also deciduous *Quercus* for the MIS 3 and 2 leading to a first interpretation of the presence of a refugium in southern French plains. But this first test was based on short cores not covering the entire MIS 2, with weak chrono-stratigraphic constraints, which did not allow a full interpretation of palynological data. Therefore, we studied three new sequences positioned in well-known palaeogeographic and chrono-stratigraphic contexts (Berné et al., 2004; Rabineau et al., 2005). They almost cover the last 30 ky. The multi-proxy approach applied on these sequences helps to better constrain the palynological signal in order to reconstruct the palaeovegetation dynamics around MIS 2. In particular, we aim at:
(1) Precisely determining the location and the vegetation structure in southern France for the LGM,
(2) Highlighting the late-glacial history of this vegetation and discussing the contribution of these refugia to present-day populations of trees,
(3) Determining the link between short climatic events and the vegetation of southern France.

2. General settings

2.1. Present-day vegetation, hydrology and sedimentology

The present-day vegetation of the studied area (Noirfalise et al., 1987) covers the northern part of the Mediterranean climatic zone and the temperate climatic zone (Fig. 2). The Mediterranean vegetation belongs to the Meso-Mediterranean belt. It is bounded by coastline southward and finishes at 500 m in altitude. It corresponds to the development of sclerophyllous forests with evergreen *Quercus* accompanied by *Laurus nobilis*. The degradation of these forests corresponds to mattorals where *Quercus ilex* forests dominate. The Supra-Mediterranean belt is mainly composed of *Quercus pubescens* associated to Buxus *sempervirens*. The temperate zone corresponds to deciduous oak mixed forests in plains (< 700 m). The temperate hills and mountains i.e. the northern part of the Alps as well as the Massif Central is characterized by the development of *Fagus* from 700 to 1000 m high. *Fagus* is mixed with *Abies* in higher mountains. Mountainous forests of conifers occur from 1450 to 2500 m high. The Alpine belt begins at ca. 2000-2300 m. The lower part is composed of Ericaceae or alpine grassland with Poaceae, Fabaceae and Cyperaceae.

The Mediterranean Sea is characterized by thermohaline circulation: surface water coming from the North Atlantic Ocean enters the Mediterranean basin while Mediterranean deep-water outflows. The circulation in the Gulf of Lions is wind-dependant (Millot, 1990). Two cold winds blowing all year long from the North and the North-west (i.e. Mistral and Tramontane) induce downwellings and deep-water formations (Fig. 2). A secondary wind, coming from the Southeast brings warm air masses sometimes blowing intensely (generally from autumn to spring) and can influence the distribution of sediments down to ten meters of bathymetry. The main surface current of the Gulf of Lions is a gyre called the North-Mediterranean current (Millot, 1999).

The shelf in the Gulf of Lions is maximum 70 km wide. The continental slope is incised by submarine canyons that develop from the shelf break to the rise (Fig. 3). The shelf is made up of terrigenous sediment mainly originating (i.e. 80%) from the Rhone River (Aloïsi et al., 1979). The smaller western rivers (i.e. Tech, Têt, Agly, Aude, Orb and Hérault) deliver the remaining fraction. In contrast, aeolian inputs are negligible (Węgrzynek et al., 1997). At the river mouth, several water layers enriched in particles are formed. The bottom nepheloid layer develops at the mouth near the bottom (Aloïsi et al., 1979; Roussiez et al., 2005). It corresponds to a continuous dense flow, which spreads over the shelf. Its influence weakens from the river mouth to the outer shelf and becomes negligible on the slope (Aloïsi et al., 1979; Monaco et al., 1999). Resuspension from the shelf is the main way to bring terrigenous particles on the slope and into the canyons (Courp and Monaco, 1990; Durrieu De Madron et al., 1999; Monaco et al., 1999; Frignani et al., 2002).

2.2. Sedimentary history of the Gulf of Lions

The shelf of the Gulf of Lions is made up of Plio-Quaternary sediments (Lofi et al., 2003; Duvail et al., 2005). Rabineau et al. (2005) outlined the depositional pattern of the last 540 ky in the Bourcart-Hérault interfluve, where the upper five sedimentary sequences were assigned to the 100 ky glacio-eustatic cycles, based on stratigraphic modelling (Fig. 4). Within a glacial/interglacial cycle, the deposition is maximum at the shelf edge during the end of sea-level fall and lowstand. Whereas most of sedimentation occurs on the inner shelf during Deglacial and Interglacial conditions, the outer shelf experiences starvation during this interval (Bassetti et al., 2004). The source of sediment at the shelf edge was probably mixed during the last glacial: there is evidence of a connection of the Hérault canyon to a large system including the Rhone and the Hérault rivers, whereas the Bourcart canyon was probably connected both to the Rhone and to a Pyrenean river (Berné et al., 2002) (Fig. 3).

2. 3. Reliability of pollen signal

The reliability of marine palynological data has been a matter of debate since the 1950's [see Beaudouin et al. (accepted) and Hooghiemstra et al. (2006) for a review]. Especially, the presence of reworked palynomorphs in terrigenous sediments was considered as evidence of the unreliability of the whole pollen signal. In contrast, many recent investigations made on terrigenous and autochthonous sediments in other parts of the world (e.g. Heusser and Balsam, 1977; Sun et al., 1999; Van der Kaars, 2001) and also in the Gulf of Lions (Beaudouin et al., 2005b; Beaudouin et al., accepted) demonstrated the suitability of marine pollen signal to reconstruct a regional vegetation even if they contain reworked palynomorphs. In particular, a study carried out on the present-day prodelta of the Rhone River (i.e. deposited under 40 m of water depth) demonstrated the stability of the pollen signal during 30 years of sedimentation despite the occurrence of storms and floods (Beaudouin et al., 2005b).

Actually, one needs to distinguish between allochthonous (i.e. terrigenous) and autochthonous sediments to understand the meaning of the marine pollen signal. Pollen grains contained in autochthonous sediments are mainly brought by winds (Beaudouin et al., accepted). On the contrary, pollen grains contained in terrigenous sediments are mainly brought by rivers and therefore come from one or several drainage basins (Heusser, 1988). In the case of the Gulf of Lions, they are incorporated into the bottom nepheloid layer at the river mouth and spread all over the shelf (Beaudouin et al., accepted). According to the physiography of the margin, terrigenous sediments can reach the sea floor. They carry by definition reworked particles and therefore reworked palynomorphs (i.e. identified Pre-Quaternary pollen and dinoflagellate cysts as well as corroded pollen grains having totally or partly lost their ektexine) when the area drained by rivers encounters older sedimentary basins. Actually, a key question is to know if the amount of pollen supplied by the erosion of previously deposited sediments is able to balance the contemporaneous pollen signal (i.e. the contemporaneous amount of pollen emitted by plants). In present-day sediments of the Gulf of Lions, reworked palynomorphs reach 5% of the palynological content while the pollen content is representative of the vegetation (Beaudouin et al., accepted). Furthermore, several multi-proxy studies made on Quaternary terrigenous sediments demonstrated that the pollen signal was sensitive to climatic variations recorded by oxygen isotopes in the same cores and therefore definitely evidenced the suitability of terrigenous marine deposits to reconstruct past vegetation dynamics (e.g. McGlone, 2001; Sánchez-Goñi et al., 2002). For example, Sánchez-Goñi et al. (2002) evidenced a clear correlation between the pollen signal and the oxygen isotopes in an area located within the Alboran Sea where 88% of sediments are terrigenous (Sánchez-Goñi et al., 2002), although rivers drain Cenozoic continental basins. Reworked palynomorphs are not mentioned but more recent studies evidenced the presence of Pre-Quaternary palynomorphs in this area within Lower Pleistocene sediments while the pollen signal is once again in correspondence with oxygen isotopes (Joannin, pers. com.).

Whatever, we cross-checked the new data with others based on literature (i.e. palynology, phylogenetic and botany) to reconstruct the probable history of vegetation in southern France.

3. Material and Method

We provide three long and high-resolution pollen records extracted from (1) core MD99-2349 (42°49.27’N, 3°43.43’E; 126 m depth), (2) core MD99-2348 (completed by the upper portion of the PROMESS drillsite PRGL1-4 situated at the same position (42°41.58’N, 3°50.50’E; 296 m depth) and (3) core MD99-2352 (43°19.15’N, 4°09.64’E; 70 m depth). Core MD99-2349 samples the lowstand palaeo-lower-shoreface at the interfluve Bourcart-Hérault on the outer shelf (Fig. 3, 4). Cores MD99-2349 and MD9923-48/PRGL1-4 sample units deposited during sea-level fall, last Glacial and early Deglacial (units 151 to 154 of Jouet et al., in press). These authors provide a detailed lithological description of both cores. Core MD99-2348 is situated on the upper slope on the Bourcart-Hérault interfluve, in a place that was not affected by mass wasting and where sedimentation rate was very high due to fall of particles from the plumes of rivers situated in the vicinity during glacial period (Jouet et al., in press). Core PRGL1-4 is made on the same site and samples the last 430 ky on a thickness of 300 m (Berné et al., 2004). The first analyses made between 1806 and 3664 cm depth are combined with the data obtained on core MD99-2348. Core MD99-2352 samples the muddy bottomsets of clinoforms of a transgressive parasequence that formed during a decrease in the Deglacial sea-level rise, around the Younger Dryas (Berné et al., 2003). These authors provide a detailed lithological interpretation of this core. It was under the direct influence of the Rhone River.

The general stratigraphy is described by a set of seismic units defined on mud penetrator chirp signal. Several radiocarbon datings made on fresh and intact macrofossils and on foraminifers from numerous cores constrain these seismic units (Rabineau, 2001; Jouet et al., in press; Berné et al., 2003). The radiocarbon datings were calibrated using Calib 5.0.2 (Stuiver et al., 2005) with the curve of Hughen et al. (2004). For datings older than 21,786 BP we used the curve of Bard et al. (1998). We applied a reservoir age of 400 years. The dates are in general coherent. Most of the chronological inversions evidenced by non-calibrated dates disappear when taking into account the calibration and its associated confidence limit (Tabl. 1). However, the radiocarbon datings on core MD99-2349 are more scattered because this core corresponds, at the time of deposition, to a very shallow environment with episodic reworkings by storms events (Jouet et al., in press). In order to minimize the reworking effect on this core, we only take into account the AMS datings made on microfossils.

This chrono-stratigraphic framework allows a comparison between palynological and climatic data (i.e. $\delta^{18}O$) from Greenland ice-cores. We chose the signal from the GRIP ice-core using the time-scale of Johnsen et al. (2001) at a resolution of 50 years. Indeed, concerning MIS 2, there is a particularly good correlation between the climatic signal of the Western Iberian and this core using this chronology (Roucoux et al., 2005).

A standard chemical treatment was applied to extract palynomorphs, using cold HCl (33%), cold HF (70%), ZnCl2 and sieving at 200µm and 10µm. A minimum of 150 pollen grains (apart from *Pinus*) was counted for each sample. To calculate percentages, we used the sum of pollen grains without *Pinus*. Contrary to continental pollen data (e.g. in lakes) where the pollen of Cyperaceae most probably originates from local herbs and are over-represented, marine terrigenous sediments contains pollen of Cyperaceae that can originate from various environments. We therefore include them as well as other herbs. Dinoflagellate cysts were determined and counted on the same lines as pollen grains. We did not calculate the relative abundance of dinoflagellate cysts because their amount was insufficient. Nevertheless, they bring supplementary information about the palaeoenvironment. All corroded and clearly identified pre-Quaternary palynomorphs were classified as reworked (Fig. 5). We distinguished reworked pollen grains from contemporaneous one on the state of the conservation of the ektexine (e.g. Haberle, 1997). A reworked pollen grain should have a partly or totally destroyed ektexine. We used the Cour's Method to calculate concentrations (Cour, 1974). All the palynological data are available in the Cenozoic Pollen Database and Climatic values (http://cpc.mediasfrance.org/aims/index.php). In terrigenous sediments, the presence of one pollen grain from a taxon cannot be considered as an evidence of the presence of the taxon within the drainage basin because of reworkings. Therefore, we focussed on the main taxa representing more than 5%. We drew a simplified diagram also displaying the confidence limits on each percentage. We did not represent the Cyperaceae and the Poaceae even if they were abundant as their ecological meaning is unconstrained. In order to better constrain the statistical significance of peaks of pollen abundances, binomial confidence limits for proportions were calculated using the program Pro-CI (available on request from G. Escarguel). Given a type I error rate $\alpha = 0.05$, these limits define the 95% confidence intervals associated to each sample percentage, i.e., the range of percentage values within which there is $1 - \alpha = 95\%$ of chance to find the unknown true (parametric) percentage (e. g. Sokal and Rohlf, 1995).

Palynozones were defined on the change of the main taxa as well as on the evolution of the abundance or reworked palynomorphs. Indeed, the abundance of reworked palynomorphs in marine sediments is linked to the importance of the erosion of the drainage basins due to (1) sea-level drops (e.g. McGlone, 2001) or (2) melting of glaciers (e.g. Haberle, 1997; Gregory and Hart, 1992). In the case of the Gulf of Lions, major sea-level drops are linked to a great increase of the abundance of reworked particles. It is the case for MIS 6, from MIS5 to 4 (J.-P. Suc, pers. com.) and from MIS3 to 2 in deep-sea terrigenous sediments (Beaudouin et al., 2004). Reworked palynomorphs were also found in abundance within the drainage basin of the Rhone River in the alpine lake of Annecy at the end of MIS3 (David et al., 2000).

4. Results

4.1. Palynological content

The palynofacies includes (1) well preserved pollen grains and dinoflagellate cysts, (2) pre-Quaternary destructured dinoflagellate cysts and pollen grains and (3) other debris (charcoals, wood debris, cuticles, stomata, epidermis...). Concentration of pollen grains is generally low (from 40 to 3000 grains/g). Concentration of dinoflagellate cysts and reworked palynomorphs respectively reach 0 to 500 cysts/g and 0 to 320 grains/g. *Pinus*, Cupressaceae, *Abies*, *Picea*, Deciduous *Quercus*, *Hippophae rhamnoides*, Poaceae, *Artemisia* and Cyperaceae constitute the main part of the pollen signal within cores MD99-2348/PRGL1-4 and MD99-2349. One hundred taxa were found in core MD99-2349. Six palynozones were defined (Fig. 6). Twenty-three Dinoflagellate cysts were determined. *Brigantedinium*, *Operculodinium centrocarpum* and *Spiniferites* are relatively frequent. Dinoflagellate cysts adapted to low saline and coastal areas (*Lingulodinium machaerophorum*) and found at river mouths and in lagoons (*Polysphaeridium zoharyi*) or in freshwater (*Concentricystes*) are relatively well represented and confirm that sediments were deposited in the lower-shoreface. Dinoflagellate cysts characterizing cold waters are present only sporadically (*Nematosphaeropsis labyrinthus*, Cf. *Pentapharsodinium dalei* and *Bitectatodinium tepikiense*). Eighty-eight taxa were found in the sequence MD99-2348/PRGL1-4. Seven palynozones were built (Fig. 7). The same dinoflagellate cysts as in core MD99-2349 were found. Freshwater or lagoon dinoflagellates are not as frequent as in core MD99-2349. Seventy-six taxa were found in core MD99-2352. The dominant taxa are *Pinus*, Deciduous *Quercus*, evergreen *Quercus*, Cupressaceae, *Corylus*, *Ulmus*, *Betula*, Poaceae, Cyperaceae and *Artemisia*. Three palynozones were created (Fig. 8). Dinoflagellate cysts are relatively abundant representing 25% of the palynomorphs from 1515 to 290 cm depth: they are mainly represented by *Brigantedinium*, *Spiniferites*, Cf. *Pentapharsodinium dalei* and *Operculodinium centrocarpum*. From 290 to 152 cm depth, dinoflagellate cysts are rare and only represented by some *Spiniferites*. In the upper part of the core (from 90 to 10 cm depth), *Concentricystes* is the only taxon to be represented: it may characterize the influence of the Rhone River.

In all sequences, the evolution of the abundance of pollen from the main taxa does not follow the evolution of reworked palynomorphs (Fig. 6, 7 and 8).

4.2. Correlation of cores and comparison with global climatic changes

The cores display comparable pollen fluctuations in terms of variation but not abundance (Fig. 9). We therefore propose a correlation based on the seismic stratigraphy and the radiocarbon datings. The time-window recorded by our cores is small and consequently, the resolution of pollen data is high, reaching ca. 70 years in core MD99-2349 and 100 years in core MD99-2348. Pollen curves in the latter core shows slight fluctuations difficult to correlate with the pollen signal from core MD99-2349. The cause of this characteristic will be explained further. The variations of abundances of the main taxa match relatively well with the GRIP δ18O record for such a short time-window. Two synchronous common pollen features shared by two or all cores are noteworthy. The first feature corresponds to the great increase of deciduous *Quercus* and *Quercus ilex* t. associated with the decrease of *Artemisia* and reworked elements correlated with the Holocene (palynozones MD48-A, MD49-A and MD52-A). In the sequence MD99-2348/PRGL1-4, the apparent Holocene increase of deciduous *Quercus* from 2% reaching 14% is dated at 14,880±250 cal. BP at 25 cm depth. The highest sample carries a similar signal to present-day sediments from the Gulf of Lions (Beaudouin et al., accepted). In fact, the upper 25 cm (i.e. only 3 samples) correspond to condensed levels recording the Interstade 1 (IS1), the Younger Dryas and the Holocene, the pollen signal representing a mean of the vegetation changes through these climatic changes. The second main feature is found at the base of sequences MD99-2349 and MD99-2348/PRGL1-4. It corresponds to the development of the curve of reworked palynomorphs followed by the increase of *Picea*, *Abies* and deciduous *Quercus* to the detriment of the Cupressaceae (palynozone MD49-E, MD49-D and MD48-G). In core MD99-2349, the bottom part of the pollen signal (i.e. zone MD49-E) is reworked according to the sedimentary facies. Nevertheless, reworkings do not affect levels situated above 1442 cm also containing a low amount of *Picea* and *Abies*. The radiocarbon datings confirm that the great increase of reworked palynomorphs corresponds to the sea-level drop between MIS3 and 2. The associated and following vegetation pattern (i.e. the decrease of Cupressaceae and the increase of *Picea* and *Abies*) is situated within the same sedimentary unit (U151) in both cores and is dated at ca. 28 ky cal. BP in core MD992349 and up to ca. 25-24.5 ky cal. BP according to core MD99-2348/PRGL1-4. The H2 event is partly identified (with the presence of *Neogloboquadrina pachyderma* sinistra) in the upper part of zone MD48-G corresponding to the base of core MD99-2348 (Flores et al., 2005). The H2 event could correspond to the palynozone MD49-C in core MD99-2349 according to the chrono-stratigraphy and would be characterized by the development of *Artemisia* and the decrease of temperate taxa. From ca. 28 to 25.5 ky cal. BP, the Gulf of Lions seems to experience an increase of dryness at the end of which the H2 event is identified. But the effect of the latter is not clearly recorded by vegetation. The same pattern occurs in the Western Mediterranean. In western Iberia (between 40°N and 43°N), the MIS 3 vegetation was made up of *Pinus*, deciduous *Quercus*, *Betula* and Cupressaceae associated with Ericaceae, Poaceae and *Artemisia* (Roucoux et al., 2005). In detail, from ca. 27.5 to 24 ky cal. BP deciduous *Quercus* disappears (Roucoux et al., 2005). This phase is followed by the H2 event recorded by ice-rafted debris. But the response of the vegetation is not clear for this event. On the southern part of the Portuguese Margin, the response of the vegetation to H2 event is characterized by a slight decrease of Ericaceae and fluctuations of *Artemisia* (Turon et al., 2003). In the Alboran Sea, H2 event is found within a succession of peaks of semidesert taxa beginning at 27 ka cal. BP and finishing at 24 ka cal. BP (Combourieu-Nebout et al., 2002). In Italy at Lago di Monticchio (Allen et al., 2000), the pollen of *Quercus* also experiences a strong decrease at 26 ky cal. BP. The phase of *Picea* and *Abies* in MD99-2349 (i.e. zone MD49-D) could correspond to the peak of temperate taxa found in the Alboran Sea around ca. 25.5 cal. BP (Combourieu-Nebout et al., 2002). But it does not correspond to any vegetation change in core MD9923-48/PRGL1-4 as well as in North West Iberia (Roucoux et al., 2005). This correlation hypothesis implies that the IS3 is not well-recorded in the Gulf of Lions like in North West Iberia (Roucoux et al., 2005). According to the seismic data, zones MD48-B to MD48-D corresponding to U154 (above the discontinuity D70) are not recorded in core MD99-2349 where it should be represented by a condensed interval. Zone MD48-D (from ca. 20.5 to 18.3 ky cal. BP) corresponds to a high amount of *Picea*, deciduous *Quercus* and *Artemisia*. Deciduous *Quercus* is more abundant at the bottom of the zone while *Artemisia* increases upward. MD48-C is characterized by a decrease in *Picea*, *Abies* and *Pinus*, while Cupressaceae and *Artemisia* increase. Flores et al. (2005) attribute these levels to the H1 event (from foraminifer’s assemblages). Zone MD48-B records a slight increase of *Picea* and deciduous *Quercus* and could correspond to IS2 according to the chrono-stratigraphy. H1 is also well-marked in other Mediterranean sites. It is characterized by a well-marked development of the curve of semidesert taxa (including *Artemisia*) in the Alboran Sea (Combourieu-Nebout et al., 2002) and by a severe decrease of Ericaceae on the Portuguese Margin (Roucoux et al., 2005; Turon et al., 2003). Core MD99-2352 records the last 15 ky and should record IS1 and the following Younger Dryas. It cannot be correlated to core MD99-2348 as this period corresponds to three samples in the latter core (i.e. the first 25 cm of sediments). Zone MD52-C is characterized by the dominance of *Artemisia*, *Hippophae rhamnoides* and Cupressaceae (from 14,960±240 to 11,870±230 cal. BP) except from 11,870±230 to 10,950±190 cal. BP corresponding to an increase of *Betula*. The bottom part of the core is characterized by the low amount of *Pinus* associated with a high percentage of reworked palynomorphs. Zone MD52-B (from 10,830±220 cal. BP up to the upper discontinuity) is characterized by the development of *Corylus* and Cupressaceae. *Pinus* as well as reworked elements increase in this zone. In core MD99-2352, the Holocene is represented by a condensed interval dated at ca. 5,310±130 cal. BP likely formed during a sudden sea-level rise after the Younger Dryas (Berné et al., 2003).

5. Discussion

5.1. Location and structure of the populations of trees

In the Gulf of Lions, (1) the high amount of pollen of Cupressaceae, *Abies*, *Picea*, and deciduous *Quercus*, (2) their reaction fitting climatic changes (at least evidenced for the 28-26 ky cal. BP event and the H1 event) and (3) the fact that their abundance does not follow the evolution of the abundance of reworked particles suggest the presence of these trees in the basins drained by the Rhone and the Pyreneo-Languedocian rivers during the MIS 3 and through the LGM. *Pinus* was also present. The signal of *Pinus* is known to be difficult to interpret in marine sediments because it is sorted by currents unlike other bisaccate pollen grains (Heusser, 1988). The abundance of *Pinus* is modulated by pollen production and also by the fluctuation of sea-level through sedimentary supplies or sea-level changes. We can attest that *Pinus* was present in the Rhone and the Pyreneo-Languedocian drainage basins although we can't give any further conclusions concerning its percentage evolution. This conclusion is in agreement with other studies carried out in the area (Beaulieu and Reille, 1984; Cheddadi et al., 2006).

Even if the evolution of pollen curves can be compared for what concerns long-term changes between core MD99-2348 and MD99-2349, the abundance of each taxon is different in each core. Core MD99-2349 shows an amount of *Abies* and *Picea* higher than core MD99-2348 for the same time-window. This difference can't be linked to a sorting of pollen grains: a study made on present-day sediments from the Gulf of Lions demonstrated that pollen content was similar from the coast to the edge of the shelf (Beaudouin et al., accepted). This difference may be more likely due to a double origin of the sediments, i.e. coming on the one hand from the Pyreneo-Languedocian Rivers and on the other hand from the Rhone River according to the palaeogeography (Fig. 3). This phenomenon is found in present-day sediments of the Gulf of Lions: the pollen signal in the western part of the shelf is different from that of the eastern part. This reflects the different vegetation within the areas drained by the Rhone River and the Pyreneo-Languedocian Rivers. From this point of view, the pollen contained within seismic units U151 and U152 in core MD99-2349 has been brought by the Agly/Aude/Orb/Hérault palaeoriver draining the Pyrenean Mountains and the plains of the Languedoc-Roussillon. It is the closest channel from the sampled area (Fig. 3). Sediments of sequence MD99-2348/PRGL1-4 were deposited at a deeper bathymetry (i.e. at 130 m depth during the lowstand) and have also received abundant inputs from the Rhone River connected to the Hérault canyon, i.e. 20 meter above and 30 km eastwards. The area drilled by core MD99-2349 has been relatively protected from these Rhone River inputs because the Agly/Aude/Orb/Hérault palaeoriver was the most important flow (Rabineau, 2001). Furthermore, the Rhone River was connected to several canyons at the same time, i.e. at least to the Petit-Rhone (Beaudouin et al., 2004) and the Hérault canyons certainly dividing the power of its tributaries. This scheme also explains the difference between the curves of reworked palynomorphs in cores MD99-2349 and MD99-2348/PRGL1-4 for what concerns short-term variations. We therefore suggest a difference of vegetation between the eastern and the western part of the Gulf of Lions, the Rhone drainage basin having less *Picea*, *Abies* and deciduous *Quercus* and more herbs and shrubs (Poaceae, Cyperaceae, *Artemisia* and *Hippophae rhamnoides*).

The significance of pollen signal in terrigenous sediments cannot be interpreted like a signal extracted from hemipelagic sediments or from continental sediments (peat and little lakes) constituting the main source of palynological data in the literature. The high amount of pollen grains of a taxon (here *Picea*, *Abies* or deciduous *Quercus*) cannot be taken as an evidence for a forest. According to studies carried out on present-day sediments of the Gulf of Lions, the most abundant pollen taxa are found close to the river (riparian woodland) and in the southern part of the drainage basin (Beaudouin et al., 2005b; Beaudouin et al., accepted). During the

Glacial, populations of trees could have lived on the emerged shelf of the Gulf of Lions. Faure et al. (2002) suggested that during lowstands, shelves constitute a source of freshwater and would represent "coastal oasis" while continental interior would desiccate. The shelf of the Gulf of Lions, relatively flat and made of clays could have favoured the installation of trees.

5.2. Other evidences for the presence of high latitude populations of trees

According to the long French and Spanish lacustrine sites [Les Echets near Lyon, Bouchet lake (Massif Central) and La Grande Pile (Vosges)] (Fig.1), *Picea* would have been totally absent from France since 30 ky cal. BP (Woillard, 1978; Beaulieu and Reille, 1984, 1992; Reille and Beaulieu, 1988). Its recolonization would have occurred at 4.5 ky cal. BP from eastern Europe through the Alps (Huntley and Birks, 1983). This route was confirmed by phylogenetic studies (Collignon and Favre, 2000; Gugerli, 2001). Nevertheless, Collignon and Favre (2000) also identified a genetically different population of *Picea* living in the Southern Alps while the populations encountered in the northern Alps, Jura and Vosges mountains are similar. Southern populations of *Picea Abies* are particularly well adapted to Mediterranean climatic conditions (i.e. to droughts). Collignon and Favre (2000) combining their phylogenetic data with palynological data hypothesized that these trees would originate from a refugium situated in northern Apennines. However, according to Ravazzi (2002) and Scotti et al. (2000), the population from Southern Alps would be a relict. Therefore, the pollen signal found in the Gulf of Lions is not surprising: *Picea* was present at relatively high latitudes from at least 30 ky cal. BP and through the LGM. The results found in the present study suggest that their area restricted later (i.e between ca. 16 to 14.5 cal. BP). However, it is not possible to deduce if the population of *Picea* of the Gulf of Lions contributed genetically to the southeastern present-day relict. In fact, the absence of pollen from *Picea* in lacustrine sequences is due to the fact that they record a local vegetation and to the fact that *Picea* pollen grains are heavy and do not spread regionally (Triat-Laval, 1978).

The history of *Abies* was a matter of debate for several years in particular in the Pyrenees (Jalut et al., 1982; Huntley and Birks, 1983; Beaulieu and Reille, 1984; Reille, 1991; Reille and Lowe, 1993). Terhürne-Berson et al. (2004) recently clarified its history. They found evidences for an important refugium of *Abies* in the Pyrenean Mountains as well as in northwestern Italy from macrorests and pollen data. In detail, the Pyrenean refugium is not documented by the Spanish low altitude site of Banyoles (Pérez-Obiol and Julià, 1994) as first suggested by Terhürne-Berson et al. (2004) but instead the site of La Borde situated northward at 1660 m (Reille, 1990; Terhürne-Berson, pers.com). *Abies* was present in Greece and in Italy from the Glacial and during the Late-Glacial (Tzedakis, 1993; Tzedakis et al., 2002). It started to spread in France since 9 to 8.5 ky cal. BP in the Alps and in the Pyrenees and finally reached the Massif Central at ca. 5.5 ky cal. BP. The populations of the Massif Central and the Alps share the same genetic imprint and would originate from southeastern France and/or northern Italy (Terhürne-Berson et al., 2004). The presence of a Pyrenean refugium would explain the genetic singularity of the Pyrenean populations of *Abies alba* compared with the other European populations. The presence of *Abies* in southern France is also attested by marine pollen data from the Gulf of Lions. One again, the absence of *Abies* pollen grains in French and Spanish lacustrine sites can be explained by the fact that this pollen cannot be transported very far (Triat-Laval, 1978).

The European history of deciduous *Quercus* is now considered to be well constrained. According to the most recent study based on the European Pollen Database (Brewer et al., 2002), deciduous *Quercus* might be absent from France, northern Italy and northern Spain during the Last Glacial. The trace of pollen found in these countries would be an echo of southern refugia situated in southern Spain, southern Italy, southern Balkan Peninsula and Black Sea. Deciduous *Quercus* spreads from these refugia northwards during the Late

Glacial. It was severely affected by the cooling and the drying of the Younger Dryas (11.5 to 12.5 ky cal. BP). Populations would have persisted in secondary refugia southward to a line from the Pyrenees to the Balkan. Then, deciduous *Quercus* re-expanded from 11.5 ky cal. BP to reach Scandinavia at ca. 6.5 ky cal. BP. The presence of deciduous *Quercus* in plains of southern France during the Last Glacial (as suggested by our data) is a particularly controversial point. Concerning southern France, northern Spain and northern Italy at the LGM and the deglaciation, available sites of the European Pollen database are scarce and mostly situated in mountains: in the Pyrenees, they are at least 1600 m-high (except one site situated at 880 m of altitude), in the Massif Central there are at least 1000 m-high and in the Alps they are at least 1900 m-high. Closed lakes record relatively local vegetation compared with marine sediments. Even if these pollen grains are transported from plains to higher altitudes in open environments, the absence of pollen grains of deciduous *Quercus* at high altitudes does not mean that the tree was not present in plains. The site of Banyoles is the only one to be situated in plains at 173 m of altitude (Pérez-Obiol and Julià, 1994). It contains a small amount of pollen of deciduous *Quercus* at ca. 27 ky BP. Then, pollen of deciduous *Quercus* regularly but not frequently occur (15 occurrences are recorded in 27 spectra at a constant pollen concentration). The frequency starts to increase before 15 ky cal. BP (11 occurrences are recorded in 12 spectra) but may be correlated to the general decrease in pollen fluxes. This small amount of pollen may be an echo of regional refugia. Phylogenetic studies (Petit et al., 2002) identified the three refugia (Balkan Peninsula, Italy and Spain). But, they also evidenced a genetically different population of trees spread on the western side of Spain. They suggest that it could originate from a refugium situated in the Ebro Valley i.e. a few hundred km southward to Banyoles. Our data suggesting the presence of deciduous *Quercus* in plains of southern France up to ca. 16 ky cal. BP is not in contradiction with such a high latitude refugium. However, the population of southern France was certainly very fragile according to the low amount of its pollen in the sediments. It was not present in the Rhone drainage basin during the deglaciation (from at least 14.5 ky cal. BP). The increase of deciduous *Quercus* in the Rhone drainage basin begins between 11 and 10.7 ky cal. BP corresponding to the second expansion of deciduous *Quercus* (Brewer et al., 2002) linked to the warming of the Holocene. This increase of pollen abundances in the Gulf of Lions is also synchronous with the increase of pollen abundances in northwestern Spain.

The Late-Glacial history of *Picea*, *Abies* and deciduous *Quercus* in plains is still difficult to reconstruct from our marine data, due to the presence of hiatuses and to the weak thickness of the Holocene recorded in the studied sites. In the Rhone drainage basin, the pollen of *Pinus*, *Betula*, Cupressaceae, *Hippophae rhamnoides* and herbs constitute the main part of the pollen signal during the Late-Glacial (Triat-Laval, 1978) confirming the signal of core MD99-2352. The charcoal analyses of caves from the plain of Roussillon show the local presence of *Pinus sylvestris* and Juniperus but neither *Abies* nor *Picea* at ca. 12.5 ky cal. BP (Heinz and Thiebault, 1998). Deciduous *Quercus* could have been present. It seems that *Abies*, *Picea* and deciduous *Quercus* also disappeared from the Pyreneo-Languedocian river drainage basins during the deglaciation. But this hypothesis has to be tested.

The existence of southern France relicts during the Last Glacial Maximum is also attested for another mesophilous tree, i.e. *Fagus sylvatica*, (Magri et al., 2006) while its echo is not well-recorded in cores from the Gulf of Lions. This could be due to the low density of the population or to its situation, i.e. far from rivers. The fact that these populations of trees didn’t spread during the deglaciation is in favour of the existence of relicts rather than refugia s.s. A refugium is considered in our point of view as a population which spreads out of its area while a relict does not spread even if it can survive. The data from the Gulf of Lions are therefore in favour of the first model for what concerns the location of refugia (i.e. situated in southern Mediterranean peninsula) and in favour of Tzedakis (2004) for what concerns the northern tree limit of southern France during the Last Glacial Maximum.

It is worth noting that the ultimate northern relicts attested by phylogenetic studies (i.e. in north-eastern Spain and south-eastern France) even if going through rapid climatic deteriorations, didn't expand during the climatic amelioration of the post-glacial while populations from Southern Spain, Italy, Balkan and Eastern Europe started to spread. Their non-expansion could be linked to their physiology and/or an effect of competition with other trees like *Pinus*. The impact of mammals (i.e. grazing) is also a factor to take into account. The ground competition of seeds with other plants is also particularly important for what concerns colonization. But, the spatial colonization of several taxa competing in a context of climate change is not yet understood. The study of cores situated in front of the Pyreneo-languedocian Rivers, northern Spain margin, eastern part of the Gulf of Lions and covering the late-glacial and the Holocene would help to clarify this point.

5.3. Climatic implications

MIS 2 climate is known to be less variable than the MIS 3's even if millennial-scale fluctuations still occur. Therefore, it is considered as almost constant during the LGM and generally treated as such in a time-window ranging from 24 to 19 ky cal. BP (i.e. 18±2 ky 14C BP) (e.g. Elenga et al. 2000). However, the apparent climatic stability of the LGM is purely relative compared to the high variability of MIS 3. In fact, the variability of the δ18O recorded in GRIP ice-core is higher than the 8.2 ky event which had an effect on vegetation dynamics (Alley and Ágústsdóttir, 2005). Recent studies documented the effect of short-climatic changes from ca. 30 ky to 16 ky cal. BP on the western European climate (Chondrigianni et al., 2004) and vegetation (Combourieu Nebout et al., 2002; Roucoux et al., 2005). The data from the Gulf of Lions also suggest a high variability of climatic parameters during the LGM. The response of the vegetation follows the same pattern as in western Iberia although its composition differs. In the Gulf of Lions, cold and arid episodes (including Heinrich events) are characterized by the decrease of *Abies*, *Picea* and deciduous *Quercus* and the increase of *Artemisia*. These trees were probably at the limit of their tolerance in terms of temperature and precipitations during the Glacial. During the most severe event (from 28 to 26 ky cal. BP) they may have disappeared from the area (less than 5% of their pollen is found in the sediment) whereas the Cupressaceae were more abundant. The latter are actually more tolerant to low temperatures and low Growing Degree Day values (Laurent et al., 2004). The response of vegetation in the Gulf of Lions supports the hypothesis of strengthened cold and arid winds in the region during Heinrich events maybe due to the strengthening of the Scandinavian Polar Highs (Cacho et al., 2000; Moreno et al., 2005; Sánchez-Goñi et al., 2002).

6. Conclusions

Sediments of the Gulf of Lions suggest the presence of *Pinus*, Cupressaceae, Betula, *Abies*, *Picea* and also deciduous *Quercus* in plains. *Abies*, *Picea* and deciduous *Quercus* would have more certainly been located in the drainage basins of the Pyreneo-Languedocian Rivers. A relict of trees in the Gulf of Lions is strongly probable as other studies, like phylogenetics combined with pollen data suggested the presence of relicts of *Picea* in South-Eastern France (Ravazzi; 2002), *Abies* in the Pyrenees (Terhürne-Berson et al., 2004) and deciduous *Quercus* in Northern Spain (Petit et al., 2002). We can't affirm that the populations of *Abies*, *Picea* and deciduous *Quercus* in the Gulf of Lions were still genetically linked to these relicts during the LGM. These certainly fragile populations were very sensitive to short climatic events (i.e. Heinrich events or not) and may have disappeared from the Gulf of Lions during the Late

Glacial. The presence of trees at such high latitudes during the late MIS 3 and the LGM may explain a part of discrepancies between models and the pollen datasets usually used for comparisons (Alfano et al., 2003; Huntley et al., 2003). Finally, the south-eastern France and the north-eastern Spain areas may represent the ultimate and smallest relicts that had descendants. The non-expansion or weak expansion of these trees during the deglaciation could be due to an effect of local competition for resources as climate warmed up. To clarify this point, we suggest studying cores from the late-glacial of south-eastern, south-western France and north-eastern Spain.

Acknowledgements

This work is part of a PhD thesis financed by the French Ministry for Research and Technology. C.B. acknowledges financial support from French Institute of Biodiversity (J.-P. Suc) and the National Science Foundation of China through post-doctoral fellowships. Data for this paper were collected within the EU project PROMESS 1 (Contract n. EVR1-CT-2002-40024) on board R/V Bavenit. Cores MD99-2348, MD99-2349 and MD99-2352 were collected during the IMAGES V cruise of the Marion Dufresne. The crews of both vessels are thanked for their assistance. This work received financial supports from the GDR Marges Program, IFREMER and the French Institute of Biodiversity (J.-P. Suc; S. Fauquette). C. B. thanks Dr. A. Bertini and the Department of Earth Sciences of Florence (Italy) for welcoming during a first year of post-doctorate. C.B. is also grateful to J. Baztan and J.-M. Laurent for improving earlier draft of the manuscript and to G. O'Mullan for improving the English. The authors thank an anonymous reviewer, P.C. Tzedakis and M.-F. Sánchez-Goñi for constructive remarks. The program Pro-CI is available on request to G. Escarguel (gilles.escarguel@univ-lyon1.fr).

References

Acherki, N., 1997. Analyse palynologique de quatre carottes du golfe du Lion. Application à la restitution de la végétation et du climat du midi de la France pendant le dernier cycle climatique et à la stratigraphie marine. Unpublished PhD Thesis, University of Montpellier 2, 157 p.

Alfano, M.J., Barron, E.J., Pollard, D., Huntley, B., Allen, J.R.M., 2003. Comparison of climate model results with European vegetation and permafrost during oxygen isotope stage Three. Quaternary Research 59, 97-107.

Allen, J.R.M., Watts, W.A., Huntley, B., 2000. Weichselian palynostratigraphy, palaeovegetation and palaeoenvironment: the record from Lago Grande di Monticchio, southern Italy. Quaternary International 73-74, 91-110.

Alley, R.B., Ágústsdóttir, A.M., 2005. The 8k event: cause and consequences of a major Holocene abrupt climate change. Quaternary Science Reviews 24, 1123-1149.

Aloïsi, J.-C., Millot, C., Monaco, A., Pauc, H., 1979. Dynamique des suspensions et mécanismes sédimentologiques sur le plateau continental du golfe du Lion. Comptes Rendus de l'Académie des Sciences de Paris D 289(13), 879-882.

Bard, E., Arnold, M., Hamelin, B., Tisnerat-Laborde, N. and Cabioch, G., 1998. Radiocarbon calibration by means of mass spectrometric 230Th/234U and 14C ages of corals. An updated data base including samples from Barbados, Mururoa and Tahiti. Radiocarbon, 40(3), 1085-1092.

Bassetti, M.A., Jouet, G., Berné, S., Taviani, M., Leroux, E., Perez-Belmonte L. 2004. Depositional history of the post-glacial transgression on the outer continental shelf of the Gulf of Lions (Western Mediterranean). American Geophysical Union, Fall Meeting 2004, 1329.

Beaudouin, C., Dennielou, B., Melki, T., Guichard, F., Kallel, N., Berné, S., Huchon, A., 2004. The Late-Quaternary climatic signal according to palynology in a deep-sea turbiditic levee (Rhône Neofan, Gulf of Lions, NW Mediterranean). Sedimentary Geology 172 (1-2), 85-97.

Beaudouin, C., Suc, J.-P., Acherki, N., Courtois, L., Rabineau, M., Aloïsi, J.-C., Sierro, F.J., Oberlin, C., 2005a. Palynology of the Northwestern Mediterranean shelf (Gulf of Lions): First vegetational record for the last climatic cycle. Marine and Petroleum Geology 22, 845-863.

Beaudouin, C., Suc, J.-P., Cambon, G., Touzali, A., Giresse, P., Pont, D., Aloïsi, J.-C., Marsset, T., Cochonat, P., Duzer, D., Ferrier, J., 2005b. Present-day rythmic deposition in the Grand Rhone prodelta (NW Mediterranean) according to high-resolution pollen analyses. Journal of Coastal Research 21 (2), 292-306.

Beaudouin, C., Suc. J.-P., Escarguel, G., Arnaud, M., Charmasson S., Accepted. The significance of pollen signal in present-day marine terrigenous sediments: the example of the Gulf of Lions (western Mediterranean Sea). Geobios.

Beaulieu, J.-L. de, Reille, M., 1984. A long Upper Pleistocene pollen record from Les Echets, near Lyon, France. Boreas 13, 111-132.

Beaulieu, J.-L. de, Reille M., 1992. The last climatic cycle at La Grande Pile (Vosges, France)- A new pollen profile. Quaternary Science Reviews 11, 431-438.

Bennett, K.D., Tzedakis, P.C., Willis, K. J. 1991. Quaternary refugia of North European Trees. Journal of Biogeography 18, 103-115.

Berné, S., Aloïsi, J.C., Baztan, J., Dennielou, B., Droz, L., Dos Reis, T., Lofi, J., Méar, Y., Rabineau, M., 2002. Notice de la carte morpho-bathymétrique du Golfe du Lion. IFREMER et Région Languedoc Roussillon, Brest, pp. 48.

Berné, S., Baton, J.M., Delpeint, A., Dennielou, B., Duval, F., Field, M.E., Lericolais, G., Le Roux, E., Satra, C., Taviani, M., 2003. Deglacial history of the Rhone prodelta from detailed morphology and preliminary stratigraphic data. In: F. Trincardi (Editor), Comdelta. ISMAR-CNR, Bologna, Italy, Aix en Provence, France, pp. 7-8.

Berné, S., Rabineau, M., Flores, J.A., Sierro, F. J., 2004. The impact of Quaternary Global Changes on Strata Formation. Oceanography 17(4), 93-103.

Brewer, S., Cheddadi, R., Beaulieu, J.-L. de, Reille, M. and contributors, 2002. The spread of deciduous *Quercus* throughout Europe since the last glacial period. Forest Ecology and Management 156, 27-48.

Cacho, I., Grimalt, J.O., Canals, M., 2002. Response of the Western Mediterranean Sea to rapid climatic variability during the last 50,000 years: a molecular biomarker approach. Journal of Marine Systems 33-34, 253-272.

Carrión, J.S., 2004. The use of two pollen records from deep-sea cores to frame adaptative evolutionary change for humans: a comment on "Neanderthal extinction and the millennial-scale climate variability of OIS 3" by F. d'Errico and M.F. Sánchez-Goñi, Quaternary Science Reviews, 23(9-10), 1217-1219.

Cheddadi, R., Vendramin, G.G., Litt, T., François, L., Kageyama, M., Lorentz, S., Laurent, J.-M., Beaulieu, J.-L., Sadori, L., Jost, A., Lunt, D., 2006. Imprints of glacial refugia in the modern genetic diversity of *Pinus sylvestris*. Global Change Biology 15(3), 271-282.

Collignon, A.M., Favre, J.M., 2000. Contribution to the Postglacial History at the Western Margin of *Picea Abies*' Natural Area Using RAPD Markers. Annals of Botany 85, 713-722.

Combourieu-Nebout, N., Turon, J.-L., Zahn, R., Capotondi, L., Londeix, L., Pahnke, K., 2002. Enhanced aridity and atmospheric high-pressure stability over the western Mediterranean during the North Atlantic cold events of the past 50 k.y. Geology 30 (10), 863-866.

Cour, P. 1974. Nouvelles techniques de détection des flux et des retombées polliniques: études de la sédimentation des pollens et des spores à la surface du sol. Pollen et Spores 16, 1, 103-141.

Courp, T., Monaco, A., 1990. Sediment dispersal and accumulation on the continental margin of the Gulf of Lions: sedimentary budget. Continental Shelf Research 10 (9-11), 1063-1087.

David, F., Farjanel, G., Jolly, M.-P., 2000. Enregistrement de l'histoire de la vegetation tardiglaciaire et holocène dans un grand lac : le lac d'Annecy (France).

Davis M.B., Shaw R.G. 2001. Range shifts and adaptative responses to Quaternary climate change. Science 292, 673-679.

D'Errico, F., Sánchez-Goñi, M.F., 2003. Neanderthal extinction and the millennial-scale climatic variability of OIS 3. Quaternary Science Reviews 22, 769-788.

Durrieu De Madron, X., Castaing, P., Nyffeler, F., Courp, T., 1999. Slope transport of suspended particulate matter on the Aquitanian margin of the Bay of Biscay. Deep-Sea Research Serie 2, 46, 2003-2027.

Duvail, C., Gorini, C., Lofi, J., Le Strat, P., Clauzon, G., Tadeu dos Reis, A., 2005. Correlation between onshore and offshore Pliocene–Quaternary systems tracts below the Roussillon Basin (eastern Pyrenees, France). Marine and Petroleum Geology 22, 6-7,747-756

Elenga, H., Peyron, O., Bonnefille, R., Jolly, D., Cheddadi, R., Guiot, J., Andrieu, V., Bottema, S., Buchet, G., Beaulieu, J.-L. de, Hamilton, A., Maley, J., Marchant, R., Pérez-Obiol, R., Reille, M., Riollet, G., Scott, L., Straka, H., Taylor, D., Van Campo, E., Vincens, A., Laarif, F., Jonson, H., 2000. Pollen-based biome reconstruction for southern Europe and Africa 18,000 yr BP. Journal of Biogeography 27, 221-234.

Faure, H., Walter, R. C., Grant, D.R., 2002. The coastal oasis: ice age springs on emerged continental shelves. Global and Planetary Change 33, 47-56.

Flores, J.A., Sierro, F.J., Pérez-Folgado, M., Colmenero-Hidalgo, E., Gravalosa, J.M., Bárcena, M.A., Grimalt, J., Berné, S., Dennielou, B., Curtis, J.H., Hodell, D.A., PROMESS 1 Scientific Party members. 2005. Abrupt climatic changes during the last climatic cycles in the Gulf of Lions (Western Mediterranean) revealed by micropaleontological and geochemical tools. European Geosciences Union (EGU). Geophysical Research Abstract, Vienna, pp.02208.

Frignani, M., Courp, T., Cochran, J.K., Hirschberg, D., Vitoria i Codina, L., 2002. Scavenging rates and particle characteristics in and near the Lacaze-Duthiers submarine canyon, northwest Mediterranean. Continental Shelf Research 2, 2175-2190.

Gregory, W.A., Hart, G.F., 1992. Toward a predictive model for the palynological response to sea-level changes. Palaios 7(1), 3-33.

Gugerli, F., Sperisen, C., Büchler, U., Magni, F., Geburek, T., Jeandroz, S., Senn, J., 2001. Haplotype variation in a mitochondrial tandem repeat of Norway spruce (*Picea Abies*) populations suggests a serious founder effect during postglacial re-colonization of the western Alps. Molecular Ecology 10, 1255-1263.

Haberle, S., 1997. Upper Quaternary vegetation and climate history of the Amazon Basin: correlating marine and continental pollen record. In: Flood, R.D., Piper, D.J.W., Klaus, A., Peterson, L.C., (Eds). Proceedings of the Ocean Drilling Program, Scientific Results 155, 381-396.

Heinz, C., Thiébault, S., 1998. Characterization and palaeoecological significance of Archaeological Charcoal Assemblages during Late-Glacial and Post-Glacial phases in southern France. Quaternary Research 50, 56-68.

Heusser, L.E., 1988. Pollen distribution in marine sediments on the continental margin off northern California. Marine Geology 80, 131-147.

Heusser, L.E., Balsam, W.L. 1977. Pollen Distribution in the Northeast Pacific Ocean. Quaternary Research 7, 45-62.

Hewitt, G.M., 1999. Post-glacial re-colonization of European biota. Biological Journal of the Linnean Society 68, 87-112.

Hooghiemstra, H., Lézine A.-M., Leroy, S.A.G., Dupont, L., Marret, F., 2006. Late Quaternary palynology in marine sediments: A synthesis of the understanding of pollen distribution patterns in NW African settings. Quaternary International 148(1), 29-44.

Hughen, K.A., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J.W., Bertrand, C.J.H., Blackwell, P.G., Buck, C.E., Burr, G.S., Cutler, K.B., Damon, P.E., Edwards, R.L., Fairbanks, R.G., Friedrich, M., Guilderson, T.P., Kromer, B., McCormac, F.G., Manning, S.W., Bronk Ramsey, C., Reimer, P.J., Reimer, R.W., Remmele, S., Southon, J.R., Stuiver, M., Talamo, S., Taylor, F.W., van der Plicht, J., Weyhenmeyer, C.E., 2004. Marine radiocarbon age calibration, 26 - 0 ka BP. Radiocarbon 46, 1059-1086.

Huntley, B., Birks, H.B.J., 1983. An Atlas of Past and Present Pollen Maps for Europe:0-13000 years ago. Cambridge University Press, Cambridge, 667 p.

Huntley, B., Alfano, M.J., Allen, J.R.M., Pollard, D., Tzedakis, P.C., Beaulieu de, J.-L., Grüger, E., Watts, B., 2003. European Vegetation during Marine Oxygen Isotope Stage-3. Quaternary Research 59, 195-212.

Jalut, G., Delibrias, G., Dagnac, J., Mardones, M., Bouhours, M., 1982. A palaeoecological approach to the last 21000 years in the Pyrénees : the peat bog of Freychinède (alt. 1350 m, Ariège, South France). Palaeogeography, Palaeoclimatology, Palaeoecology 40, 321-359.

Johnsen, S.J., Dahl-Jehnsen, D., Gunderstrup, N., Steffensen, J.P., Claussen, H.B., Miller, H., Masson-Delmotte, V., Sveinbjornsdottir, A.E., White, J., 2001. Oxygen isotope and palaeotemperature records from six Greenland ice-core stations: Camp Century, Dye-3, GRIP, GISP2, Renland and NorthGRIP. Journal of Quaternary Science 14, 299-307.

Jouet, G., Berné, S., Rabineau, M., Bassetti, M.A., Bernier, P., Dennielou, B., In press. Shoreface migration at the shelf edge and sea-level changes around the Last Glacial Maximum (Gulf of Lions, NW Mediterranean). Marine Geology.

Konnert, M., Bergmann, F., 1995. The geographical distribution of genetic variation of silver fir (*Abies alba*, Pinaceae) in relation to its migration history. Plant Systematics and Evolution

196, 19-30.

Laurent, J.-M., Bar-Hen, A., François, L., Ghislain, M., Cheddadi, R., 2004. Refining vegetation simulation models: From plant functional types to bioclimatic affinity groups of plants. Journal of Vegetation Science 15, 739-746.

Lebreton, V., Renault-Miskovsky, J., Sémah, A.-M., 2004. La chronologie pollinique de la fin du Pliocène, du Pléistocène et de l'Holocène en Europe. Stations éponymes et historiques ; nouvelles données. In: Sémah, A.-M., Renault-Miskovski, J. (Eds). L'Evolution de la Végétation depuis deux millions d'années. Saint-Etienne, Errance, pp. 30-52.

Lofi, J., Rabineau, M., Gorini, C., Berné, S., Clauzon, G., Clarens, P. de, Dos Reis, T., Mountain, G.S., Ryan, W.B.F., Steckler, M., Fouchet, C., 2003. Plio-Quaternary prograding clinoform wedges of the Western Gulf of Lions continental margin (NW Mediterranean) after the Messinian Salinity Crisis. Marine Geology 198, 289-317.

McGarry, S.F., Caseldine, C., 2004. Speleothem palynology: an undervalued tool in Quaternary studies. Quaternary Science Reviews 23, 2389-2404.

McGlone, M.S., 2001. A late Quaternary pollen record from marine core P69, southeastern north island, New Zealand. New Zealand Journal of Geology and Geophysics 44, 69-77.

Millot, C., 1990. The Gulf of Lions' hydrodynamics. Continental Shelf Research 10(9-11), 885-894.

Millot, C., 1999. Circulation in the Western Mediterranean Sea. Journal of Marine Systems 20, 423-442.

Monaco, A., Durrieu De Madron, X., Radakovitch, O., Heussner, S., Carbonne, J., 1999. Origin and variability of downward biogeochemical fluxes on the Rhone continental margin (NW Mediterrean). Deep-Sea Research Serie 1, 46, 1483-1511.

Moreno, A., Cacho, I., Canals, M., Grimalt, J.O., Sánchez-Goñi, M.F., Shakleton, N., Sierro, F.J., 2005. Links between marine and atmospheric processes oscillating on a millennial time-scale. A multi-proxy study of the last 50,000 yr from the Alboran Sea (Western Mediterranean Sea). Quaternary Science Reviews 24, 1623-1636.

Noirfalise, A., Dahl, E., Ozenda, P., Quézel, P., 1987. Carte de la végétation naturelle des états membres des communautés européennes et du conseil de l'Europe. Office des publications officielles des Communautés européennes, Luxembourg, 2nd edition, 78 pp.

Pérez-Obiol, R., Julià, R., 1994. Climatic Change on the Iberian Peninsula Recorded in a 30,000-yr Pollen Record from Lake Banyoles. Quaternary Research 41, 91-98.

Petit, R.J., Brewer, S., Bordacs, S., Burg, K., Cheddadi, R., Coart, E., Cottrell, J., Csaikl, U.M., Van Dam, B., Deans, J.D., Espinel, S., Fineschi, S., Finkeldey, R., Glaz, I., Goicoechea, P.G., Svejgaard Jensen, J., König, A.O., Lowe, A.J., Flemming Madsen, S., Matyas, G., Munro, R.C., Popescu, F., Slade, D., Tabbener, H., Vries, S. G.M. de, Ziegenhagen, B., Beaulieu, J.-L. de, Kremer, A., 2002. Identification of refugia and post-glacial colonisation routes of European white oaks based on chloroplast DNA and fossil pollen evidence. Forest Ecology and Management 156, 49-74.

Rabineau, M., 2001. Un modèle géométrique et stratigraphique des séquences de dépôts quaternaires sur la marge du golfe du Lion: enregistrement des cycles climatiques de 100 000 ans. Unpublished Thesis, University of Rennes, France, 445 p.

Rabineau, M., Berné, S., Aslanian, D., Olivet, J.-C., Joseph, P., Guillocheau, F., Bourillet, J.-F., Ledrezen, E., Granjon, A., 2005. Sedimentary processes in the Gulf of Lion: A record of 100,000 years climatic cycles. Marine and Petroleum Geology 22(6-7), 775-804.

Ravazzi, C., 2002. Late Quaternary history of spruce in southern Europe. Review of Palaeobotany and Palynology 120, 131-177.

Reille, M., 1991. Quelques exemples de séquences polliniques polluées par de la matière organique intruse: conséquences pour l'histoire de la végétation des Pyrénées (France). Palynosciences 1, 113-138.

Reille, M., Beaulieu, J.-L. de, 1988. History of the Würm and Holocene vegetation in Western Velay (Massif Central, France): a comparison of pollen analysis from three corings at the lac du Bouchet. Review of Palaeobotany and Palynology 54, 233-248.

Reille, M., Lowe, J. J., 1993. A re-evaluation of the vegetation history of the eastern Pyrenees (France) from the end of the last glacial to the present. Quaternary Science Reviews 12, 47-77.

Roucoux, K.H., Abreu de, L., Shakleton, N.J., Tzedakis, P.C., 2005. The response of NW Iberian vegetation to North Atlantic climate oscillations during the last 65 ky. Quaternary Science Reviews 24, 1637-1653.

Roussiez, V., Aloïsi, J.-C., Monaco, A., Ludwig W., 2005. Early muddy deposits along the Gulf of Lions shoreline : A key for a better understanding of land-to-sea transfer of sediment and associated pollutant fluxes. Marine Geology 222-223, 345-358.

Sánchez-Goñi, M.F., Cacho, I., Turon, J.-L., Guiot, J., Sierro, F.J., Peypouquet, J.-P., Grimalt, J.O., Shackleton, N.J., 2002. Synchroneity between marine and terrestrial responses to millennial scale climatic variability during the last glacial period in the Mediterranean region. Climate Dynamics 19, 95-105.

Scotti, I., Vendramin, G.C., Matteotti, L.S., Scarponi, C., Sari-Gorla, M., Binelli, G., 2000. Postglacial recolonization routes for *Picea Abies* K. in Italy as suggested by the analysis of sequence-characterized amplified region (SCAR) markers. Molecular Ecology 9, 699-708.

Stewart, J.R., 2003. Comment on “Buffered Tree Population Changes in a Quaternary Refugium: Evolutionary Implications”. Science 299, 825a.

Sokal, R. R., Rohlf, F. J., 1995. Biometry (third edition). Freeman and Co., New York 887 p.

Stewart, J. R., Lister A., M., 2001. Cryptic northern refugia and the origin of the modern biota. Trends in Ecology and Evolution 16(11), 608-613.

Stuiver, M., Reimer, P. J., Reimer, R. W., 2005. CALIB 5.0. http://radiocarbon.pa.qub.ac.uk/calib/

Sun, X., Li, X., Beug, H.-J., 1999. Pollen distribution in hemipelagic surface sediments of the South China Sea and its relation to modern vegetation distribution. Marine Geology 156, 211-226.

Taberlet, P., Cheddadi, R., 2002. Quaternary Refugia and Persistence of Biodiversity. Science 297, 2009-2010.

Terhürne-Berson, R., Litt, T., Cheddadi, R., 2004. The spread of *Abies* throughout Europe since the last glacial period: combined macrofossil and pollen data. Vegetation History and Archaeobotany 13, 257-268.

Triat-Laval, H., 1978. Contribution pollenanalytique à l'histoire tardiglaciaire de la végétation de la basse vallée du Rhône. Unpublished Thesis, University of Aix-Marseille 3, France, 343 p.

Turon, J.-L., Lézine, A.-M., Denèfle, M., 2003. Land-sea correlations for the last glaciation inferred from a pollen and dinocyst record from the Portuguese margin. Quaternary Research 59, 88-96.

Tzedakis, C., 1993. Long-term tree populations in northwest Greese through multiple Quaternary climatic cycles. Nature, 364, 437-440.

Tzedakis, P.C., 2004. The Balkans as prime glacial refugial territory of European temperate trees In: Griffiths, H.I., Krystufek, B & Reed, JM (eds). Balkan Biodiversity. Pattern and process in the European hotspot., 49-68, Kluwer, Dordrecht.

Tzedakis, P.C., Lawson, I.T., Frogley, M.R., Hewitt, G.M., Preece, R.C. 2002. Buffered Tree Population Changes in a Quaternary Refugium: Evolutionary Implications. Science 297, 2044-2047.

Tzedakis, P.C., Lawson, I.T., Frogley, M.R., Hewitt, G.M., Preece, R.C. 2003. Comment on “Buffered Tree Population Changes in a Quaternary Refugium: Evolutionary Implications”. Science 299, 825b.

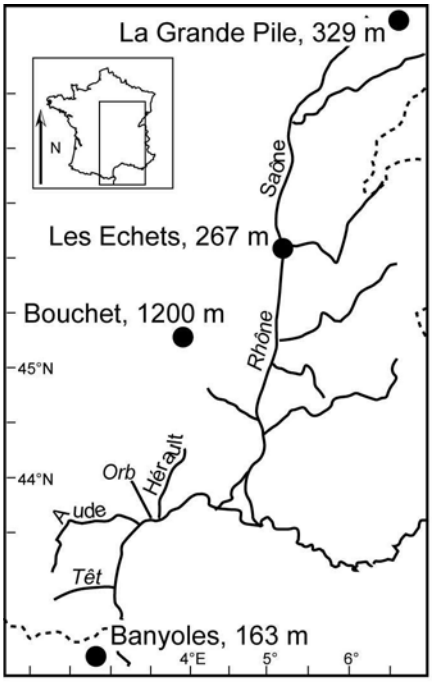
Van der Kaars, S. 2001. Pollen distribution in marine sediments from the south-eastern Indonesian waters. Palaeogeography, Palaeoclimatology, Palaeoecology 171, 341-361.
Węgrzynek, D., Jambers, W., Van Grieken, R., Eisma, D., 1997. Individual particles analysis of western Mediterranean sediments cores, Rhône suspended matter and Sahara aerosols, Investigation of inputs to the sediments. Marine Chemistry 57, 41-53.
Willis, K.J. Van Andel, T.H., 2004. Trees or not trees: The environments of central and eastern Europe during the Last Glaciation. Quaternary Science Reviews 23, 2369-2387.
Woillard, G.M., 1978. Grande Pile Peat Bog: a continuous Pollen Record for the Last 140,000 Years. Quaternary Research 9, 1-21.

Table captions

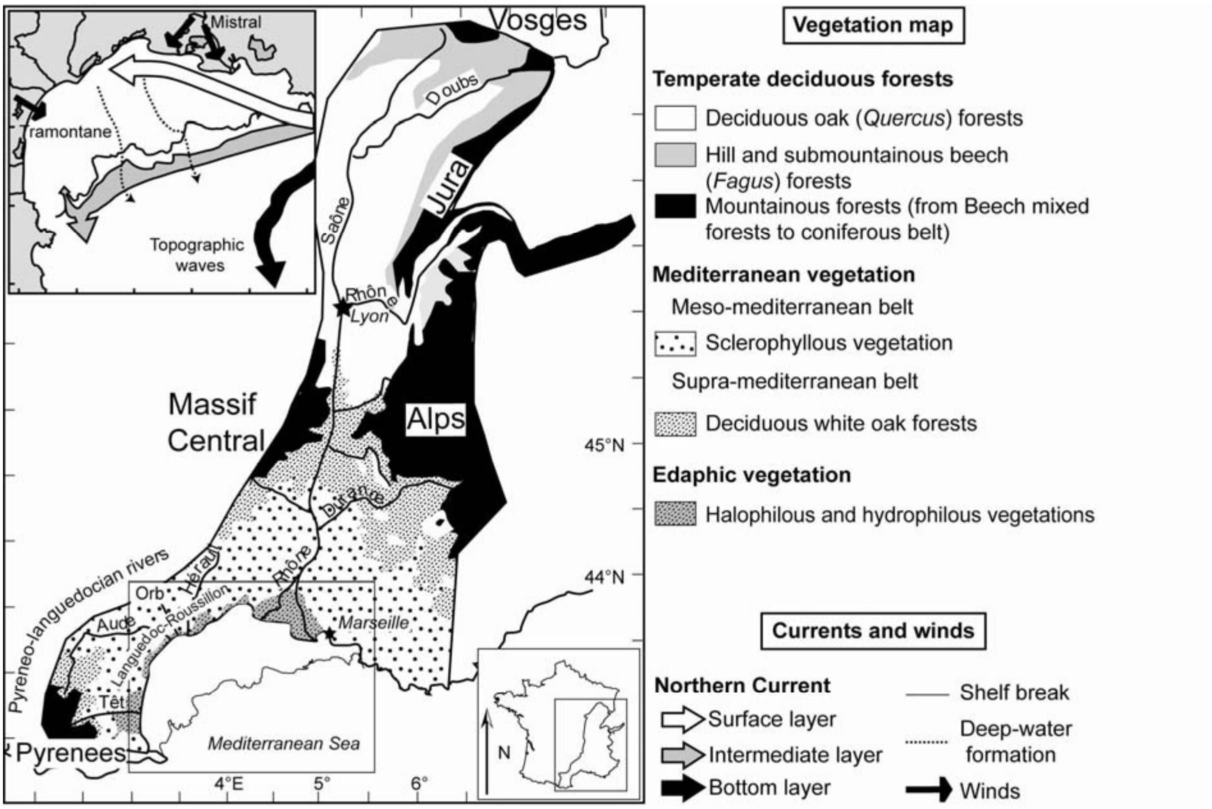
Tabl. 1. Radiocarbon datings made on cores MD99-2349, MD99-2348 and MD99-2352.

Figures captions

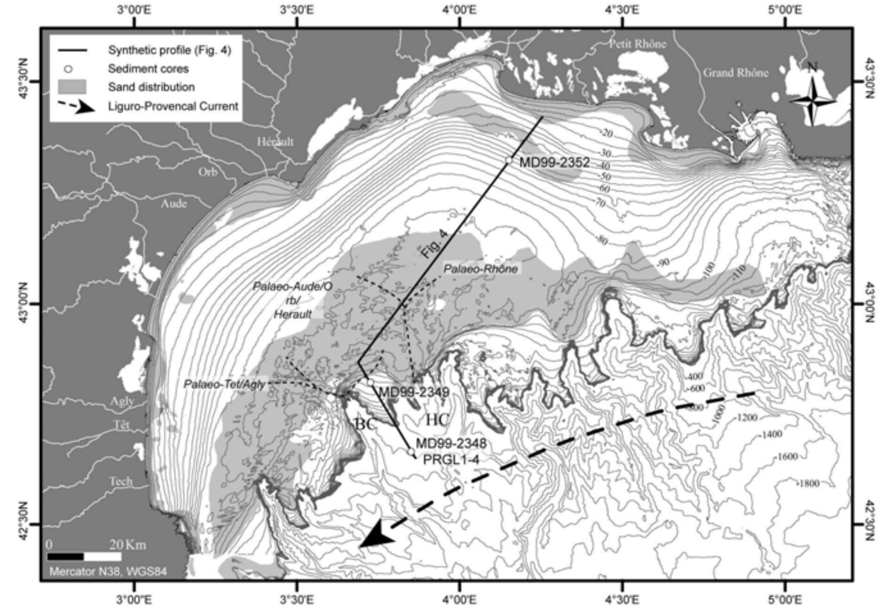
Fig. 1. Location of lacustrine French and Spanish sites covering the last 30 ky and generally used for vegetation reconstructions.
Fig.2. Simplified vegetation map of the present-day vegetation and main currents and winds in the Gulf of Lions (from Noirfalise et al., 1987 and Millot, 1990).
Fig. 3. Location of studied sites and palaeogeography.
Fig. 4. Interpreted composite line drawing displaying major seismic units of the studied area and location of cores, from Berné et al. (2004) and Jouet et al. (in press).
Fig. 5. Example of different state of conservation of pollen grains in core MD99-2349. a,b, well-preserved pollen grains of *Picea* displaying a well conserved structure; c, reworked pollen grain of Pinaceae recognized by its non-structured appearance.
Fig. 6. Simplified pollen diagram of core MD99-2349 and corresponding seismic units. For each taxon, the grey area delimited by the two continuous curves corresponds to the 95% confidence belt associated to the observed (sampled) percentage of pollen. Black and white stars correspond to levels dated by radiocarbon and seismic correlations respectively. Thick lines correspond to the seismic limits. Wavy lines correspond to discontinuities visible on the sediment.
Fig. 7. Simplified pollen diagram of core MD99-2348/PRGL1-4 and corresponding seismic units. For each taxon, the grey area delimited by the two continuous curves corresponds to the 95% confidence belt associated to the observed (sampled) percentage of pollen. Black stars correspond to levels dated by radiocarbon. Thick lines correspond to the seismic limits.
Fig. 8. Simplified pollen diagram of core MD99-2352 and corresponding seismic units. For each taxon, the grey area delimited by the two continuous curves corresponds to the 95% confidence belt associated to the observed (sampled) percentage of pollen. Black stars correspond to levels dated by radiocarbon. Wavy lines correspond to discontinuities visible on the sediment.
Fig. 9. Synthetic view of the correlations between palynological signals of cores and isotopic records from GRIP ice-core.



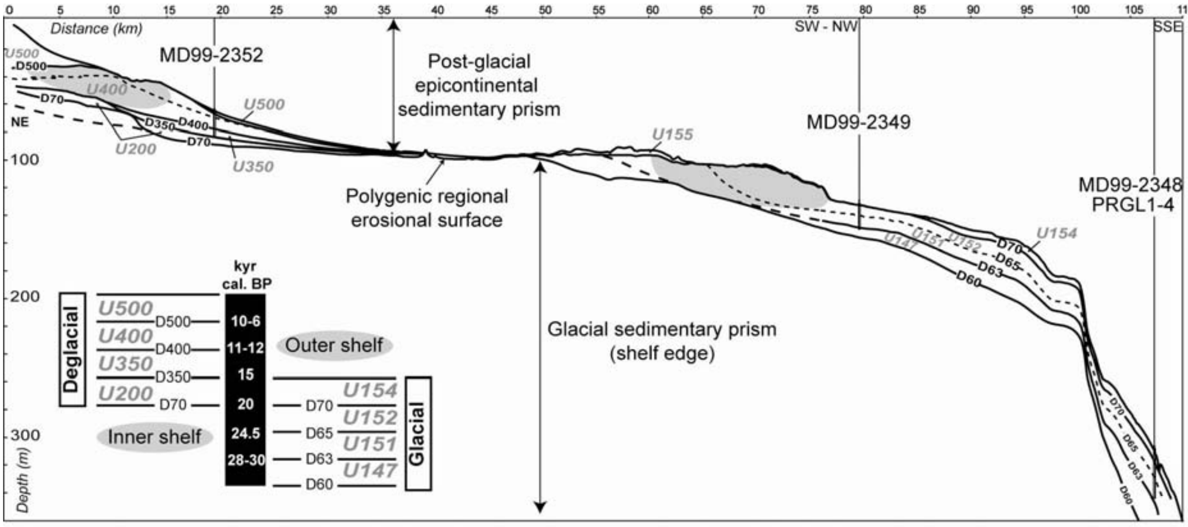
Beaudouin et al., Fig.1



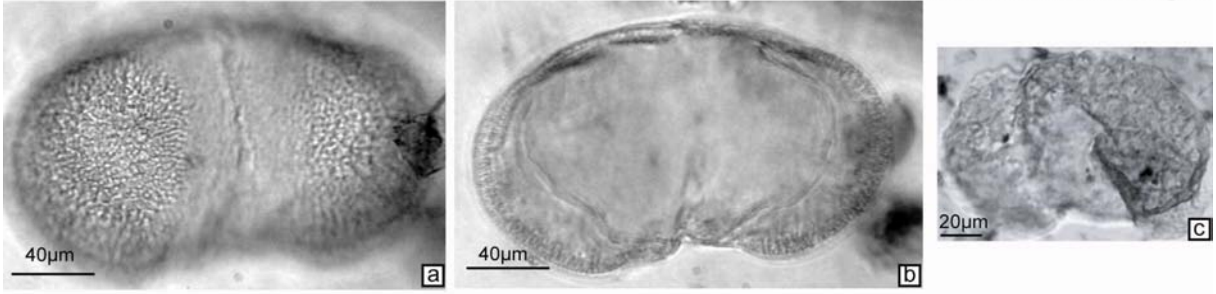
Beaudouin et al. Fig. 2



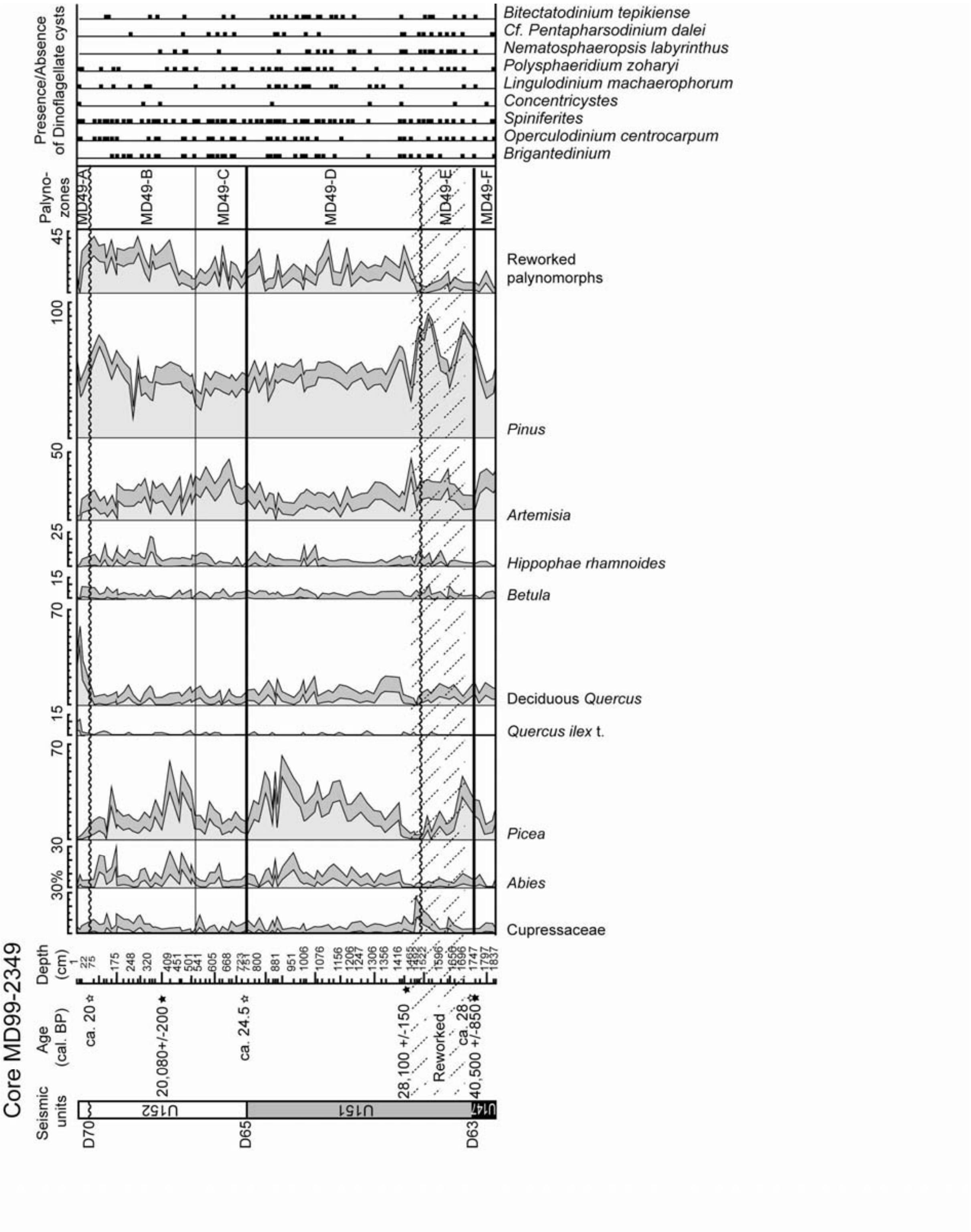
Beaudouin et al., Fig. 3



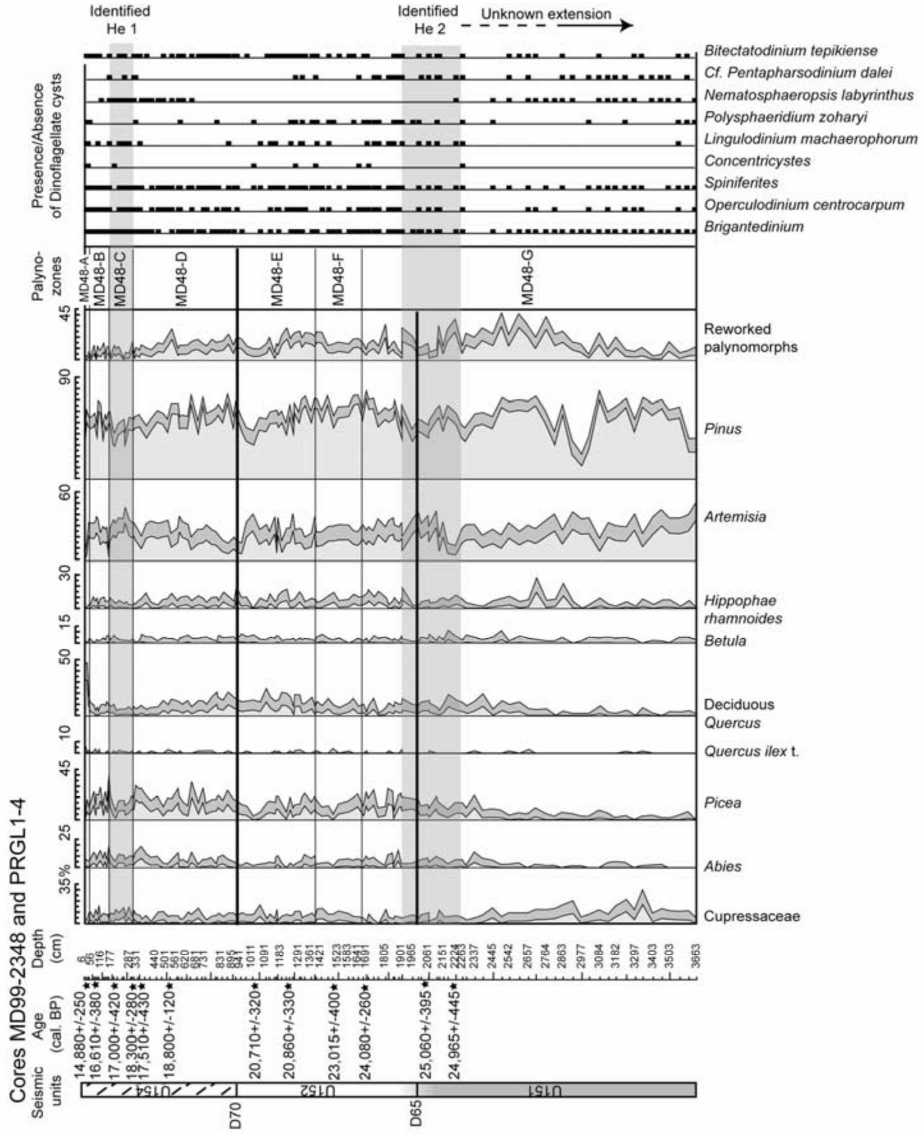
Beaudouin et al., Fig. 4



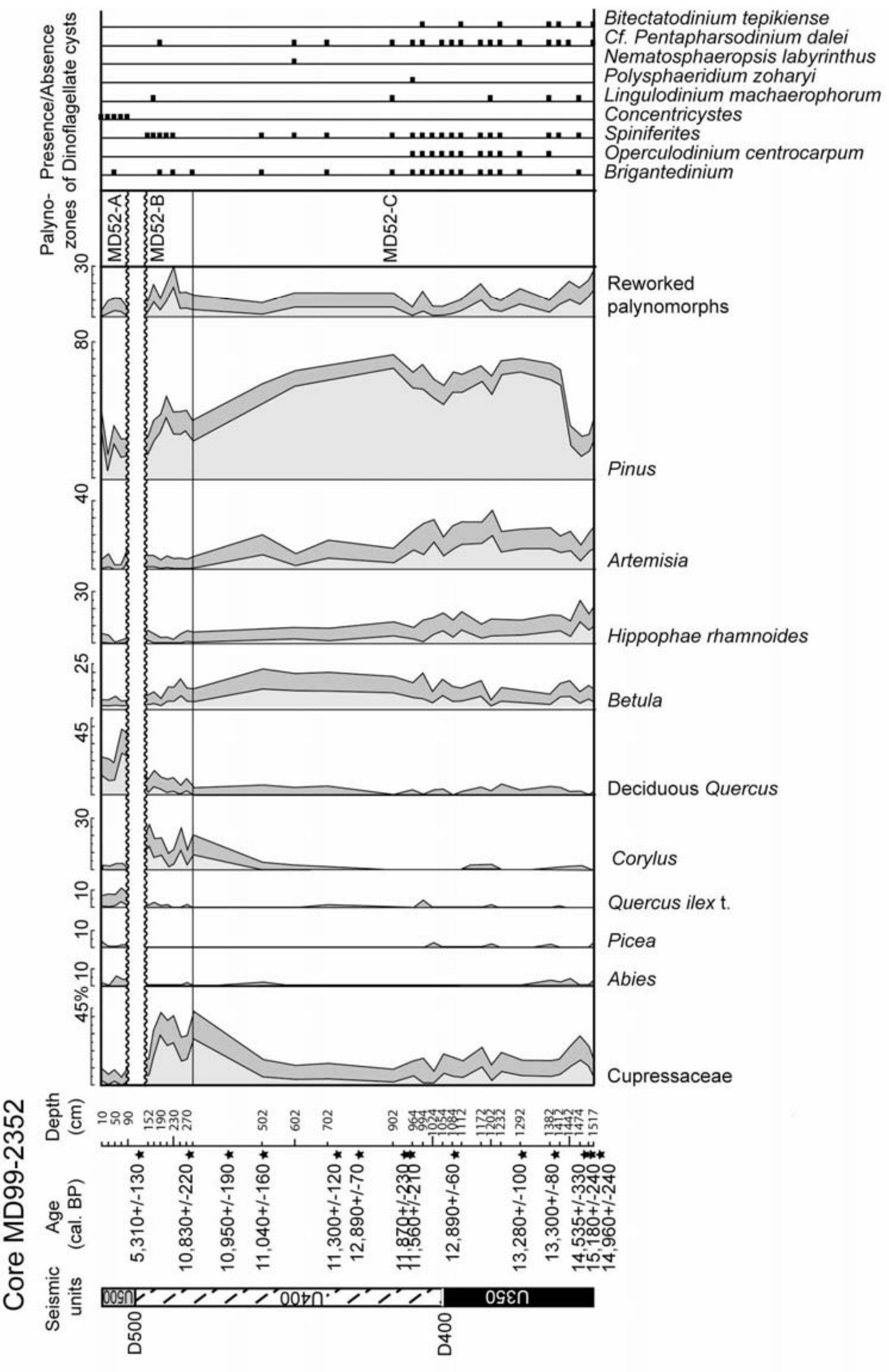
Beaudouin et al., Fig. 5



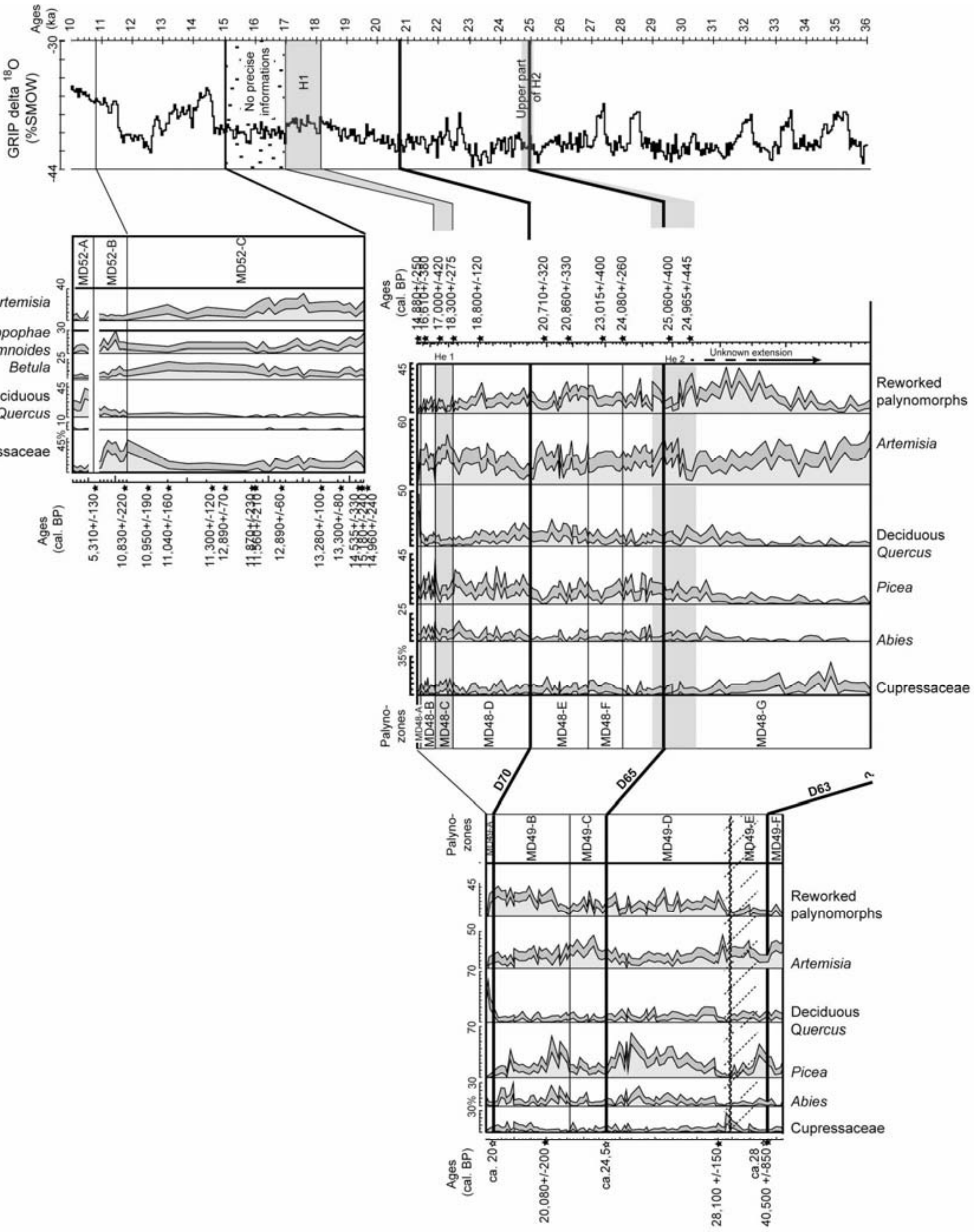
Beaudouin et al., Fig. 6



Beaudouin et al., Fig. 7



Beaudouin et al., Fig. 8



Beaudouin et al., Fig. 9

Core	**Depth (cm)**	**Material**	**C14 Ages**	**Cal Ages (Year BP)**		**Relative Area**	**Technic**	**Reference**	**Taken into account**
				Lower limit	**Upper Limit**				Yes
MD99-2348	25	Foraminifers	13020 ± 40	14633	15125	1	AMS	Géochron	Yes
MD99-2348	80	Foraminifers	14350 ± 60	16230	16993	1	AMS	CAMS108010	Yes
MD99-2348	190	Foraminifers	14640 ± 60	16578	17414	1	AMS	CAMS108011	Yes
MD99-2348	300	Foraminifers	15380 ± 70	18025	18576	1	AMS	CAMS108012	No
MD99-2348	360	Foraminifers	14960 ± 70	17083	17937	1	AMS	CAMS108013	Yes
MD99-2348	518	Foraminifers	15890 ± 70	18678	18915	1	AMS	CAMS108014	Yes
MD99-2348	1018	Foraminifers	17910 ± 80	20395	21030	1	AMS	CAMS108015	Yes
MD99-2348	1231	Foraminifers	18060 ± 60	20535	21187	1	AMS	Géochron	Yes
MD99-2348	1498	Foraminifers	19750 ± 90	22613	23417	1	AMS	CAMS108016	Yes
MD99-2348	1680	Bulk forams >200 µm	20500 ± 80	23819	24346	1	AMS	LLNL-L397-77703	Yes
MD99-2348	2058	Foraminifers	21240 ± 110	24665	25455	1	AMS	CAMS108017	Yes
MD99-2348	2218	Foraminifers	21150 ± 120	24520	25410	1	AMS	CAMS108018	Yes
MD99-2349	397	Benthic Foraminifera and Ostracod valves	17340 ± 90	19880	20285	1	AMS	Poz-7851	Yes
MD99-2349	533-538	Shells (*Cyprina* sp.)	19635 ± 150	22528	23071	1	Classic	LY-11900	No
MD99-2349	902	Shells (*Cyclichna* sp.)	20,570 ± 100	23868	24433	1	AMS	Poz-7852	No
MD99-2349	1074	Shells (*Varicorbula Gibba*)	21150 ± 70	24709	25013	0.72	AMS	LLNL-CAMS-96163	No
MD99-2349	1218	Shell (*Nucula* sp.)	21190 ± 100	24617	25414	1	AMS	Poz-7854	No
MD99-2349	1458	Shells (*Chlamys islandica*)	19910 ± 480	22597	23824	1	Classic	LY-11899	No
MD99-2349	1441	Microshells	24300± 140	27930	28250	-	AMS	Poz-14903	Yes
MD99-2349	1600	Shells	52400 ± 2900	-	-	-	AMS	LLNL-CAMS-96164	No
MD99-2349	1736-1738	Foraminifers	35900 ± 800	40120	41840	-	AMS	LLNL-CAMS-96165	Yes
MD99-2349	1760	Shells	>54000	-	-	-	AMS	LLNL-CAMS-96166	No
MD99-2352	123	Acanthocardia echinata	4 955 ± 45	5173	5443	0.98	Classic	LLNL-95846	Yes
MD99-2352	286	Nucula sp.(nucleus)	9890 ± 60	10606	11056	1	AMS	Poz-3842	Yes
MD99-2352	401-403	Turitella communis	10000 ± 50	10761	11136	1	AMS	Poz-3843	Yes

MD99-2352	519-521	small benthic forams (>63 µm) + few bivalvia, gastropods and ostracods	10070 ± 60	10880	11200	0.96	AMS	Poz-3844	Yes
MD99-2352	731	Turitella communis	10310 ± 50	11178	11422	0.93	AMS	Poz-3845	Yes
MD99-2352	799-801	mixed benthic forams (>63 µm) + few bivalvia, gastropods and ostracods	11320 ± 60	12817	12955	1	AMS	Poz-3846	Yes
MD99-2352	928-932	Corbula gibba	10590 ± 50	11635	12097	1	AMS	Poz-3848	No
MD99-2352	948	Corbula gibba	10 475 ± 40	11351	11766	0.93	Classic	LLNL-95847	Yes
MD99-2352	1105-1107	mixed benthic forams (>63 µm) + few bivalvia, gastropods and ostracods	11340 ± 50	12832	12953	1	AMS	Poz-3849	Yes
MD99-2352	1305-1307	Ammonia beccarii or Elphidium crispum + few bivalvia	11820 ± 50	13184	13383	1	AMS	Poz-3850	Yes
MD99-2352	1393	Corbula gibba	11 840 ± 40	13212	13381	1	Classic	LLNL-95848	Yes
MD99-2352	1494	Turitella communis.	12 855 ± 40	14205	14865	1	Classic	LLNL-95849	Yes
MD99-2352	1505	Mya truncata	13 245 ± 40	14945	15417	1	Classic	LLNL-95850	Yes
MD99-2352	1534-1536	Mytilus sp.	13 090 ± 50	14716	15202	1	Classic	LLNL-98908	Yes

Tabl. 1