

Progress in palynology of the Gelasian-Calabrian stages in Europe: ten messages

Progrès dans la palynologie des étages Gélasien et Calabrien en Europe : dix messages

Suzanne A.G. Leroy

*Institute for the Environment, Brunel University, Uxbridge UB8 3PH, West London, UK**E-mail address:* suzanne.leroy@brunel.ac.uk (S.A.G. Leroy)

Fax +44-1895-269736

Abstract

Europe has at present the most extensive network of palynological sites covering the Late Pliocene and the Early Pleistocene or roughly the Gelasian-Calabrian Stages. This paper covers ten points of recent progress in the palynology of this time period: 1) the contribution of palynology to truly global stratigraphy, 2) the existence and steps of vegetation succession after a glacial period, 3) the causes for the disappearance from Europe of some taxa, 4) the location and the types of vegetation refugia, 5) the causes of the low arboreal pollen representation in glacial times, 6) the extent of extreme glacial conditions, 7) the input of long marine records to short terrestrial ones, 8-9) cyclopalynostratigraphy for wiggle matching dating and duration estimations and, finally, 10) short glacial periods and long interglacial ones in an obliquity-forced climate.

Résumé

L'Europe a pour l'instant le réseau le plus étendu de sites palynologiques couvrant le Pliocène et le Pléistocène Ancien ou bien encore les étages Gélasien-Calabrien. Cette publication présente en 10 points des progrès récents de la palynologie pour cette période : 1) la contribution de la palynologie à une stratigraphie vraiment globale, 2) l'existence même et les étapes des successions de la végétation après une période glaciaire, 3) les causes de la disparition en Europe de quelques taxons, 4) la localisation et les types de refuges de la végétation, 5) les causes de la faible représentation du pollen d'arbres, 6) l'étendue des conditions glaciaires extrêmes, 7) l'influence des longs enregistrements marins sur les enregistrements terrestres courts, 8-9) la cyclopalynostratigraphie utilisée pour la datation par appariement des ondulations des courbes et pour l'estimation des durées, et finalement en 10) les périodes glaciaires courtes et interglaciaires longues sous un climat forcé par l'obliquité.

Keywords: Palynology; Vegetation; Europe; Lakes; Pliocene; Pleistocene; Gelasian; Calabrian*Mots clés :* Palynologie ; Végétation ; Europe ; Lacs ; Pliocène ; Pléistocène ; Gélasien ; Calabrien

European Late Pliocene-Early Pleistocene (2.58 to 0.78 Ma), roughly equivalent to the Gelasian and Calabrian Stages (GCS, 2.58 to 0.99 Ma), palynological sequences are a rich source of palaeoenvironmental information (Figs. 1 and 2). The focal point of sites of that age was located in western central Europe in the 1950s and 1960s and it progressively moved to the south of Europe after the 1980s. The interpretation of palynological records evolved during that half century of research. Two main factors have played a part: a change of mindset especially under the push of multiproxy high-resolution investigations usually applied to the last glacial-interglacial period and progress in marine drilling technology providing first-quality sequences covering the last million years continuously.

The Gelasian and the Calabrian Stages (Figs. 1 and 2) are examined together because they have more in common with each other than with the preceding stage, the Piacenzian, and the following Stage, the Ionian. The scientific attraction of this Late Pliocene-Early Pleistocene period has recently further increased, as the earliest arrival of hominids in Europe has been pushed back to the Early Pleistocene in sites such as Orce and Atapuerca Gran Dolina in Spain, Vallonnet and Pont-de-Lavaud in France and Campo Grande di Ceprano in Italy (Falguères, 2003). Terrestrial, especially lake, sediments are a crucial archive for understanding the environment where hominids lived and evolved.

However, it is only in some rare cases that it is possible to attribute absolute ages to sites of that time. Marine sequences are often better dated but they do not record as well vegetation on the continent as additional taphonomical factors affect their pollen spectra (Hooghiemstra et al., 2006). Pollen diagrams from marine cores are mostly concentrated in the Mediterranean basin with very few sequences in the North Sea and none in the European Atlantic Ocean (Fig. 1 and 2). Establishing durations of terrestrial sequences in the absence of a robust chronology has depended for a long time on the correlation of these sequences to local and then regional palynostratigraphic schemes, relying on the disappearance of palynotaxa, and too often without a multiproxy collaboration, especially between palynologists and sedimentologists. One of the palynostratigraphies that has been followed most extensively throughout Europe for more than 50 years is that of Zagwijn and co-workers in the Rhine and Meuse estuaries (Zagwijn, 1989, 1992; de Jong, 1988). It was one of the first and covered apparently a large part of the last 3 Ma. For a long time, other European regional

studies made extensive attempts to correlate to it (Lona, 1971; Szafer, 1954; Walker, 2005; Suc and Zagwijn, 2003; Zagwijn and Suc, 1984). In the absence of a good alternative, it became the dominant ideology. However most of the Dutch pollen diagrams were derived from short sections, often with no other information besides the presence or absence of some pollen taxa considered as chronological markers. Drees (2005) offers a critical review of this local palynostratigraphy on the Dutch side of the basin and Kemna (2005) for the German side.

This paper will present ten aspects of the Gelasian-Calabrian palynology based on some new ideas structured as a review of recent progress. In addition, we are going to use some criticism of the Dutch palynostratigraphy (and derived information on vegetation and climate) as a base for discussion.

1. The contribution of palynology to some stratigraphical choices

After a brief summary of the present state of the GCS stratigraphy, this section examines the contribution of palynology to the ongoing discussion on boundaries and names for the period around the beginning of the Quaternary.

There has been and still is a lot of confusion about where the Quaternary and the Pleistocene start and it does not seem that this problem will be easily resolved in the near future. Hence any serious paper dealing with that time period has the onerous task of explaining which definition is being used. Officially the Pliocene-Pleistocene boundary (PPB) is located at the sapropel layer 'e' of the Vrica stratotype, Italy, near the top of Olduvai chron (1.67 Ma) (Fig. 2). This is the limit ratified in 1983 by the International Commission on Stratigraphy (ICS). The age has recently been updated by astrochronology and cyclostratigraphy and now is 1.79 Ma. The age of the sapropel 'e' has become now with the new chronology: 1.806 Ma. However the first glacial periods with open vegetation in Europe started at 2.58 or 2.6 Ma (pre-cyclostratigraphy: 2.4 Ma), at the Gauss-Matuyama transition, with the three typical marine isotopic stages (MIS) 100, 98, and 96 (Fig. 2) (Shackleton, 1995). The preparation of these cold MIS is already seen in MIS 104 and 102. Often this is taken as the informal base of the Quaternary. The creation of a special name for the period between the unofficial base of the Quaternary and the official base of the Pleistocene, or from 2.6 to 1.8 Ma (the newly created Gelasian, see below), makes sense as this period has several unique features in terms of climate, vegetation, fauna, and human evolution and migration. Several authors have already made such propositions in the past: e.g. Menke and Behre (1973) proposed the Cenocene which lasted from c. 2.5 Ma (Ekholt cold stage with probable almost Arctic conditions) to c. 1 Ma (Osterholz interglacial) in an attempt to distinguish these climatic fluctuations from later, more glacial, ones.

The subdivisions in stages of the Late Pliocene and the Early Pleistocene are the following:

- the Gelasian Stage = Upper Pliocene, starts at MIS 103, 20 ka above Gauss/Matuyama boundary, astrochronological age of 2.589 Ma, ratified in 1996 (Rio et al., 1998) (Fig. 2);
- the Calabrian Stage = from the base of the Pleistocene, at MIS 65, only 25 ka below top of Olduvai Chron, astrochronological age 1.795 Ma, until the top of Jaramillo sub-chron, at MIS 25, at about 0.99 Ma. This is a more complex Global Boundary Stratotype Section and Point than the preceding one as only the base of the Pleistocene has been ratified in 1985 (Aguirre and Pasini, 1985) (Fig. 2), but not that of the Quaternary.

At recent INQUA (International Union for Quaternary Research) congresses, it was agreed to consider changing again the PPB and put it back at 2.58 Ma. In addition, other drastic changes are taking place pushed by the Neogene stratigraphic commission. The Neogene system could be modified to last until the present (Pillans, 2004). This would decouple again the Pleistocene base and the Quaternary base. It is likely that the fate of the Quaternary in this new thinking would be to disappear altogether (Pillans, 2004).

In 1996 the INQUA and ICS jointly proposed that the Early-Middle boundary of the Pleistocene should be at the Brunhes-Matuyama magnetic reversal boundary, at 0.781 ka (Fig. 2) but this has not yet been ratified (Gibbard and van Kolfschoten, 2005).

The period covered by the Gelasian-Calabrian Stages (GCS) is delimited by the two main periods of shift in astronomical forcing: precession to obliquity at the Gauss-Matuyama at 2.6 Ma and obliquity to eccentricity at top of Jaramillo at 0.9 Ma (Fig. 2). The difference between the end of the Early Pleistocene and the end of the Calabrian covers a 200 ka-long period of transition between obliquity and eccentricity forcing.

Palynology can contribute to these stratigraphical aspects at two levels: first in relation to trends, secondly in relation to details within a climatic cycle. Regarding the trends, Suc et al. (1997) present vegetation changes across these important boundaries in various parts of the world. At the Gauss-Matuyama transition, vegetation changes in Europe and N-W Africa show the strongest modifications with the first glacial periods that are expressed by opening of the landscape in Europe and by extension of the Sahara southwards (Fig. 3). In the Crotona pollen diagram covering the PPB, vegetation does not show large changes at the PPB; and in addition cyclic vegetation changes forced by wide-amplitude climatic changes are already detected below. Sufficient sampling and time resolutions can provide excellent data to support the choice of a boundary position, reaching the level of details within a climate cycle. This is complementary to oxygen isotopic data (changes in ocean and ice volume), as pollen represents what is happening on the continent. Therefore the double approach (isotope and pollen) is an absolute requirement to define a valid boundary representing global (land and ocean) changes.

2. Vegetation succession in a GCS glacial-interglacial cycle

No vegetation successions were observed for the Late Pliocene and Early Pleistocene in the Dutch pollen diagrams (de Jong, 1988). For a long time in Middle Europe (especially in the Netherlands), it was believed that there was “no clear succession in the immigration of forest elements” (de Jong, 1988) and that the migration pattern of the early Holocene had no equivalent before 1 Ma ago. We will present examples of vegetation succession in glacial-interglacial cycles of southern and middle Europe in the GCS (and much earlier), and then we analyse the successive steps within a cycle. We provide an example from two successive studies of the PPB stratotype in Italy, the second one having acknowledged the existence of vegetation successions.

2.1. Steps of vegetation successions

When obvious vegetation successions became evident in southern European sites as early as the Gelasian Stage, e.g. in Nogaret in France (Leroy, 1990; Leroy and Seret, 1992; Leroy et al., 1999) and in Croton in Italy (Combourieu-Nebout and Vergnaud-Grazzini, 1991; Combourieu-Nebout, 1993), it became possible to re-analyse middle and northern European sites and to find them there too. We give two examples one in Germany and one in England. In Schleswig-Holstein (northern Germany, hence at a latitude north of The Netherlands), the site of Lieth (Fig. 1) shows several cycles of vegetation succession before 1.7 Ma (Menke, 1975). New analysis of the same data suggests an age at least as old as 2.4 Ma for the first cycle of vegetation succession (Pross and Klotz, 2002). The pollen diagram of the type-site for the Pastonian in East Anglia (c. 1.8 Ma) displays clear and complex steps of vegetation succession as well (West, 1980) (Fig. 1). Shifts of vegetation belts from wetter to drier were reconstructed in N-W Africa in the ODP (Ocean Drilling Programme) Site 658 from 2.6 Ma onwards, but here a combination of more factors is taking place not just vegetation succession in any one spot but also a change in the transport of the pollen grains mostly by changes in the strength of the trade winds (Leroy and Dupont, 1994; Dupont and Leroy, 1995). When going further back in time, complex vegetation successions have also been observed, such as in the site of Ptolemais (Greece) (Fig. 1) during the Early Pliocene (Steenbrink et al., 2003) and at an earlier time in the Messinian, but less clearly (Steenbrink et al., 2000).

Adequate comparisons to the climatic cycles of Late Pliocene-Early Pleistocene sites such as Nogaret (France; Leroy, 1990; Leroy and Seret, 1992; Leroy et al., 1999) and Lefte (Italy; Ravazzi and Rossignol-Strick, 1995) can be made in order to establish typical successive steps of vegetation development (Fig. 4). These steps are: open vegetation (steppe or tundra), dry open woodland, deciduous forest, mixed forest, conifer forest (often *Picea* or *Abies*) reflecting climatic change from dry and cold, to warmer but still dry, to warm and humid, and finally cool and still humid (Leroy and Ravazzi, 1996, 1997) (Fig. 4). Similar cycles in marine sites at lower latitudes have been observed in Semaforo and Vrica (Italy; Combourieu-Nebout, 1993, 1995). The lag of precipitation on temperature was already underlined by Grichuk (1964) and by van der Hammen et al. (1971) making dry and warm interglacial beginnings and cool and wet interglacial ends. Some clear exceptions to this pattern are however found in a series of northern Italian sites where the glacial periods do not correspond to open vegetation but to the development of a coniferous forest (C. Ravazzi, pers. comm.; Bertini, 2001) linked to a decrease of temperature but not of humidity.

Vegetation successions are usually from the end of a glacial period to the end of an interglacial period with no backward successions (Fig. 4). This one-way succession of taxa is also seen in the diagram of the marine record ODP Site 658 (NW Africa: Leroy and Dupont, 1994; Dupont and Leroy, 1995).

2.2. The example of the PPB stratotype

Two successive studies were undertaken at Croton (Italy), the PPB stratotype (Figs. 1 and 2). The results obtained are very different as the second study took place after the Milankovitch cycles became a reality for vegetation reconstruction. This edifying example shows the influence of the time resolution estimated satisfactory at the time of the field sampling. In the first palynological study (Combourieu-Nebout, 1987; Combourieu-Nebout and Vergnaud-Grazzini, 1991), the time resolution was c. 82 samples on > 1 Ma, i.e. a sample every 12 ka; hence Milankovitch cyclicities were missed. In addition a correlation with the Dutch palynostratigraphy was proposed, as was usually done then. Fortunately in the second study (Combourieu-Nebout, 1993), a shorter section of the outcrop was chosen and the time resolution reached this time 78 samples in c. 180 ka, hence a sample every 2.3 ka. This approach finally allowed differentiating Milankovitch cycles as well as detailed steps of vegetation succession within a climatic cycle.

3. The causes of the disappearance of some taxa from Europe

In this section we present some taxa that have disappeared from Europe as known from pollen analysis (with special attention to *Parrotia*) with help from macrofossil identification (such as seeds and leaves); we then review the causes of their disappearance.

Several GCS genera and species are now absent from Europe, but have survived elsewhere (such as *Carya* and *Tsuga* in China and N. America), whereas others seem to have completely disappeared. For example, the three Early Pleistocene lakes of Bòbila Ordis (Spain) contain a range of palynotaxa from plants that have now disappeared from

Europe (*Tsuga*, *Carya*, *Eucommia ulmoides*, *Parrotia persica*, *Parthenocissus*, *Pterocarya fraxinifolia*) or of which some species survive only in very limited areas of southern Europe (*Zelkova abelicea* and *sicula*) (Leroy, 1990; Leroy et al., 1997, 2001; Løvlie and Leroy, 1995). Some detailed leaf and seed macroflora confirm this diversity loss in the GCS; but owing to the higher taxonomical level of identification of this technique, it also appears that more species are extinct now than it emerged from the pollen record only. The leaf sites of Crespià (Spain), Bernasso and Nogaret (France) (Roiron, 1983, 1992; Leroy and Roiron, 1996) revealed one clear fossil species with no direct modern affinity: *Carpinus suborientalis*. In the Calabrian section of Lefte, Italy (Figs. 1 and 2), a larger range of Tertiary taxa, detected by their pollen, wood, fruits or seeds, is still present: such as *Chamaecyparis*, *Glyptostroboxylon*, *Liquidambar*, *Nyssa*, *Phellodendron* and *Staphylea* (Ravazzi, 1995). Fruits, seeds and related structures in a compilation of Italian sites (Martinetto, 1999) reveal the presence of *Juglans bergomensis*, *Magnolia cor* and *Phellodendron elegans* (extinct species) until possibly 0.8 Ma ago (later than in the Netherlands where they had disappeared before 1.8 Ma).

An important contributor to the European palynoflora, that is still often misidentified, is *Parrotia persica* (Hamamelidaceae) (Fig. 5). This tree now grows only on the northern slopes of the Alburz Mountains, Northern Iran (Leroy and Roiron, 1996; Kazancı et al., 2004) and in the Alsan valley of the Caucasus (Binka et al., 2003), but was frequent in southern Europe: France, Spain, Italy, etc.

Taxodiaceae such as *Sequoia* and *Taxodium-Glyptostrobus* were present in Europe (e.g. Bertini, 2003). The case of their time-transgressive disappearance is well illustrated by their maintenance until c. 1.9 Ma in the Crotone site (Combourieu-Nebout, 1993) and their earlier disappearance in the Languedoc-Roussillon, France (Suc, 1980). Only a series of long records throughout Europe would help establish a satisfying time frame of disappearance. Their asynchronous disappearance is easily explained by the existence of several refugia. The precise moment of the disappearance of most of these taxa, often termed Tertiary, is still unknown.

The hypothesis for disappearance causes that has been largely shared by palynologists and biogeographers in the 1960s was the geography of Europe with its west east Alpine mountain range. It was thought that this acted as a barrier for plants pushed south of it by glaciations (C. and E. Reid in West, 1977). On the contrary, to explain the disappearances we follow the hypothesis formulated by Bennett et al. (1991) who indicate that the tree taxa which spread into and across northern Europe from the south during the postglacial still occur in the south or the east of Europe; and that the vanishing of trees at the ends of interglacials is caused by tree population dying where they are rather than a migration back to refugia. For the following interglacial, colonisation of the north started with whatever plants were available in refugia. This concept has a direct implication: the maintenance in Europe of populations of the tree species characteristic of northern Europe throughout the Quaternary must have depended (and will) on the persistence of populations of these taxa in southern refugia during warm stages as well as cold stages (Bennett et al., 1991). In general, the disappearance of plants in Europe is caused by their non-survival in the last of its refugia during glacial times. This could be due to factors such as illness in refugia, decrease in number of refugia, conditions too drastic for the ecological range of the species, or competition.

The transition between obliquity forcing and eccentricity forcing at 1-0.8 Ma ago would have firstly shortened the duration of interglacials and therefore decreased the number of species that are successful to expand from the refugia to colonise Europe, and secondly lengthen the glacials and therefore facilitate disappearances.

In conclusion for this section, we can say with confidence that first there are more plants that have disappeared than palynology alone can suggest; and that secondly the south is the genetic pool for the whole of Europe, or in other words its source of genetic diversity, and worth protection as such.

4. Vegetation refugia

The idea of distant refugia having an influence on the Netherlands has been challenged for a long time by palynologists working in the Rhine and Meuse estuary (de Jong, 1988). The absence of vegetation succession was believed to be related to the proximity of trees during cold stages. After a review of refugia types, this section is devoted to a discussion of known refugia and potential ones, as well as to colonisation routes from refugia to the rest of Europe.

4.1. Refugia types

The precise location of glacial refugia is impossible to establish for each climatic cycle. It is important to note that pollen diagrams from sites in full glacial refugia are still rare, even for the last climatic cycle, and probably that none yet show the maintenance of many species of deciduous trees during the last glacial period. However areas that served as glacial refugia often for many species of plants and animals (including humans) can be narrowed down to three different types: mountains and plains (coastal or not).

The type, most frequently mentioned, is the mid-mountain belt where a mosaic of habitats can be preserved at various altitudes and exposures to the sun and the wind. This variety of ecological niches allowed the survival of a rich diversity of plants and animals during glacial times. These mid-mountains are: the Apennines, the Balkans, the Alps including the Eastern Alps, and the Carpathians (Huntley and Birks, 1983; Leroy et al., 1996; Watts et al., 1996; Willis, 1994). A very good analogue of how some European mountains looked during glacial times is what can be found now in

the Tien Shan Ranges or on the North slopes of the eastern Alburz. A belt of mixed forest separates the steppe and the alpine meadows.

Coastal areas have also been suggested as refugial types (Iversen, 1958). The evidence however remains less robust until now as it is based on pollen analysis only. Examples include the Saint-Macaire maar lake in the Languedoc coastal plain and the lower Rhone valley (Leroy et al., 1994).

Plains in central Europe, although an a-priori hostile environment during glacial times, have to be considered on the base of tree charcoal finds undoubtedly dated of the last full glacial period (Willis et al., 2000; Carcaillet and Vernet, 2001). Pollen diagrams of the Hungarian plain during the Pleniglacial have always shown the presence of arboreal pollen. It was long presumed that the trees were not growing *in situ*; but that the presence of the arboreal pollen grains was due to long-distance transport by wind or even laboratory contamination (Willis et al., 2000). During the full-glaciation, the concentration of tree pollen declined dramatically, perhaps as much as three orders of magnitude. This trend is thought to be indicative of a reduction in plant biomass and the presence of few, if any, trees on the landscape (Willis et al., 2000). A detailed charcoal analysis, including species identification and radiocarbon dating, showed however the presence of charcoal of trees in soils. Taxa represented include mostly needle-leaf species *Pinus sylvestris*, *Pinus cembra*, *Betula* sp., *Picea* sp., *Juniperus* sp., *Larix* sp., and also some broad-leaf ones: *Carpinus betulus* and *Salix* sp. (Willis et al., 2000; Willis and van Andel, 2004). This is explained by the survival of microenvironmental “oases” that were of sufficient warmth and humidity to allow the existence of small pockets of thermophilous fauna and flora during the full-glaciation (Willis et al., 2000). Carcaillet and Vernet (2001) list a series of sites in south-western central and eastern Europe where macrocharcoal analyses have shown evidence of the presence of trees during full-glacial time.

4.2. Colonisation routes based on DNA studies

The rapid expansion northward as the climate warmed after a glacial period would be from populations at the northern range of a refugium, and would involve sequential colonisations by long-distance migrants; this is the founder mechanism (Hewitt, 2003). It predicts that the rapid long-distance colonization of Northern Europe or any similar colonization would produce broad genome areas of reduced variability (Hewitt, 2003). On the other hand, population movements within mountainous refugial regions of southern Europe would have been shorter and slower and retained more genetic variability (Hewitt, 2003). It has become apparent over the last 20 years that many species of plants and animals are geographically subdivided by narrow hybrid zones. These are deduced to be the products of secondary contact between two genomes or taxa that have diverged in separate refugia and met as they expanded their ranges (Hewitt, 2003). Using DNA similarity, it is possible to infer from which ice age refugia populations emanated that now occupy different parts of the species range. The colonization routes of some twelve species from combined DNA similarity and fossil evidence are now available (Hewitt, 2000, 2003). Three patterns of expansion have been recognized: a) The grasshopper pattern or the Balkan expansion: *Alnus glutinosa* and *Fagus sylvatica* follow this pattern; b) The hedgehog pattern or the South-North strips: *Quercus* sp. and *Abies alba*; and c) The bear pattern or the E-W embrace: *Arvicola terrestris*. These cases confirm Iberia, Italy and the Balkans as distinct major glacial refugia for most species; while Turkey, Greece and the Caucasus also appear significant.

In conclusion for section 4, the present evidence indicates that the mountains are the most important type of refugium for most angiosperms, with several gymnosperms also present in central and eastern Europe. Some areas of Europe and adjoining ones to the east (such as the Taurus mountains and the Caucasus along the Pontic Range) have not yet been closely studied by palynology and by DNA investigations and could still reveal new key refugial areas.

5. Causes for the low AP representation in glacial times

In section 4, we have shown by anthracology that some trees survived in some cases in glacial times in locations that are not optimal. The low arboreal pollen (AP) representation in pollen diagrams remains however problematical. Influx of pollen grains has been shown to drop considerably during glacial times. This is caused by both low tree cover (unless demonstrated otherwise by for example charcoal presence) and low pollen production. Whereas the former is the result of a direct relationship with the absence of trees, the latter is less well known. Low pollen production is also a response to poor weather and to low [CO₂]. Firstly, work on pollen productivity in the northern boreal forest (Autio and Hicks, 2004) has revealed that during years of inclement weather conditions arboreal pollen productivity of the following year can be dramatically reduced. Secondly, glacial times caused lower than present global [CO₂] reaching < 200 μmol.mol⁻¹ (Petit et al., 1999). Experiments on *Ambrosia artemisiifolia* in greenhouses have shown that when [CO₂] is low; the pollen production is low too (Fig. 6). The number (at 370 μmol.mol⁻¹, present concentration) and the number and size (at 600 μmol.mol⁻¹, projected increase) of floral spikes increased (Ziska and Caulfield, 2000) in comparison to pre-industrial values of 280 μmol.mol⁻¹ (Fig. 6). We suggest therefore that low [CO₂] during glacial times might have been an important factor for the under-representation of trees in pollen diagrams.

6. The extent of the cold or dry climates during GCS glaciations

The main reason why vegetation succession was not seen in the Meuse/Rhine estuaries was long believed to be climate that was less cold in the Lower Pleistocene than later and “in this case the warmth-loving trees did not have to immigrate from a very distant region” (de Jong, 1988). However, we are going to show that the climate must have been sufficiently unfavourable to cause the opening of the landscape at least for a few millennia in each glacial period.

In northern Europe, an attempt has been made to reconstruct palaeotemperatures in Lieth, Germany (Pross and Klotz, 2002). Although the glacial periods are too often expressed by pollen-barren sediment, some glacial periods are well represented in the pollen diagram. The seasonality and the temperature of the coldest month were more extreme during glacial times. Suggested analogues for the first cold stage are the Moscow basin (Russia) and southern New England.

But it is worth looking further south and further back in time to detect earlier phases of cooling and drying. The sites of lake 2 of Bòbila Ordis (Leroy, 1988), Saint-Macaire (Leroy et al., 1994) and Bernasso (Suc, 1978; Leroy and Roiron, 1996; Leroy, 1990) illustrate very open landscapes linked to glacial times; the deciduous tree pollen percentages drop to < 10%, and only occasionally disappear completely. The sites of Tres Pins and lake 1 of Bòbila Ordis in north-eastern Spain (Leroy, 1997; Løvlie and Leroy, 1995), and Nogaret in southern France (Leroy and Seret, 1992) show most of a climatic cycle and, in each of them, a short cold and/or dry period is detected. Zone Mb2 of Leffe, which has a duration of 1500 years, (Ravazzi and Rossignol-Strick, 1995) is very open also. Pollen spectra indicate that it was already very dry at 3.5 Ma in NW Africa and that during the GCS glacial MIS correspond to a latitudinally wide Sahara (Leroy and Dupont, 1994; Dupont and Leroy, 1995) (Fig. 3). The investigations on marine cores covering the last climatic cycle off the Saharan coast has clearly demonstrated that during GCS glacial MIS it is dry in NW Africa (Hooghiemstra, 1989; Hooghiemstra et al., 2006). Ptolemais diagrams (Greece) show that cooler or drier periods were cyclically present very early on and well before the period considered here (Steenbrink et al., 2000, 2003).

In conclusion for section 6, continuous favourable conditions seem never to have existed over the last > 6 Ma. The environment has always been fluctuating and plants, animals and humans had to adapt continuously to them. Regular periods of landscape opening led to relying on glacial refugia for survival.

7. The beneficial influence of long marine records on short terrestrial analyses

The aim of this section is to show that progress made on long marine cores has an immediate positive impact on terrestrial stratigraphy, first as an eye opener on the record discontinuity and the presence of hiati often longer than the available records, and secondly as a way to obtain better ages.

During the last fifty years, one of the main areas of progress in Quaternary Sciences has been made on long and continuous sequences, mostly marine ones owing to programmes such as DSDP (Deep Sea Drilling Project) and ODP.

Terrestrial sites (peat bogs, river back-swamps, lakes) generally suffer of small thicknesses of sediment and hence short time spans represented in the sequences. Because of the dating limitations, it remains difficult to correlate them to each other. Following the rules of stratigraphy, terrestrial sites first receive a local name. This reasonable measure naturally led to a multiplication of local stratigraphical schemes, not always very robust, and to very tentative correlations between regions, e.g. the Dutch, German, Italian and the British Quaternary stratigraphic schemes (Gibbard and van Kolfschoten, 2005; Lona, 1950; Pross and Klotz, 2002; Walker, 2005). This is true already for sites older than the last interglacial. The inconsistent age of the Holsteinian interglacial with its *Pterocarya* marker is a good illustration of this. It is only recently that it has been equated to MIS 11 (de Beaulieu and Reille, 1995).

It is not until recently that some correlations of the sites forming local stratigraphies to MIS have been proposed, but for many it will remain impossible to correlate to MIS. Many sites that have contributed to build up the Early Quaternary Dutch palynostratigraphy will never fit into cyclostratigraphy.

In conclusion for section 5, from the point of view of stratigraphy, we fully agree with Gibbard and van Kolfschoten (2005: p. 446): “today the burden of correlation lies in equating local, highly fragmentary, yet high-resolution terrestrial and shallow-marine sediments on the one hand, with the potentially continuous, yet comparatively low resolution, ocean isotope sequence on the other”. It is necessary to add that marine records with resolutions similar to that of continental sites are more often found now, such as the annual varves of the Santa Barbara basin, off California, and of the Cariaco basin, off Venezuela. The analysis of the cores taken off-shore the NW Iberian coast reaches a centennial resolution.

8. Limited absolute dating methods and alternative solutions

Few absolute and relative dating techniques are available for the Late Pliocene-Early Pleistocene period. Clearly there is a technique gap here that, if solved, would revolutionise the science of Quaternary research. At the moment, we are still constrained to promote an alternative solution: the use of the wiggle matching method (such as in radiocarbon dating) of environmental proxyrecord, and this is developed in this section.

Walker (2005) mentions Potassium/Argon, Argon/Argon, Electron Spin Resonance and Fission Track for the absolute dating methods available to the GCS with amino acid diagenesis as a relative dating method; whereas oxygen isotope stratigraphy, tephrochronology and palaeomagnetism can be used for finding age equivalence. The presence of

volcanic activity often leads to radiometric dates that allow the development of stratigraphical hypotheses, for example the sites of Bernasso (c. 2.0 Ma) and Nogaret (2.0 Ma) in southern France (Leroy and Seret, 1992; Leroy and Roiron, 1996; Leroy et al., 1999) and Pula in Hungary (3.05 to 2.0 Ma) (Willis et al., 1999). Working outside volcanic regions leads to reliance on relative dates such as biozones (appearance/disappearance of plants, micro-mammals and megafauna) and the identification of magnetic field reversals.

Long marine chronologies are built on a combination of proxies such as magnetostratigraphy, foraminifera and other microfossil stratigraphy, but mostly on cyclostratigraphy (tuning of proxies such as oxygen isotopes to astronomical periodicities; Channel, 1995).

Short sections containing a climatic signal could be wiggle matched to a part of the long marine oxygen isotope curve. The term “wiggle matching”, derived from radiocarbon dating calibration, is considered to be better than “curve matching” (Gibbard and van Kolfshoten, 2005), because it suggests a higher level of detail. The record of Nogaret is believed to be one of the first cases of wiggle matching for the GCS: e.g. Nogaret to MIS 75 (Leroy, 1990; Leroy and Seret, 1992; Leroy et al., 1999) (Figs. 1 and 7). The wiggle matching is supported by the age of the regional volcanic activity (K/Ar: 2 to 1 Ma), large mammals from the Saint-Vallier biozone (2.1-1.8 Ma) and the influence of eccentricity on obliquity causing slightly longer cycles between 2.2 and 2.0 Ma (Raymo et al., 1989). Another site near Nogaret is Bernasso. Its interglacial is placed between MIS 81 and 73 (Leroy and Roiron, 1996). For lake 1 of Bòbila Ordis, Spain, a correlation of a sequence (with > 1 climatic cycle) to MIS on the basis of the presence of a common magnetic subchron (the Cobb mountain subchron at 1.2 Ma ago; Fig. 2) and rodent teeth has been proposed, i.e. MIS 35 (Løvlie and Leroy, 1995). The vegetation cycles in Crotona were correlated to MIS 97 to 89 (4.5 cycles) (Combourieu-Nebout, 1993). An attempt was made to correlate vegetation succession cycles and oxygen isotopes cycles for the site of Stirone, Italy (Bertini, 2001; Fauquette and Bertini, 2004). The Pejark Marsh, in Australia, dating for the Early-Middle Pleistocene transition (Wagstaff et al., 2001) may cover MIS 30–17, dated to between about 1.03 and 0.68 Ma ago.

One caveat for the wiggle matching approach is the potential lag of one proxy in regard to another. When working at the scale of cyclopalynostratigraphy, the lag is minimal, to the contrary of what is suggested in Gibbard and van Kolfshoten (2005). Investigations in marine sequences of both typical marine proxies (dinocysts, isotopes on foraminifera) and typical terrestrial proxies (pollen) have demonstrated the lag of the latter proxies to be c. 5-6 ka at the beginning of the last interglacial (Sanchez-Goñi et al., 1999; Kukla et al., 2002). This is caused partially by the different response of the ocean temperature/ice volume and of the land to climatic change but probably also by the boundary definition and problem of dating of the terrestrial sites (Kukla et al., 2002).

However “vegetation in Iberia ... responds immediately ... to SST (sea surface temperature) changes on millennial time scales during MIS 3” within the resolution of the record which is a few hundred years (Roucoux et al., 2005).

Another case study appears to show a lag of more than 10 ka, but it results from problems of taphonomy. The normal event in lake 1 of Bòbila Ordis has been correlated to the Cobb mountain magnetic subchron (Løvlie and Leroy, 1995). It is found towards the end of an interglacial, MIS 35, whereas the same subchron in a marine sequence corresponds to a glacial MIS. The main reason is the low sedimentation rate in the marine setting that affects the acquisition of the magnetic signal by relocation.

In ODP Site 658, oxygen isotopes lag behind pollen by 5 to 7 ka (Dupont and Leroy, 1995). In conclusion for section 6, the era of palynostratigraphy is over. It is now replaced by wiggle matching of pollen proxy records to MIS. This is part of the cyclopalynostratigraphical approach (for more on this, see section 9).

9. Duration of records

In this section, we propose that, in the absence of absolute dating, cyclopalynostratigraphy is used to obtain satisfactory estimations of durations for the observed changes at the scale of Milankovitch cycles. We review sites with independent relative time control: terrestrial then marine, because they will further confirm the assumption that the glacial-interglacial cycles expressed as vegetation successions are indeed taking place at the periodicity of the obliquity (c. 41 ka). Then we use cyclopalynostratigraphy to reconsider durations of some published sequences without (or with poor) age control in order to obtain a more realistic duration estimate.

9.1. Lacustrine laminates and chronologically-controlled marine records

Annually laminated sediment is relatively rare. It usually forms under anoxic conditions inhibiting bioturbation. Such environments may be found at the bottom of lakes, usually deep lake such as maars. In two cases, lamination has helped in estimating the duration of vegetation zones in the GCS: one in France and one in Italy. The Nogaret maar is mostly filled with calcareous laminates rich in diatoms, interbedded with pyroclastic layers and silt (Leroy and Seret, 1992). The laminates are the result of annual deposition with at least 3 seasons represented (Fig. 8) with an average of 216 $\mu\text{m}\cdot\text{yr}^{-1}$. Some sections of Leffe, which are annually laminated, have provided an estimated sedimentation rate of 280-400 $\mu\text{m}\cdot\text{yr}^{-1}$ (Ravazzi and Rossignol-Strick, 1995; Ravazzi and Moscariello, 1998). In these two cases, the laminate counts have allowed light to be thrown on the duration of some vegetation cycles, confirming their forcing by obliquity.

As summarised in Channell (1995), it is now over 30 years since it was first demonstrated that orbital cycles are preserved in the climatic records of deep-sea sediments (Shackleton and Opdyke, 1973; Hays et al., 1976). Hays et al. (1976) adjusted their initial timescale to bring the peak of variance of obliquity cycles to the same frequency calculated for obliquity by astronomers, and were thus the first to use cyclostratigraphy as a means of tuning timescales. It has now been established that climatic cycles were forced by obliquity (41 ka) during the Gelasian Stage and the Early Pleistocene (Imbrie et al., 1993; Ruddiman et al., 1989; Raymo et al., 1989; Shackleton et al., 1995) with a transitional period between 1 and 0.78 Ma ago during which the eccentricity becomes progressively stronger (Fig. 2). In ODP Site 658, pollen and isotopes are fluctuating in parallel and both display the periodicity of obliquity (Dupont and Leroy, 1995).

9.2. Astrochronology for palynostratigraphy: a drastic reduction in durations

If we accept the simple hypothesis that on average all the climatic cycles of the GCS are forced by obliquity and if a pollen diagram has reached a sampling resolution high enough to highlight glacial-interglacial vegetation successions, then we have an indirect tool to estimate the durations of the deposit formation: by considering that each cycle of vegetation succession is 41 ka long.

Counting the number of these cycles (one of the aspects of cyclopalynostratigraphy) provides a more accurate estimation of duration and increases the probability of fitting sequences correctly either in the magneto-stratigraphy or in the marine oxygen isotopic stratigraphy. A re-analysis of a series of sites (Valle Ricca, Stirone, Pietrafitta, Senèze, Mizzen and Lieth, location on Fig. 1) shows completely different durations from those published (Fig. 9). Fig. 9 shows a drastic reduction of the duration estimates, for some, of more than 10 times.

The sequence of Lieth, Germany, originally correlated to the Reuverian up to the Menapian (Menke, 1975), thus lasting more than 1.5 Ma long (Fig. 9), has recently been estimated to have lasted 0.9 Ma from the Praetiglian to the Eburonian (Pross and Klotz, 2002). But if we apply strictly the obliquity-forcing concept, the vegetation cycles being 8 or 10 in number, then it is only 0.33 to 0.41 Ma long; hence a further reduction of c. three times has to take place.

Finally for section 9, the reaction of vegetation to obliquity has been demonstrated in marine and in terrestrial environments. The cyclopalynostratigraphical approach provides a new tool for dating by wiggle matching (section 8) and for obtaining duration estimations (section 9.3). It becomes therefore essential that sampling and time resolutions of the pollen diagrams be increased until the main steps of vegetation successions are found.

The problem of poor estimations for sedimentation rates leads not only to a wrong appreciation of environmental change rate, but also to something fundamental at the beginning of a project, the choice of sampling step.

10. Short glacial and long interglacial stages

The Quaternary is generally seen as an Ice Age with long glacials and short interglacials. Although this is true for the last 780 ka, it is not accurate for the period before 990 ka. The aim of this section is to show for the GCS the relative smaller time span of glacials versus interglacials.

Within a climatic cycle the question is where to place the boundaries between glacial and interglacial stages, or between cold and warm stages. Although a global definition has not been proposed by the ICS, in principle in ocean sediment cores, the boundaries are placed at mid-points between temperature maxima and minima as reconstructed from the oxygen isotope analysis (Gibbard and van Kolfschoten, 2005). This is a practical convention, but it does not reflect what happens in the environment on land. Moreover the isotopes are not an accurate proxy for temperature for the Late Pliocene-Early Pleistocene as other factors are interfering. An older definition for an interglacial is “a temperate period with a climatic optimum at least as warm as the present interglacial in the same region” (Gibbard and van Kolfschoten, 2005).

For the Gelasian and Calabrian time period, it is better to turn to pollen records. The boundaries in Europe are usually placed between periods of open landscapes and landscapes covered by vegetation, not necessarily the mathematical midpoint between the worst and the best conditions. According to location, these better conditions vary, and for the area of study they often are a dry open woodland (Fig. 4), in other words fairly close to what the vegetation was at the beginning of the Holocene.

The GCS are characterized from the vegetation point of view by short glacials with open landscape and long interglacials with closed forests (Fig. 10). This has been derived from a survey of the following palynological diagrams: Stirone (400 m asl, Italy; Lona and Bertoldi, 1973; Bertolani et al., 1979), Pietrafitta (220 m asl, Italy; Lona and Bertoldi, 1973; Pontini and Bertini, 2000), Valle Ricca (marine site, Italy; Urban et al., 1983; Arias et al., 1990), Senèze (590 m asl, France; Elhaï, 1969), Nogaret (690 m asl, France; Leroy and Seret, 1992), Leffe (490 m asl, Italy; Ravazzi and Rossignol-Strick, 1995) and Crotona (marine site now exposed, Italy; Combourieu-Nebout, 1993, 1995).

A comparison of successions under forcing by obliquity or by eccentricity leads to the following three observations (Fig. 10): (a) Based on a synthesis of pollen diagrams, it appears that the duration of the glacial period is much shorter in an obliquity-forced cycle (< ¼ of 41 ka) than in an eccentricity-forced cycle (> 4/5 of 100 ka). As a corollary, the duration of an interglacial period is twice as long in an obliquity-forced cycle; hence in the more recent

interglacials the successions have to take place at a much faster pace and/or can accommodate fewer species. This has a direct impact on diversity in localities far from refugia. (b) The number of cycles (and therefore of deep modification of the vegetation cover and biodiversity) is 2.5 times higher in the Late Pliocene- Early Pleistocene than in the Middle-Late Pleistocene. The chances of losing species in the glacial refugial areas are hence also increased because they undergo more dynamic conditions. (c) The difference between glacial and interglacial environmental conditions is however less extreme than in the Middle-Late Pleistocene, especially owing to less drastic glacial periods.

In the case of a super-interglaciation caused by global warming, more taxa are expected to be able to come out of refugia and colonise Europe. This super-interglaciation would bear a lot of similarities to an interglacial forced by obliquity.

11. Ten messages

We summarise here the messages from each of the ten sections.

- 1. Palynology is an integral part of stratigraphy when it puts forward major steps in vegetation changes. It is clear that changes at 2.56 Ma ago are more important than at 1.8 Ma ago. Palynology (land) must be complementary to oxygen isotopes (ocean and ice) to establish boundaries that have a global (land and ocean) scope.
- 2. Vegetation successions linked to Milankovitch cycles been in evidence throughout Europe at least from 2.6 Ma ago. They are known at least from the Messinian.
- 3. Besides increasingly drastic glacial periods, survival conditions within glacial refugia should be taken equally into consideration for taxa disappearance.
- 4. Vegetation refugia might have been of different types, but mid-mountain settings are the most frequent. Sites near Europe such as the Taurus Mountains and the Pontic Range should become the target of further investigations as they had an impact on Europe.
- 5. During glacial times, trees may have been more widespread out of traditional refugia than suggested by pollen diagrams. Trees often seem insignificant in pollen diagrams, because their pollen productivity is affected by bad weather/climate and low [CO₂].
- 6. Cold and/or dry glacial periods were extreme enough to cause an opening of the landscape outside refugia at the beginning of the GCS already.
- 7. Terrestrial sites have benefited immensely from progress made by investigations on long marine cores, especially in the shocking realisation of the gaps in terrestrial stratigraphy and in the fact that most schemes of correlation between GCS continental stratigraphies are obsolete.
- 8. Wiggle matching of pollen proxy records to the marine oxygen isotopic record (one of the aspects of cyclopalyostratigraphy) is an improvement for sites that lack absolute dates.
- 9. Cyclopalyostratigraphy is also a tool to improve estimation of durations and dating.
- 10. The interglacial part of a climatic cycle forced by obliquity is longer than its glacial part. The obliquity-forced interglacials are longer (maybe up to three times) than the eccentricity-forced interglacials. A super-interglaciation forced by global warming would bear similarities with a GCS interglacial.

12. Future

The results of this analysis of ten aspects of Quaternary palynology have a bearing on the following three components of research project planning.

12.1. Choice of favourable localities

From this review and analysis, it is clear that the choice of localities in regard to the taphonomy of pollen is crucial for the quality of data derived.

The causes for the absence of vegetation succession observation in the Dutch pollen diagrams are not actually climatic, but more taphonomical. Pollen sites came from unfavourable sedimentation environments such as oxbow lakes, flood plains and backswamps, which are short, discontinuous and/or integrate the pollen of a wide catchment. Sites such as fluvio-lacustrine sequences (Rhine-Meuse Graben and estuaries) should be avoided. Another unfavourable setting is that of Lake 3 of Bòbila Ordis, Spain, that has provided a 30 m-long sequence of homogenous pollen spectra (Leroy, 1987). The proposed explanation is that the sediment has been homogenised by under-water springs similar to that found in the present-day lake of Banyoles. The North Sea is not a good location for informative pollen diagrams in the GCS because the area was part of the Great European Delta (Ekman, 1999). Up to now, no pollen diagrams have been derived from the north-east Atlantic along western Europe for the GCS, probably because the wind direction, mostly from the west, is not favourable to pollen transport (Hooghiemstra et al., 2006).

On the contrary, it seems that small and deep lakes such as maar lakes provide favourable sequences, covering several climatic cycles, for example the maars of Senèze (Elhaï, 1969) and Nogaret (Leroy and Seret, 1992) in France. The sedimentary basin of Bòbila Ordis near Banyoles (Spain) has also provided sequences that show glacial-interglacial

vegetation cycles in less than 30 m, from a sediment formed in a quiet settling setting (a sinkhole without spring in a region of subsidence in the southern piedmont of the Pyrenees).

12.2. Decision on sampling resolution

The concept that climatic cycles should be visible in the sediment and in the vegetation reconstruction, constrains the researcher in his/her decision on how to map and how to sample. It is crucial to make sure that the steps of vegetation succession are identified. If vegetation successions cannot be detected, then the sediment is unsuitable for glacial-interglacial palaeoenvironmental and palaeoclimatic reconstructions. In the case of the lake 1 of Bòbila Ordis, the sampling resolution of the second cycle had to be doubled (Leroy, in preparation); in the case of the Plio-Pleistocene boundary stratotype at Crotone, the resolution of part of the marine sequence was increased from one sample per 300 cm to one sample per 70 cm to reveal the impact of obliquity on vegetation (Combourieu-Nebout 1987, 1993). This actually still remains far from the sampling resolution used in many Holocene diagrams for establishing the steps of vegetation succession.

12.3. Some prime locations for long continental sequences

New investigation could turn towards the Atlantic Ocean. The blatant absence of long marine sections with pollen record at the latitude of Europe may be rectified by the selection of sites with favourable wind transport conditions. The area off the Iberian Peninsula has yielded excellent diagrams for the last 150 ka. Also long lacustrine sections should be investigated. This now becomes possible owing to the new technology developed and used by the International Continental Drilling programme (ICDP) for deep lake drilling already used in the Qinghai, Malawi and Titicaca lakes. Long records going back continuously to the GCS in Europe should be searched, although maybe only a combination of long maar lake records is possible in a first instance.

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Fig. 1. Location map of Gelasian-Calabrian sites. For the precise location of Lamone, see Bertini (2003). For the other sites, see references in text.
Fig. 1. Carte de localisation des sites Gélasiens et Calabriens. Pour la localisation précise de Lamone, voir Bertini (2003). Pour les autres sites, voir les références dans le texte.

Fig. 2. Cyclostratigraphy of the Gelasian (Late Pliocene) and Calabrian (most of the Early Pleistocene). ODP 658 from 3.7 to 1.7 Ma (MIS 149/Gi 9 to 60) from Leroy and Dupont (1994); Vrica from c. 2.6 to 1.3 Ma from Combourieu-Nebout (1987) and 2.46 to 2.1 Ma (MIS 96 to 90) from Combourieu-Nebout (1993) (black outline); Senèze, 2.21 to 2.01 Ma (MIS 85 to 76) from Elhaï (1969) and Roger et al. (2000); Leffe from top Olduvai to base of Jaramillo from Ravazzi and Rossignol-Strick (1995) and Ravazzi et al. (2005). Ages after Gibbard and van Kolfschoten (2005). Some marine isotopic stages (MIS) are given in the fourth column. CM: Cobb Mountain subchron. M: Matuyama.

Fig. 2. Cyclostratigraphie du Gélasien (Pliocène Récent) et Calabrien (la plupart du Pléistocène Ancien). ODP 658 de 3,7 à 1,7 Ma (MIS 149/Gi 9 à 60) de Leroy et Dupont (1994) ; Vrica de c. 2,6 à 1,3 Ma de Combourieu-Nebout (1987) et 2,46 à 2,1 Ma (MIS 96 à 90) de Combourieu-Nebout (1993) (contour noir) ; Senèze, 2,21 à 2,01 Ma (MIS 85 à 76) de Elhaï (1969) et Roger et al. (2000) ; Leffe du haut de l'Olduvai à la base de Jaramillo de Ravazzi et Rossignol-Strick (1995) et Ravazzi et al. (2005). Ages d'après Gibbard et van Kolfschoten (2005). Quelques étages isotopiques marins sont donnés dans la quatrième colonne. CM : Cobb Mountain subchron. M : Matuyama.

Fig. 3. Trends in ODP Site 658 pollen diagram (prepared by Dupont and adapted from Dupont and Leroy, 1995). Smoothing on 9 samples (c. 45 ka) to eliminate the impact of obliquity forcing. CCA: Chenopodiaceae, Caryophyllaceae and Amaranthaceae. Note the increase in CCA and the decrease of Tropical forest at 2.6 Ma.

Fig. 3. Tendances dans le diagramme du site ODP 658 (préparé par Dupont et adapté de Dupont et Leroy, 1995). Lissage sur 9 échantillons (c. 45 ka) pour éliminer l'impact du forçage par l'obliquité. CCA : Chenopodiaceae, Caryophyllaceae et Amaranthaceae. À noter : l'augmentation en CCA et la diminution de la forêt tropicale à 2,6 Ma.

Fig. 4. Typical succession of the main arboreal pollen/trees for temperate Europe during a glacial-interglacial cycle forced by obliquity.

Fig. 4. Succession caractéristique des principaux types de pollen d'arbres et d'arbres eux-mêmes pour l'Europe tempérée durant un cycle glaciaire-interglaciaire forcé par l'obliquité.

Fig. 5. Photos 1 and 2 of *Parrotia persica* (herbarium) and 3 and 4 of *Parrotia persica* (fossil from Bòbila Ordis) (Photos: S. Leroy). All in polar view. Some morphological characteristics: crenate outline in polar view (see 3), dented colpi (see 1) and columella in lumen centre (see 2). Size: c. 35 µm in polar view.

Fig. 5. Photographies 1 et 2 de *Parrotia persica* (herbier) et 3 et 4 de *Parrotia persica* (fossile de Bòbila Ordis) (Photos : S. Leroy). Tous en vue polaire. Quelques caractéristiques morphologiques : contour en créneau en vue polaire (voir 3), colpes dentés (voir 1) et columelles dans le centre de la lumière (voir 2). Taille : c. 35 µm en vue polaire.

Fig. 6. Pollen production versus CO₂ concentration (adapted from Ziska and Caulfield, 2000).

Fig. 6. Production pollinique contre la concentration en CO₂ (adapté de Ziska et Caulfield, 2000).

Fig. 7. Wiggle matching of the Nogaret pollen diagram to oxygen isotopes of ODP Site 607 (benthic foraminifera, Ruddiman et al. (1989) with the chronology of Cande and Kent (1995)).

Fig. 7. Appariement d'ondulations de courbes du diagramme de Nogaret et des isotopes de l'oxygène de l'ODP 607 (foraminifères benthiques, Ruddiman et al. (1989) avec la chronologie de Cande et Kent (1995)).

Fig. 8. Laminites of Nogaret sediment in thin section in polarised light (Photo: G. Seret). In blue the diatom bloom of spring, in yellow the deposition of neoformed carbonate crystals of summer, and in black the detrital deposition of autumn and winter. Average annual thickness: 216 µm (between double arrow).

Fig. 8. Laminites du sédiment de Nogaret en lames minces en lumière polarisée (Photo : G. Seret). En bleu, l'explosion printanière des diatomées, en jaune le dépôt de cristaux de carbonate néoformés en été, et en noir le dépôt détritique de l'automne et de l'hiver. Épaisseur annuelle moyenne : 216 µm (entre la double flèche).

Fig. 9. Revision of the duration of a series of GCS sites. For Senèze according to Roger et al. (2000). Palynostratigraphy of the Netherlands according to Zagwijn (1996). g. = glacial, i. = interglacial, c. = complex.

Fig. 9. Révision de la durée d'une série de sites GCS. Pour Senèze selon Roger et al. (2000). Palynostratigraphie des Pays-Bas selon Zagwijn (1996). g. = glaciaire, i. = interglaciaire, c. = complexe.

Fig. 10. Relative durations (in ka) of glacial and interglacial periods under an eccentricity versus an obliquity-forced climatic cycle.

Fig. 10. Durées relatives (en ka) des périodes glaciaires et interglaciaires d'un cycle climatique forcé par l'excentricité comparativement à un cycle forcé par l'obliquité.

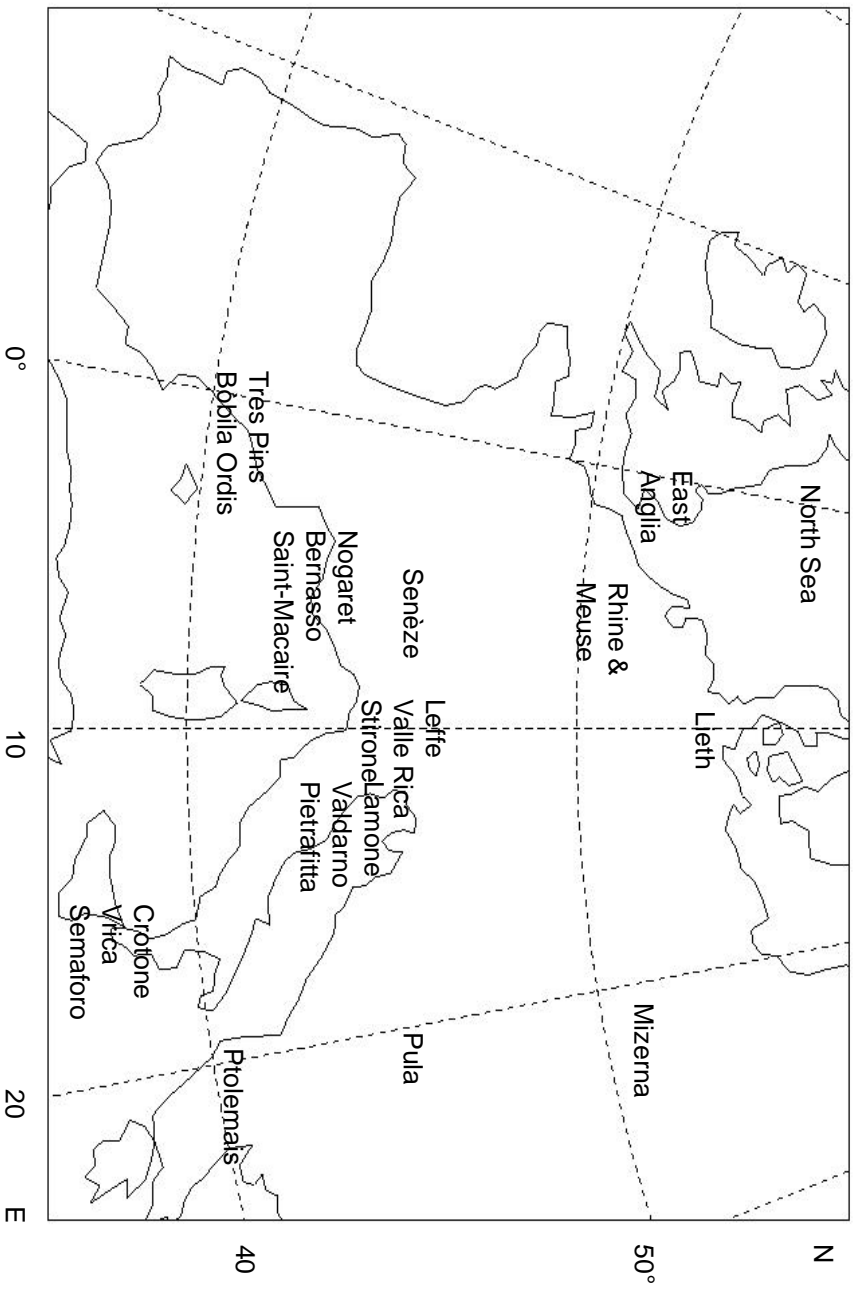


Fig. 1 Leroy

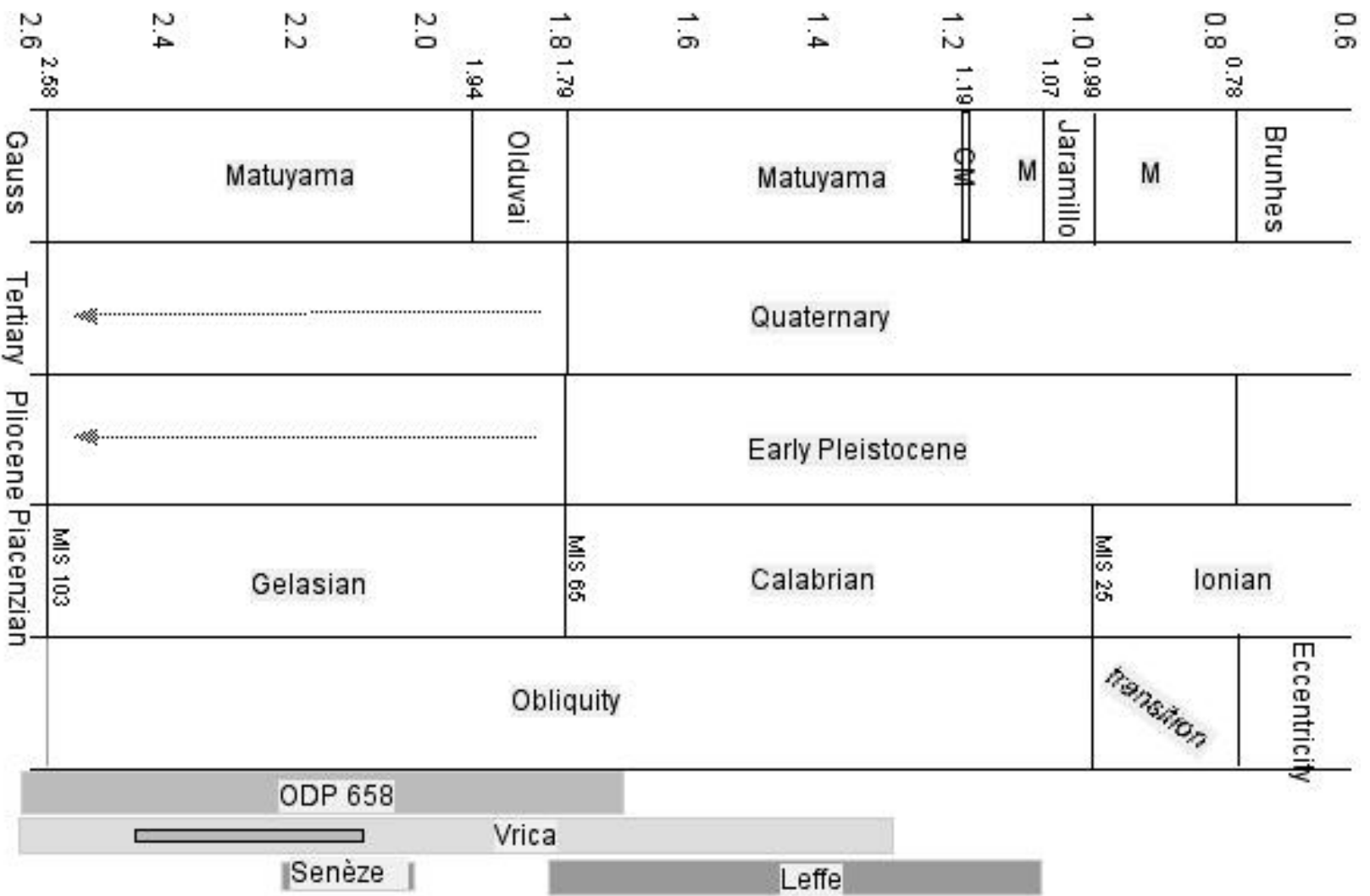


Fig. 2 Leroy

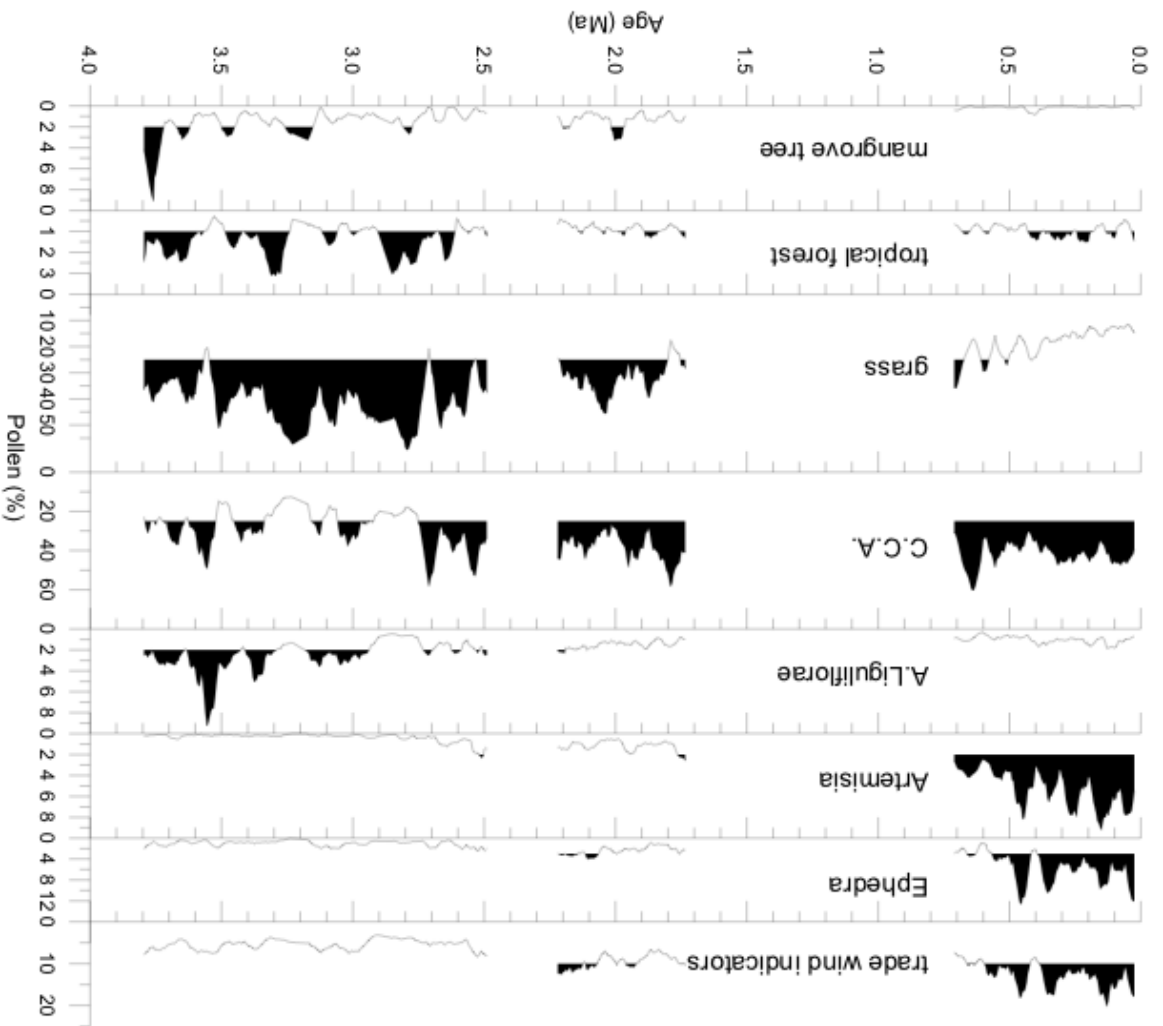


Fig. 3
Leroy

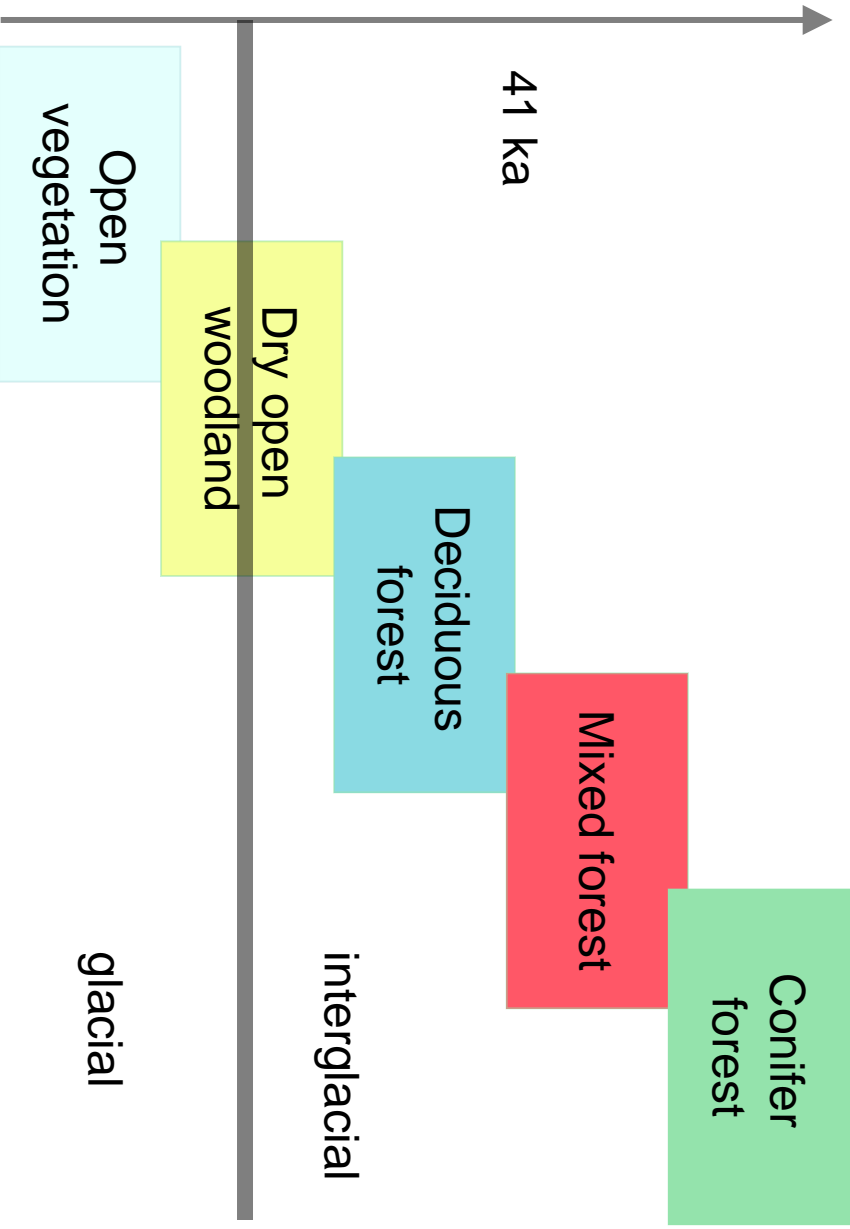


Fig. 4 Leroy



10 μm

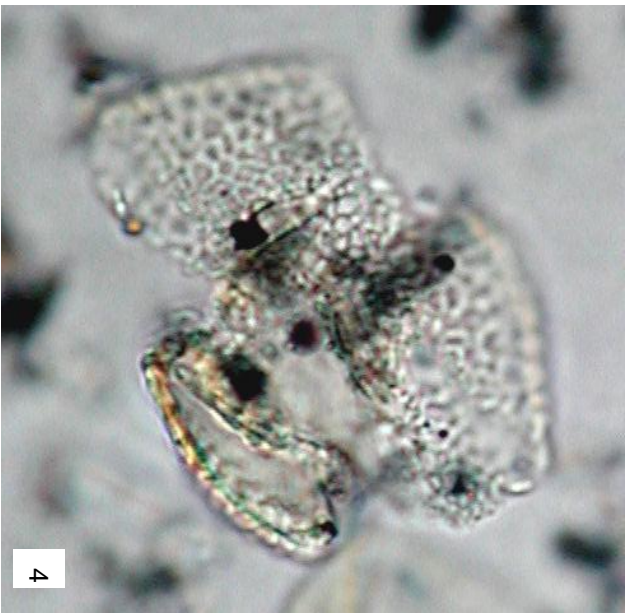


Fig. 5 Leroy

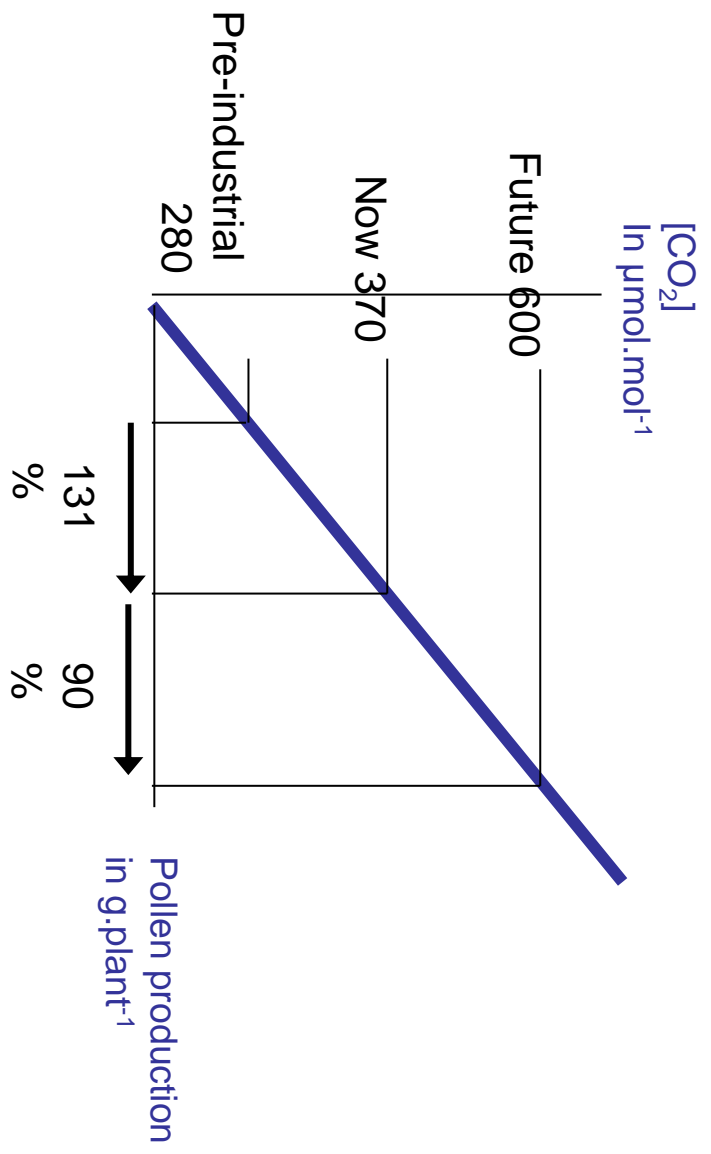


Fig. 6 Leroy

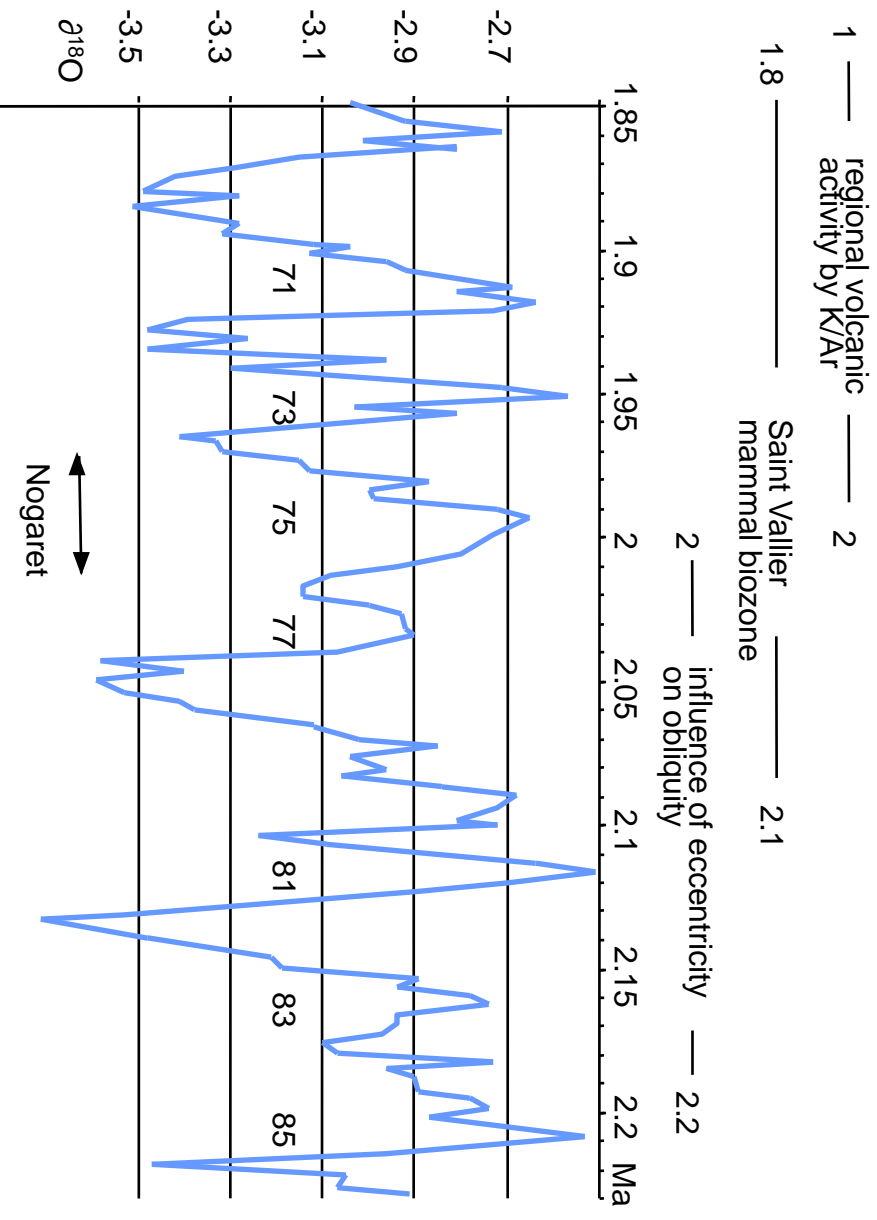


Fig. 7 Leroy

Fig. 8 Leroy

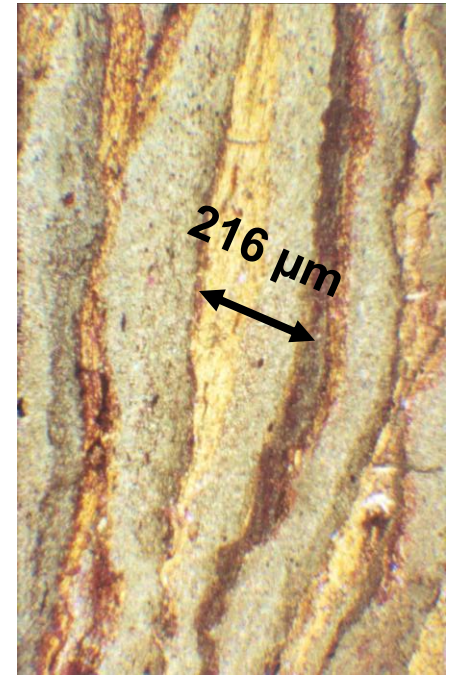


Fig. 9 Leroy

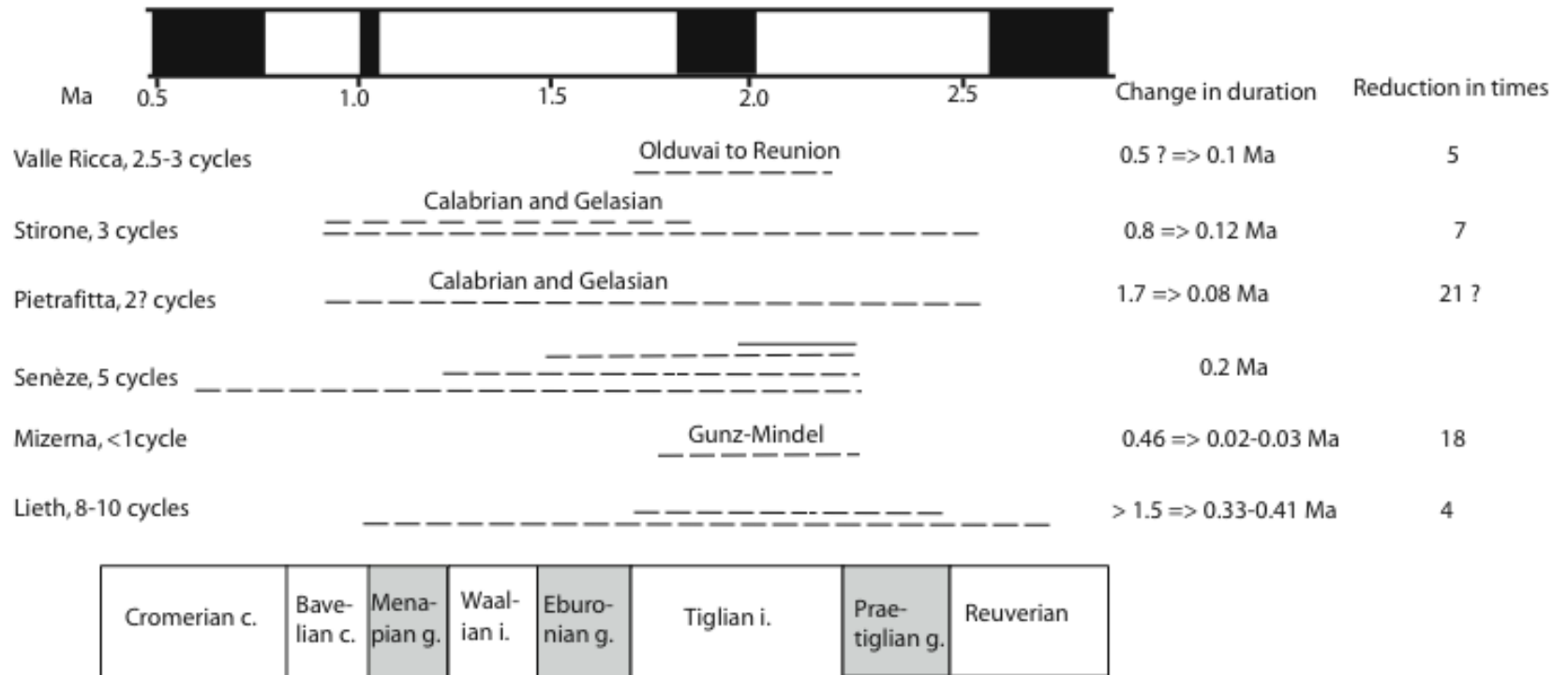


Fig. 10 Leroy

