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The Zanclean palaeofloras around the Mont-Dore strato-volcano: A window into upper Neogene vegetation and environments in the Massif Central (Puy de Dome, France) *

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Abstract

New Pliocene macrofloras and microfloras perfectly preserved from the Mont-Dore (Puy-de-Dôme, Massif central, France) have been reinvestigated. Samples come from different stratigraphical levels collected from three localities, Lac Chambon, La Gratade and Pont de Chocol. The $^{40}\text{Ar}/^{39}\text{Ar}$ radiometric datings bracketing the Chambon Lake and La Gratade fossil-bearing horizons give 4.46 ± 0.05 Ma and 3.94 ± 0.04 Ma, respectively, representative of the Zanclean Stage (= Brunssumian B and C), a period of the early Pliocene (5.32 to 3.6 Ma), much older than previously thought (i.e., Piacenzian). Pont de Chocol is considered to be close biostratigraphically, or even identical in age to La Gratade. Detailed morphological evaluation of leaf morphotypes completed with pollen analysis contributed to the better taxonomic knowledge of these palaeofloras. The overview focuses on floristic and phytostatigraphical characteristics of the defined stratigraphical units and their dating and

correlation with previously defined palaeofloristic units of the Massif central. The study provides detailed identifications of plants representing 11 gymnosperms among which Pinaceae (pollen and winged seeds), Cupressaceae including “Taxodioid” pollen grains and Sciadopitaceae families (only pollen). Besides, different angiosperm trees and shrubs have been determined from both micro- and macro-remains. Fagaceae is the most diversified with several foliage of beech and deciduous oaks, while diversified Juglandaceae contribute mainly as abundant leaf remains of *Carya*, *Pterocarya* and *Juglans*; Ulmaceae with numerous leave of two *Zelkova* species, and also *Ulmus*. Various other deciduous dicotyledonous such as *Alnus*, *Betula*, *Carpinus*, *Populus*, *Acer laetum* and *A. interrigenum* are well documented. Leguminosae are recorded by a small number of leaflet imprints. Evergreen shrubs of Buxaceae (*Buxus pliocenica*) are scarce. All these taxa contributed to a rich biodiversity of these Pliocene assemblages. All three sites point toward riverine forest habitats dominated by hygrophilic diversified woody plants while in the surrounding plains and slopes the thermophilic elements were scarce and mesophilic taxa abundant as temperate elements. This vegetation can be compared with mixed mesophytic forests depicting a climate cooling during the two considered periods (*ca.* 4.46 and 3.95 Ma).

Keywords:

Macroflora

Microflora

Palaeovegetation

Pliocene

Mont-Dore

Massif central

Europe

1. Introduction

Tertiary volcanogenic deposits of the Puy de Dôme (Massif central, France) have been explored for a long time and are a place of interest to palaeobotanists because of the abundance and well-preserved micro- and macrofossil plants. The earliest written record of Mont-Dore region fossil flora dates back to the end of the 19th century (Boulay, 1892). This work summarized all the discoveries that pointed vegetated Tertiary landscapes from the

French Massif central (Varennes, Perrier, Niac, Pas de la Mougudo, Ceyssac, Saint-Vincent, Joursac, La Gratade and Pont de Chocol).

During the first half of the 20th century, Grangeon and Rudel (1959) reported some fossil plants in Chambon Lake outcrops and detailed the taxonomic studies; the flora which should belong to this locality contains a small assemblage of 9 species: *Bambusa cambonensis* N. Boul. (*Arundinaria metake* Sieb.), *Alnus glutinosa* Gaertn., *Fagus sylvatica* L., *Fagus pliocenica* Sap., *Populus tremula* L., *Ulmus effusa* Willd., *Acer pseudocampestre* Ung., *Acer Nicolai* N. Boul. (affinity *A. opulifolium* Willd.), *Carpinus betulus* L., and one family, Poaceae. Later, this study was completed by Elhai and Rudel (1961) with a microfossil analysis. La Gratade and Pont de Chocol were studied by Grangeon and Rudel (1962); most of the fossil flora samples come from La Gratade outcrop, with 23 taxa identified as *Torreya nucifera* Sieb. et Zucc., *Potamogeton quinquenervis* N. Boul., *Salix* sp., *Populus tremula* L., *Populus alba* L., *Betula macrophylla* Heer, *Alnus glutinosa* Gaertn., *Carpinus orientalis* Mill. (fruits and leave), *Carpinus*, *Corylus avellana* L., *Fagus sylvatica* Sap., *Castanea vesca* Gaertn., *Quercus hispanica* Rer., *Quercus* sp., *Zelkova ungeri* Kovats, (*crenata* and *acuminata*), *Ulmus* sp., *Juglans regia* L., *Carya* sp., *Acer laetum* C.A. Mey, *Acer* sp., and *Tilia* sp. Then a detailed microfloral study was produced by Elhai and Rudel (1965) from the lignite clay from Pont de Chocol. The microflora of La Gratade has not been previously studied. Today, all these sites are widely scattered in the literature, most of them are not updated and not well constrained by radiometric dates. The more recent and detailed updates concern only the Miocene plant assemblage of Murat in the French Massif Central (Roiron, 1991; Legrand, 2003, 2010).

Recent harvests of macroflora were gathered by J.F. Pastre from 3 localities: Chambon Lake (LCh), La Gratade (LG) and Pont de Chocol (PTC), combined with new radiometric datations, bring us to complete and synthesize the results of former inventories. Despite the local character of such fossil records and the inequitable representation of ancient vegetation, they provide invaluable information about the history and distribution of the floristic elements and offer a great potential for identifying past environmental elements, making a contribution to a new picture of the palaeofloristic biodiversity in this area. The results of the palaeoenvironmental investigations are partly comparable but also complete earlier investigations with the description of 28 new taxa in Chambon Lake outcrop, as well as two species in La Gratade and Pont Chocol. The aims of the present study were: (i) to document, describe and determine the three new collections of plant fossils of Chambon Lake, Pont Chocol and La Gratade outcrops which were recently collected by one of us (JFP), (ii) to

compare these fossil plant collections to the one recovered and published by Grangeon and Rudel (1959, 1962) from the same area, (iii) to compare the Zanclean flora of these areas to other selected Pliocene floras in the Massif central region and from Western Europe, and (iv) to infer the palaeoecology of the three areas during the early Pliocene, using evidence from macrofossils and published data from dispersed pollen and spores.

2. Location and geological settings

The three fossiliferous outcrops studied in this article are all located in the French Massif central, in the periphery of the Mont-Dore strato-volcano (Fig. 1). They were deposited in lacustrine environments reworking contemporaneous pyroclastites and giving tuffite deposits.

The fossiliferous outcrop of the Chambon Lake (Altitude 866 m asl) is situated on the right bank of the Couze Chambon river downstreams from the Chambon Lake and to the West of the strombolian cone of the Tartaret (45.575° N, 2.929° E; Fig. 1). It was discovered in 1985 in trenches of *ca.* 1 m-depth dug for the electrification of a campground. The foliar imprints are contained in nodules of tuffites up to 30 cm in diameter. These nodules are higgledy-piggledy incorporated in a tuffaceous silty matrix which also contains some blocks of bedded sandy tuffites with volcanic minerals (alkali feldspars, biotite...). These facies characterize a secondary outcrop due to a major landslide localized in the N-E part of the lake and giving the hills situated to the east and bordering the lake. This landslide originated in the Dent du Marais cirque situated to the North and bordered by the diatreme of basaltic breccia of the Saut de la Pucelle (Besson et al., 1977). If this landslide, which is not covered by the scoriae of the Tartaret, is probably Holocene in age, the material embedded in this landslide is much older. Alkali-feldspars found in the sandy tuffites of the outcrop and attributed to a contemporaneous pyroclastic activity are used hereafter to infer the age of the foliar imprints thanks to $^{40}\text{Ar}/^{39}\text{Ar}$ dating method. If this outcrop offers a particular context due to its nodules, it is probably contemporaneous of the cinerites of the lake Chambon, which outcrop sporadically on the northern shore of the lake and in the hills situated near the parking of the beach (Besson, 1978).

The fossiliferous outcrops of the Pont de Chocoll and La Gratade are situated near the hamlet of La Gratade in the valley of the brook of Fontsalade, *ca.* 3 km to the South of the town of Rochefort-Montagne. The outcrop of Pont de Chocoll (961 m asl) is located in the bed of the stream of Fontsalade, 50 m downstream the bridge on the path of the hamlet of Chez Chocoll (45.656° N, 2.808° E; Fig. 2). It corresponds to bedded grey tuffites rich in foliar

imprints. Other tuffites can be found in some places on the left bank slope where they are found associated with weathered trachytic pumices beds as well as small blocks of trachyte. The outcrop of La Gratade (941 m asl) belongs to the same sedimentary unit. It is situated at about the half height of a small ravine tributary of the brook of Fontsalade, *ca.* 100 m to the NW of the mill of La Gratade (45.660° N, 2.806° E; Fig. 2). It is made of white to pale grey-bedded tuffites outcropping on *ca.* 2 m high that we also samples for $^{40}\text{Ar}/^{39}\text{Ar}$ dating purpose.

The granitic basement outcrops in the valley to the South and to the North of the study area. The position of the tuffites, which are several tens of metres thick, is anachronistic. It is very probable that they correspond to a lacustrine infilling of a maar crater opened in the basement. The first formation of the Mont-Dore *sensu stricto* which covers these tuffites corresponds to the “Grande Nappe” (= ignimbrite) of rhyolitic fibrous pumices which can be seen along the road D80, north from La Gratade and which is dated at 2.77 ± 0.07 Ma (Nomade et al., 2017).

3. Material and methods

3.1. Macroflora

Plant fragments were recovered by splitting clay containing the impression/compression fossils. Minimal preparation with fine needles was performed to fully expose the plant organs when needed. Cuticles are often present but were not studied here. The images were processed and measurements obtained using Nikon binocular loupe and Canon Elements. The taxonomic determinations established in this study are based exclusively on the gross morphological characters of the gathered specimens, whereas special attention is paid to the morphological details of lamina venation and margin outline of the leaves. The morphological terminology is based on the descriptions of Hickey (1973), Dilcher (1974) and L.A.W.G. (1999). Two major treatments serve as a basis for the data presented here: besides several preliminary papers consulted (Grangeon, 1956; Roiron, 1991; Legrand, 2003, 2010), foliage are compared with and herbarium specimens and living material. The analyses are based on detailed comparisons of individual elements with the living analogues according to detailed morphological and anatomical studies. For palaeoenvironmental reconstruction, the Nearest Living Relative method (Mosbrugger and Utescher, 1997) assumes that the fossil taxon had a climate tolerance and habitat similar to that of its nearest living relative.

All the studied new macrofossil specimens are housed at the LGP (CNRS, Meudon). Ancient collections were not revised in this work.

3.2. Microflora

The three samples were first treated with 37% hydrochloric acid (HCl) to dissolve the carbonate, and after washing, the residue was treated with 52-62% hydrofluoric acid to dissolve silica. The residue obtained by chemical dissolution of the mineral sample was further processed with KOH to extract the organic material from the mineral. The organic residue material was washed and centrifuged at 3600 rpm for 10 min. The residue from the casting ring was applied to a glass slide, dried, and after the addition of glycerine gelatine, it was covered with a cover slip. A transmitted light microscope (Leica) with $\times 400$ and $\times 1000$ magnifications (without oil immersion) was used for identification, and $\times 400$ was used for the counting of pollen and spores. Pollen and spore identification was accomplished using Henri Elhaï reference database. Other published keys and pollen atlases were also used as well as atlases of recent pollen (Reille, 1992, 1995).

3.3. Ar/Ar sampling and analytical method

About 500 g of the pale grey-bedded tuffites (La Gratade hereafter) and of the sandy tuffites (Mdo hereafter) from La Gratade and Chambon Lake sites were sampled. After wet sieving, we kept the 600 μm to 1 mm fraction. From this fraction we picked 20 pristine K-feldspars crystals for each sample. These crystals were irradiated 1:30 hours in the B1 tube of the Osiris reactor (Irradiation 35; CEA Saclay Center, France). After irradiation, 9 and 10 crystals for Mdo and Gratade samples were individually loaded in a copper sample holder. The sample holder was then put into a double vacuum Cleartran window. Each crystal was then fused using a Synrad CO₂ laser at 15% of nominal power (*ca.* 25 W). The extracted gas was purified for 10 min by two hot GP 110 and two GP 10 getters (ZrAl). Argon isotopes (³⁶Ar, ³⁷Ar, ³⁸Ar, ³⁹Ar and ⁴⁰Ar) were analysed by mass spectrometry using a VG5400 equipped with an electron multiplier Balzers 217 SEV SEN coupled to an ion counter. Neutron fluence J for each sample was calculated using co-irradiated Alder Creek Sanidine (ACs-2 hereafter) standard with an age of 1.193 Ma (Nomade et al., 2005) and the total decay constant of Steiger and Jäger (1977). J-values computed from standard grains is $0.00067860 \pm 0.00000339$ and $0.00068750 \pm 0.00000344$ for Mdo and La Gratade, respectively. The ⁴⁰Ar/³⁹Ar age is a not a direct method and relies on the precise measurements of the ³⁹Ar produced in the nuclear reactor; for this, we used a natural K-feldspars standard (i.e., crystals extracted from rock of known age) that was irradiated under the same conditions than the sample of interest. The J-value was therefore the weighted mean and corresponding standard

deviation based on the measurements of 3 to 6 standard crystals (in our case, Alder creek sanidine). This J flux factor was used to quantify the Neutron induced ^{39}Ar made from ^{39}K in the nuclear reactor that can varied as a fonction of the irradiation duration and position of the sample with respect to the irradiation schuttle and cannot be predicted from previous irradiation.

Mass discrimination was estimated by analysis of Air pipette throughout the analytical period, and was relative to a $^{40}\text{Ar}/^{36}\text{Ar}$ ratio of 298.56 (Lee et al., 2006). Procedural blank measurements were computed after every two or three sample crystals, depending on the beam measured. For 10 min static blank, typical backgrounds are *ca.* $2.0\text{-}3.0 \times 10^{-17}$ and $5.0\text{-}6.0 \times 10^{-19}$ mol for ^{40}Ar and ^{36}Ar , respectively. The precision and accuracy of the mass discrimination correction was monitored by weekly measurements of air argon of various beam sizes.

4. Results

4.1. $^{40}\text{Ar}/^{39}\text{Ar}$ datations

Full analytical details for individual crystal are given in Tables S1 and S2 (Appendix A). Results are presented as probability diagrams in Fig. 3. In this figure, individual crystal age uncertainties are given at 1σ -level and the weighted mean age uncertainties are quoted at 2σ -level, including J uncertainties. In both sample we found only one main population of crystal as shown by the unimodal probability diragrams (Fig. 3). Despite a slight excess scattered, meaningful weighted mean ages of 3.94 ± 0.04 Ma (MSWD = 1.9) and 4.46 ± 0.05 Ma (MSWD = 2.0) can be calculated for La Gratade and Mdo, respectively. It is worth noting that three crystals from Mdo displayed very low precision (Fig. 3) due to their low radiogenic content (i.e., 38 to 78%; see Appendix A for details). Removing these crystals from the weighted mean age does not change the weighted mean age reported above for this sample. These two ages are interpreted as the age of eruption of the volcanic material found in the two studied sites.

4.2. Floristic composition

4.2.1. Pollen analysis and palynofacies

All studied samples yielded well preserved sporomorphs suitable for detailed palynological analysis in Table 1, showing that the floras are in agreement with the $^{40}\text{Ar}/^{39}\text{Ar}$ datations. In detail, pollen grains of gymnosperms and angiosperms were very frequent in all

samples. Fern and cryptogam spores were rare. In all, 437 pollen grains (of which 3% are herbaceous taxa) were identified at Chambon Lake, 414 pollen grains (of which 6% herbaceous) at Pont de Chocol, and 359 pollen grains (of which 11% herbaceous) at La Gratade, excluding the Fungus spores and the Algae. The number of terrestrial spermatophyte taxa found in each level varies from 30 to 40 species. The list of taxa is fairly similar in the four sites as well as between samples from each site (Table 1).

The vegetation indicates a forest physiognomy in the 3 different deposits, with Arboreal Pollen (AP) ranging from 88 to 97%. Poaceae are rare (0.7-1.7%); other herbaceous species are represented by few pollens of Cyperaceae, Apiaceae, Rosaceae, *Nuphar*, Caryophyllaceae, Amaranthaceae, Leguminosae, Papaveraceae, *Helianthemum*, Lamiaceae, and Ranunculaceae. The maximum diversity is reached in Pont de Chocol deposits. Ericaceae frequency increase is noted in La Gratade and Pont de Chocol outcrops.

In the different palynological samples, *Pinus diploxylon* type is always dominant with pollen values between 25 and 34% while *Cathaya* is recorded with only 1-1.6% and *Pinus haploxylon* with values between 0.8 and 2.3%. *Pinus* are mainly accompanied by *Picea* (5.7-14.5%); higher frequencies are recorded in the Chambon Lake. *Picea* pollen percentages lower than 5% in extant vegetation are considered as an indication of regional presence (Hicks, 1994; Huntley and Birks, 1983); two different *Tsuga* species recorded together between 3 and 7.2%, *Abies* 4.4-10% and *Sciadopitys* 6% in LCh, 1% in La Gratade, but the taxa is absent from Pont de Chocol.

Pollen grains of Cupressaceae (including “Taxodioid” pollen types) are represented with few pollens, respectively 0.7-2.3% and 0.4-4.6%, with lower frequencies recorded in La Gratade and Pont de Chocol areas. Angiosperms are more diversified. Deciduous oaks were always present with low values of 3.6% and peaking at 6% in Pont de Chocol and 12% in La Gratade. *Carya* percentages are between 2.1 and 5%. Others arboreal taxa are *Fagus* with range frequencies of 1-5.8%, *Pterocarya* (1.7-2.4%), *Juglans* (1-3%), and *Ulmus-Zelkova* (1.6-2.6%). *Nyssa* is recorded with only one pollen in LCh and PTC. The absence of *Engelhardia* (Sapotaceae) is worth to be mentioned. Non pollen palynomorphs (NPP) were scarced; among them the freshwater Botryococcaceae algae *Botryococcus braunii* Kützing, 1849 is a common element in the different deposits, with 6-13.4% in Chambon Lake and Pont de Chocol and a lower representation in La Gratade (1.2 %). Several epiphyllous fungi are observed.

Several remarks can be expressed. The forests found in both successions are always relatively dense, with a thick forest canopy. Herbs which have entomophilous pollen

dissemination are practically absent in the three outcrops (4-12%); the list of present-day taxa extinct in the region is the same or very similar, showing the presence of many trees living today in warm-temperate Asia, North America and Caucasia associated with still extant species. Very similar vegetations are shown at both sites with, however, slightly differences in the frequencies of the different taxa. There is an indication for a pollen rain coming from several vegetational belts, as it results from the mixing of montane, mesophilous and hygrophilous elements. A homogenous forest formation characterizes the three outcrops. *Sciadopitys* is not recorded in La Gratade deposit. Sporomorph assemblages show the apparent predominance of “arctotertiary” (including warm temperate and temperate) and cosmopolitan floristic elements. The palaeotropical and palaeotropical/warm temperate taxa were represented by a single pollen of *Nyssa* both in La Gratade and Pont de Choccol outcrops.

Concerning the presence of some arboreal taxa, few observations are useful to interpret the different records and to locate them in the chronological scale. First of all, we note the permanence of many mesothermic taxa such as *Carya*, *Juglans*, *Pterocarya*, *Liquidambar*, and *Zelkova*. *Liquidambar* disappeared from The Netherlands at the end of the Reuverian or at the beginning of the Praetiglian in Koningsbosch (Zagwijn, 1960) and in Normandie (Clet-Pellerin, 1983); it is absent in altitude but remains present in south Europa (Bertini and Martinetto, 2008; Suc et al., 2018), *Engelhardtia* disappeared at the end of the Miocene in The Netherlands (van der Hammen et al., 1971). “Taxodioid” Cupressaceae disappeared in Netherlands at 2.5 Ma (Zagwijn, 1974), during the Praetiglian in Normandy (Clet-Pellerin, 1983), at 3 Ma in Languedoc (Suc, 1980), and at 1.6 Ma in North Italy (Bertini and Martinetto, 2008; Suc et al., 2018).

The optical characterization of the micro-organic matter (palynofacies) in Table 1 highlights different environments: in Chambon Lake, two classes of organic matter are recognized. The first one shows a high percentage of particulate organic matter (POM = 85%) composed of diversified terrestrial plant fragments (mainly yellow-brown wood and cuticles, palynomorphs dominated by pollen contribute only to 10% of the POM total). It also contains opaque phytoclasts (up to 5% of the total of the organic matter). The second class is the amorphous organic matter with no recognizable elements (AOM = 15%).

La Gratade organic matter content is composed with POM (80%) dominated by sporomorphs and AOM which contributes for 20%. In Pont de Choccol, 3 classes are described: POM (50%), AOM (45%) and carbonized particles (COM = 5%).

Zooclasts and fungus spores are absent from the different palynofacies records.

4.2.2. Macroflora composition

The Recent collectings at three sites, Chambon Lake, La Gratade, Pont de Chocoll in the Mont-Dore (Puy de Dôme, France) has resulted in the recovery of numerous plant specimens (Table 2; Figs. 4-10). The palaeobotanical dataset is mainly composed of foliages (impressions, sporadically carbonized compressions) and less frequently of fruits and seeds. The plant fossil material of Chambon Lake is abundant and with an excellent quality of preservation. Most of the leaves are entire; they are preserved in a fine, regularly laminated sediment, while in other sites the deposited material is quite damaged and is characterized by numerous fragmented and small sized samples.

Most of the recorded angiosperm genera are present in the pollen analysis. In previous macroflora researches, only 9 taxa have been described from the Lake Chambon outcrops: *Bambusa cambonensis*, *Alnus glutinosa* Gaertn., *Fagus sylvatica* L., *Fagus pliocenica* Sap., *Populus tremula* L., *Ulmus effusa* Willd., *Acer pseudocampestre* Ung., *Acer Nicolai* N.B. (aff. *A. opulifolium* Willd.), *Carpinus betulus* L., and Poaceae (Marty, 1912; Grangeon and Rudel, 1959). With the new collection described in this paper the former floristic record is extended by 23 additional taxa. Angiosperms, which apparently prevail in macroflora, are documented either by numerous leaves and leaflets or less frequently by fruits and seeds or needles (Table 2). Fagaceae are by far the most diversified and the most abundant in the Chambon Lake assemblage. It comprises at least one more beech species: *F. grandifolia* type (Fig. 5(A, B)), associated with abundant leaves of *F. sylvatica* L. (Figs. 4(A), 5(I)) and two other different oak species (*Q. Roburoides* Gaud. (Fig. 5(C-E)) and *Q. hispanica* Rér. (Figs. 4(F), 5(F), 6(I, J)). Betulaceae are abundantly represented by diversified *Alnus* species including *A. glutinosa* Gaertn. (Fig. 4(J)), *A. stenophylla* Sap. et Mar. (Fig. 4(G-I)), *Alnus* sp., as well as *Betula subpubescens* Goepp., *B. macrophylla* (Goerpp) Heer (Fig. 4(B-E)), *Betula alnoides* Buch. Ham.ex D. Don (Fig. 8(D)), *Betula* sp. (Fig. 4(H)), *Carpinus betulus* L. (Fig. 9(G)) and *Carpinus orientalis* Sap. (Fig. 9(I)). Salicaceae (*Salix* sp.) are not common in the different deposits. Leaves of *Ulmus braunii* type (Fig. 8(A)), *Zelkova ungeri* aff. *Z. acuminata* Planch. (Fig. 7(C)) and *Zelkova ungeri* aff. *Z. crenata* Spach. (Figs. 5(A), 7(A, B, D)), *Carya minor* Sap. et Mar. (Figs. 6(G), 8(C)), and *Pterocarya* sp. (Fig. 8 (F, H, I)) are well documented. In addition, a few interesting, though very poorly represented accessory elements have been collected that correspond to the ancient morpho-species and well preserved fossil leaves of *Acer laetum* Unger (Fig. 6(A)), *Acer integerrimum* (Viv.) Mass. (Fig. 6(B)), *Acer sanctae-crucis* Stur (Roiron, 1991) (Fig. 6 (C, D)) as well as an unidentifiable *Acer* sp., *Buxus pliocenica* Saporta et Marion (two leaf specimens), and *Cornus distans* type (Fig. 7(G, H)).

Leguminosae are represented by the morphotype element *Leguminophyllum* sp. 1 (Fig. 8(E)) and a set of unidentified taxa including *Dicotyphyllum* sp. 1 (Fig. 9(J)), *D.* sp. 2 (Fig. 9(E)), *D.* sp. 3 (Fig. 8(B)), *D.* sp. 4 (Fig. 7(I)), and *D.* sp. 5 (Fig. 6(H-K)). Few fruits or seeds of *Carpinus suborientalis* Sap. (syn. *C. tschonoski* Maxim, 1881) (Fig. 10(I)), *Carpinus betulus* L. (Fig. 10(D)), *Betula* sp. (Fig. 10(A-C)), *Alnus* sp. (Fig. 10(F)), *Pinus* sp. (Fig. 10(H)), *Picea* sp. (Fig. 10(G)) and *Tsuga* (Fig. 10(E)), as well as one needle of *Abies ramesi* Sap. (Fig. 9(K)) and one of *Tsuga* sp. (Fig. 7(J)) are recorded in the macroflora.

The Chambon Lake macroflora assemblage, apart from the great number of specimens, is considered to be fairly diverse with a well preserved macroflora comprising 33 taxa identified at this stage (former study and this paper; Table 2), including at least 10 gymnosperms, the presence of some of them being demonstrated by both reproductive and few vegetative organs. With a few winged seeds and numerous pollen, *Abies ramesii* Sap., ?*Tsuga* or *Picea* sp. are poorly represented in the macroflora but are abundant in the pollen flora. *Pinus* L. and *Sciadopitys* (Thunb.) Siebold et Zucc. are only documented by well distinguishable pollen that are particularly numerous in all fossiliferous layers of the site.

Comparatively, La Gratade and Pont de Chocol, both located between the Roche Tuilière and Sanadoire in the South and Rochefort-Montagne in the North, are more monotoneous. The great majority of the 23 plant taxa formerly described from La Gratade site show great similarities with the Chambon macroflora. Taxa identified by Grangeon and Rudel (1962) are *Potamogeton quinquenervis* N. Boul., *Salix* sp., *Populus tremula* L., *Populus alba* L., *Betula macrophylla* Heer, *Alnus glutinosa* Gaertn., *Carpinus orientalis* Mill. (fruits and leave), *Carpinus paucinervia* Andreansky, *Corylus avellana* L., *Fagus sylvatica* Sap., *Castanea vesca* Gaertn., *Quercus hispanica* Rer., *Quercus* sp. (groupe *Q. drymeja*), *Zelkova ungeri* Kovats (*crenata* and *acuminata*), *Ulmus* sp., *Juglans regia* L., *Carya* sp., *Acer laetum* C.A. Mey, *Acer* sp., *Tilia* sp., and *Torreya nucifera* Sieb. et Zucc. In the present paper only 10 taxa were identified (Table 2); *Quercus* leaves are abundant but predominantly incomplete, the species was probably the local dominant species in the area with *Alnus* sp., *A. stenophylla*, *Betula subpubescens*, *Fagus sylvatica*, *Fagus grandifolia*, and *Zelkova* type *Z. crenata*. Among these species only *Fagus grandifolia* was not recorded previously.

Pont de Chocol new record is a smaller and very similar assemblage with 12 taxa: *Pteridium aquilinum* (L.) Kuhn, *Alnus glutinosa* Gaertn., *Alnus kefersteinii* Ung., *Alnus viridis*?, *Quercus hispanica*, *Quercus* sp., *Q. roburoides* Ber., *Ulmus* type *U. braunii*, *Zelkova* type *Z. acuminata* Planch, and *Dicotyphyllum* sp. 3 which probably belongs to the Leguminosae.

Herbaceous remains, excluding Poaceae, are totally absent from the macroremain assemblages of the three deposits. Ferns are recorded in Pont de Chocoll with one sample (*Pteridium aquilinum* (L.) Kuhn). Buxaceae and gymnosperms are lacking in the small macrofloral collection from La Gratade and Pont de Chocoll, but this absence does not mean that they were not present in the palaeoflora.

4.2.3. Vegetation reconstruction

There is no apparent correspondance between the macro- and microfossil records. Macroflora indicates preferentially local vegetation while microflora records a wider environment and provides quantitative data. The combined analyses constitute a comprehensive part of environment and allow for a more accurate differentiated reconstruction of the vegetation types and environments. According to zonal and azonal vegetation of the different sites was quite diverse but not totally uniform. First, in the micro- and macro-analyses arboreal elements prevail and few plants are indicative of open landscapes; apart from taxa with a wide ecological range (*Ulmus* and *Zelkova*), the presence of few dispersed Leguminosae leaflet (found only in LCH and PTC) and reduced humid heliophilous forest with *Sciadopitys*, *Nyssa* and “Taxodioid” Cupressaceae might indicate the presence of more open areas. The minor contribution of herbaceous plants in the different palynological pollen records (Elhai and Rudel, 1961, 1965; Elhai et al., 1963; this study) is difficult to interpret, as suggested by Favre et al. (2008) and not well aligned with the presence of some heliophilous taxa (Leguminosae) which are recorded in the different outcrops.

Four main vegetation types well known in the Neogene are identified. The aquatic vegetation type is absent from the macroflora; diversified aquatic plants (*Potamogeton*, *Sparganium*, *Nuphar*) and abundant *Botryococcus* records point to the presence of a waterbody with stagnant or slowly moving water (Guy-Ohlson, 1992) according to palynological analysis. They are only recorded with high frequencies in the two deposits of Chambon Lake and Pont de Chocoll. Only few taxa represent the riparian azonal vegetation with *Alnus* sp., *Alnus glutinosa*, *Alnus stenophylla*, *Betula macrophylla*, *Betula subpubescens*, *Betula* sp., *Salix* sp., *Fraxinus* sp., and *Acer laetum*. Pollen and macroremains are encountered in all deposits. The occurrence of *Sciadopitys* pollen may indicate a swampy vegetation as found in the Neogene of Bresse where for the first time in Western Europe macroremains support a different ecology than extant species (Philippe et al., 2002). Possibly, *Sciadopitys* may underline a moist broad similar to that occupied by the extant species *S. verticillata*, an

endemic of Southern Japanese mountains under leaved forest, temperate maritime climate with high rainfall and moisture. *Sciadopitys* lives there under more severe thermal conditions, i.e., it withstands three to six months of cold weather (mean temperature less than 15°C) (Willard 1994).

Most of the elements dominating the assemblage (deciduous Fagaceae, *Carpinus*, etc.) belong to the broad-leaved forests outside swampy and flooded habitats and covered large parts of the studied areas. Diversified *Fagus* species dominated the flora in the area of Chambon with a clear predominance of *Fagus sylvatica* while the deciduous oaks and especially *Quercus robur* and *Quercus hispanica* were predominating locally in the forest of PTC and LG. Some, more likely mesophytic woody elements are better represented, e.g., *Zelkova*, *Acer* spp., deciduous Juglandaceae, namely *Carya*, *Pterocarya* and *Juglans* may have entered both mesophytic and non-flooded areas together with *Ulmus*, *Fraxinus* and Salicaceae. Some shrubs (cf. Buxaceae) are relatively rare in the fossil macrofloras. In areas with poor substratum, the pine trees were probably forming pure stands, although the high amount of pollen in the assemblage allows us to suppose that this element was spreading also on sites with higher soil fertility forming a mixed oak-beech-pine forest and belonged to mesophytic representatives of mixed coniferous and broad-leaved deciduous forests.

The last vegetation type constitutes the highland vegetation with the development of conifer forests with *Picea*, *Abies* and *Tsuga*.

Termophilous elements (megathermic and mega-mesothermic elements *sensu* Fauquette et al. 2007) such as some Hamamelidaceae, Lauraceae, Sapotaceae, *Symplocos* and others, which may indicate the Mixed Mesophytic Forest of East Asia, are largely absent. As it is revealed by previous and present studies, the assemblage is floristically characterized by the apparent predominance of ‘arctotertiary’ elements (Mai, 1991; Ferguson and Knoblock, 1998) whereas thermophilic elements are quite rare. The simultaneous occurrence of these units and elements attests to a relatively humid, warm-temperate climate. Modern analogues of the studied outcrops might be the rich mesophytic deciduous forest of the Eastern part of North America, Northern China and Caucasus.

5. Discussion

Pliocene plant assemblages in the French Massif central occur at localities variously dated and in various stage of exploration. Based on published fossil floras for most of them, it appears that most micro- and macroflora assemblages may be less stratigraphically controlled than assumed in several former studies, as demonstrated by Bellon (1971) and Gibert et al.

(1977) with the first radiometric controls for several Miocene outcrops in Cantal (Massif central, France).

Based on palynological data, the discussed floristic assemblages of the Chambon Lake, La Gratade and Pont de Choccol areas emphasise the presence of temperate deciduous elements mixed with abundant Pinaceae as typical for the Neogene of Europe. A “Villafranchian” age (3.58-1.7 Ma) was estimated for these three assemblages by comparison with the detailed climatic reconstructions established in The Netherlands by Zagwijn (1960) for the last 5 myr based on pollen analysis, which stimulated comparable palynological researches. The new $^{40}\text{Ar}/^{39}\text{Ar}$ dates obtained for Chambon Lake (4.46 ± 0.05 Ma) and La Gratade (3.94 ± 0.04 Ma) places the deposits in the Zanclean (= Brunssumian; 5.32-3.58 Ma). The Zanclean is first subdivided into three climatic periods: warm (Brunssumian A from 5.33 to ca. 4.75 Ma, cooler (Brunssumian B from ca. 4.75 to ca. 4.00 Ma), and the warmest phase (Brunssumian C from ca. 4.00 to ca. 3.60 Ma) (Suc and Zagwijn, 1983; Zagwijn and Suc, 1984; Suc et al., 1995). Recently, new ages extrapolated from the climatostratigraphic interpretation of the DSDP site 380 pollen record were proposed for the Brunssumian A (5.45-4.08 Ma), the Brunssumian B (5.08-3.94 Ma), and the Brunssumian C (3.94-3.37 Ma) by Popescu et al. (2010).

Pinus has an important place in the palynological records, whereas *Abies*, *Picea*, *Sciadopitys* and *Tsuga* are also important components of the vegetation. The deciduous component of the forest is diversified with *Acer*, *Betula*, *Carpinus*, *Corylus*, *Fagus*, *Carya*, *Pterocarya*, *Juglans*, *Quercus*, *Tilia*, *Ulmus*, and *Zelkova*, with high abundance of *Sequoia*-type (concurrent with abundant *Taxodium*-type) and regular occurrence of *Symplocos* and Sapotaceae (Zagwijn, 1960; Roche et al., 2004). These taxa are sometimes associated with several morphotypes (*Tricolporopollenites edmundi*, *T. librarensis*, *T. megaexactus* and *T. microhenrici*) which cannot be considered as valid taxa (Suc et al., 2018).

By comparing our data with micro- and macrofloras recognized in nearby regions with similar datations, it appears that the floristic composition of the lower Pliocene is not uniform. Some analogies might also be drawn with the record from the same altitudinal range in the upper Miocene lacustrine diatomite deposits from Murat (Massif central, Cantal) dated by the K/Ar method to 5.34 ± 0.3 Ma (Roiron, 1991, corrected in Kovar-Eder et al., 2006). Murat macroflora includes *G. europaeus*, *Sequoia abietina*, *Abies ramesi*, *Pinus* sp., *Picea* sp., *A. ducalis*, *A. cecropiifolia*, *Alnus viridis*, *Alnus* sp. (cf. *A. kefersteinii*), *Betula* sp., *Carpinus suborientalis*, *Carpinus betulus*, *C. orientalis*, *Q. hispanica*, *Q.* sp. (cf. *Q. macranthera*), *Q. kubinyi*, *Z. zelkovifolia* (aff. *Z. crenata* and *Z. acuminata*), *Ulmus campestris*, *U.* sp. (cf. *U.*

fulva), *Celtis australis*, *Populus tremula*, *Carya minor*, *Juglans regia*, *Phellodendron* sp. (cf. *P. amurense*), *Cedrela* sp., *A. integerrimum*, *A. sanctae-crucis*, *A. campestre*, *A. opulifolium*, *A. platanooides*, *A. tricuspidatum*, *H. helix*, *Ilex* sp. (aff. *Ilex cornuta*), *Tilia tomentosa*, *Dombeyopsis lobata*, *Berberis* sp. (cf. *B. regeliana*), *Ceratophyllum demersum*, *Crataegus* sp. (cf. *C. douglasii*), *Prunus acuminata*, *Rosa* sp. (cf. *R. californica*), cf. *Photinia*, and *Bambusa* sp.

The microfossil analysis (Durand and Rey, 1964) gives the following results: *Pinus* (59%), *Picea* (31%), *Abies* (1%), Cupressaceae, *Tsuga*, *Carya*, *Pterocarya* (total 3.5%), *Sciadopitys*, *Sequoia*, *Taxodium*, *Nyssa* (total 3%), *Betula*, *Alnus*, *Quercus*, *Ulmus*, *Fagus* (total 2%), and herbaceous plants (1%). The thermophilic elements such as “Taxodioid” Cupressaceae are scarce while mesophilic taxa are abundant as *Alnus*, *Carpinus*, *Acer*, *Zelkova*, deciduous *Quercus*, *Carya*, etc. Lauraceae are recorded by Legrand (2011) and Hamamelidaceae are lacking. This vegetation may indicate a climate change at the end of the Miocene with a continuous decline in Chambon Lake palaeoflora. The lack of *Sassafras*, *Cedrela* and *Phellodendron* differentiates the Chambon Lake from Murat and may indicate a new significant climate change between 5.34 and 4.4 Ma or an overall cooler aspect due to higher elevation and may relate to the cooler phase of the Zanclean B (= Brunssumian B) in Chambon Lake. In La Gratade and Pont de Choccol, pollen records prove otherwise that microthermic elements are regressing while the mesothermic members are increasing, as seen in the warmest phase of the Zanclean C.

The Massif central results do not fit well with the general evolution of leaf and microfloras described from different Pliocene deposits of lowland from Western Europe. These different deposits include only a few common elements. In Northwestern Europe localities, high *Sequoia* content are recorded at Susteren (Zagwijn, 1960) and La Londe (Clet-Pellerin, 1983) but are absent from the Mont-Dore and Cantal records.

Pliocene of the so-called “Hagenau terrace” and lowlands of the Rhine River in Northern Alsace, France, has yielded numerous fossil plant remains (Geissert, 1974, 1979; Geissert and M  nillet, 1979; Geissert et al., 1990) dated from the early to late Pliocene without independent dating. Most of the elements dominating the Auenheim assemblage show high similarities with the Mont-Dore outcrops and described as *Fagus*, deciduous *Quercus*, *Carpinus*, Salicaceae, and Ulmaceae, belonging to the deciduous mesophytic to moist riparian broad-leaved forests outside swampy and flooded habitats. Only a few woody elements are swamp plants, *Taxodium*, *Alnus*, *Nyssa*, and *Fraxinus*. Mesophytic woody elements are better represented, e.g., *Zelkova*, *Acer* spp., *Buxus*, *Carpinus*, and Rosaceae. *Carya* and *Pterocarya*

may have entered both mesophytic and riparian non-flooded areas together with *Ulmus*, *Zelkova*, *Fraxinus*, *Gleditsia*, and *Salicaceae*. Also all recorded gymnosperms except *Taxodium*, such as *Ginkgo*, *Pinaceae*, and *Torreya* belong to mesophytic representatives of mixed coniferous and broad-leaved deciduous forests in the Northern Hemisphere.

Thermophilous elements, such as evergreen *Fagaceae*, *Lauraceae* and others, which would indicate the Mixed Mesophytic Forest of East Asia, are largely absent. Exceptions are *Cathaya* and *Craigia*, two relict living genera, which deviate from their ancestors in their more thermophilous character (Kvacek et al. 2008; Teodoris et al. 2009).

Conifers are represented by some more boreal elements, such as *Picea* and *Abies*, typical of the mixed coniferous and broad-leaved deciduous forests. This is a characteristic feature of most late Pliocene floras of Europe. Rare subtropical/evergreen elements occur; typical plants of the European Pliocene (*Sassafras*, *Torreya*) are also present, which may correspond to the altitudinal level of the Auenheim site.

Between North and South a thermic gradient is significant. The Northern Mediterranean area is characterized by dominance of arboreal pollen, suggesting a dense forest cover (Suc et al., 1995) with the presence of mega-mesothermic elements (*Cupressus*, *Cedrela*, *Laurus*, *Persea*) from records in South localities of Cessenon (Zanclean) situated near Murviel (Hérault, France) (Roiron, 1991, corrected in Kovar-Eder et al., 2006) and the early Pliocene plant assemblage of Pichegu (Gard, France) (Roiron and Ambert, 1990, corrected in Kovar-Eder et al., 2006). The plant assemblage of Cessenon includes: *Abies* sp., *Pinus* sp., *Glyptostrobus europaeus*, cf. *Sequoia*, *Cupressus* cf. *sempervirens*, *Laurus primigenia*, *P. leucophylla*, *Quercus coccifera*, *Quercus ilex*, *Q. hispanica* (aff. *sessiliflora*), *Q. kubinyii*, *Alnus ducalis*, *Populus tremula*, *Salix* sp., *Prunus* sp., *Cedrela* sp., *Nerium oleander*, and *Fraxinus* cf. *oxycarpa*. The leaf assemblage contains only a few subtropical taxa such as *Glyptostrobus* or *Cedrela*, absent from the Mont-Dore flora, some riparian elements such as *Populus*, *Salix* and *Platanus*, and plants with Mediterranean nearest relatives such as *Cupressus*, *Laurus nobilis*, *Q. ilex*, *Q. coccifera*, *Nerium*, etc. This assemblage is compared with the Californian vegetation, the similar extant model where subtropical humid taxa live mixed with more xerophilic plants (Kovar-Eder et al., 2006). The microflora of Cessenon is more diversified and includes conifers such as *Cathaya* and *Cedrus*, mesophilic deciduous broad-leaved taxa such as *Liquidambar*, *Parrotia*, *Carya*, and Mediterranean elements such as *Pistacia*, *Olea* and *Phillyrea* (Suc, 1980). Hence at the beginning of the Pliocene, the climatic conditions in Languedoc show a decrease in summer rainfall (Roiron, 1991).

The early Pliocene plant assemblage of Pichegu (Gard, France) includes (Roiron, 1991, corrected): *Ginkgo adiantoides*, *Abies* cf. *spectabilis*, *Tsuga* cf. *caroliniana*, *Chamaecyparis polymorphum*, *D. ungeri*, *L. nobilis*, *L. primigenia*, *O. heeri*, cf. *Persea gratissima*, *P. leucophylla*, *L. europaea*, *Ulmus pyramidalis*, *Zelkova zelkovifolia* (aff. *Z. crenata* and aff. *Z. acuminata*), *Carya minor*, *Pterocarya denticulata*, *Fagus gussonii*, *F. pliocenica*, *Quercus faginea*, *Q. hispanica* (aff. *Q. sessiliflora*), *Q. ilex*, *Q. kubinyii*, *Q.* cf. *castaneifolia*, *Alnus ducalis*, *Carpinus betulus*, *C. orientalis*, *C. suborientalis*, *C.* cf. *tschonoskii*, *Populus alba*, *P. balsamoides*, *P. nigra*, *P. tremula*, *Salix* sp., *Acer tricuspidatum*, *A. sp.*, and *Bambusa* sp. The assemblage is rich in mesophilic taxa and riparian elements. Some xerophilic taxa such as *Carpinus orientalis*, *Q. ilex* and *L. nobilis* are present. In addition, the record contains megamesothermic taxa such as subtropical Lauraceae and Celastraceae. There are no taxodioids in the macrofossil record but the pollen diagram shows a decrease in Cupressaceae (including Taxodiaceae) from the base to the upper part of the section (Suc, 1980). The disappearance of taxodioids in Languedoc at that time is certainly caused by the Mediterranean-type climate with dry summers (Suc, 1984; Girard et al., 2019).

6. Conclusions

The plant material recovered from Chambon Lake, La Gratade and Pont Chocot (Puy-de-Dôme) and newly dated to 4.46 ± 0.05 Ma and 3.94 ± 0.04 Ma by $^{40}\text{Ar}/^{39}\text{Ar}$ are among the taxonomically richest lower Pliocene floras in the French Massif central. The plant assemblage of micro- and macrofloras added complementary data of both autochthonous and allochthonous origin. It comprises at least 76 different taxa (pollen flora and macroflora), a number considerably increased with the recent collect of macrofossil material. It consists mainly of broad-leaved deciduous angiosperms (*Fagus*, *Quercus*, *Pterocarya*, *Carya*, *Ulmus*, *Zelkova*, *Betula*, and *Acer*) and conifers (*Pinus*, *Tsuga*, *Abies*, *Picea*, and Cupressaceae including members of the former Taxodiaceae family). According to comparisons with the current data, the Zanclean palaeoflora indicates the occurrence of extensive riparian woods throughout the wetlands, together with deciduous mesophytic and mid altitude forests at the slopes of the surrounding hills, developed in a relatively warm temperate and humid climate. These new plant findings offer a unique opportunity to enrich our still fragmentary knowledge of lower Pliocene palaeovegetation and to gain a more accurate picture of the plant succession and palaeoenvironmental history of the French Massif central region.

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Table and Figure captions

Table 1. Palynological results of LCh, LG and PTC outcrops (Puy-de-Dôme, France).

Table 2. Summary of the macrofloristic composition of the studied localities of Chambon lake, La Gratade, and Pont de Chocol, including the NLR (Near Living Relatives; Mosbrugger and Utescher, 1997) and frequency groups: *, single (1 specimen); **, 2-5 specimens; ***, 6-15 specimens; ****, predominant (>16 specimens). Locality: LCh, Chambon Lake; LG, La Gratade; PTC, Pont de Chocol. Botanical organs studied: L, leave; S, seed; F, fruit.

Fig. 1. Geographical and geological map of the Chambon Lake area (Massif Central, France), modified from Besson et al. (1977). 1: Scree; 2: Recent alluvium; 3: Landslide; 4: Basaltic fall of the Tartaret; 5: Strombolian scoriae of the Tartaret; 6: Basaltic breccia of the Saut de la Pucelle; 7: Cinerites of the Lake Chambon; 8: Nuées ardentes deposits; 9: Trachyte; 10: Soshonite lava-flow; 11: Basaltic lava-flows; 12: Oligocene clayey sands; 13: Cristalline basement; 14: 90 m-high cliff; 15: Summit depression; 16: Fossiliferous outcrop.

Fig. 2. Geographical and geological map of La Gratade and Pont de Chocol area (Massif Central, France), modified from Brousse and Tempier (1981) BRGM geological map 1/50,000 Bourg-Lastic (infoterre.brgm.fr). 1: Granitic basement (La Bourboule granite); 2: Tuffites from la Gratade; 3: "Grande Nappe" rhyolitic ignimbrite; 4: Volcano-sedimentary deposits; 5: Soshonite with pyroxene, amphibole and plagioclase phenocrystals; 6: Soshonite with pyroxene, biotite, plagioclase and sanidine phenocrystals; 7: Potassic trachybasalt (aphyric or with rare olivine, pyroxene and plagioclase phenocrystals); 8: Basalt with pyroxene, amphibole and plagioclase phenocrystals; 9: Tephrite with pyroxene, amphibole, plagioclase and h  yne phenocrystals; 10: Ankaramite with olivine and pyroxene phenocrystals; 11: Quaternary alluvium; 12: Fault; 13: Brook; 14: Habitations; 15: Fossiliferous outcrops: A, Pont-de-Chocol; B, La Gratade.

Fig. 3. $^{40}\text{Ar}/^{39}\text{Ar}$ relative probability distributions for the Chambon Lake and La Gratade outcrops.

Fig. 4. **A.** LCh-1a: *Fagus sylvatica* L. **B, C.** LCh-2a: *Betula macrophylla* Goerpp.; LCh-2b: *Quercus hispanica* **D, E.** LCh-2a: margin and veination details. **F.** *Quercus hispanica* Rér. **G-I.** LCh-2d: *Alnus* cf. *stenophylla* L.; **H:** LCh-31a: *Betula* sp. **J.** LCh-21: *Alnus glutinosa* L. Scale bars: 1 cm.

Fig. 5. **A, B.** LG-1: *Fagus* type *grandifolia*; **B:** detail of leaf margin with small tooth (arrows). **C:** LCh-28: *Quercus* type *Q. roburoides* Gaud. **D, E.** LG-2: *Quercus* type *Q. roburoides* Gaud. **F.** LCh-69: *Quercus hispanica* Rér. **G.** LCh-65: *Fagus pliocenica* Sap. **H.** LCh-20: *Zelkova* cf. *Z. crenata* Spach. **I.** LCh-7a: *Fagus sylvatica* L. Scale bars: 1 cm.

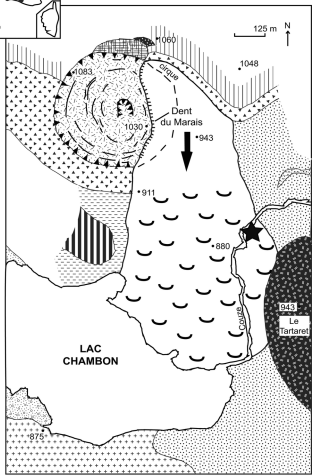
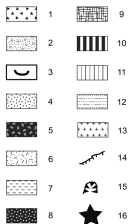
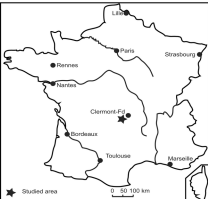
Fig. 6. **A.** LCh-38: *Acer laetum pliocenicum* Saporta et Marion. **B.** LCh-13f: *Acer integerrinum* (Viv.) Mass. **C-E.** PTC-35: *Acer sanstae-crucis* Stur (Roiron); **C:** General view; **D, E:** veination and margin details. **F.** LCh-61a: *Populus nigra* L. **G.** LCh-48: *Carya minor* Saporta et Mar. **H, K.** LCh-2: *Dicotyphyllum* sp. 5. **I.** LCh-27: *Quercus hispanica* Rér. **J.** PTC-17a: *Quercus hispanica* Rér.; PTC-17b: *Fagus sylvatica* L. Scale bars: 1 cm (A-D, F, G), 1 mm (E).

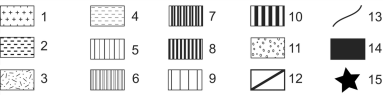
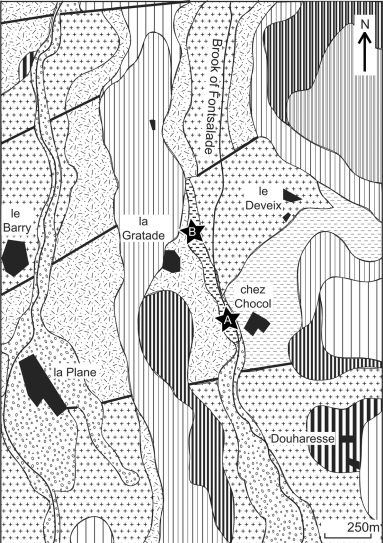
Fig. 7. **A, B.** LG-9b: *Zelkova ungeri* aff. *crenata* Spach. **C.** LCh-72: *Zelkova ungeri* aff. *Zelkova acuminata* (petiolate leaf fold). **D.** LCh-49: *Zelkova ungeri* aff. *Z. crenata* Spach. **E.** LCh-39b: *Zelkova ungeri* aff. *crenata* Spach. **F.** LCh-39d: *Zelkova ungeri* aff. *Z. crenata* Spach. **G, H.** LCh-37a: *Cornus* type *distans*. **I.** LCh-51: *Dicotyphyllum* sp. 4. **J.** LCh-30: *Tsuga* sp. needle. Scale bars: 1 cm (A-I), 2 mm (J).

Fig. 8. **A.** LCh-18: *Ulmus braunii* Heer. **B.** LCh-11: *Dicotyphyllum* sp. 3. **C.** LCh-48: *Carya minor* Sap. et Mar. **D.** LCh-19: *Betula alnoides* Buch.-Ham. ex D. Don. **E.** LCh-5: *Leguminophyllum* sp.1 cf. *Cassia* sp. **F.** LCh-42a: *Pterocarya* sp. **G.** PTC-22: Cuticular cells with laterocytic stomatal type. **H, I.** LCh-39d: *Pterocarya* sp. Scale bars: 1 cm (A-F, H), 25 µm (G).

Fig. 9. **A-C.** PTC-34A: *Leguminophyllum* sp. 2; **A:** General view; **B, C:** venation details. **D.** LCh-22: *Leguminophyllum* sp. 4. **E.** LCh-25a: *Dicotyphyllum* sp. 2. **F, G.** LCh-51b: *Carpinus betulus* L. **H.** Monocotyledon epiderm (?*Bambusa* sp.). **I.** LCh-20C: *Carpinus suborientalis* Sap. **J.** PTC-34b, *Dicotyphyllum* sp. 1. **K.** LCh-23: *Abies ramesi* Sap. Scale bars: 5 mm.

Fig. 10. **A-C.** LCh-2: *Betula* sp., seeds. **D.** LCh-30d: *Carpinus betulus*, akene. **E.** LCh-46: *Tsuga* sp., seed cone. **F.** LCh-30c: *Alnus* sp., strobili. **G.** LCh-2d: *Picea* sp. **H.** LCh-13d: *Pinus* sp. **I.** LCh-13a: *Carpinus suborientalis* Sap. **J.** LCh-13b: Black circular fungi on leaf. **K.** LCh-13c: epiderm incertae sedis (petal?). Scale bars: 1 cm (A-G), 500 μ m (I-K).

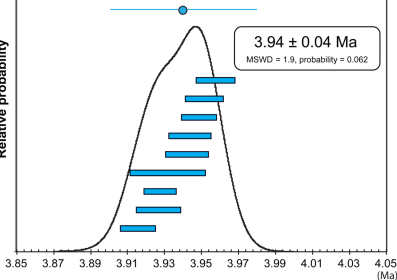




GRATADE

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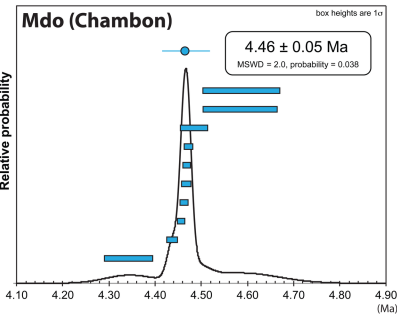
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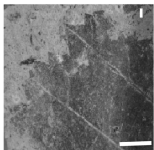
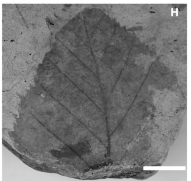
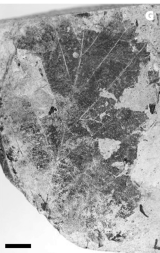
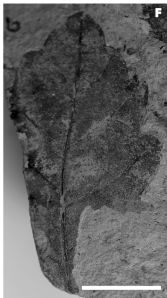
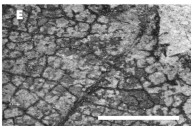
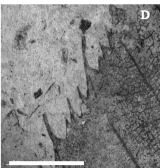
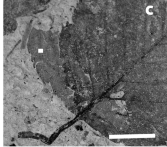
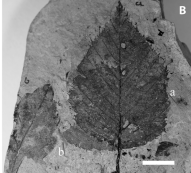


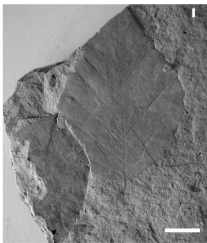
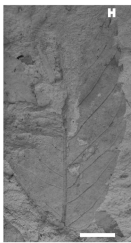
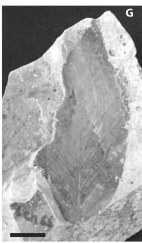
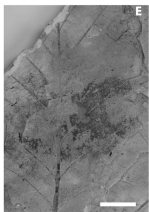
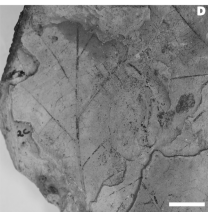
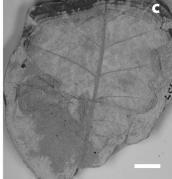
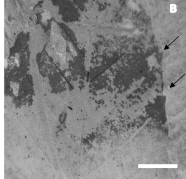
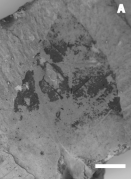
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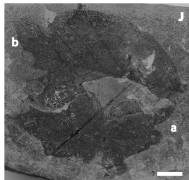
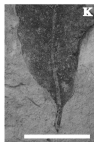
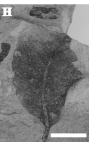
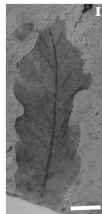
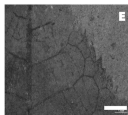
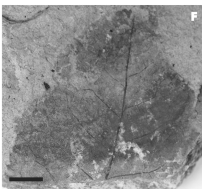
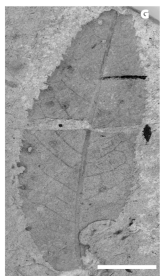
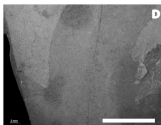
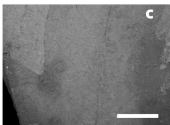
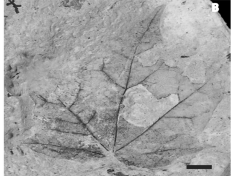
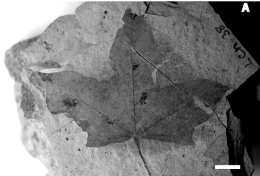
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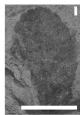
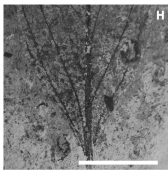
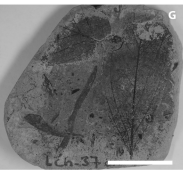
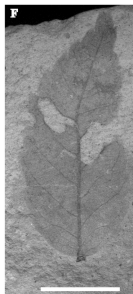
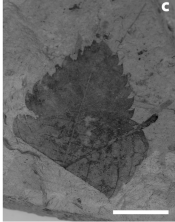
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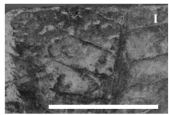
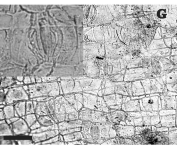
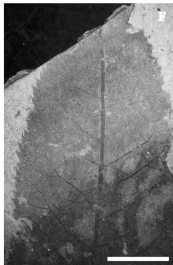
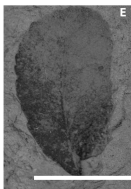
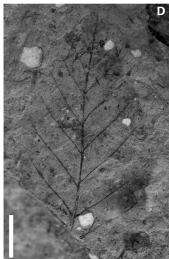
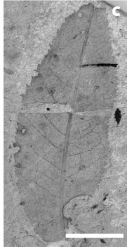
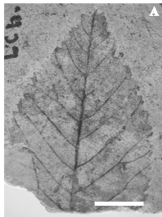


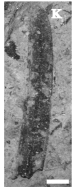
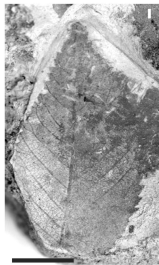
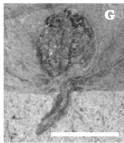
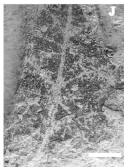
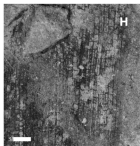
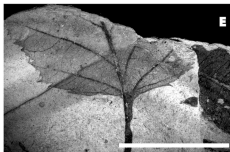
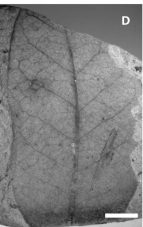
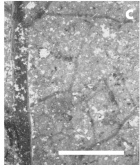
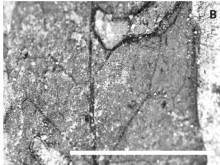


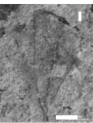
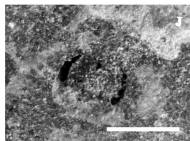
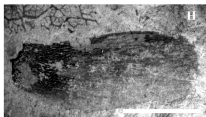
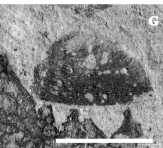
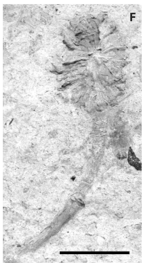
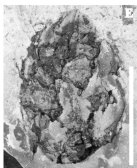
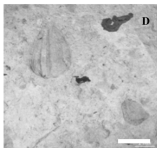
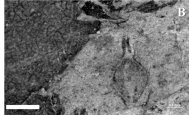
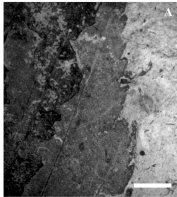












	CHAMBON LAKE		LA GRATADE		PONT DE CHOCOL	
	Nbr	%	Nbr	%	Nbr	%
<i>Pinus sylvestris</i> - type	131	30	90	25	140	34
<i>Pinus haploxylon</i> -type	10	2.3	3	0.8	8	2
<i>Cathaya</i>	7	1.6	4	1.1	4	1
<i>Abies</i> sp.	68	15.5	18	5	24	6
<i>Picea</i> sp.	53	12	20	5.4	22	5.3
<i>Cedrus</i> sp.	3	0.7	2	0.5	4	1
<i>Sciadopitys</i> sp.	26	6			4	1
<i>Tsuga</i> type 1	28	12	12	3.3	18	4.3
Cupressaceae (Juniperus- <i>Cupressus</i> pollen-type)	3	0.7			5	1.2
Cupressaceae ("Taxodioid" pollen-types)	10	2.3	8	2.2	2	0.4
<i>Sequoia-Taxodium</i>	10	2.3				
<i>Juglans</i> sp.	2	1.4	10	3	4	1
<i>Carya</i> sp.1	6	1.4	18	5	14	3.4
<i>Carya</i> sp.2			4	1.1	4	1
<i>Pterocarya</i> sp.			6	1.7	10	2.4
<i>Platycarya</i> sp.	1	0.2	1	0.3		
<i>Liquidambar</i> sp.	2	0.4			2	0.5
<i>Nyssa</i>			1	0.3	1	0.2
<i>Quercus deciduouus</i> pollen-type	18	4.1	39	11	25	6
<i>Quercus ilex</i> type	2	0.4	4	1.1	3	0.7
<i>Fagus</i> sp.	5	1	21	5.8	16	3.8
<i>Carpinus</i> sp.					4	1
<i>Tilia</i> sp.			6	1.7	3	0.7
<i>Castanea</i> sp.					4	1
<i>Corylus</i> sp.	1	0.2	12	3.3	6	1.4
<i>Ulmus/Zelkova</i>	7	1.6	10	3	11	2.6
<i>Acer</i> sp.	1	0.2			1	0.2
<i>Alnus</i> sp.	11	2.5	9	2.5	17	4.1
<i>Betula</i> sp.	16	4	13	3.6	16	4
<i>Buxus</i> sp.			1	0.3	1	0.2
Total AP (Arborean Pollen)	424	97	317	88.3	390	96
Poaceae	3	0.7	6	1.7	4	1
Poaceae (<i>Bambusa</i> type)					1	0.2
Cyperaceae	1	0.2	6	1.7	1	0.2
type <i>Juncus</i>						
Apiaceae Saniculoideae			1	0.3	1	0.2
<i>Nuphar</i> sp.					1	0.2
<i>Typha</i> sp.					1	0.3
Ericaceae	4	1	15	4.2	12	3
Caryophyllaceae	1	0.2				
<i>Centaurea</i>	1	0.2				
Amaranthaceae					1	0.3
Caprifoliaceae			1	0.3		
Leguminosae			6	1.7	4	1
<i>Lamium</i> sp.			2	0.6		
Ranunculaceae	1	0.2	1	0.3	1	0.2
Rosaceae	3	0.7	7	2	2	0.5
Triletes spores			1	0.3	1	0.2
<i>Osmunda</i>					2	0.5
Unidentified pollen grains					2	0.4
Indeterminable pollen grains	2	0.4			7	1.7
Total NAP (Non arborean pollen)	16	3	42	11.7	24	6
AP+NAP	437	100	359	100	414	100
<i>Osmunda</i>					2	0.4
<i>Botryococcus</i> sp.	28	6	4	1.2	66	13.4
<i>Spirogyra</i> sp.	1	0.2	1	0.3		
Unidentified microplankton	10	2	4	1.2	11	2.2
<i>Cyanobacteria</i> sp.					1	0.2
<i>Arcella</i> sp.	1	0.2				
total Pollen + Non Pollinic Palynomorphs (NPP)	478		368		492	
Organic matter						
POM (Particulate Organic Matter)		85		80		50
AOM (Amorphous Organic Matter)		15		20		45
COM (Carbonized Organic Matter)		0		0		5

TAXA	LCH	LG	PTC	FREQUENCY	NLR	DISTRIBUTION	ILLUSTRATIONS
Fungi				*			Fig. 10(J)
Monocotyledons	L			**			Figs. 9(H), 10
<i>Pteridium aquilinum</i> (L.) Kuhn			L	*	<i>Pteridium aquilinum</i> (L.) Kuhn (syn. : <i>Pteris aquilina</i> Linné)	Europa	
<i>Abies ramesi</i> Sap.	S			*			Fig. 9(K)
<i>Picea</i> sp.	S			**	<i>Picea</i> sp./ <i>Tsuga</i> sp.		Fig. 10(G)
<i>Tsuga</i> sp.	SF			*	<i>Tsuga</i> sp.		Figs. 7(J), 10(E)
<i>Pinus</i> sp.	S			*	<i>Pinus</i> sp.		Fig. 10(H)
Poaceae	L			**	Poaceae		
<i>Buxus pliocenica</i> Sap. et Marion 1876	L			*	<i>Buxus sempervirens</i> L.	Europa	
<i>Fagus pliocenica</i> Sap.	L						Fig. 5(G)
<i>Fagus grandilolia</i> Ehrh. 1788	L	L		*/*	<i>Fagus grandifolia</i> Ehrh. 1788	North America	Fig. 5(A, B)
<i>Fagus sylvatica</i> L. 1753	L			****	<i>Fagus sylvatica</i> L. 1753	Europa	Figs. 4(A), 5(I)
<i>Quercus roburoides</i> Gaudin	L	L	L	***/**	<i>Quercus</i>		Fig. 5(D, E)
<i>Quercus hispanica</i> Rér.	L	L	L	***/**		Europa	Figs. 4(F), 6(I, J)
<i>Quercus macranthera</i> Fish et Mey	L	L	L	*/**		Caucasia	
<i>Alnus glutinosa</i> (L.) G aertn.1790	L/F	L	L	***/**	<i>Alnus glutinosa</i> (L.) G aertn.1790	Eurasia	Figs. 4(J), 10(F)
<i>Alnus</i> cf. <i>stenophylla</i> Sap. et Mar.	L			*			Fig. 4(G-I)
<i>Alnus</i> sp.	L	L	L	***/**	<i>Alnus</i> sp.		
? <i>Alnus viridis</i> (Chaix) DC. 1805	L	L	L		<i>Alnus viridis</i> (Chaix) DC. 1805	Europa	
<i>Betula alnoides</i> Buch.-Ham. ex D.Don	L					Asia (China, Japan)	Fig. 8(D)
<i>Betula macrophylla</i> (Goerpp.) Heer	L			*****	<i>Betula macrophylla</i> (Goerpp) Heer		Fig. 4(B-E)
<i>Betula</i> sp.	1/F/S	L	L	***/**	<i>Betula</i> sp.		Figs. 4(H), 10(A-C)
<i>Betula subpubescens</i> Goepp.		L	L	*/*			
<i>Populus tremula</i> L. 1753	L			**	<i>Populus tremula</i> L. 1753	Europa	
<i>Populus</i> sp.	L			**	<i>Populus</i> sp.		
<i>Populus nigra</i> L.	L			*	<i>Populus nigra</i> L.	Eurasie	Fig. 6(F)
<i>Carpinus betulus</i> L.1753	1/F		L	**/**	<i>Carpinus betulus</i> L. 1753	Europa	Figs. 9(G), 10(D)
<i>Carpinus suborientalis</i> Sap. (syn. <i>C. tschonoski</i> Maxim 1881)	1/F					Caucasia	Figs. 9(I), 10(I)
<i>Fraxinus excelsior</i> L.			L	*	<i>Fraxinus excelsior</i> L.	Europa	
<i>Cornus type distans</i>	L			*		Europa	Fig. 7(G, H)
<i>Ulmus type braunii</i> Heer	L		L	**/**	<i>Ulmus campestris</i> L.		Fig. 8(A)
<i>Ulmus type fulva</i> Michx				*	<i>Ulmus rubra</i> Muehl.	North America	
<i>Zelkova ungeri</i> aff. <i>Z. acuminata</i> Planch.	L		L	***/*	<i>Zelkova acuminata</i> P lanch. (syn. <i>Z. serrata</i> Mak.	Asia (China, Japan)	Fig. 7(C)
<i>Zelkova ungeri</i> aff. <i>Z. crenata</i> Spach.	L	L		**/*	<i>Z. crenata</i> Spach.	Caucasia	Figs. 5(A), 7(A, B, D)
<i>Carya minor</i> Sap. et Mar.	L	L	L	***/**		North America	Figs. 6(G), 8(C)
<i>Pterocarya</i> sp.	L			**			Fig. 8(F, H, I)
<i>Acer laetum pliocenicum</i> Sap. et Mar. (syn.: <i>A. integerrimum</i> (Viv.) Mass. (Roiron 1991)	L			**	<i>Acer laetum</i> Mey (syn. <i>A. cappadocicum</i> Gleditsch.	Caucasia, Asia	Fig. 6(A)
<i>Acer integerrimum</i> (Viv.) Mass	L						Fig. 6(B)
<i>Acer sanctae-crucis</i> Stur (Roiron 1991)	L			*			Fig. 6(C, D)
<i>Acer</i> sp.	L			*	<i>Acer</i> sp.		
<i>Leguminophyllum</i> sp. 1	L			*	Fabaceae		Fig. 8(E)
<i>Leguminophyllum</i> sp. 2			L	*			Fig. 9(A-C)
<i>Dicotyphyllum</i> sp. 1	L			*	Incertae sedis		Fig. 9(J)
<i>Dicotyphyllum</i> sp. 2	L			*	Incertae sedis		Fig. 9(E)
<i>Dicotyphyllum</i> sp. 3	L			*	Incertae sedis		Fig. 8(B)
<i>Dicotyphyllum</i> sp. 4	C			*	Incertae sedis		Fig. 7(I)
<i>Dicotyphyllum</i> sp. 5	L			*	Incertae sedis		Fig. 6(H, K)