CLAMP-based palaeoclimatic analysis of the late Miocene (Tortonian) flora from La Cerdanya Basin of Catalonia, Spain, and an estimation of the palaeoaltitude of the eastern Pyrenees

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Abstract

We analyse the late Miocene (early Tortonian) climate of the La Cerdanya Basin (Catalonia, Spain) using the Climate Leaf Analysis Multivariate Program (CLAMP) based on an assemblage comprising twenty-nine dicot leaf taxa. Results show a mean annual temperature of 11.4 ± 2.1ºC. The coldest mean monthly temperature was 1.8 ± 3.4ºC while the warmest was 21.6 ±2 .5ºC. Growing season was 6.8 ± 1.1 months in duration. Precipitation during this period was 1082 ± 317 mm, reaching 661 ± 38 mm in the three wettest consecutive months, while in the three driest months it was 194 ± 229 mm. These results indicate a permanently humid temperate climate, with warm and wet summers. Compared with published palaeoclimatic results obtained using the Coexistence Approach method, our CLAMP analysis indicates lower temperatures and higher rainfall during the driest month. The climatic parameters are consistent with the occurrence of a temperate mixed evergreen and broadleaf deciduous fossil assemblage in the late Miocene of the La Cerdanya Basin. The assemblage contains more taxa in common with coeval localities from northern and central Europe than with Mediterranean sites; its closest modern analogue is with the montane flora from Honshu Island (Japan). Palaeoaltitudinal estimation using the terrestrial lapse rate method suggests that the La Cerdanya Basin was positioned at 1100–1550 m during early Tortonian times. These results challenge previous palynological and isotopic studies that inferred a palaeoaltitude of c. 600 m in early Tortonian-Messinian times.

Keywords

Neogene; Iberia; leaf physiognomy; upland vegetation; palaeoclimate; Pyrenean uplift

1. Introduction

The collision between the African and Eurasian plates during the latest Cretaceous and the Paleogene produced important orogenic belts across Europe, e.g., the Betic Chain, the Pyrenees, the Alps or the Caucasus. The uplift of these mountain ranges influenced the atmospheric air distribution and the palaeoclimate (Kocsis et al., 2014), increasing the latitudinal climatic gradient across Europe (Fauquette et al., 2007). For instance, in the middle Miocene, central and eastern Europe was covered by mixed broadleaf and coniferous forests (Mai, 1989; Kovar-Eder, 2003; Utescher et al., 2007), while in the south, evergreen forests flourished (Utescher et al., 2007). During the late Miocene (Tortonian), the climate became wetter with higher rainfall

(Utescher et al., 2007; Böhme et al., 2011) and the flora distribution across Europe became more complex (Bruch et al., 2004). Palaeogeography (Bruch et al., 2004), atmospheric circulation patterns (Wanner et al., 2001) and palaeotopography (Sokol and Bližňák, 2009; Bartolini et al., 2009) have all been claimed as the key factors stimulating floristic regionalism. In line with this increasing complexity, the late Miocene flora from La Cerdanya has been characterised as a mixed evergreen and broadleaf deciduous forest (Martín-Closas, 1995; Barrón, 1996a) and differs from most southern European floras, which formed evergreen sclerophyllous–laurophyllous forests (Barrón et al., 2010).

The taxonomy of macroscopic plant remains from the early Tortonian of La Cerdanya has been studied since the 19th Century (Rérolle, 1884-1885; Villalta and Crusafont, 1945; Menéndez-Amor, 1955; Barrón, 1992, 1996a, 1996b, 1996c; Barrón and Diéguez, 1994; Martín-Closas et al., 2006; Barrón et al., 2014). In parallel, palynological studies from the Miocene of La Cerdanya were first performed with a taxonomic and biostratigraphic scope by Jelgersma (1957) and later by Bessedik (1985) in the lignite pit-mines from the Estavar, Prats-i-Sansor and Sanavastre providing a Tortonian age. More recently, Barrón (1996a, 1996d, 1997a, 1997b) studied the palynological record of these sites in comparison with macro remains, while Zetter and Ferguson (2001) described a particular new pollen taxon.

The significance of the La Cerdanya leaf flora for palaeoecology motivated the studies of Álvarez-Ramis and Sanz-Peciña (1979), Álvarez-Ramis et al. (1979), Sanz de Siria (1980, 1985), Álvarez-Ramis (1981, 1983). Álvarez-Ramis and Golpe-Posse (1981) determined five plant communities, including aquatic plants, riparian and swamp vegetation, lowland and high-altitude slope forests, and upland vegetation. In order to understand the processes involved in the origin of fossil plant assemblages from the Miocene of La Cerdanya, Martín-Closas (1995) and Martín-Closas et al. (2005) carried out plant biostratinomic and palynofacies analyses. A number of taphofacies were distinguished, mainly determined by the mechanisms that transported plant remains to the palaeolake, and by the local palaeogeography.

In recent years, interest in analysing the La Cerdanya Miocene flora to determine palaeoclimate and palaeoaltitude has increased. Agustí et al. (2006), and Suc and Fauquette (2012) compared the pollen record from the Messinian of La Cerdanya with that of the neighbouring coastal basin of El Rosselló (Roussillon), in French Catalonia. They concluded that the composition of the vegetation of the eastern Pyrenees during the latest Miocene (Messinian) was similar to that of sea-coast localities, leading to the assumption that most of the recent Pyrenean altitude was reached by isostatic compensation during Pliocene and Quaternary times. Recently, Huyghe et al. (2020) compared the composition of the stable isotopes from different fossil groups (micromammals, molluscs and charophytes) from the El Rosselló and La Cerdanya basins in order to gain new insights into the palaeoaltitude of La Cerdanya during the Messinian. The results revealed again that the La Cerdanya Basin was at a much lower altitude in the Messinian (approximately 600 m a.s.l) than today (ca. 1100 m a.s.l.) and that this altitude was possibly inherited from previous (early Tortonian) times.

As regards the early Tortonian, a similar result was obtained in the central Pyrenean Prüedo Basin, by Ortuño et al. (2013), based on palynological and magneto-telluric analyses. No significant difference in palaeoaltitude was found between the early Tortonian vegetation of the studied locality, located now at ca. 2500 m.a.s.l, and the coeval coastal localities. Barrón et al. (2010, 2016) estimated the earlyTortonian and early Messinian palaeoclimate of La Cerdanya, using the Coexistence Approach (CA) with palynomorphs and macrofloral remains. They concluded that there were no significant changes to the plant composition in La Cerdanya across that time span. As regards the climate, it was humid and warm with a marked seasonality, while precipitation was similar to today (Barrón et al., 2016).

The aim of the present study is to estimate the palaeoclimate of the La Cerdanya Basin during the early Tortonian, based on CLAMP and to compare the inferred climate parameters with previous results. Comparison with the climatic parameters and floristic composition of other early Tortonian palaeobotanical sites in Europe, and with extant plant localities provided in the CLAMP dataset, sheds new light on the palaeoenvironmental conditions of the La Cerdanya Basin during the early Tortonian. Furthermore, the results obtained were used to estimate the palaeoaltitude of the La Cerdanya during the early Tortonian, which allows for a discussion of previous palaeoaltitudinal studies in this palaeogeographic area.

2. Geological setting

The Pyrenees is the east-west-oriented mountain range bounding the north of the Iberian Peninsula. It rose mainly during the Palaeogene as a result of the collision between the Iberian and European plates. By the end of the Oligocene and the beginning of the Miocene, approximately 25 Ma ago, the Pyrenees had developed the fold-and-thrust structure the chain has today (Muñoz, 1992).

During the late Miocene, a rosary of pull-apart basins were formed in relation to a complex intramontane strike-slip fault generically called La Tet (Têt) fault, which crossed the eastern Pyrenean Axial Zone in a WSW–ENE direction (Cabrera et al., 1988). The largest of these basins is the La Cerdanya Basin (Fig. 1).

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The Neogene stratigraphic record of the La Cerdanya Basin is formed of two lithostratigraphic units, informally known as the Lower and Upper Neogene units (Cabrera et al., 1988). The Lower Neogene Unit, with a thickness of 800 m, is Vallesian (early Tortonian) in age (late Miocene, MN 9−10 biozones), which is a land mammal stage equivalent to the early Tortonian (Hilgen et al., 2012), and lies unconformably, or by fault, upon a Palaeozoic basement (Agustí and Roca, 1987; Anadón et al., 1989). This unit contains the leaf assemblage studied herein. On the other hand, according to Agustí and Roca (1987), the Upper Neogene Unit was deposited during the Turolian (latest Miocene, MN 13 biozone), which is a land mammal stage largely equivalent to the Messinian (Hilgen et al., 2012). It is up to 200 m thick and is restricted to the southwestern part of the basin, near Bellver de Cerdanya, where it lies unconformably upon the Lower Neogene Unit and separated from it by a significant stratigraphic gap representing about 1.5 Myr (Cabrera et al., 1988).

The sedimentation of the Lower Neogene Unit was largely controlled by the La Tet fault, resulting in a significant asymmetry in the thickness of the Neogene deposits. In the south of the La Cerdanya Basin, close to this main fault, the lacustrine deposits reach up to several hundred metres in thickness, while to the north of the basin, which corresponds to the passive basin margin, may be only a few metres thick. Furthermore, the La Cerdanya Basin is divided in two sub-basins by a structural high near the localities of Sanavastre, Prats-i-Sansor and Das. The northeastern part of the basin, corresponding to Puigcerdà sub-basin, filled in with conglomerate, sand and ochre lutites deposited in alluvial and fluvial environments. These deposits change laterally to grey sands, lutites and lignite to the southwest, near the structural high, where palustrine and deltaic conditions prevailed (Cabrera et al., 1988). In the other sub-basin located in the southwestern, called the Bellver sub-basin, the Lower Neogene Unit well-laminated clay and diatomite, representing deposition in a eutrophic and meromictic palaeolake (Cabrera et al., 1988; De las Heras et al., 1989; Martín-Closas et al., 2006). These lacustrine deposits contain the leaf flora studied herein (Fig. 2). The diatomite of this unit results from the accumulation of the silica frustules of a low diversity assemblage of diatoms (Haworth and Sabater, 1993). The monotonous well-laminated diatomite and clay deposits occasionally interrupted by orange-coloured ferruginous horizons, rich in hydrated calcium and iron phosphate (anapaite) nodules or crusts, corresponding to lacustrine hardgrounds that indicate temporary cessation of sedimentation (De las Heras et al., 1989). Geochemical markers studied by De las Heras et al. (1989), and the almost total absence of bioturbation, suggest that anoxic conditions prevailed during the deposition of the diatomite and clay, which explains the exceptional preservation of morphological characters in the fossil leaves. However, diagenetic processes enhanced the dissolution of organic matter, limiting to some extent the preservation of leaf cuticles.

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3. Material and methods

3.1. Palaeobotanical assemblage

Twenty-nine morphospecies from the Vallesian (early Tortonian) plant assemblage of La Cerdanya with sufficient preservation quality of the leaf shape have been selected for this study and the fossils are stored at the Museu de Ciències Naturals de Barcelona with quotation numbers MGB 89666−MGB 89699 (Table 1, Figs. 3−5). Most of them are complete adpressions or were authigenically limonitized, showing an excellent preservation of the leaf characters, but rarely with cuticles preserved.

-----------------------------------Insert Table 1 near here------------------------------------

The fossil leaves were obtained from the Vallesian (early Tortonian) stratigraphic succession in the lacustrine unit (mainly clay and diatomite) of the Bellver sub-basin (42º 22’ 04’’N; 01º 46’ 42’’E) from the La Cerdanya Basin (Fig. 2). The plant remains were collected after systematic sampling of a number of outcrops, whose location was provided by Martín-Closas et al. (2005). These remains correspond to different plant beds of the Lower Neogene Unit, which have been attributed to the mammal biozones MN9 and/or MN10, by Agustí and Roca (1987). These biozones represent, at most, a time span of 2.3 Myr (11.2–8.9 Ma), according to Hilgen et al. (2012). However, the total time span of the diatomite and clay unit was probably less than this, considering that it results from an indefinition in the biostratigraphic range of the mammal assemblages found in the La Cerdanya Basin (Agustí and Roca, 1987). Although the precise time span of the plant-bearing beds studied herein is difficult to ascertain, a number of authors have concluded that climate change during the Vallesian (early Tortonian) was moderate to nil, by comparing plant remains from different localities within La Cerdanya (Barrón et al., 2016) or in other coeval European basins (Utescher et al., 2017). In consequence the beds studied herein will be considered homogeneous in terms of palaeoclimatic evolution.

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3.2. CLAMP

Leaves are one of the most climate-sensitive plant organs and have been long used as a climatic proxy in non-marine environments (Wolfe, 1993). For this purpose, Wolfe (1993) and later Wolfe and Spicer (1999) developed CLAMP (Climate Leaf Multivariate Program Analysis), a method based on leaf physiognomy to estimate the climate of the past. CLAMP is a free-access program (http://clamp.ibcas.ac.cn/) that uses 31 physiognomic leaf features of woody dicot angiosperms such as leaf shape, laminar size, margin type or tooth morphology to characterise the palaeoclimate. It correlates the physiognomy of leaves from plants with the climate that they grow including 378 meteorological stations distributed worldwide, with the climatic data gathered at these stations for more than 30 years. This information is compared with physiognomic leaf data obtained from a fossil leaf assemblage to estimate the palaeoclimate of the studied fossil plant's locality. CLAMP multivariate analysis uses Canonical Correspondence Analysis (CANOCO).

According to Wolfe (1993), at least 20 woody dicot taxa are needed to obtain reliable palaeoclimatic parameters. In this study 29 leaf morphotypes were obtained. To estimate the most suitable calibration for the palaeoflora from La Cerdanya, we first used the global calibration algorithm (PhysgGlobal) (http://clamp.ibcas.ac.cn). The results plotted the studied plant assemblage within non-monsoonal sites (Fig. 6A-B), leading us to use a second, non-monsoonal calibration, the "Physg3brcAZ_Calibration", to perform the CLAMP analysis. It is based on 144 locations, mostly belonging to the northern hemisphere but excluding the alpine localities, where prevailing temperatures are below zero. This calibration was favoured since freezing temperatures are not expected for the Miocene of the La Cerdanya Basin, where thermophyllous taxa such as palms or Sapotaceae occurred (Barrón, 1996a). To minimise sporadic effects of exceptional meteorological phenomena, such as heavy storms, we used a calibration grid, GRIDMet3bcrAZ Calibration (Spicer et al., 2009).

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The CLAMP webpage provides a score sheet to be filled in with the enquired information of the leaf characters (Wolfe, 1993). The information requested corresponds to 31 specific shape features of leaves (Table S1). In the case of highly polymorphic leaves, such as *Quercus drymeja* Unger, *Q. hispanica* Rérolle and *Acer tricuspidatum* Bronn, the whole range of character variation displayed by one species has been marked on the score sheet. Leaf features that were missing due to insufficient preservation or were simply not present, were left blank on the score sheet.

CLAMP online analytical tool (http://clamp.ibcas.ac.cn/CLAMP_Run_Analysis.html) provides information on the following climatic parameters: MAT (mean annual temperature), WMMT (warmest month mean temperature), CMMT (coldest month mean temperature), GROWSEAS (length of the growing season), GSP (growing season precipitation), MMGSP (mean monthly growing season precipitation), 3-WET (precipitation during the three wettest consecutive months), 3-DRY (precipitation during the three driest consecutive months) and RH (relative humidity). Values of MAT, WMMT and CMMT are expressed in degrees Celsius (ºC); GROWSEAS is expressed in months; GSP, MMGSP, 3-WET and 3-DRY are in centimetres (cm); and RH is a percentage (%) Specific humidity (SH) in g/kg and enthalpy (ENTHAL) in kJ/kg.

Comparison between our CLAMP results and those of the Coexistence Approach (CA) method used by Barrón et al. (2016), needed an adaptation of some parameters, as follows:

(1) Precipitation. The precipitation parameters provided by CLAMP give the rainfall during the growth period of plants (GSP), while CA shows the mean annual precipitation (MAP). The two different ways of characterising precipitation have been homogenized using the Tanrattana et al. (2020) equation, which defines the

minimum mean annual precipitation (MAP) as a function of the growth season precipitation (GSP), its length (GROWSEAS), and the precipitation during the driest months (3-DRY), as follows:

$$MAP = GSP + (12 – GROWSEA) x (3-DRY/3) \qquad (1)$$

Additionally, all precipitation parameters from CLAMP were converted from cm to mm.

Other precipitation parameters also differ between the two methods. CLAMP analysis provides the precipitation of the three wettest and three driest consecutive months (respectively, 3-WET and 3-DRY), while CA analysis shows a value for only the wettest and the driest month (MPwet and MPdry, respectively). To compare the results, the second and third months' precipitation lacking from the CA method were estimated, based on the CLAMP database. As a reference for this, the present-day locality of Kannami (Honshu Island, Japan) was chosen since it displays a 3-WET rainfall fluctuation close to that of the Vallesian (early Tortonian) of La Cerdanya. Based on the climatic record of this locality, the rainfall of the second and third wettest consecutive months would be, respectively, 12% and 20% less wet than the values of the rainiest month. For the 3-DRY values, present-day Beaufort (South Carolina, USA) bears the closest resemblance to the Vallesian (early Tortonian) of La Cerdanya. In this case, the precipitation of the second and third months would be, respectively, 3% and 6% less dry than the driest month.

(2) Temperature. The average values for MAT (mean annual temperature), WMT (warmest month temperature) and CMT (coldest month temperature) obtained using CA, are taken as equivalent to the MAT, WMMT and CMMT, respectively, from the CLAMP analysis.

3.3. Palaeoaltitude estimates

The estimation of the palaeoaltitude in the La Cerdanya during the Vallesian (early Tortonian) is based on the terrestrial lapse rate method proposed by Axelrod (1965) and refined by Wolfe (1992). Recently, Gregory-Wodzicki (2000) and Spicer (2018) concluded that the difference in elevation (ΔZ), between two localities (one upland and one lowland) may be derived from the difference in surface temperature (MAT) and the terrestrial lapse rate (2).

$$\Delta Z = (T_{high} – T_{low})/\gamma \qquad (2)$$

Where T_{high} corresponds to the MAT of the upland locality, T_{low} to the MAT of the lowland locality, and γ to the terrestrial rate, which is a constant representing the variation of the temperature versus altitude in a particular latitudinal belt. This value depends on parameters such as the state of the atmosphere, moisture, albedo of the ground surface, among other (Wolfe, 1992). From the former expression the terrestrial lapse rate can be obtained as follows (Wolfe, 1992):

$$\gamma = |MAT_{interior} – MAT_{coastal}| / \Delta Z \qquad (3)$$

In order to calculate the terrestrial lapse rate of the Iberian Peninsula during the Vallesian (early Tortonian), we used the MAT values obtained from two localities, where quantitative palaeoclimatic data are available, the inland Zaratán, located near Valladolid, NE Spain (Bruch et al., 2004; Fauquette et al., 2007) and Alborán, offshore Andalucía (South Spain), considered herein as the coastal locality (Jimenez-Moreno et al., 2010). The results indicate a terrestrial lapse rate of 3.6 (ºC/km).

4. Results

Twenty-nine morphotypes of dicotyledonous leaves from the Vallesian (early Tortonian) of La Cerdanya were used for palaeoclimatic reconstruction (Table S1). The CLAMP results suggest a MAT of 11.4±2.1ºC (Tables 2 and S1). A significant contrast is observed between the WMMT, at 21.6±2.5ºC and the CMMT, at 1.8±3.4ºC, indicating seasonality in plant growth, which lasted for 6.8±1.1 months (GROWSEAS). These values suggest that the temperature was over 10ºC for at least half the year, given that CLAMP is configured to consider that plants cease growing at temperatures below 10ºC (Körner, 2016 and R. Spicer personal communication, 2020).

The precipitation during the Vallesian (early Tortonian) in La Cerdanya was high, at 1082±317 mm during the growing season. This would allow for precipitation of 153±59 mm MMGSP. Based on the equivalence algorithm proposed by Tanrattana et al. (2020), the MAP would correspond to 1418 mm. As with temperature, a contrast is found in precipitation levels, with the three driest months (3-DRY) at 194±59 mm, being some three times lower than the three wettest months (3-WET), at 661±229 mm. The RH was 75.9±8.6 %.

The palaeoclimatic results obtained for the Miocene of La Cerdanya are better understood by comparing them with the Köppen climate types (Köppen 1900). Based on these criteria, the palaeoclimate of the Vallesian (early Tortonian) in La Cerdanya would come within the range of a temperate, fully humid climate with warm summers (Cfb-type climate).

--Insert Table 2 near here------------------------------

The palaeotemperature values obtained from CLAMP are used for inferring the palaeoaltitude of the La Cerdanya during the Vallesian (early Tortonian) following the terrestrial lapse method (equation 2). T_{high} corresponds to the MAT of the La Cerdanya while two coastal localities with a similar palaeoaltitude as La Cerdanya provided the $T_{coastal}$ in equation 2. The latter localities are Povoa located 1000 km west from La Cerdanya, in the Atlantic coast of Portugal, and Terrassa (Catalonia) situated ca. 150 km south-east from the studied zone at the Miocene palaeo-seacoast. The MAT from Povoa (13.7–17 ºC) was taken from Bruch et al. (2004) which is also provided in Table 4 . The MAT variation results in a palaeoaltitude variation ranging 639–1556 m a.s.l with a mean palaeoaltitude of 1097 m a.s.l. for the La Cerdanya Vallesian (early Tortonian). On the other hand, the MAT of 16-18ºC estimated for Terrassa by Sanz de Siria (1997, see Table 4) would provide an altitudinal range of 1277-1833, with a mean height of 1555 m a.s.l. during the Vallesian. In consequence, a mean range of 1100–1550 m a.s.l. is proposed here as the Vallesian (early Tortonian) paleoaltitudinal range of the La Cerdanya Basin.

5. Discussion

The Vallesian (early Tortonian) flora of La Cerdanya represents one of the few known intramontane plant localities from this age in southern Europe. The palaeoclimatic results suggested by CLAMP and the estimation of the palaeoaltitude of La Cerdanya during the late Miocene afford new insights from previous studies based on macroflora - and microflora from the same basin and other coeval European localities.

5.1. Comparison with previous palaeoclimatic studies from La Cerdanya

A palaeoclimatic study of the Vallesian (early Tortonian) from La Cerdanya Basin was provided by Barrón et al. (2016), based on the Palaeoflora database (Utescher and Mosbrugger, 2015. www.Palaeoflora.de) and using the Coexistence Approach (CA) method. This method was introduced by Mosbrugger and Utescher (1997) and is based on the assumption that the fossil plant taxa had similar climatic requirements to their nearest living relatives (NLR). Climatic intervals are then generated from comparing the fossil assemblage with the CA database obtained from extant species and looking for the best matches to propose a palaeoclimatic hypothesis.

The temperature values results of Barrón et al. (2016) based on the Vallesian (early Tortonian) macroflora of La Cerdanya are somehow similar to the values obtained here (Table 3). However, the MAT would be in the range 11.7–16.2ºC, which is 0.3−4.8ºC warmer than the MAT obtained by CLAMP. The CMMT values are almost equal. By contrast, the WMMT is approximately 4ºC higher in the results by Barrón et al. (2016), reaching 26.1ºC. These higher temperatures would put the Vallesian (early Tortonian) palaeoclimate of La Cerdanya within Köppen’s Cfa-type climate range, while a Cfb-type climate is obtained by CLAMP.

The comparison between the two methods reveals compatible figures for the

MAP. Based on macroflora, Barrón et al. (2016) provided a MAP ranging from 1098 mm to 1355 mm, which is slightly less than the MAP calculated herein (1418 mm). However, the distribution of rainfall across the year is significantly different depending on the method used. The precipitation of 3-WET was three times higher than that of 3-DRY according to CLAMP. By contrast, Barrón et al. (2016) noted that rainfall could increase, by a factor of approaching seven, to 520 mm for 3-WET from 77 mm for 3-DRY, indicating a stronger seasonality in terms of precipitation.

------------------------------------Insert Table 3 near here-----------------------------------

The differences between the palaeoclimatic results obtained by Barrón et al. (2016) through CA and ours through CLAMP may be due to the composition of the macrofloral assemblage considered for palaeoclimate analysis. The two studies share only 33 % of the taxa used, since species belonging to ferns, conifers and monocot angiosperms are not analysed by CLAMP, which is based exclusively on the leaf physiognomy of woody dicotyledonous angiosperms. For instance, needles and winged seeds of Pinaceae, i.e., *Abies* and *Pinus*, are abundant in the fossil record of La Cerdanya and were used for CA (Barrón et al., 2016). However, some of them show evidence of significant taphonomic selection by wind transport, suggesting that they might provide a regional climatic signal rather than local information (Martín-Closas et al., 1995, 2005). Among the Cupressaceae, the genus *Cryptomeria* was used by Barrón et al. (2016) to provide the minimum precipitation value and is therefore significant in their results. However, *Cryptomeria* was widespread and diverse in the European Miocene (Denk et al., 2011), while it is nowadays represented by a single species, *Cryptomeria japonica*, which is a relict in Japan (Millien-Parra and Jaeger, 1999). This suggests that the actualistic palaeoclimatic information provided by *Cryptomeria* could be biased and is certainly limited in comparison to the range of environmental conditions that this genus could have withstood during the Miocene (Utescher et al., 2014).

Differences in the MAT values between both methods occur as well. This disparity could lie on the species selected to define the MAT range in the CA approach. For instance, the MAT values provided by Barrón et al. (2016) for the Vallesian (early Tortonian) La Cerdanya Basin were obtained from the Paleoflora dataset, with the minimum MAT defined by *Quercus coccifera/ilex* (11.7ºC) and the maximum by the highest temperature tolerance of *Cryptomeria* (16.2ºC). However, in some regions *Q. ilex* is growing under a MAT range of 7−17ºC (San-Miguel-Ayanz et al., 2016) and *Cryptomeria* in a MAT of 21ºC (Fang et al., 2011). This suggests that a larger range of the MAT could be plausible matching better with the figures estimated here using CLAMP.

Another difference between CA and CLAMP is that hydrophytic plants are not included in the CLAMP database. According to Mai (1985), hydrophytic plants are able to survive a wide array of land climate conditions, because they grow in water, thus making them poor indicators of atmospheric variables. The same author reported, for instance, that hydrophytic plants were resilient to the Quaternary climatic changes, with the Neogene subtropical *Brasenia*-complex surviving through several Pleistocene interglacials in Europe.

5.2. Comparison with other Tortonian localities of Europe

Mai (1989) and Kvaček (2010) observed that a latitudinal gradient impinged the European Miocene vegetation. In the northern and central parts of Europe, plants that adapted to moderate temperatures and high precipitation regimes prevailed (e.g., *Betula*, *Quercus*, *Acer* or *Alnus*), while in the south, i.e., Iberian, Italian and Balkan peninsulas, species that tolerate warm temperatures, such as laurels and leguminous plants, dominated. However, local heterogeneity has also been recognised across the continent (Mai, 1989). For instance, in the case of the Iberian Peninsula, a study by Jiménez-Moreno et al. (2010), based on pollen analysis, described a regional climatic gradient overlying the more general European latitudinal pattern during the Tortonian. These authors distinguished three major Iberian climatic belts. (1) The southern part of the Iberian Peninsula (Andalusia) was dominated by open scrubland composed of herbs and shrubs (savannah-like vegetation). This vegetation was conditioned by high mean annual temperatures (17−25ºC) and relatively arid conditions with a precipitation of 355−875 mm per year. (2) The second belt would correspond to the central part of the Iberian Peninsula, where the climate was characterised by higher precipitation levels, at 600–700 mm per year, but almost equal mean annual temperatures (16−25ºC). This belt includes the Zaratán locality (Valladolid province, central Spain) which is situated at the same latitude as the coeval palaeobotanical site of Terrassa (Catalonia, eastern Spain), discussed below. The flora from this belt is well characterised by the assemblages from the Zaratán site, including Cistaceae, Cupressaceae, Ericaceae and *Plantago* (Jimenez-Moreno et al., 2010). A similar plant assemblage, but with more abundant leguminous plants (*Acacia*, *Caesalpinia*, *Colutea*, *Podocarpium*), was described by Sanz de Siria (1985) in the palaeobotanical site of Terrassa. (3) The northern Iberian belt includes localities in the Pyrenees and Cantabrian mountains (Jiménez-Moreno et al., 2010), which are situated today in significant topographic highs (≈1000 m a.s.l). The reference locality is La Cerdanya, with a palaeotemperature range of 15.5−19.8ºC and an annual precipitation of 1100−1600 mm. The vegetation of this palaeogeographic belt was mainly characterised by mixed evergreen and broadleaf deciduous forests, dominated by taxa such as *Quercus*, *Fagus*, *Alnus*, *Acer*, *Zelkova*, *Taxodium* , *Cathaya*, *Pinus* and *Abies* (Barrón, 1996a), and contrasts with the vegetation of neighbouring lowland localities in eastern Iberia and southern Europe.

The palaeoclimatic data from La Cerdanya differ significantly from the coeval sites equivalent in latitude. An example of this is the Samos site in Greece (Bruch et al., 2004). This locality provided a MAT of 16.5−19.4ºC, which is 5ºC warmer than La Cerdanya, and a coldest monthly temperature that is approximately 8ºC warmer than La Cerdanya. Furthermore, the MAP of Samos is 500 mm lower than that of La Cerdanya. Similar climatic signal to Samos is estimated for Terrassa, located near the Miocene palaeo-coastline in the Vallès-Penedès Basin, approximately one hundred kilometres south of the La Cerdanya Basin. Based on the estimations carried out by Sanz de Siria (1997), the Vallesian (early Tortonian) MAT for Terrassa was 16-18ºC, up to 7ºC warmer than the coeval La Cerdanya. Hence, the climate of the upper Miocene of La Cerdanya would have been wetter and colder than those localities from a similar latitude and at near sea level.

The climate and many plant taxa of the Vallesian (early Tortonian) La Cerdanya Basin are akin to those of some coeval plant localities in Central Europe (Table 4, Fig. 7). For instance, Massenhausen (Germany) provided a similar MAT (13.3−13.8ºC) and CMT (0.1−4.1ºC) to La Cerdanya (Bruch et al., 2004). Similar figures were obtained in the coeval locality of Wörth (Austria), with a MAT of 9.1−16.4ºC (Utescher et al., 2017).

----------------------------------Insert Figure 7 near here--------------------------------------

Precipitation is as important as temperature for climate characterisation. The MAP value for the Vallesian (early Tortonian) in la Cerdanya is similar to that of Neuhaus in Austria which was 897−1297 mm (Utescher et al., 2017). Other comparable MAPs provided by these authors were in Lohnsburg (Austria), with 897−1187 mm per year, and Chiuzbaia (Romania), with 897−1297 mm (Utescher et al., 2017). These similarities highlight the peculiar climatic characteristics of La Cerdanya during the Vallesian (early Tortonian) that might be related with the relative height of this basin.

---------------------------------------Insert Table 4 near here----------------------------------

5.3. Comparison with previous palaeoaltitudinal studies from La Cerdanya

The palaeoaltitudinal estimation presented here shows that La Cerdanya Basin was approximately between 1100−1550 m a.s.l at Vallesian (early Tortonian) time. These values indicate similar or even a higher altitude for this basin during the Vallesian (early Tortonian) than today. Nowadays the bottom of the La Cerdanya valley has a mean altitude of around 1100 m a.s.l but the Vallesian (early Tortonian) outcrops reach higher altitudes, up to 1300 m a.s.l, e.g. near the village of Meranges, revealing that the bottom of La Cerdanya Basin was clearly higher than the mean altitude of the present-day valley.

Our results match well with the tectonosedimentary studies carried out by Puigdefàbregas et al. (1992) in the Pyrenees, which concluded that La Cerdanya was completely uplifted in the Miocene. However, in the first half of the 20th Century the hypothesis was already formulated that a strong late Cenozoic erosion of the Pyrenean Chain almost wiped out the topography created during the Paleogene fold-and-thrust formation of the chain. Thus, Birot (1937) and De Sitter (1954) interpreted the high plateaus surrounding the La Cerdanya Basin (e.g., Cambredase and Puigpedrós) as the geomorphological product of that erosion.

Recent studies about the palaeoaltitude of the latest Miocene La Cerdanya basin began with Suc and Fauquette (2012), who compared the palynological fossil assemblages from the latest Miocene of La Cerdanya with coeval records from El Rosselló Basin, concluding that during the Turolian (latest Miocene, MN11– MN13) the palaeoaltitude of La Cerdanya was barely 200 m a.s.l. These results were refined recently by Huyghe et al. (2020), who obtained, for the same Turolian (Messinian) deposits, a palaeoaltitude of 600 m a.s.l based on data provided by the stable isotope composition of oxygen from mammal teeth, charophyte gyrogonites and terrestrial gastropod shells. Furthermore, they interpreted this height as inherited from the Vallesian (early Tortonian) and concluded that the uplift of the La Cerdanya Basin to its present mean altitude of 1100 m a.s.l was reached by isostatic compensation in post-Miocene times.

To date the only palaeoaltitude estimation of the Pyrenean Chain in the Vallesian (early Tortonian) was obtained by Ortuño et al. (2013) in the Prüedo Basin, in the Valh d'Aran (Central Pyrenees) located 150 km west from La Cerdanya. They showed that Prüedo Basin, which is now at about 2500 m a.s.l., was in the Vallesian (early Tortonian) barely at 700-1000 m height, based on magnetotelluric and palynological studies.

Several reasons may explain the significant differences between the results obtained here for the La Cerdanya Vallesian (early Tortonian) based on CLAMP and the terrestrial lapse method with those from the Turolian (late Messinian) based on pollen and isotopic analyses. First, the Vallesian and Turolian stratigraphic units in La Cerdanya are separated by an angular unconformity associated to significant erosion and a stratigraphic gap of about 1.5 Myr, which may account for a part of the uplift and palaeolatitudinal differences between both ages. Second, pollen records generally provide a more comprehensive overview of local and regional vegetation than leaves, which are exclusively local markers (Ferguson, 1985; 1995). Pollen might include the climatic signal of the surrounding lowlands, especially because the latest Miocene floras were dominated by wind-pollinated species, which are usually megaproducers of pollen that can travel far away from their production site (Traverse, 2007). This would lead to a lower altitude estimation. Last, analyses based of the oxygen isotopy of mammal teeth, non-marine molluscs and charophyte gyrogonites are far from being based on sound estimates of the isotopic fractionation biases. At least for charophytes, Anadón et al. (2002) experimentally demonstrated that charophyte calcification rarely is in equilibrium with the environment.

In order to better comprehend the precise uplift of the La Cerdanya Basin, future studies based on CLAMP could be applied to leaf floras from the Vallesian (early Tortonian) lowlands surrounding the Pyrenean Chain, which would allow to test these results based on an estimation of the palaeoaltitude using the enthalpy. There are plant beds already known from the L'Empordà Basin, i.e. La Bisbal (Sanz de Siria, 1981) and the Vallès-Penedés Basin. i.e. Terrassa (Sanz de Siria, 1993; 1997). However, the available leaf floras from these localities are from historical collections, which appear to have collection biases and do not contain sufficient taxa for CLAMP. New excavations are needed to improve the dataset.

5.4. Comparison of the Vallesian (early Tortonian) La Cerdanya vegetation with localities showing similar climate parameters provided by the CLAMP database

The CLAMP webpage (http://clamp.ibcas.ac.cn/) provides information on the climatic parameters from current localities used to build the CLAMP database that show similar climate parameters to a particular palaeoflora. This allows for a comparison of the Neogene leaf flora from La Cerdanya and the living plant communities that grow within similar climatic parameters (Fig. 6B). Ten localities in Japan, distributed along the northern coastal range of Honshu Island (coordinates 37º16'N, 140º54.5'E), have a Cfb-type climate and provided climatic results that better match those from the fossil flora studied herein (Fig. 8). These ten localities are covered by temperate broadleaf forests, with mixed deciduous and evergreen plants. This vegetation dominates in both the highlands (700−1600 m a.s.l) and lowlands of the eastern part of the island, showing a change westward, where the precipitation decreases (Miyawaki, 1984). The western localities, i.e., Sanze, Takinosawa, Tazawa-ko and Nibetsu are dominated by *Fagus, Daphniphyllum, Sasa, Ilex* and *Lindera*, while the wetter sites in the east of the island, i.e., Chuzenji-ko, Umedaira, Kidogawa 1 and 2, Aoba and Mt. Tokura are mainly composed of *Fagus*, *Ulmus*, *Acer* and *Fraxinus*, these being more similar in composition to the Vallesian (early Tortonian) flora from La Cerdanya. This is particularly the case in Chuzenji-ko, which is located at 1300 m a.s.l. and is surrounded by forests mainly composed of *Fagus* and *Quercus* and, to a lesser degree, *Ulmus*, *Acer* and *Fraxinus*.

------------------------------------Insert Figure 8 near here-----------------------------------

6. Conclusions

CLAMP is applied for the first time to quantitatively evaluate the climatic parameters of the upper Miocene (early Tortonian) of the La Cerdanya Basin (eastern Pyrenees, Catalonia, Spain). The climatic results acquired through this method indicate a temperate palaeoclimate with fully humid and warm summers, which falls within the Cfb-type climate range of Köppen's classification. The results presented herein differ from previous palaeoclimatic analyses, which hypothesised a long, hot, dry season for the upper Miocene of the La Cerdanya Basin, leading to the supposition that the vegetation in the eastern Pyrenees was similar to that of coastal and lowland areas of the same age.

The Vallesian (early Tortonian) vegetation from La Cerdanya is similar to present-day vegetation from mountainous areas in the northeast of Honshu Island (Japan), including woody dicots belonging to the genera *Quercus, Fagus, Ulmus*, *Acer* and *Fraxinus* supporting the hypothesis that the chain was already at a significant topographic height during the early Tortonian.

The palaeoaltitudinal estimation using the terrestrial lapse rate method shows that during the Vallesian (early Tortonian) La Cerdanya was about 1100−1550 m a.s.l pointing to a similar or higher palaeoaltitude than in the presentIn order to refine the late Miocene altitude of La Cerdanya, future studies using other methods could be applied. For instance, the enthalpy value which is provided through CLAMP could be used. This method would compare the enthalpy obtained from the intramontane flora of La Cerdanya with the neighbouring coeval floras from the coastal basins of Vallès-Penedès or l'Empordà to provide the palaeoaltitude of La Cerdanya. However, this will require new sampling to properly estimate the palaeoaltitude, since the recorded floras from historical collections appear to be biased by the sampling method. These studies might shed light to characterize properly the uplift evolution of the Eastern Pyrenees in the Neogene and to gain a detailed view of the Neogene upland vegetation in South Europe.

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Figure captions

Figure 1: Simplified geological setting of the Miocene in the La Cerdanya Basin, modified from Cabrera et al. (1988).

Figure 2: Stratigraphic section through the Miocene units of the La Cerdanya Basin (Bellver sub-basin) with the location of the plant remains studied herein (modified from Roca, 1986). Chronostratigraphic attribution according to Agustí and Roca (1987). See the location of the section in Fig. 1.

Figure 3: Fossil leaf taxa from the Vallesian (early Tortonian) of the La Cerdanya Basin, used for the CLAMP database. A: *Daphnogene* sp. (MGB 89667-a). B: *Laurophyllum pseudoprinceps* (MGB 89666). C: *Buxus pliocenica* (MGB 89668). D: *Parrotia pristina* (MGB 89688-a). E: *Cercidiphyllum* sp. (MGB 89669-a). F: *Populus tremulaefolia* (MGB 89671). G: *Cassia* sp. (MGB 89672-a). H: Fabales sp. indet. 1 (MGB 89698-1). I: Fabales sp. indet. 2 (MGB 89698-2). Scale bar 1 cm.

Figure 4 Fossil leaf taxa from the Vallesian (early Tortonian) of the La Cerdanya Basin, used for the CLAMP database. A: *Zelkova zelkovifolia* (MGB 89674-a). B: *Ulmus plurinervia* (MGB 89675). C: *Quercus drymeja* (MGB 89676). D: *Q. mediterranea* (MGB 89677). E: *Q. hispanica* (MGB 89678). F: *Q. kubinyii* (MGB 89679). G: *Fagus pristina* (MGB 89680). H: *F. gussonii* (MGB 89681). I: *Juglans* sp. (MGB 89682). J: *Carya serrifolia* (MGB 89683). K: *Carpinus grandis* (MGB 89684). Scale bar 1 cm.

Figure 5: Fossil leaf taxa from the Vallesian (early Tortonian) of the La Cerdanya Basin, used for the CLAMP database. A: *Betula insignis* (MGB 89685). B: *Alnus occidentalis* (MGB 89687). C: *Acer tricuspidatum* (MGB 89691). D: *Acer integerrimum* (MGB 89689). E: *Acer pyrenaicum* (MGB 89690). F: *Acer palaeosaccharium* (MGB 89694). G: *Cedrela* sp. (MGB 89695). H: *Tilia vidali* (MGB 89696). I: *Aralia multifida* (MGB 89697). Scale bar 1 cm.

Figure 6: Canonical Correspondence Analysis graph with location of meteorological stations of CLAMP localities used for this study. **A**: CCA graph axes 1-2 with the palaeobotanical site of La Cerdanya (red square). Triangles correspond to present-day localities with monsoonal climate, while dots are localities with a non-monsoonal climate. B: CCA graph axes 2-3 with the palaeobotanical site of La Cerdanya (red square). Orange squares correspond to present-day American localities, blue triangles to Japanese localities, purple pentagon to Puerto Rico localities and brown dots to Oceanian localities. Meteorological sites plotted by CLAMP without a clear geographical situation were not represented in this figure.

Figure 7: European palaeogeographical map of the Tortonian. Dots represent the location of the European Tortonian palaeobotanical sites providing palaeoclimatic information for comparison. The La Cerdanya plant locality studied herein is marked with a star. Localities are numbered as in Table 4.

Figure 8: Location of the present-day sites in Honshu Island (Japan) supplying the most similar climatic parameters to those from the Vallesian (early Tortonian) of the

La Cerdanya Basin. 1: Chuzenji-ko. 2: Umedaira. 3: Kidogawa 1. 4: Kidogawa 2. 5: Aoba. 6: Mt. Tokura. 7: Sanze. 8: Takinsawa. 9: Tazawa-ko. 10: Nibetzu.

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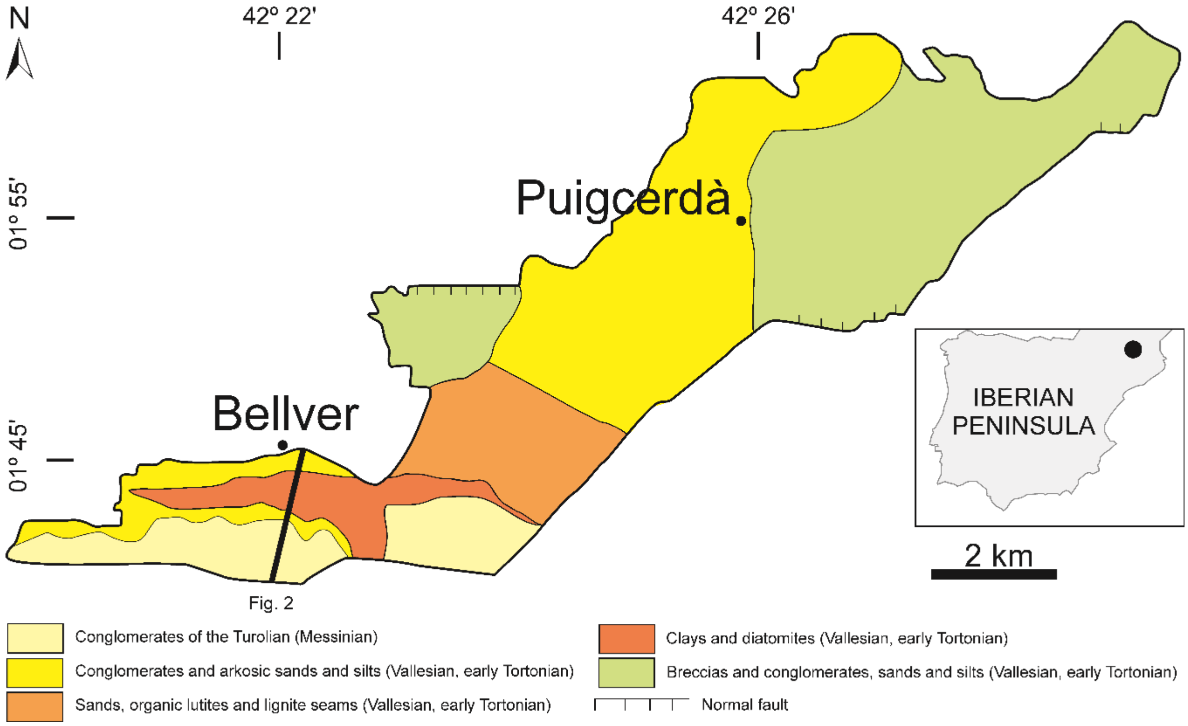
Table 2: Palaeoclimatic results provided by CLAMP for the Vallesian (early Tortonian) of La Cerdanya.

Table 3: Comparison of results obtained through CLAMP (this study) and through CA (Barrón et al., 2016) for the Vallesian (early Tortonian) of the La Cerdanya Basin.

Table 4: Climatic parameters of other Vallesian (early Tortonian) palaeobotanical sites in Europe.

Supplementary material

Table S1: CLAMP scoresheet filled in with leaf shape features of 29 taxa from the La Cerdanya Basin.



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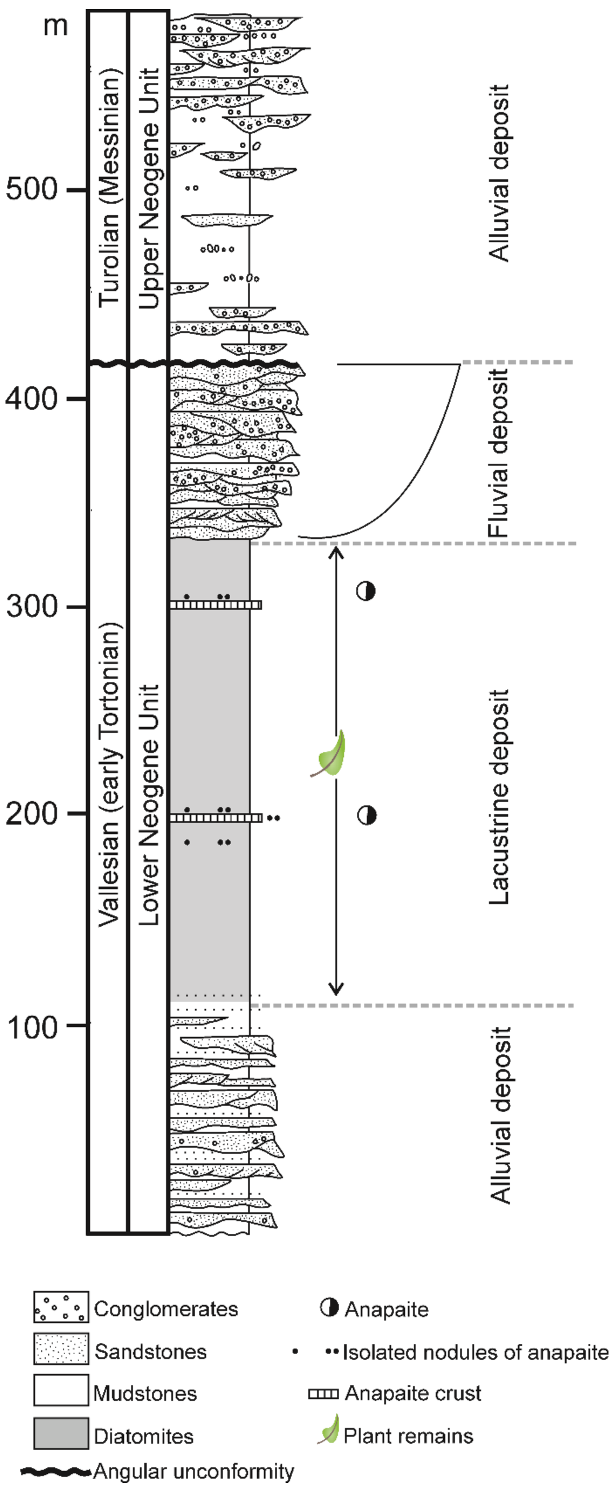

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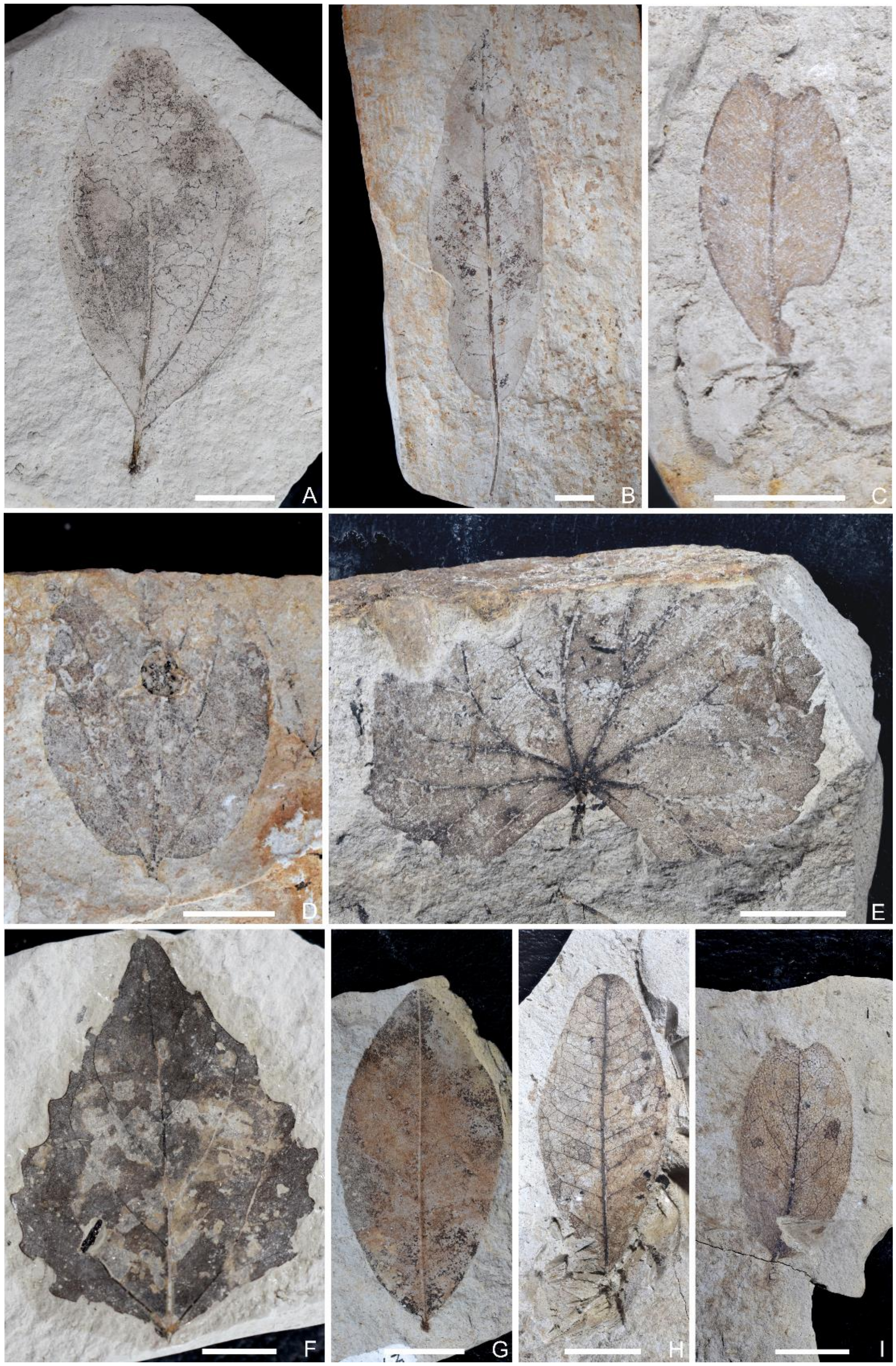

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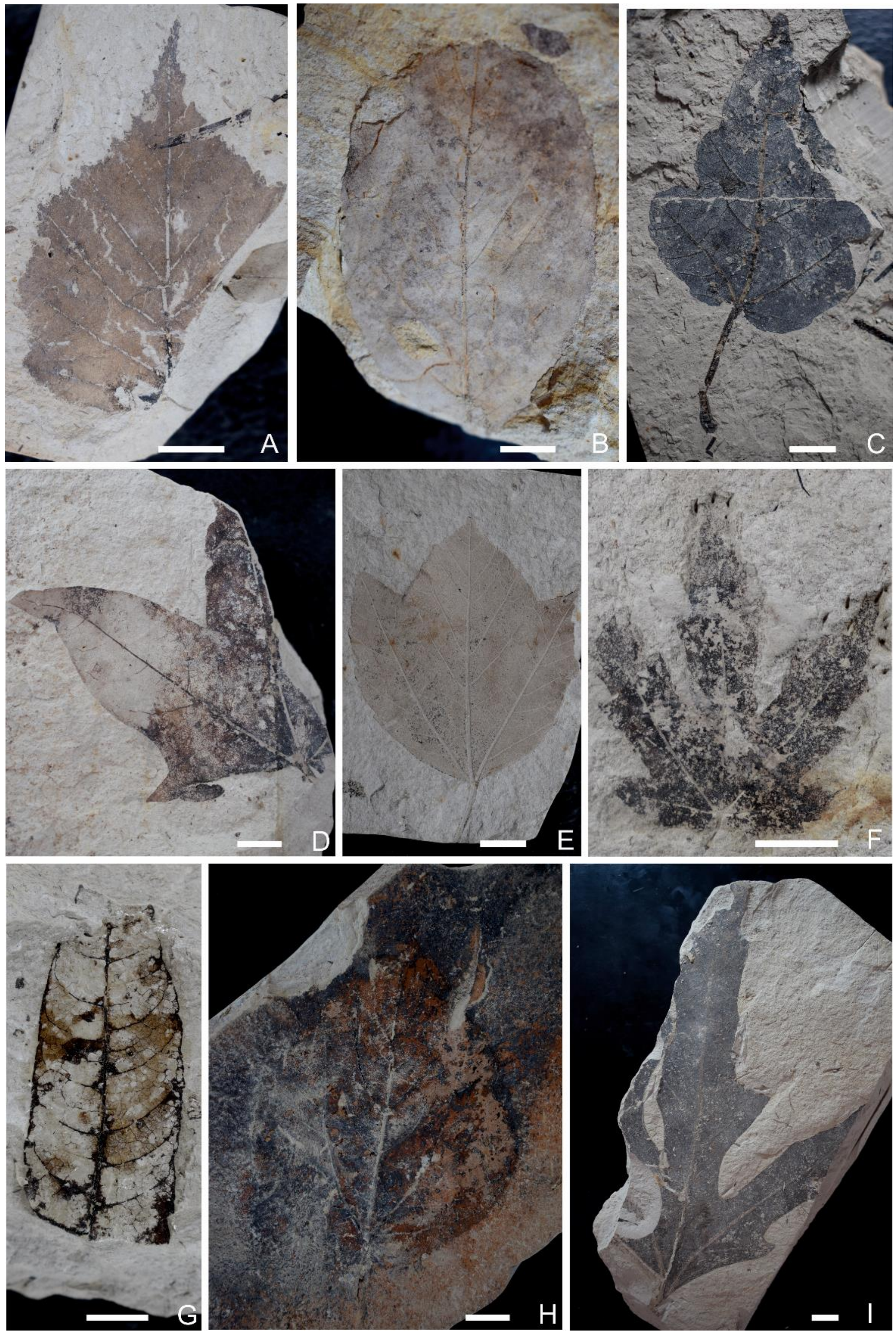

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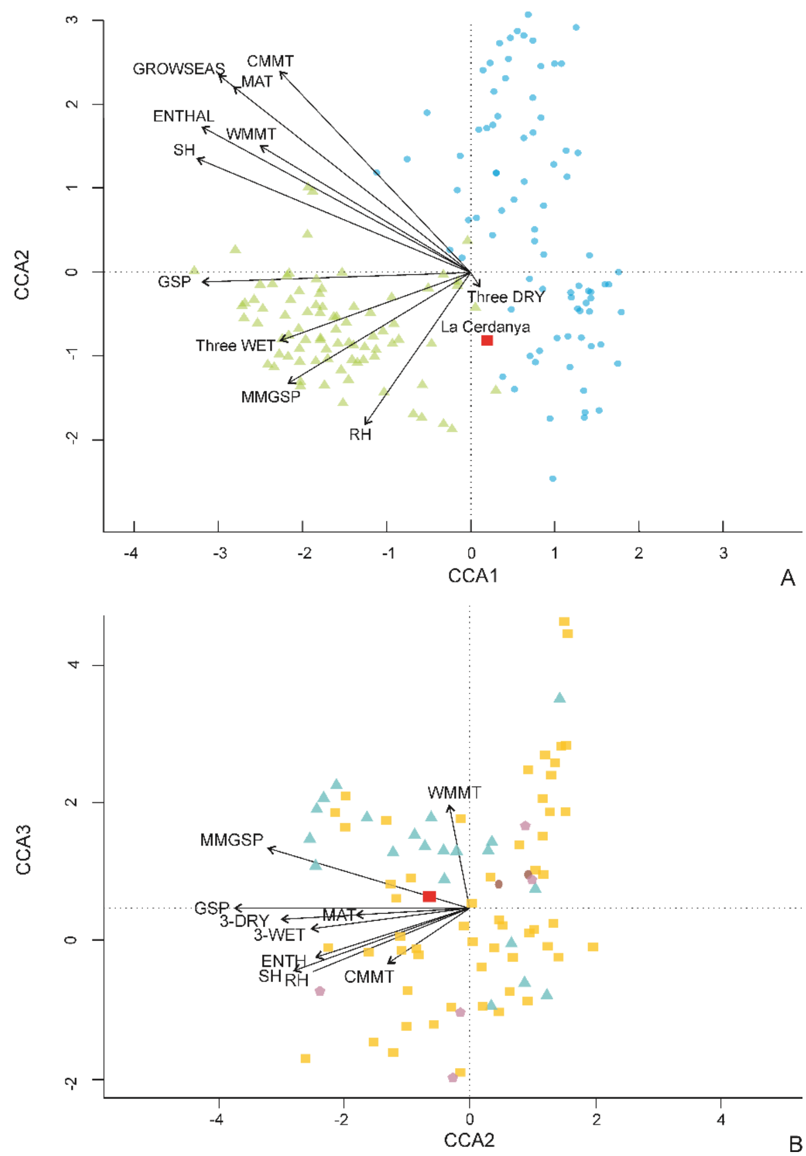

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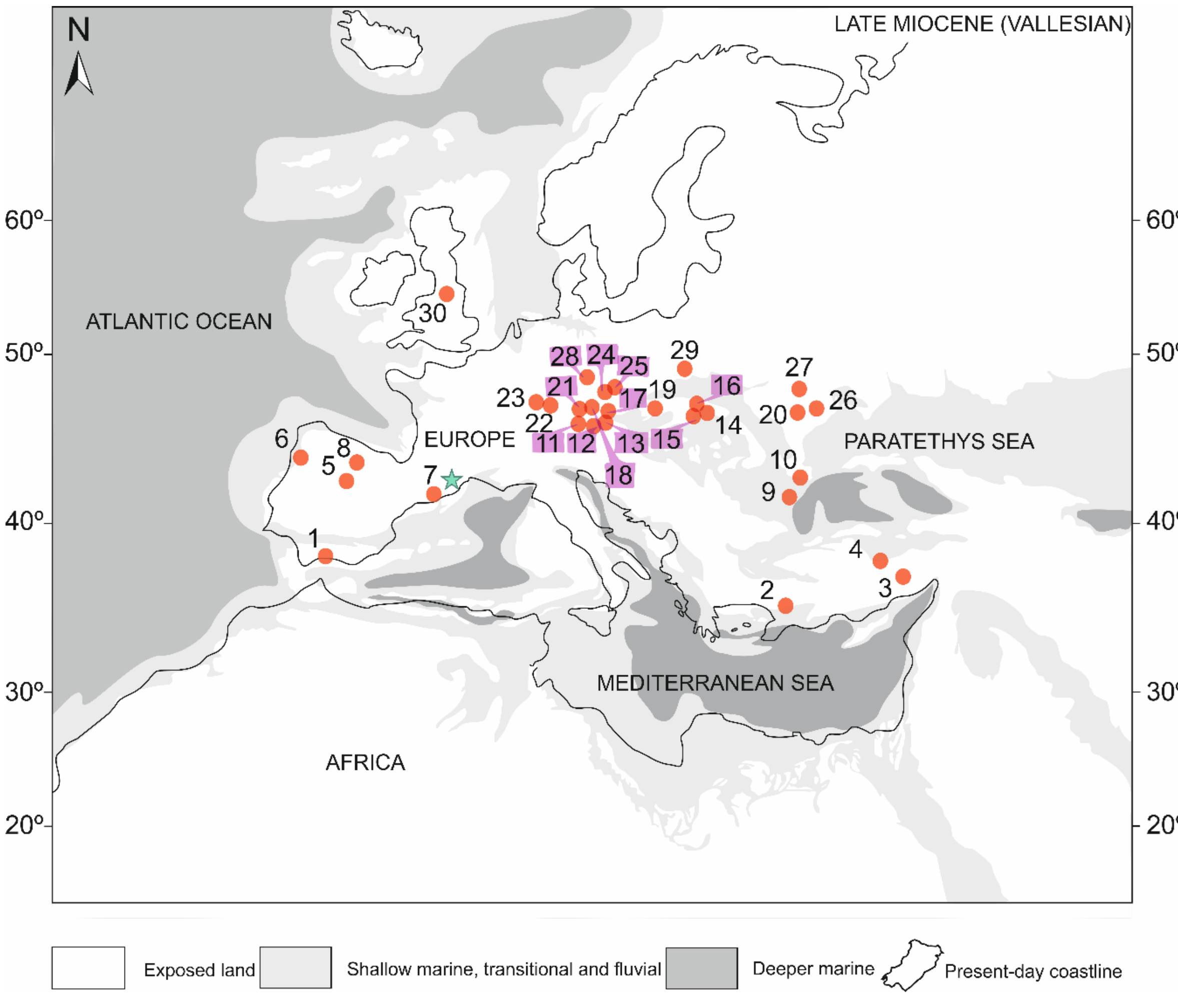

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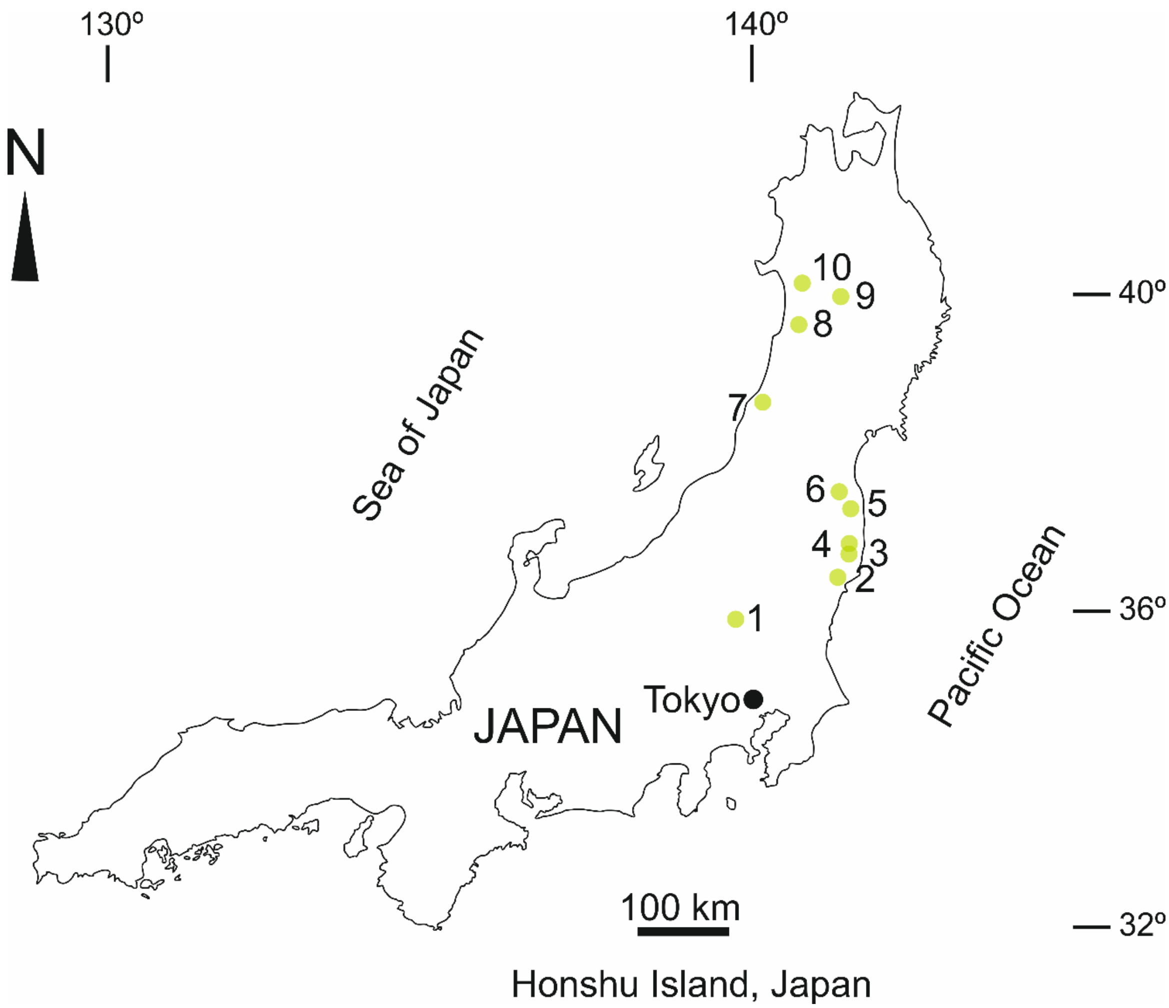

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Magnoliopsids of the Vallesian from La Cerdanya	
Or. Laurales Berchtold and Presl	Or. Fagales Enler
Fam. Lauraceae Jussieu	Fam. Fagaceae Mortier
Daphnogene sp.	*Quercus drymeja* Unger
Laurophyllum pseudoprinceps Weyland and Kilpper	*Quercus mediterranea* Unger
	Quercus hispanica Rérolle
	Quercus kubinyii Czeczott
Or. Buxales Reveal	*Fagus pristina* Saporta
Fam. Buxaceae Dumortier	*Fagus gussonii* Massalongo and Scarabelli
Buxus pliocenica Saporta and Marion	Fam. Juglandaceae De Candolle Ex Perleb
Or. Saxifragales Brechtold and Presl	*Juglans* sp.
Fam. Hamamelidaceae	*Carya* sp.
Parrotia pristina Ettingshausen	Fam. Betulaceae Gray
Fam. Cercidiphyllaceae	*Carpinus grandis* Heer
Cercidiphyllum sp.	*Betula insignis* Gaudin
	Alnus occidentalis Rérolle
Or. Malpighiales Martius	
Fam. Salicaceae Mirbel	Or. Sapindales Brechtold and Presl
Populus tremulaefolia Saporta	Fam. Sapindaceae Jussieu
	Acer tricuspidatum Bronn
Or. Fabales Bromhead	*Acer integerrimum* Viviani
Cassia sp.	*Acer pyrenaicum* Rérolle
Fabales sp. indet. 1	*Acer palaeosaccharium* Sturr
Fabales sp. indet. 2	Fam. Meliaceae
	Cedrela sp.
Or. Rosales Brechtold and Presl	
Fam. Ulmaceae Mirbel	Or. Malvales Dumortier
Zelkova zelkovifolia Bůžek and Kotlaba	Fam. Malvaceae
Ulmus plurinervia Unger	*Tilia vidali* Rérolle
	Or. Apiales Nakai
	Aralia multifida Saporta

Table 1: Taxonomic list of the morphospecies recognised in the flora assemblage studied herein, from the Vallesian of La Cerdanya**.**

	MAT (ºC)	CMMT (ºC)	WMMT (ºC)	GROWSEAS (months)	GSP (mm)	MMGSP (mm)	3-WET (mm)	3-DRY (mm)	RH (%)
Vallesian from La Cerdanya	11.4±2.1	1.8±3.4	21.6±2.5	6.8±1.1	1082±317	153±59	661±38	194±22	75.9±8.6

Table 2: Palaeoclimatic results provided by CLAMP for the Vallesian of La Cerdanya.

Climatic parameters	MAT (ºC)	CMT (ºC)	WMT (ºC)	MAP (mm)	3-WET (mm)	3-DRY (mm)
CLAMP (present study)	11.4±2.1	1.8±3.4	21.6±2.5	1418	661±38	194±229
CA from macroremains (Barrón et al., 2016)	11.7−16.2	0.4−3.8	25.1−26.1	1098−1355	397−520	77−118

Table 3: Comparison of results obtained through CLAMP (this study) and through CA (Barrón et al., 2016) for the Vallesian of the La Cerdanya Basin.

	Locality	Present-day coordenates UTM	Present-day altimetry (m a.s.l)			MAT (ºC)	CMT (ºC)	WMT (ºC)	MAP (mm)	Reference
	La Cerdanya (Spain)	42º 22’ 04’’N; 01º 46’ 42’’E	1000-1300	Leaf	Vallesian	11.4	1.8	21.6	1418	Present study
					Today	9	-3−2	14−18	700−1000	
1	Andalucía (Spain)	36º30’06’’N; 41º53’20’’W	27	Pollen	Vallesian	16.8−24.7	-	-	388−873	Jimenez-Moreno et al. (2010)
					Today	17	1-−9	30−36	250−800	
2	Samos (Greece)	37º45’26’’N; 26º58’30’’E	700	Pollen	Vallesian	16.5−19.4	9.6	26−27.9	830−1281	Bruch et al. (2004)
					Today	17.9	12	29	746	
3	Elaziğ (Turkey)	41º01’07’’N; 28º51’56’’E	1403	Pollen	Vallesian	15.6−21.3	5−13.3	24.7−28.1	-	Akgün et al. (2007)
					Today	12.4	-1.6	25.9	534	
4	Sivas-Hafik (Turkey)	39º 54’37’’N; 37º15’14’’E	1733	Pollen	Vallesian	16.5−20.8	5.5−13.3	27.3−28.1	-	Akgün et al. (2007)
					Today	9.1	3.3	15.4	447	
5	Zaratán (Spain)	41º 39’27’’N; 04º 47’ 13’’W	755	Pollen	Vallesian	16−25	5−9.6	25.3−27.7	600−892	Bruch et al. (2004) ; Fauquette et al. (2007)
					Today	20	8	30	201	
6	Povoa (Portugal)	39º 22’ 00’’N 08º 90’ 00’’W	190	Leaf	Vallesian	13.7−17	2.5−8.3	23.3−26.4	735−1333	Bruch et al. (2004)
					Today	14.5	9.7	19.5	1220	
7	Terrassa (Spain)	41º 33’ 46’’N 02º 00’ 31’’E	286	Leaf	Vallesian	16−18	–	–	–	Sanz de Siria (1997)
					Today	15	8	23.1	635	
8	Burgos (Spain)	42º 20’43’’N 03º42’02’’W	937	Pollen	Vallesian	15.6−17	6.4−10.3	24.7−26.3	1146−1322	Bruch et al. (2004)
					Today	10.5	2.7	18.9	575	
9	Drenovets and Koshava (Bulgaria)	43º 41’34’’N 22º 58’ 55’’E:	121	Pollen and Leaf	Vallesian	13.3−17.2	3	–	652−1308	Ivanov et al. (2011)
					Today	8−11	0−5	25−30	700	
10	Dacian Basin (Romania)	45º40’18’’N 23º 10’ 47’’E	535	Pollen	Vallesian	13.9−19.9	6.1−12.3	27.9−28.1	529−1096	Casas-Gallego et al. (2020)
					Today	10	-2.3	20.2	625	
11	Moravska Nova Ves (Czech Republic)	48º 70’00’’N 17º 05’00’’E	191	Leaf	Vallesian	13.3−16.4	-	-	1100−1297	Utescher et al. (2017)
					Today	13	2	26	463	
12	Neuhaus (Austria)	46º 93’ 00’’N 16º08’00’’E	486	Leaf	Vallesian	13.8−18.5	-	-	897−1297	Utescher et al. (2017)
					Today	8.4	-2.8	20.5	572	
13	Vösendorf (Austria)	48º 07’ 21’’N 16º 20’ 05’’E	195	Leaf	Vallesian	14−14.9	-	-	735−1297	Utescher et al. (2017)
					Today	9.8	-0.7	19.8	631	
14	Tiszapalkonya (Hungary)	47º 88’ 50’’ N 21º05’ 50’’E	92	Leaf	Vallesian	9.1−17.6	-	-	512-1542	Utescher et al. (2017)
					Today	16	0	26	277	
15	Mindszentkálla (Hungary)	46º 87’ 00’’N 17º55’00’’E	164	Fruits and seeds	Vallesian	12.2−16.9	-	-	439-1356	Utescher et al. (2017)
					Today	11.2	-0.4	21.3	640	

16	Alcsút (Hungary)	47º 42’ 60’’N 18º 60’ 03’’E	138	Leaf	Vallesian	12.5−21.3	-	-	897−1613	Utescher et al. (2017)
					Today	10.4	-4	26.5	592	
17	Pellendorf (Austria)	48º 11’00’’N 16º 14’ 00’’E	175	Leaf, fruit and seed	Vallesian	14.4−16.6	-	-	979−1297	Utescher et al. (2017)
					Today	15	1	26	310	
18	Ebersbrunn (Austria)	48º 53’ 00’’N 15º 88’ 00’’E	393	Leaf	Vallesian	12.5−17.6	-	-	897−1613	Utescher et al. (2017)
					Today	15	1	25	310	
19	Neusiedl (Austria)	46º 93’ 00’’ N 15º 83’ 46’’E	127	Leaf	Vallesian	14−15.1	-	-	897−1430	Utescher et al. (2017)
					Today	10	-1.1	20.3	600	
20	Chiuzbaia (Romania)	47º 75’ 00’’N 23º 50’ 00’’ E	539	Leaf	Vallesian	12.5−16.4	-	-	897−1297	Utescher et al. (2017)
					Today	9.3	-3	19.4	770	
21	Lohnsburg (Austria)	48º 15’ 00’’N 13º 42’ 00’’E	524	Leaf	Vallesian	12.5-16.4	-	-	897-1187	Utescher et al. (2017)
					Today	18	-5	22	1530	
22	Massenhausen (Germany)	48º 20’ 54’’N 11º38’11’’E	472	Leaf	Vallesian	13.3−13.8	-0.1−4.1	25.6−26.4	-	Bruch et al. (2004)
					Today	7.9	-2.1	17	833	
23	Zukunft (Germany)	50º50’25’’N 12º54’25’’E	307	Fruits and seeds	Vallesian	15.3−15.5	6.6−7.9	25.7−25.9		Bruch et al. (2004)
					Today	8	4	25	930	
24	Wörth (Austria)	47º 02’00’’ N 15º75’00’’E	494	Leaf	Vallesian	9.1−16.4	-	-	735−1297	Utescher et al. (2017)
					Today	10.4	1.1	19.5	701	
25	Postorna (Czech Republic)	48º75’ 00’’N 16º 14’00’’E	162	Leaf, fruit and seed	Vallesian	12.5−21.3	-	-	897−1542	Utescher et al. (2017)
					Today	9	-2.2	18.6	519	
26	Delureni (Romania)	46º48’52’’N 24º20’41’’E	378	Leaf	Vallesian	14.4−18.1	-	-	843−1256	Utescher et al. (2017)
					Today	17	2	30	365	
27	Kucsova (Albania)	48º50’00’’N 22º35’00’’E	63	Leaf	Vallesian	2.1−22.2	-	-	201−2559	Utescher et al. (2017)
					Today	14.8	8	30	1207	
28	Mistrin (Czech Republic)	48º 97’ 00’’N 17º 17’ 00’’E	184	Leaf, fruit and seeds	Vallesian	13.5−17.4	-	-	578−1356	Utescher et al. (2017)
					Today	9.3	2	26	619	
29	Rudabánya (Hungary)	48º 38’00’’N 20º 63’ 00’’E	226	Leaf	Vallesian	15.7−22.2	-	-	1096−1864	Utescher et al. (2017)
					Today	10	-2.7	10.7	551	
30	Derbyshire (England)	53º06’40’’N 01º33’49’’W	259	Pollen	Vallesian	18.14−18.63			1164−1826	Pound (2012)
					Today	14	6	19	283	

Table 4: Climatic parameters of other Vallesian palaeobotanical sites in Europe.

Late Miocene (Vallesian) of La Cerdanya		Latitude: 42º 22’04’’N												Longitude: 01º 46’42’’E									Mean altitude: 12000 m a.s.l								**Completeness:** 0.908							
Morphotype	**Species**	**Lamina**		**Margin**										**Size**									**Apex**				**Base**			**Length : Width**					**Shape**		
		Unlobed	**Lobed**	**No teeth**	**Teeth**	**Regular teeth**	**Irregular teeth**	**Close teeth**	**Distant teeth**	**Round teeth**	**Acute teeth**	**Compound teeth**	**Compound<50%**	**Nanophyll**	**Leptophyll I**	**Leptophyll II**	**Microphyll I**	**Microphyll II**	**Microphyll III**	**Mesophyll I**	**Mesophyll II**	**Mesophyll III**	**Emarginate**	**Round**	**Acute**	**Attenuate**	**Cordate**	**Round**	**Acute**	**L:W <1:1**	**L:W 1-2:1**	**L:W 2-3:1**	**L:W 3-4:1**	**L:W >4:1**	**Obovate**	**Elliptic**	**Ovate**
1	*Daphnogene* sp.	1		1															1						1				1		1					1	
2	*Laurophyllum pseudoprinceps*	1		1																1					1				1				1			1	
3	*Buxus pliocenica*	1		1													1	1							1				1				1			1	
4	*Parrotia pristina*	1		1														1						1				1			1					1	
5	*Cercidiphyllum* sp.	1		1															1								1									1	
6	*Populus tremulaefolia*	1			1	1		1		1			1						1	1	1	1							1			1	1		1		
7	*Cassia* sp.	1		1														1							1				1				1			1	
8	Fabales sp. indet. 1	1		1														1							1				1		1					1	
9	Fabales sp. indet. 2	1		1													1						1					1				1				1	
10	*Zelkova zelkovifolia*	1			1	1		1		1	1		1				1	1							1				1			1				1	
11	*Ulmus plurinervia*	1			1	1		1			1		1					1	1						1			1			1						1
12	*Quercus drymeja*	1			1	1	1	1	1	1	1		1					1	1						1			1	1				1			1	1
13	*Quercus mediterranea*	1			1		1		1		1		1					1	1						1			1					1				1
14	*Quercus hispanica*	1			1	1		1		1	1		1					1	1						1			1				1				1	
15	*Quercus kubinyii*	1			1	1		1			1		1					1							1				1			1				1	
16	*Fagus pristina*	1			1	1			1	1	1		1					1	1						1			1				1					1
17	*Fagus gussonii*	1			1		1		1	1	1		1						1	1	1	1		1				1	1		1					1	
18	*Juglans* sp.	1		1																1						1			1				1			1	
19	*Carya* sp.	1			1		1	1			1		1						1	1					1				1				1			1	
20	*Carpinus grandis*	1			1		1	1			1	1						1							1		1				1						1

Late Miocene (Vallesian) of La Cerdanya																																					
		Lamina		Margin										Size									Apex				Base			Length : Width					Shape		
Morphotype	Species	Unlobed	Lobed	No teeth	Teeth	Regular teeth	Irregular teeth	Close teeth	Distant teeth	Round teeth	Acute teeth	Compound teeth	Compound<50%	Nanophyll	Leptophyll I	Leptophyll II	Microphyll I	Microphyll II	Microphyll III	Mesophyll I	Mesophyll II	Mesophyll III	Emarginate	Round	Acute	Attenuate	Cordate	Round	Acute	L:W <1:1	L:W 1-2:1	L:W 2-3:1	L:W 3-4:1	L:W >4:1	Obovate	Elliptic	Ovate
21	*Betula insignis*	1			1		1	1			1		1						1	1					1		1				1						1
22	*Alnus occidentalis*	1			1		1		1		1	1							1	1			1	1				1			1					1	
23	*Acer tricuspidatum*		1		1		1	1		1			1					1	1	1					1		1				1		1			1	
24	*Acer intergerrimum*		1	1																		1			1			1			1						1
25	*Acer pyrenaicum*		1		1		1		1		1		1					1							1			1			1					1	
26	*Acer palaeosaccharinum*		1		1		1		1		1		1					1							1		1				1					1	
27	*Cedrela* sp	1		1																1																	
28	*Tilia vidali*	1			1		1	1			1		1									1			1		1					1					1
29	*Aralia multifida*		1		1		1		1	1			1									1				1	1							1		1	

Palaeoclimatic values	MAT (ºC)	CMMT(ºC)	WMMT(ºC)	GROWSEAS (months)	GSP (mm)	MMGSP (mm)	3-WET (mm)	3-DRY (mm)	RH (%)	ENTHAL (Kj/kg)	SH (g/kg)
	11.4±2.1	1.8±3.4	21.6±2.5	6.8±1.1	1082±317	153±59	661±38	194±22	75.9±8.6	31.43	7.57

Table S1: CLAMP scoresheet filled in with leaf shape features of 29 taxa from the La Cerdanya Basin.