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# Palaeoclimatic reconstruction for the Late Oligocene La Val fossil site (Estadilla, Huesca, Spain) based on CLAMP and LMA

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ABSTRACT

In this paper, we reconstruct palaeoclimate for the late Oligocene (Chattian) La Val plant assemblage of Spain (NE Iberian Peninsula). Our study employs both CLAMP (Climate Leaf Analysis Multivariate Program) and LMA (Leaf Margin Analysis), the first time these two techniques have been directly compared, and is based on 25 morphotypes (representing 23 taxa) of woody dicot leaves from a single stratigraphic unit (layer LV6). Both methods have provided a similar result. Although the standard deviation of LMA is higher than CLAMP, the results of LMA are coherent with CLAMP. The palaeoclimatic variables obtained from CLAMP shows a marked contrast between WMMT and CMMT and between 3-WET (836.3 ± 145.4 mm) and 3-DRY (113 ± 33 mm). Meanwhile, the GROWSEAS (9.30 ± 0.7 months) points out that the growth season lasted almost all the year. These variations signal a seasonal contrast, showing the existence of a dry season. Results indicate a warm temperate climate with hot and dry summers. The palaeoclimatic variables obtained using CLAMP are: MAT 17.2 ± 1.7 °C, WMMT 25.5 ± 1.3 °C, CMMT 10 ± 1.8 °C and GSP 1480 ± 204 mm. The palaeoclimatic variables obtained using LMA are MAT 17.11 ± 4.61 °C (regression equation for data from East Asia) and 16.8 ± 4.7 °C (regression equation for data from Europe). The palaeoclimatic values estimated from La Val site match those obtained from other Oligocene sites from Iberia (e.g. As Pontes site) that rely on different palaeoclimate methods. These palaeoclimatic values obtained from La Val are also similar to those from several Oligocene localities (e.g. the Rot flora) in Europe and reflect peak temperature corresponding to the late Oligocene warming episode.

## 1. Introduction

Several techniques have been developed for determining quantitative terrestrial palaeoclimate parameters. These methods are mainly based on foliar physiognomic and nearest living relative techniques and include Leaf Margin Analysis (LMA) (Wolfe, 1979; Traiser et al., 2005), Climate Leaf Analysis Multivariate Program (CLAMP) (Wolfe, 1993; Yang et al., 2011), the Coexistence Approach (CA) (Mosbrugger and Utescher, 1997; Utescher et al., 2014), the Climate Amplitude Method (CAM) (Fauquette et al., 1998a, 1998b), and more recently Overlapping Distribution Analysis (ODA) (Yang et al., 2007). These methods are most often employed to reconstruct the evolution of Cenozoic palaeoclimates and are mainly applied to Neogene and Quaternary fossil floras, periods for which they are the most powerful tools available (Yang et al., 2007, 2011).

Both LMA and CLAMP are extensively utilised in contemporary palaeoclimate reconstructions. They are based on aspects of plant architecture, which are influenced by environmental conditions. LMA is a straightforward technique that depends on the correlation that exists between the proportions of toothed versus non-toothed woody dicotyledonous leaves in a given patch of non-pioneer vegetation and the Mean Annual Temperature (MAT). The advantage in using LMA is that it is simple to compute, although it returns only one climate variable (Yang et al., 2007). CLAMP is a multivariate statistical method that builds upon the foundation of LMA. CLAMP obtains the climatic signal inherent in the physiognomy of leaves of woody dicotyledonous plants and is capable of yielding values for up to 24 palaeoclimate variables (Bathia et al., 2021) and although the computational simplicity of LMA is lost, precision is greatly increased (Yang et al., 2007, 2011; Spicer et al., 2009, 2019; Zolina et al., 2020; Bathia et al., 2021). A second major advantage of CLAMP is that the fossil specimens need only be divided into morphotypes, instead of being classified taxonomically; this method

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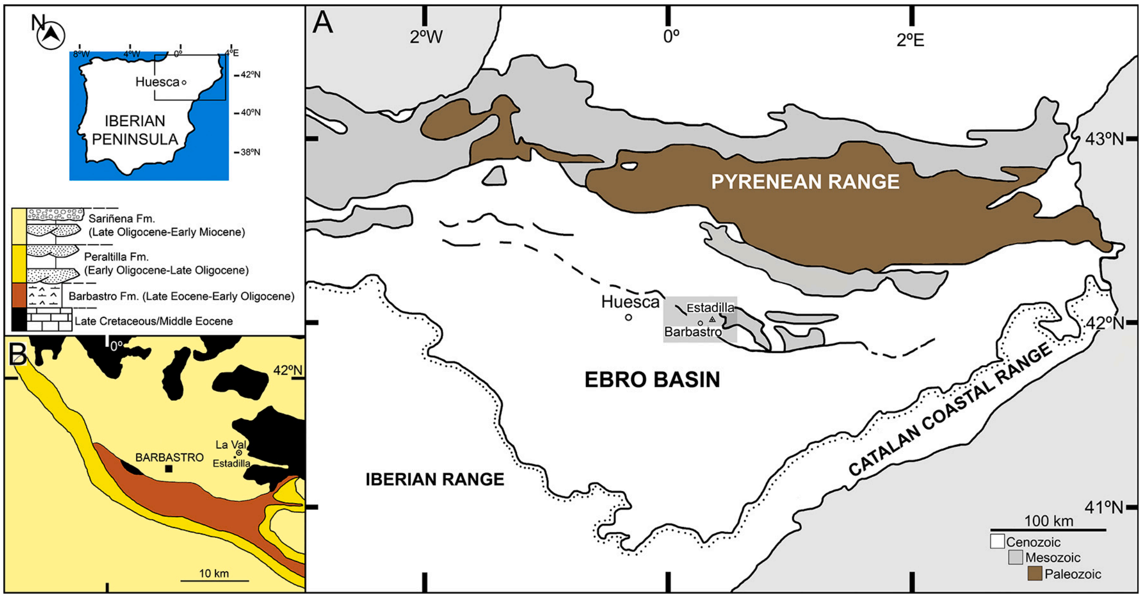


**Fig. 1.** Location and geographical and geological context of the La Val megafloral fossil assemblage, northeastern Spain. A. Simplified geological map of the northeastern region of the Iberian Peninsula with location of the study area. B. Geological map of the study area where is situated La Val fossil site with the lithostratigraphic units: Barbastro Fm. (Late Eocene-Early Oligocene), Peraltilla Fm. (Early Oligocene-Late Oligocene), and Sariñena Fm. (Late Oligocene-Early Miocene). Modified from Moreno-Domínguez et al. (2015).

is sufficiently robust even where fossil material is only partially preserved, and it can be applied effectively to fossil assemblages up to 100 million years old (Herman and Spicer, 1996). The CLAMP method gives results comparable to those of the other techniques listed above (see Liang et al., 2003; Uhl et al., 2003), although the temperature values produced by CLAMP are often lower than those derived through other methods; this variation depends on the climate regime (Spicer et al., 2011; Yang et al., 2011).

The aims of the present paper are: (1) to reconstruct the palaeoclimate of the La Val fossil site of the Iberian Peninsula by using the CLAMP and LMA methods, (2) compare the results with those of similar fossil sites in Europe, and (3) provide new insights into palaeoclimate evolution during the late Oligocene in the South of Europe.

Until now, the palaeoclimatic reconstructions for the Iberian Peninsula have focused on the Neogene period and have been based on several different techniques derived from analyses of micromammals (López-Martínez et al., 1987; Cuenca-Bescós et al., 2011), sedimentological data (Hamer et al., 2007), squamata and amphibian assemblages (Blain et al., 2009, 2018), pollen data, and fossil macroflora assemblages (Barrón et al., 2010; Barrón et al., 2016; Altolaguirre et al., 2019). Several quantitative and semi-quantitative methods, such as CA or Mutual Climatic Range, have also been used (Blain et al., 2009; Gaudant et al., 2015; Casas-Gallego et al., 2015; Casas-Gallego, 2018) and, very recently, CLAMP (Tosal et al., 2019, 2021). However to date, LMA and CLAMP have not been applied to the late Oligocene of the Iberian Peninsula.

## 2. Geological setting

The La Val fossil macrofloral assemblage (42°3′47.62″N, 0°15′3.34″E; 475 m asl) is situated approximately one kilometre to the north of Estadilla (Huesca Province, Spain) (Fig. 1, A-B). The outcrop is located at the foot of the Carrodilla Range in the Marginal Sierras of the southern Pyrenees, very close to the northern margin of the Ebro Basin (Moreno-Domínguez et al., 2016).

From both geographic and geological perspectives, the Ebro Basin is the largest continental Cenozoic basin in the northeast of Iberia and is delimited by the Pyrenees to the north (Fig. 1, A-B). The geodynamic evolution of this basin was associated with the structural development of its margins during the Alpine Orogeny, and principally to that of the Pyrenees. From the late Eocene to late Miocene, the Ebro Basin was endorheic, with large alluvial fan systems and passing into carbonate or saline lacustrine environments in the basin centre (Luzón and González, 2003; Luzón, 2005).

Upper Oligocene_Lower Miocene sedimentary rock units outcrop in the central sector of the northern Ebro Basin. These deposits comprise coarse- to fine-grained sediments belonging to the Sariñena Formation, and La Val fossil site is located in this sequence. This formation mainly consists of continental deposits of sandstones and mudstones (Luzón, 2005). These continental beds are interpreted as fluvial and alluvial-fan sediments and have long been considered to have been deposited in a large fluvial system, which existed simultaneously with several small alluvial fans (Luzón and González, 2003; Luzón, 2005; Moreno-Domínguez et al., 2016).

The Sariñena Formation is late Oligocene (Chattian) to early Miocene (Burdigalian) in age and is divided into two tectono-sedimentary units (T4 and T5, see Fig. 2), which are defined in the Ebro Basin, and related to the Alpine Orogeny (Luzón and González, 2003; Pardo et al., 2004; Luzón, 2005). It is dated by mammal assemblages and reaches up to one thousand meters thick in some areas (e.g. Luzón, 2005). Unit T4 comprises the lower and the middle part of the Sariñena Formation (Chattian_Aquitanian) and Unit T5 includes the upper part of this formation (Aquitanian_Burdigalian). La Val is stratigraphically situated in the lower part of the Sariñena Formation, and therefore dates to the Chattian (late Oligocene) (Moreno-Domínguez et al., 2016).

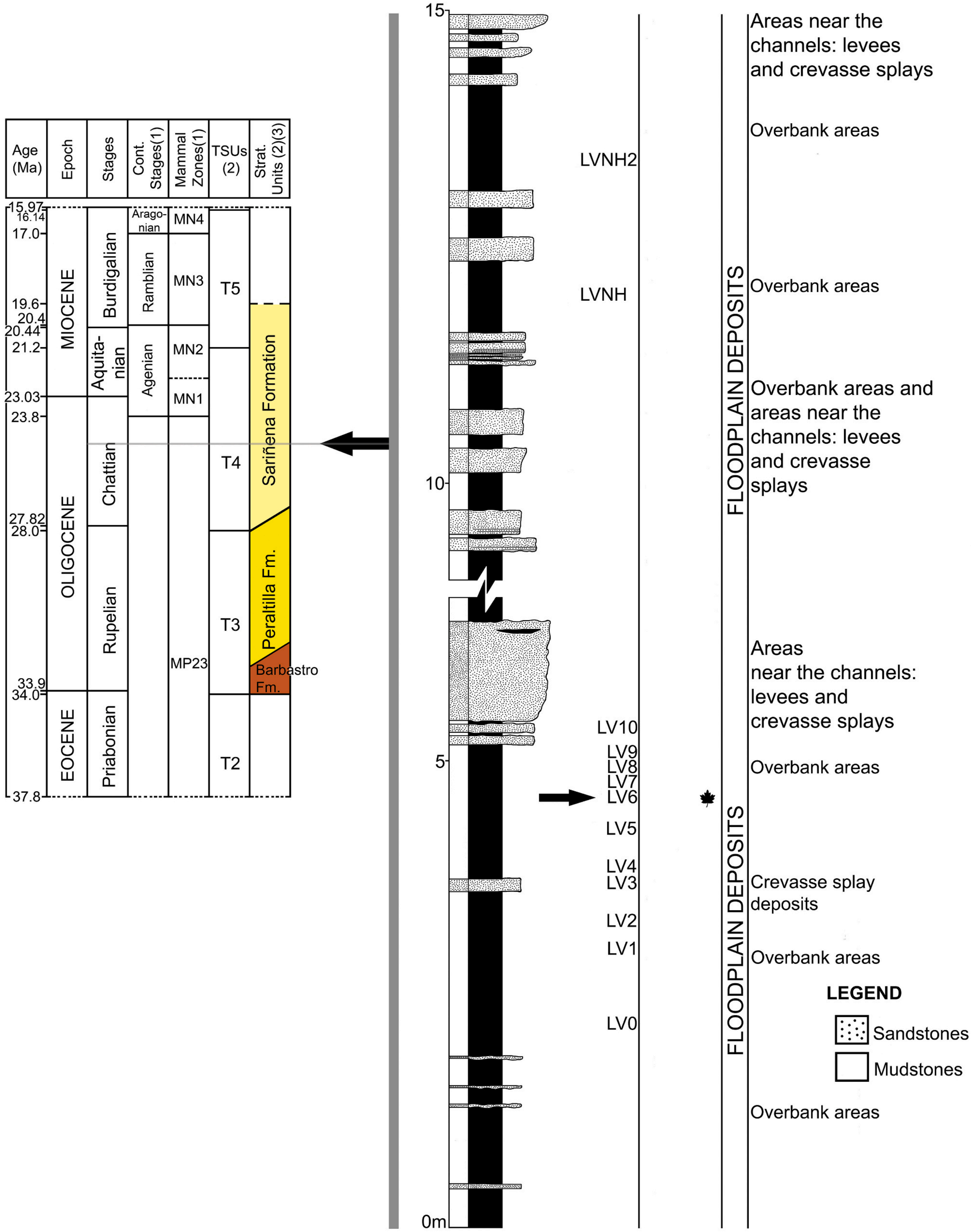


**Fig. 2.** Chronostratigraphic chart for the study area, including the position of the La Val fossil site, and schematic stratigraphic general section and sedimentological interpretation of the La Val fossil site showing the horizon where fossil layer LV6 occurs in the La Val fossil assemblage. Modified from Moreno-Domínguez et al. (2016), and data based on Pardo et al. (2004), Luzón (2005), and Sesé (2006). Strat.: Stratigraphic, TSUs: Tectosedimentary Units, Cont.: Continental, Fm.: Formation, MN: Mammal Neogene, LV: La Val, LVNH: La Val Nivel Helechos. (1) Sesé (2006), (2) Pardo et al. (2004), (3) Luzón (2005).

**Table 1**
Taxa list of the megaflora per stratigraphic layers (LV) used in LMA for La Val fossil site. It is only considered angiosperm leaves. (+: taxon is present in the stratigraphic bed, LV: La Val, LVNH: La Val Nivel Helechos).

| Stratigraphic layers | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Fossil taxon | LV0 | LV1 | LV2 | LV3 | LV4 | LV5 | LV6 | LV7 | LV8 | LV9 | LV10 | LVNH | LVNH2 |
| *Acer* cf. *haselbachense* | | | | | | | + | | | | | | |
| *Acer* sp. | | | | + | + | | | | | | | | |
| *Alnus* cf. *gaudinii* | | + | + | + | + | + | + | + | | | | | |
| *Alnus* sp. | + | + | + | + | + | + | + | | + | + | + | | |
| *Ampelopsis* sp. * | | | | | | | + | | | | | + | + |
| *Berberis andreanszkyi* | | | | | | | | + | | | | | |
| cf. *Berberis* sp. * | | | | | | | | | | | | + | |
| Betulaceae | + | + | + | + | + | + | + | + | + | + | + | + | |
| cf. *Carpinus grandis* | | | | + | | | | | | | | | |
| *Caesalpinites* sp. * | | | | | + | | | | | | | + | |
| *Celastrophyllum* sp. | | | | + | | | | | | | | | |
| *Dicotylophyllum* sp. | | | | | + | | + | | | | | + | + |
| *Daphnogene bilinica* * | | + | | + | | | | + | + | | | | |
| *Daphnogene cinnamomifolia* * | | | | | | | + | | + | | | | |
| *Daphnogene lanceolata* * | | + | | + | | | + | + | | | | | |
| *Daphnogene polymorfa* * | | + | | | + | + | + | + | + | | | | |
| *Daphnogene* sp. * | + | + | | + | + | + | + | + | + | + | + | | |
| *Engelhardia orsbergensis* | | | | | + | | + | | | | | | + |
| Fabaceae * | + | + | | | + | | + | | | | | + | |
| *Laurophyllum* sp. * | + | + | + | + | + | | + | + | | + | | + | + |
| Lauraceae * | | | | + | + | + | + | + | | | | | |
| *Leguminophyllum* sp. * | | | | | | | + | | | | | | |
| cf. *Liquidambar* sp. | | | | + | | | | | | | | | |
| *Liriodendron* sp. * | | | | | | | + | | | | | | |
| cf. *Magnolia* sp. * | | | | | | | | | + | | | | |
| *Myrica lignitum* | | | | | + | | + | | | | | | |
| *Myrica* sp. | | + | + | | + | + | + | + | | | | | |
| cf. *Myrica* sp. | | + | | + | + | | + | | | | | | |
| cf. *Parrotia* sp. * | | | | | | | + | | | | | | |
| *Quercus mediterranea* | | | | | | | + | | | | | + | |
| *Quercus* sp. * | + | | | | | | | + | | | | | |
| cf. *Rosa lignitum* | | | | | + | | + | | | | | | |
| cf. *Salix varians* | | | + | | | | | | | | | | |
| cf. *Salix* sp. * | | + | | + | + | | + | + | + | | | | |
| cf. *Typha* sp. * | | | | | + | | | | | | | | |
| Total | 5 | 12 | 6 | 14 | 18 | 7 | 23 | 12 | 8 | 4 | 3 | 8 | 4 |

## 3. La Val fossil site

To date, only three late Oligocene megafloral fossil assemblages have been studied in Iberia: Son Ferragut (Álvarez-Ramis et al., 1987), As Pontes (Barrón and Santos, 1998; Casas-Gallego and Barrón, 2020) and La Val (Moreno-Domínguez et al., 2015). The La Val fossil site is the most recent contribution to understanding the Oligocene floras of the Iberian Peninsula. The La Val fossil site was discovered in 2011, but its palaeobotanical study did not begin until 2015.

The plant taxa listed below (Moreno-Domínguez et al., 2015; Moreno-Domínguez, 2019; Table 1) are recognised from 13 distinct, fossiliferous layers at the La Val site (Fig. 2): *Acer*, *Acrostichum*, *Alnus*, *Ampelopsis*, *Berberis*, *Daphnogene*, *Dicotylophyllum*, *Caesalpinites*, cf. *Carpinus*, *Celastrophyllum*, Cupressaceae, *Engelhardia*, *Equisetum*, Fabaceae, *Laurophyllum*, *Leguminocarpon*, *Leguminophyllum*, cf. *Liquidambar*, *Liriodendron*, cf. *Magnolia*, *Myrica*, cf. *Parrotia*, *Pinus*, *Pronephrium*, *Pteridium*, *Quercus*, cf. *Rosa*, cf. *Salix*, cf. *Typha*, and Trapaceae.

The megaflora of La Val developed in fluvial areas, which were situated in medial to distal zones of large sub-aerial alluvial fans. This fossil megaflora corresponds to a riparian forest (Moreno-Domínguez et al., 2015, 2016), with *Alnus* being the most abundant taxon. However, other characteristic and important floral elements are also present, such as *Acrostichum*, which has been interpreted as a pioneer plant growing in surrounding floodplain areas in La Val (Moreno-Domínguez et al., 2016). In contrast, megaflora at As Pontes and Son Ferragut mainly correspond to lacustrine margin environments (Álvarez-Ramis et al., 1987; Barrón and Santos, 1998).

An initial palaeoecological examination of La Val suggests that *Alnus* grew on the edges of flooded areas and dominated the canopy, while taxa belonging to the Lauraceae formed the adjacent forest located behind this alder-dominated carr. Other prevalent families present at La Val were Myricaceae and Salicaceae. *Myrica* also likely formed part of the alder carr, while *Salix* was abundant along the river banks (Moreno-Domínguez et al., 2015, 2016).

## 4. Materials and methods

Despite a large number of specimens obtained from the La Val site, only layer LV6 had sufficient morphotypes and taxa to conduct CLAMP and LMA analyses. Our study is based on 25 morphotypes and 23 taxa from 63 studied specimens from layer LV6 (Figs. 3 and 4; Appendices A.1 and A.2). Their morphology and venation were scored using a process similar to that of Yang et al. (2011). Morphological observations were made using a Nikon SMZ-2 stereomicroscope, and the size template from the CLAMP website was used to measure the size of the fossil leaves. All specimens are currently stored in the Museum of Natural Science of the University of Zaragoza, Spain (Canudo, 2018).

Palaeoclimatic estimates were made using two foliar physiognomic


*(caption on next page)*

**Fig. 3.** Fossil morphotypes from La Val used for the CLAMP and LMA determination. Scale bars 1 cm. MORF-1: Betulaceae. 1 (EMPZ 2018/17-2018/90-LV6-2-1B), 2 (EMPZ 2018/17-2018/94-LV6-4-1B); MORF-2: Betulaceae. 3 (EMPZ 2018/17-2018/112-LV6-17-1A), 5 (EMPZ 2018/17-2018/135-LV6-33-1), 6 (EMPZ 2018/17-2018/159-LV6-51-1). *Alnus* sp. 4 (EMPZ 2018/17-2018/133-LV6-31-1B), 7 (EMPZ 2018/17-2019/1462-LV6-199-1); MORF-3: *Daphnogene lanceolata*. 8 (EMPZ 2018/17-2018/98-LV6-7-1A), 9 (EMPZ 2018/17-2018/131-LV6-30-2); MORF-4: cf. *Myrica* sp. 10 (EMPZ 2018/17-2018/211-LV6-94-1B). *Quercus mediterranea*. 11 (EMPZ 2018/17-2019/1433-LV6-121-1). *Myrica* sp. 12 (EMPZ 2018/17-2019/1437-LV6-132-1A), 13 (EMPZ 2018/17-2019/1459-LV6-196-1A); MORF-5: *Laurophyllum* sp. 14 (EMPZ 2018/17-2018/111-LV6-15-1). Incertae sedis. 15 (EMPZ 2018/17-2019/1425-LV6-16-1B). cf. *Salix* sp. 16 (EMPZ 2018/17-2018/148-LV6-42-1), 17 (EMPZ 2018/17-2019/1450-LV6-164-1); MORF-6: cf. *Parrotia* sp. (EMPZ 2018/17-2018/117-LV6-20-2) (Moreno-Domínguez et al., 2015 for its picture); MORF-7: *Daphnogene polymorpha*. 18 (EMPZ 2018/17-2018/147-LV6-41-1), 19 (EMPZ 2018/17-2019/1458-LV6-190-1); MORF-8: cf. *Laurophyllum* sp. 20 (EMPZ 2018/17-2018/162-LV6-54-1). *Laurophyllum* sp. 21 (EMPZ 2018/17-2019/1449-LV6-161-1), 22 (EMPZ 2018/17-2019/1454-LV6-167-1); MORF-9: *Leguminophyllum* sp. 23 (EMPZ 2018/17-2019/1428-LV6-69-1); MORF-10: Betulaceae. 24 (EMPZ 2018/17-2018/171-LV6-66-1A), 25 (EMPZ 2018/17-2018/195-LV6-86-1B), 27 (EMPZ 2018/17-2019/1432-LV6-108-1), 28 (EMPZ 2018/17-2019/1434-LV6-130-1), 29 (EMPZ 2018/17-2019/1440-LV6-134-1B). *Alnus* sp. 26 (EMPZ 2018/17-2018/192-LV6-85-2A); MORF-11: Incertae sedis. 30 (EMPZ 2018/17-2019/1429-LV6-75-1). The following fossil samples are not figured, but they also have been used for CLAMP and LMA determination (Moreno-Domínguez et al., 2015 for see their pictures). MORF-2: EMPZ 2018/17-2018/92-LV6-3-1B (*Alnus* cf. *gaudinii*), EMPZ 2018/17-2018/124-LV6-26-1A (Betulaceae); MORF-4: EMPZ 2018/17-2018/122-LV6-25-1A (*Myrica* sp.), EMPZ 2018/17-2018/151-LV6-46-1B (*Myrica lignitum*); MORF-5: EMPZ 2018/17-2018/201-LV6-87-1A (cf. *Laurophyllum* sp); MORF-7: *Daphnogene polymorpha*. EMPZ 2018/17-2018/170-LV6-64-1, EMPZ 2018/17-2018/174-LV6-67-1B; MORF-8: EMPZ 2018/17-2018/168-LV6-63-1A (*Laurophyllum* sp.). Specimens stored in the Museum of Natural Science of the University of Zaragoza (Spain).

techniques: LMA and CLAMP. It has long been known that there is a strong correlation between the percentage of species with entire leaf margins and mean annual temperature (MAT) (Wolfe, 1978, 1981; Su et al., 2010) and this percentage increases in direct proportion to the MAT (Wolfe, 1978). LMA essentially uses a lineal regression equation, where it is demonstrated that the proportion of woody dicotyledons with untoothed leaves has a strong correlation to mean annual temperature; however, this relationship is known to vary between different regions (Su et al., 2010). In view of the latter, two regression equations have been considered for comparing the results. The first equation corresponds to Northern Hemisphere, which is based on southeastern Asia data (Wolfe, 1979), while the second regression equation is based on European vegetation data (Traiser et al., 2005), which is the geographic area in which the La Val fossil assemblage is located and utilised herein (Appendix A.2).

As previously mentioned, CLAMP exploits the relationship between leaf form and environmental conditions. Our study followed the procedure outlined on the official CLAMP website (http://clamp.ibcas.ac.cn/, also see Yang et al., 2007, 2011) for the application of CLAMP at the La Val site, including the available datasets and spreadsheets. The following palaeoclimatic values have been estimated from 31 different leaf physiognomic parameters displayed by fossil morphotypes from layer LV6 at the La Val fossil site (see Appendix A.1): 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 three consecutive wettest months), 3-DRY (precipitation during three consecutive driest months), RH (relative humidity), SH (specific humidity), and ENTHAL (Enthalpy).

Two calibration dataset files were used in our analysis: Physg3brcAz and GRIDMet3brAZ. The first meteorological calibration dataset (Physg3brcAz) consists of 144 modern vegetation sites, mostly from temperate regions of the Northern Hemisphere, although these data set lacks samples from areas that experience extreme cold (Yang et al., 2011). The second data set, GRIDMet3brAZ, corresponds to gridded meteorological data from that same suite of locations included in Physg3brcAz. According to Yang et al. (2011) (also see http://clamp.ibcas.ac.cn/), the meteorological datasets are likely to be biased towards local climates influenced by the presence of the vegetation itself and therefore are likely to represent local instead regional climate. Here, the gridded datasets have been used, since they may represent more accurately the regional climate.

## 5. Results

Estimates for all palaeoclimatic variables were obtained by employing CLAMP and LMA methods along with their standard deviations as a measure of statistical uncertainty (Table 2, Appendices A.1 and A.2). Graphs of the palaeoclimatic variables of CLAMP are shown in the Figs. 5, 6, 7 and 8, and created using the free online version of CLAMP. The two employed equations of LMA resulted in similar results (Table 2; Appendix A.2): 17.1 ± 4.6 °C (equation of Wolfe, 1979) and 16.8 ± 4.7 °C (equation of Traiser et al., 2005). The results from CLAMP indicate a MAT of 17.2 ± 1.7 °C, which is very similar to that of LMA, and not statistically different when uncertainties are taken into consideration.

### 5.1. CLAMP (Climate Leaf Analysis Multivariate Program)

Twenty-five morphotypes from layer LV6 from the La Val fossil megafloral assemblage were scored (see Figs. 3, 4 and Appendix A.1). The completeness statistics provided by the CLAMP analysis is 0.702 (Appendices A.5 and A.6), which is above the 0.6 cut off for reliability (see Yang et al., 2011), meaning that our results are likely to be accurate.

The first variable to consider is MAT, which is estimated to be 17.2 ± 1.7 °C (15.5 to 18.9 °C). The WMMT variable ranges from 24.2 to 26.8 °C (25.5 ± 1.3 °C), while CMMT ranges from 8.1 to 11.8 °C (10 ± 1.8 °C). So, it seems there was a marked seasonal contrast in temperature. In La Val, the GROWSEAS is 9.3 ± 0.7 (from 8.6 to 10); this datum is consistent with the winter temperature range, which could have dipped below 10 °C for short periods of time. Concerning the rainfall, GSP ranges from 1276 to 1684 mm (1480 ± 20.4 mm), corresponding to an average of 156.2 ± 26 mm per month (MMGSP). The precipitation for the three wettest months (3-WET) range from 690.9 to 981.7 mm (836.3 ± 145.4 mm) and the precipitation for the three driest months (3-DRY) ranges from 80 to 146 mm (113 ± 33 mm). This variation between 3-WET and 3-DRY variables indicates a strong seasonal contrast, showing the existence of a dry season. Mean annual relative humidity (RH) is 54.7 ± 5.10% (49.6 to 59.8%). Lastly, the results of SH and ENTHAL are estimated to have been 6.8 ± 1 g/kg and 31.7 ± 0.45 kj/kg, respectively.

### 5.2. LMA (Leaf margin analysis)

Fig. 9 shows the number of angiosperm taxa and the number of fossil specimens obtained from all layers identified in La Val, as well as the

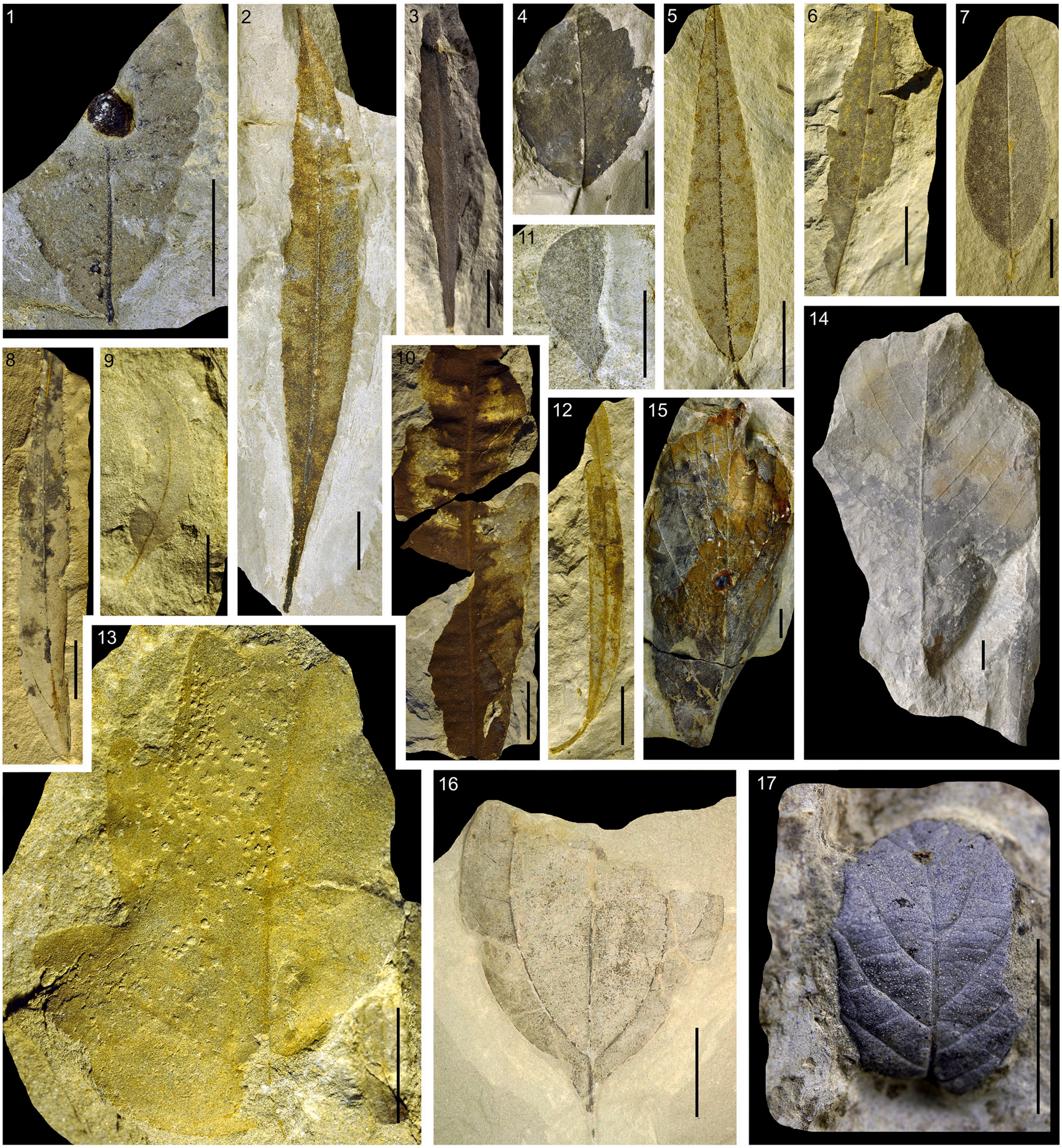


**Fig. 4.** Fossil morphotypes from La Val used for the CLAMP and LMA determination. Scale bars 1 cm. MORF-12: cf. *Rosa lignitum*. 1 (EMPZ 2018/17-2019/1431-LV6-87-2B); MORF-14: *Myrica lignitum*. 2 (EMPZ 2018/17-2019/1436-LV6-131-1B). Incertae sedis. 3 (EMPZ 2018/17-2019/1463-LV6-199-2); MORF-15: *Ampelopsis* sp. 4 (EMPZ 2018/17-2019/1441-LV6-140-1); MORF-16: *Laurophyllum* sp. 5 (EMPZ 2018/17-2019/1443-LV6-154-1A); MORF-17: *Acer* cf. *haselbachense*. 6 (EMPZ 2018/17-2019/1446-LV6-156-1B); MORF-18: *Laurophyllum* sp. 7 (EMPZ 2018/17-2019/1447-LV6-157-1A); MORF-19: *Laurophyllum* sp. 8 (EMPZ 2018/17-2019/1453-LV6-166-1B); MORF-20: Incertae sedis. 9 (EMPZ 2018/17-2019/1457-LV6-186-1); MORF-21: Incertae sedis. 10 (EMPZ 2018/17-2019/1456-LV6-171-1B); MORF-22: Fabaceae. 11 (EMPZ 2018/17-2019/1461-LV6-197-1); MORF-23: Incertae sedis. 12 (EMPZ 2018/17-2019/1451-LV6-165-1); MORF-24: *Liriodendron* sp. 13 (EMPZ 2018/17-2019/1466-LV6-200-2A); MORF-25: *Alnus* sp. 14 (EMPZ 2018/17-2019/1464-LV6-200-1A), 15 (EMPZ 2018/17-2019/1468-LV6-201-1). Other taxa used for determinating LMA: *Daphnogene cinnamomifolia*. 16 (EMPZ 2018/17-2019/1442-LV6-148-1). *Quercus mediterranea*. 17 (EMPZ 2018/17-2019/1426-LV6-19-1A). The following fossil sample is not figured, but they also have been used for CLAMP and LMA determination (Moreno-Domínguez et al., 2015 for see its picture): MORF-13: EMPZ 2018/17-2018/213-LV6-96-1 (*Engelhardia orsbergensis*). Specimens stored in the Museum of Natural Science of the University of Zaragoza (Spain).

**Table 2**
Palaeoclimatic variables from stratigraphic level LV6 obtained from the La Val fossil site using CLAMP and LMA.

| CLAMP (Climate Leaf Analysis Multivariate Program) | | |
|---|---|---|
| LA VAL-LV6 | | |
| Palaeoclimatic variables | | (*) SE |
| MAT [°C] | 17.2 (15.5–18.9) | ± 1.7 |
| WMMT [°C] | 25.5 (24.3–26.8) | ± 1.3 |
| CMMT [°C] | 10 (8.1–11.8) | ± 1.8 |
| GROWSEAS [month] | 9.3 (8.6–10) | ± 0.7 |
| GSP [cm] | 148 (127.6–168.4) | ± 20.4 |
| MMGSP [cm] | 15.6 (13–18.2) | ± 2.6 |
| 3-WET [cm] | 83.6 (69–98.1) | ± 14.5 |
| 3-DRY [cm] | 11.3 (8–14.6) | ± 3.3 |
| RH [%] | 54.7 (49.6–59.8) | ± 5.1 |
| SH [g/kg] | 6.8 (5.8–7.8) | ± 1.0 |
| ENTHAL [Kj/Kg] | 31.7 (31.2–32.1) | ± 0.4 |
| *Sampling Error (SE) | | |

| LMA (Leaf Margin Analysis) | |
|---|---|
| LA VAL-LV6 | |
| Palaeoclimatic variables MAT [°C] | |
| MAT East Asia (Wolfe, 1979) | MAT Europe (Traiser et al., 2005) |
| 17.1 | 16.8 |
| MAT East Asia ± σ[MAT] | MAT Europe ± σ[MAT] |
| 12.5–21.7 | 12.1–21.6 |
| σ[MAT] (Wilf, 1997) | σ[MAT] (Wilf, 1997) |
| 4.6 | 4.7 |

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 three consecutive wettest months, 3-DRY: precipitation during three consecutive driest months, RH: Relative Humidity, SH: Specific Humidity, ENTHAL: Enthalpy. MAT East Asia: Mean Annual Temperature based on southeastern Asia data from equation of Wolfe (1979), MAT Europe: Mean Annual Temperature based on European vegetation data from equation of Traiser et al. (2005). σ [MAT]: standard deviation or sampling error calculated according to the equation of Wilf (1997). LV6: stratigraphic layer number 6, SE: Sampling Error.

results of the regression equations for the entire flora. These 13 layers vary in the total number of leaf taxa and collected specimens, as well as the values of temperature obtained for each of the layers. This variation can be explained easily by differences in sampling effort and differences in taphonomy at each level (Uhl et al., 2003). Applying the regression equations for East Asia and Europe to level LV6 of La Val, the calculated MAT is 17.1 °C (sampling error of MAT ±4.6) and 16.8 °C (sampling error of MAT ±4.7) respectively (Appendix A.2; Fig. 9). These LMA results were consistent with those of CLAMP. The layers LV3 and LV6 have been the most thoroughly sampled at La Val, with LV6 yielding the most taxa and thus the most reliable temperature estimate (Fig. 9): 17.1 ± 4.6 °C. LV3 (14 taxa) seems to be affected by taphonomic processes, and its diversity is much lower than that of LV6 (23 taxa) or LV4 (18 taxa) (Fig. 9). In general, La Val appears to exhibit a low diversity of taxa in relation to other Iberian fossil megaflora assemblages (Barrón et al., 2010). This might be due to the sedimentary environment and the deciduous nature of the forests that once existed in La Val (Moreno-Domínguez, 2019). Alders formed dense forests, keeping out the leaves from other vegetation from reaching the sedimentation areas (Spicer, 1981; Moreno-Domínguez et al., 2015). The alders were able to produce a greater number of leaves in relation to other fossil plant groups, as is the case in layer LV3 in La Val (Moreno-Domínguez et al., 2015; Moreno-Domínguez, 2019).

Low taxonomic diversity may influence the application of LMA, although there is currently no consensus on the minimum number of taxa necessary for reliably performing LMA (see e.g. Steart et al., 2010 for details on a suggested minimum taxa diversity for LMA). In general, the more species used in LMA, the lower the uncertainties (Steart et al., 2010). According to Uhl et al. (2003), the quality of the LMA temperature estimates greatly depend on the number of taxa and the number of the fossil specimens collected. They considered only those localities which provided at least 15 taxa. Using this criterion, we considered the LV6 layer to yield the most accurate temperature because twenty three fossil taxa have been identified from 233 specimens collected from this site, including twelve taxa with entire margins (e.g., lacking lobes and/or teeth) (Appendix A.2).

## 6. Discussion

The Oligocene was a period characterised by large and sudden climatic changes, most of which were mainly associated with palaeogeographic and eustatic changes and fluctuations in the volume of the Antarctic ice sheet (Zachos et al., 2001; Wappler, 2010). The formation of the first permanent Antarctic ice sheet during the earliest Oligocene led to a substantial drop in global sea level (Ivany et al., 2006; Wappler, 2010). This epoch was a time of relatively high global temperatures and precipitations influenced by a high degree of seasonality. The marine and terrestrial isotope records of Central Europe reveal a marked fall in mean annual temperatures during the Oligocene compared with the Eocene (Zachos et al., 2001; Mosbrugger et al., 2005). This climatic context significantly affected plant communities, in that they had to acclimatise to these new climatic conditions by adapting to seasonal periods of decreased precipitation and lower temperatures. In this context, the European plant communities were mainly formed by broadleaved, subtropical evergreen rain forests which prevailed throughout (Mai, 1995). Laurel forests were also common, and are one of most widespread vegetation types of Europe during the Cenozoic (Barrón et al., 2010). However, temperate deciduous vegetation and mixed deciduous forests began to spread throughout Europe, gradually replacing the previous vegetation (Mai, 1989, 1995; Postigo-Mijarra et al., 2009; Barrón et al., 2010).

During the late Oligocene, the vegetation that developed in La Val represented a subtropical notophyllous broadleaved evergreen forest, with similarities to those seen in extant forests (for modern vegetation types see Wolfe, 1979). The palaeoclimatic data obtained from LMA and CLAMP for La Val also appear to suggest this type of vegetation: this site consisted of 52% of entire-margined leaves and had a MAT (CLAMP) of 17.2 ± 1.7 °C, MAT (LMA) 17.1 ± 4.6 °C. Modern subtropical notophyllous broadleaved evergreen forests are characterised by a proportion of 40 to 60% entire-margined leaves and a range of MAT from 13 to 20 °C. In such forests, Lauraceae, Theaceae, Magnoliaceae, and Fagaceae tend to dominate, being families of tropical affinities (Wolfe, 1979). By contrast, the subordinate vegetation is constituted by many elements of temperate affinities, such as Betulaceae, Salicaceae, Juglandaceae, Rosaceae, Aceraceae, and Altingiaceae. These plant families could be floristically over-represented in areas in which these taxa are subordinate components, as their remains dominate in parautochthonous deposits of disturbed areas such as floodplains, riverbanks, and highly volcanic terrains (Ferguson, 1995). Therefore, broad-leaved deciduous species can be also dominant in azonal successional vegetation, such as

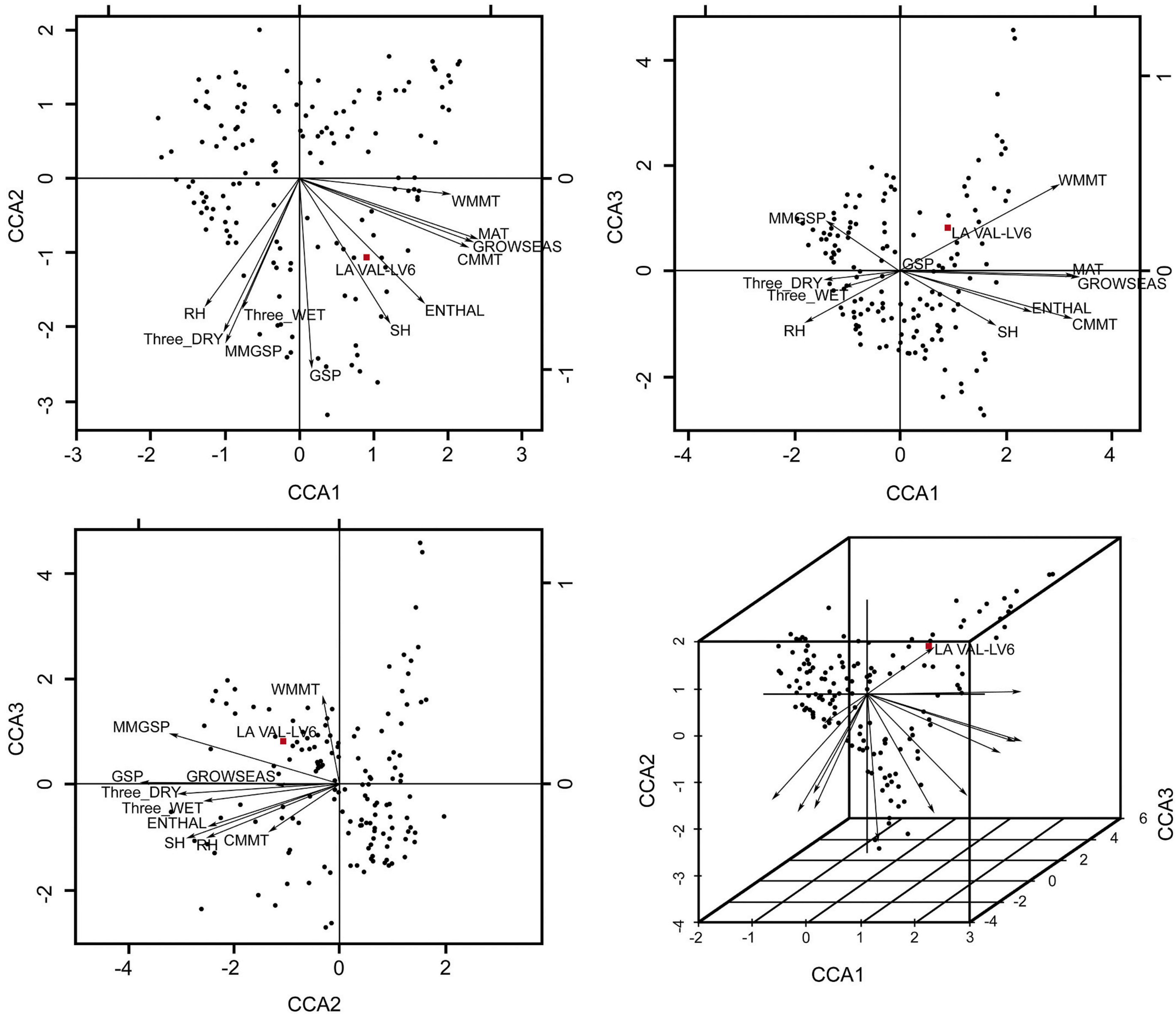


**Fig. 5.** Graphs of two-dimensional and three-dimensional views of the Physg3brcAZ calibration dataset (black circles). The position of the climate vectors are shown by black arrows. Red square corresponds to La Val fossil flora (LV6). Graphs are generated by the CLAMP Online website. CCA1, CCA2 and CCA3 are the axes 1, 2 and 3 respectively. CCA: Canonical Correspondence Analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

riparian forests, in regions in which the primary forests are otherwise broad-leaved evergreen (e.g. central and southern China, southern Japan) (Wolfe, 1979). Considering the fact that the fossil assemblage from La Val represents vegetation that mainly grew on disturbed areas, such as riverbanks (Moreno-Domínguez et al., 2016), it can be expected that species of azonal vegetation (e.g. *Alnus*) were dominant and, therefore, their leaves are over-represented in the studied assemblages. Although Lauraceae, Myricaceae, and Magnoliaceae were also part of the vegetation of La Val, Betulaceae (*Alnus*) dominated in this fossil megafloral assemblage. However, this over-representation is not problematic in CLAMP or LMA scoring because relative abundance is not a function of the physiognomic profile (Spicer et al., 2005).

### 6.1. Wider Implications

The values obtained for palaeotemperature variables for the La Val fossil assemblage are analogous to those derived from other climate proxies (Fig. 10). When comparing the palaeoclimatic variables between these palaeofloras (Mosbrugger et al., 2005), MAT (15.5–18.9 °C) and WMMT (24.3–26.8 °C) from La Val are similar to co-eval temperature data from other parts of Eastern and Central Europe (Fig. 10). In contrast, the CMMT values calculated for La Val and Eastern Europe are higher than those of Central Europe (Fig. 10). In the studied palaeofloras from Central Europe, CMMT ranges from 2 °C to 7 °C (Mosbrugger et al., 2005; Utescher et al., 2000; Uhl et al., 2007), which are lower than those

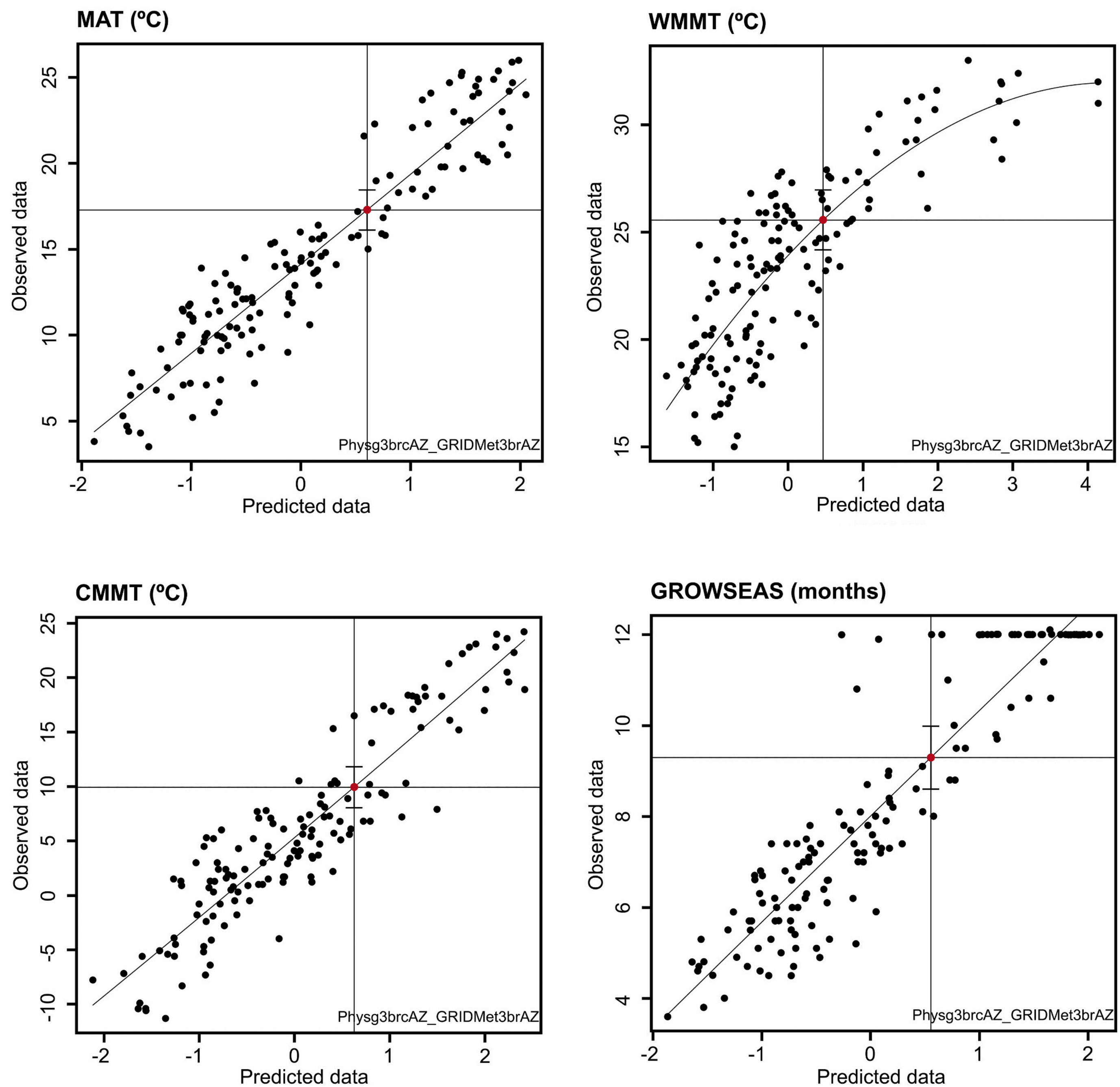


**Fig. 6.** CLAMP regression plots for MAT (Mean Annual Temperature); WMMT (Warm Month Mean Temperature); CMMT (Cold Month Mean Temperature) and GROWSEAS (Length of the Growing Season). Graphs are generated by the CLAMP Online website. Modern calibration sites are shown as black circles and the La Val fossil site (LV6) as red solid circle. The uncertainties (± 1 s.d.) are shown as a vertical bar. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of the La Val palaeoflora (8.1–11.8 °C) and Eastern Europe (Fig. 10). These differences in CMMT values could be explained in several different ways. On the one hand, it could be due to the latitudinal position of the Iberian Peninsula in southern Europe. Perhaps, the CMMT values could reflect a latitudinal gradient with regional differences already in the late Oligocene (Casas-Gallego, 2018), as is suggested for the Miocene (Bruch et al., 2007; Fauquette et al., 2007). Being further south, the Iberian Peninsula would have experienced warmer winters compared to other regions in Europe. On the other hand, a certain diachrony among these fossil sites could explain these values, as some they could represent different orbital configurations than that at the Iberian fossil site of La Val. According to Mosbrugger et al. (2005), during the Oligocene a cooling period occurred until the end of this interval when a new period marked by a temperature peak began, known as the Late Oligocene Warming (Zachos et al., 2001; Mosbrugger et al., 2005; Utescher et al., 2015; Liu et al., 2018). At the

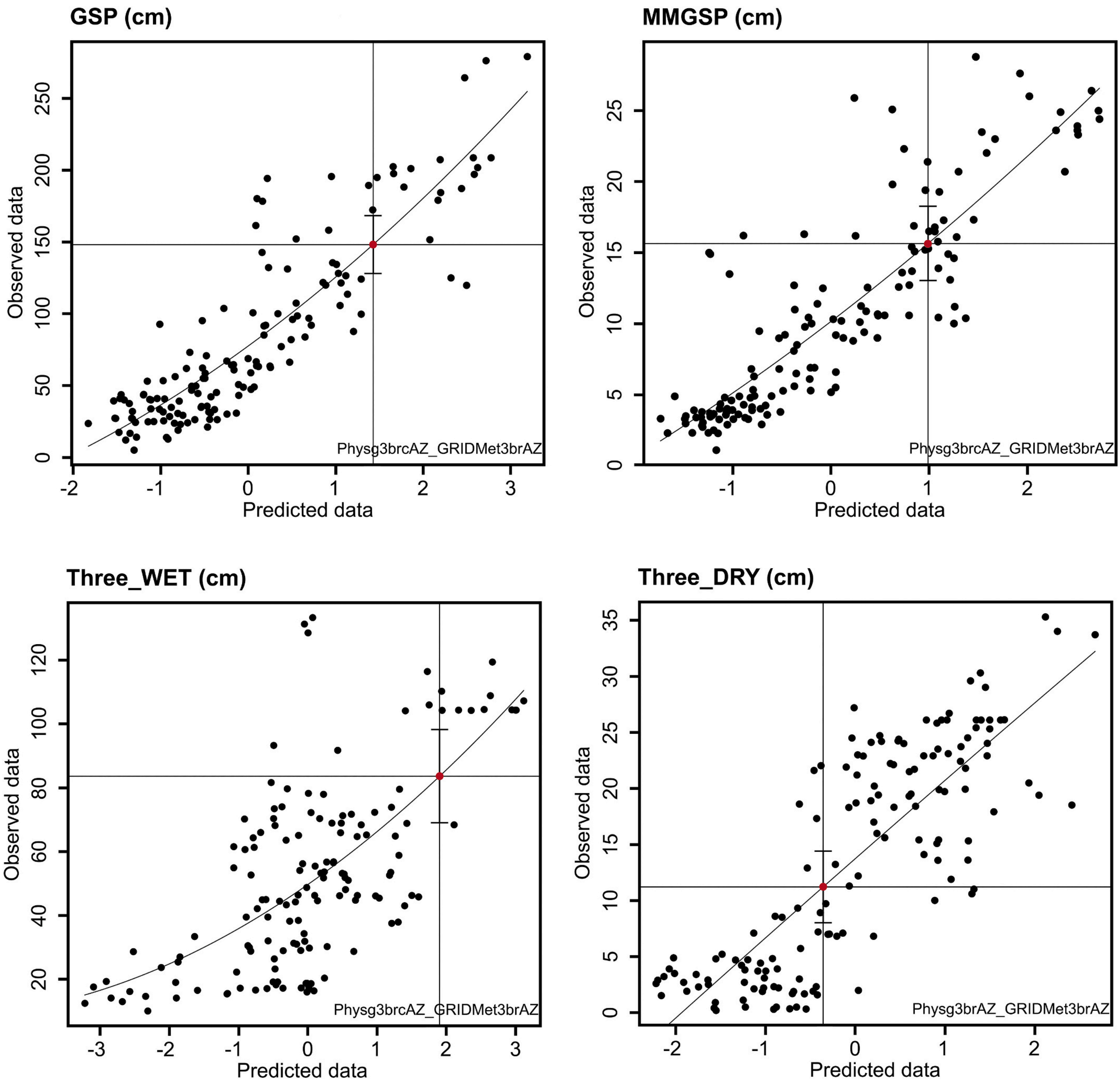


**Fig. 7.** CLAMP regression plots for GSP (Growing Season Precipitation); MMGSP (Mean Monthly Growing Season Precipitation); Three-WET (Precipitation during the three Wettest Months) and Three-DRY (Precipitation during the three Driest Months). Graphs are generated by the CLAMP Online website. Modern calibration sites are shown as black circles and the La Val fossil site (LV6) as red solid circle. The uncertainties (±1 s.d.) shown as a vertical bar. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Oligocene–Miocene boundary (at ca. 23 Ma), a new strong glacial event was followed by a series of lesser intensity, intermittent glaciations (Paul et al., 2000; Zachos et al., 2001).

The average predicted rainfall at La Val (1276–1684 mm) is significantly higher than all other palaeofloras in Europe of a similar age, except for an Aix-en-Provence fossil site (Fig. 10) (Tanrattana et al., 2020). This is because megafloral fossil assemblages that grew in fluvial depositional settings, such as the riparian environments at La Val, may reflect microclimatic conditions, which would have been cooler and wetter than the regional climate signal as it does today in floral assemblages (Spicer et al., 2005). However, it should be also noted that CLAMP tends to overestimate precipitation, particularly of the dry months in warm climates (Spicer et al., 2011).

Recent palaeoclimatic estimates have been calculated using CA and CLAMP methods for several Cenozoic megafloras and pollen datasets from the Iberian Peninsula (e.g., Barrón et al., 2010; Casas-Gallego,

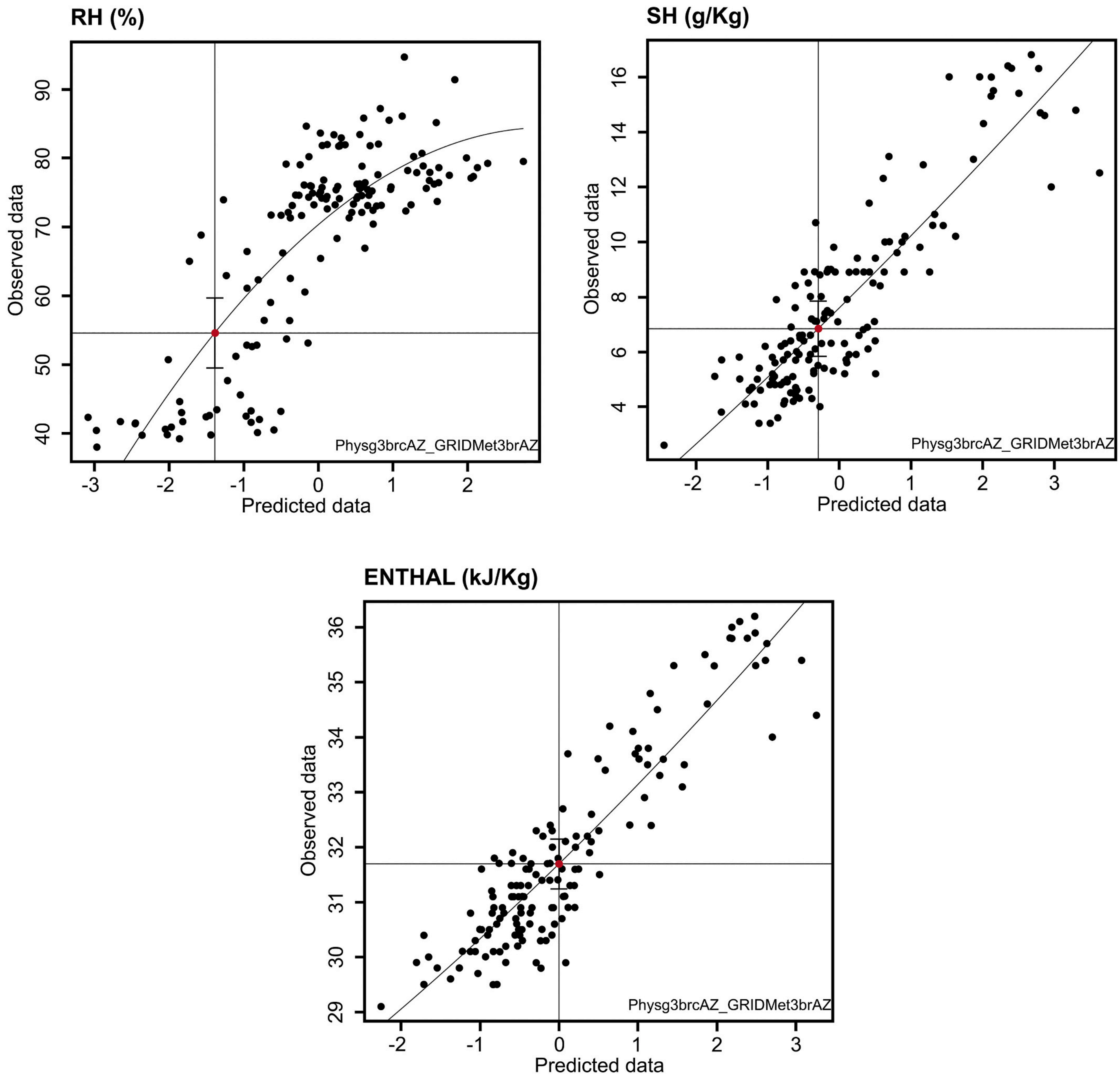


**Fig. 8.** CLAMP regression plots for RH (Relative Humidity); SH (Specific Humidity) and ENTHAL (Enthalpy). Graphs are generated by the CLAMP Online website. Modern calibration sites are shown as black circles and the La Val fossil site (LV6) as red solid circle. The uncertainties shown as (±1 s.d.) a vertical bar. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2018; Tosal et al., 2019, 2021). These palaeoclimate analyses are limited to the Oligocene Cervera site (CA, CLAMP) (Rupelian; Barrón et al., 2010; Tosal et al., 2019), As Pontes (CA) (Rupelian_Chattian; Barrón et al., 2010; Casas-Gallego, 2018) and La Val (LMA, CLAMP) (Chattian; Moreno-Domínguez and Cascales-Miñana, 2016). Although the LMA values obtained for La Val have a higher standard deviation than CLAMP and CA values, there is substantial overlap in estimates when comparing these three Oligocene fossil assemblages; however, WMMT and rainfall values from Cervera are higher than in La Val and/or As Pontes (Fig. 10).

According to Postigo-Mijarra et al. (2009), the palaeobotanical data appear to reveal a decline in MAT during the Oligocene in Iberia. This cooling is maintained until the end of the Oligocene until the period of warming that is likely represented in the fossil sites of La Val and As Pontes (Casas-Gallego, 2018). In general, the Iberian Oligocene palaeoclimatic data obtained from three different methods (LMA, CLAMP, and CA) are very similar to one another and provide a consistent quantitative overview. These values seem to be slightly above the central European values (Fig. 10), in particular the CMMT. This may again

| STRATIGRAPHIC LAYERS | NUMBER OF SPECIMENS | NUMBER OF TAXA | NUMBER OF ENTIRE-MARGINED TAXA | PROPORTION OF ENTIRE-MARGINED TAXA | LMA T [°C] East Asia Wolfe (1979) | LMA T [°C] Europe Traiser et al. (2005) |
|---|---|---|---|---|---|---|
| LV0 | 18 | 5 | 3 | 0.60 | 19.5±10.6 | 19.3±10.8 |
| LV1 | 70 | 12 | 7 | 0.58 | 18.9±6.7 | 18.8±6.9 |
| LV2 | 26 | 6 | 1 | 0.17 | 6.2±5.1 | 5.7±5.2 |
| LV3 | 454 | 14 | 6 | 0.43 | 14.2±5.3 | 13.9±5.4 |
| LV4 | 178 | 18 | 8 | 0.44 | 14.7±4.8 | 14.4±4.9 |
| LV5 | 58 | 7 | 3 | 0.43 | 14.2±7.5 | 13.9±7.7 |
| LV6 | 233 | 23 | 12 | 0.52 | 17.1±4.6 | 16.8±4.7 |
| LV7 | 78 | 12 | 8 | 0.67 | 21.5±7.2 | 21.4±7.4 |
| LV8 | 23 | 8 | 6 | 0.75 | 24.0±9.3 | 24.0±9.6 |
| LV9 | 6 | 4 | 2 | 0.50 | 16.4±10.8 | 16.2±11.1 |
| LV10 | 10 | 3 | 1 | 0.33 | 11.3±10.2 | 10.9±10.4 |
| LVNH | 170 | 8 | 4 | 0.50 | 16.4±7.6 | 16.2±7.8 |
| LVNH2 | 45 | 4 | 1 | 0.25 | 8.7±7.6 | 8.3±7.8 |
| ALL LAYERS COMBINED | 1369 | 35 | 18 | 0.51 | 16.8±3.7 | 16.6±3.8 |

**Fig. 9.** Application of LMA to the macroflora of La Val. For every single layer and subsample number of specimens, the number of taxa, the number of entire-margined taxa and the proportion of entire margined taxa are given. Data only for the angiosperm leaves.

be a signal of a climatic and vegetational gradient between southern and northern Europe. Accordingly, Utescher et al. (2020) have noted the existence of distinct spatio-temporal patterns of plant diversity, forming different vegetational belts across Europe. Thus, during the Oligocene they have defined three belts: the first corresponds to temperate broadleaved deciduous and mixed needleleaved-broadleaved deciduous forests situated between 40 and 50°N, the second includes thermophilous mixed mesophytic and evergreen broadleaved forests between 40 and 30°N, in which the vegetation of La Val was situated, and finally a belt of tropical vegetation situated below 30°N.

Based on the Köppen-Geiger climate classification for the modern day, Utescher et al. (2009) combined several climate variables from fossil floras of Central Europe over the last 45 million years to infer their present-day climate equivalents (see Kottek et al., 2006 for details of these current type climates). Using this approach, we hypothesize Cfa-Csa-Cfb type climates for the late Oligocene European megafloral assemblages. In the case of La Val, its present-day climate equivalent may correspond to Cfa-Csa types since there is a strong degree of similarity among the palaeoclimatic of the Rott and La Val floras (Utescher et al., 2009; Fig. 10). These climatic types indicate a warm temperate climate with hot and dry summers (Csa) or a warm temperate climate with fully humid and hot summers (Cfa). From relative abundance of fossil galls that appear in the leaves recovered in La Val, Moreno-Domínguez (2018) suggested the existence of a seasonal climate with a dry season, which would be equivalent to the climatic Csa type. Nowadays, this climate type is prevalent in the southwest of the Iberian Peninsula (Peel et al., 2007).

## 7. Conclusions

This study provides the first quantitative palaeoclimatic reconstruction for the Late Oligocene of the Iberian Peninsula based on CLAMP and LMA methods. This reconstruction allows for the following conclusions: (1) The palaeoclimatic variables based on CLAMP resulted in a MAT of 17.2 ± 1.7 °C, WMMT of 25.5 ± 1.3 °C, CMMT of 10 ± 1.8 °C and GSP of 1480 ± 204 mm. The climatic variable based on LMA resulted in a MAT of 17.11 ± 4.61 °C (regression equation for data from East Asia) and 16.8 ± 4.7 °C (regression equation for data from Europe); (2) Values for MAT and WMMT obtained from La Val-LV6 flora are analogous to those derived from Central Europe during the Late Oligocene; (3) From the palaeoclimatic point of view, the La Val-LV6 palaeoflora is analogous to the Rott palaeoflora; (4) The palaeoclimatic data obtained from three different methods (LMA, CLAMP and CA) for the Iberian Oligocene sites are very similar to each other. The palaeoclimatic parameter, CMMT, appears to be slightly above central European values, which could be due to a climatic and vegetational gradient between southern and northern Europe; (5) During the Late Oligocene (Chattian), a warm temperate climate with hot and dry summers existed in the NE of the Iberian Peninsula. This period was marked by a temperature peak corresponding to the Late Oligocene Warming.

The quantitative palaeoclimatic data obtained for La Val-LV6 serve as a foundation for further investigations: firstly, CLAMP and LMA methods can be applied to all layers with macroflora to determinate the palaeoclimatic trend in the same fossil site; secondly, other types of palaeoclimatic methods can also be applied for comparing with CLAMP and LMA; and finally, these results can be compared with other plant fossil assemblages.

## Declaration of Competing Interest

The authors declare that they have no known competing financial

| GEOGRAPHICAL AREAS | | PALEOCLIMATIC TECHNIQUES | PALEOFLORA | PALEOCLIMATIC VARIABLES | | | | | Koeppen type climate |
|---|---|---|---|---|---|---|---|---|---|
| | | | | MAT [°C] | WMMT [°C] | CMMT [°C] | GSP [mm] | MAP [mm] | |
| IBERIAN PENINSULA | NW SPAIN (La Coruña) | CA | [7] AS PONTES (palynomorphs) (upper Chattian) | 16.80-18.40°C | 27.30-27.90°C | 10.60-12.50°C | — | 1096-1355 mm | [7] Aw, Am |
| | | | [7] AS PONTES (palynomorphs) (lower Chattian) | 16.50-18.30°C | 27.30-27.90°C | 9.60-10.90°C | — | 1096-1278 mm | |
| | | | [6] AS PONTES (palynomorphs) (Rupelian/Chattian) | 17.20-18.40°C | 27.30-27.80°C | 6.60-7.0°C | — | 1300-1322 mm | — |
| | | | [7] AS PONTES (palynomorphs) (Rupelian) | 16.80-18.30°C | 27.30-27.90°C | 10.60-10.90°C | — | 1096-1278 mm | [7] Aw, Am |
| | EBRO BASIN (Lérida) | | [6] CERVERA (leaves) (Rupelian) | 17-18.50°C | 27.20-27.80°C | 5.60-11.70°C | — | 1255-1355 mm | — |
| | | CLAMP | [8] CERVERA (leaves) (Rupelian) | 14.81-18.81°C | 23.34-28.74°C | 5.09-11.89°C | 1679-2645 mm | — | — |
| | PREPYRENEAN MARGINAL SIERRAS (Huesca) | CLAMP (this study) | LA VAL (leaves) (Chattian) | 15.55-18.95°C | 24.30-26.83°C | 8.15-11.85°C | 1276-1684 mm | — | Cfa, Csa |
| | | LMA [3](this study) | | 12.17-21.62°C | — | — | — | — | |
| | | LMA [1](this study) | | 12.50-21.71°C | — | — | — | — | |
| FRANCE | AIX-EN-PROVENCE BASIN | CLAMP | [9] AIX-EN-PROVENCE (leaves)(Chattian) | 20.30°C | 26.13°C | 13.92°C | 1440.30 mm | 1524.49 mm | — |
| CENTRAL EUROPE | LOWER RHINE BASIN | CA | [2] ROTT (leaves) (Chattian) | 16.50-20.80°C | 26.00-27.80°C | 5.00-13.30°C | — | 843-1281 mm | [5] Cfa, Csa |
| | | | [2] ENSPEL (leaves) (Chattian) | 15.90-16.60°C | 25.70-26.40°C | 5.00-6.20°C | — | 979-1076 mm | — |
| | | | [2] ENSPEL (fruits and seeds) (Chattian) | 15.70-16.80°C | 24.70-25.10°C | 5.00-6.20°C | — | 1096-1194 mm | — |
| | | | [4] ENSPEL (Chattian) | 14.40-16.60°C | — | — | — | — | — |
| | | CLAMP | | 12.50°C | — | — | — | — | |
| | | LMA | | 9.20-12.70°C | — | — | — | — | |
| | MOLASSE BASIN | CA | [2] HAUSCHAM (leaves, fruits and seeds) (Chattian) | 15.60°C | 25.60-26.80°C | 2.20-5.00°C | — | 979-1322 mm | — |
| | | | [2] EBNAT-KAPPEL (leaves) (Chattian) | 16.50°C | 26.50-27.90°C | 5.60-7.00°C | — | 979-1213 mm | — |
| | | | [2] USM (Untere Süßwassermolasse) (leaves, fruits and seeds) (Chattian) | 16.50-16.60°C | 26.00-26.80°C | 4.80-5.80°C | — | 897-1355 mm | — |
| | | | [4] USM (MONOD-RIVAZ) (Chattian) | 15.90-16.60°C | — | — | — | — | — |
| | | CLAMP | | 17.10°C | — | — | — | — | |
| | | LMA | | 21.90-27.80°C | — | — | — | — | |
| | | CA | [2] Upper UMM (Untere Meeresmolasse) (leaves, fruits and seeds) (Chattian) | 16.50-16.60°C | 26.00-26.00°C | 4.80-5.80°C | — | 897-1355 mm | — |
| | WEISSELSTER AND LAUSITZ BASIN | | [2] KLEINSAUBERNITZ (leaves) (Chattian) | 12.60-16.70°C | 20.10-26.00°C | 4.30-7.10°C | — | 735-1335 mm | [5] Cfa, Csa, Cfb |
| | | | [4] KLEINSAUBERNITZ (Chattian) | 14.40-15.60°C | — | — | — | — | |
| | | CLAMP | | 15.90°C | — | — | — | — | |
| | | LMA | | 19.90-20.20°C | — | — | — | — | |
| | | CA | [2] BOCKWITZ OPEN-CAST (leaves) (Chattian) | 14.00-17.00°C | 25.70-27.90°C | 1.80-6.20°C | — | 1090-1213 mm | [5] Cfa |
| EASTERN EUROPE | EUXINIAN BASIN (Bulgaria) | | [7] BALCHIK (palynomorphs) (Chattian) | 15.60-17.20°C | 24.70-27.80°C | 5.0-7.0°C | — | 740-1322 mm | — |
| | WESTERN PIRIN Mts. (Bulgaria) | | [7] BREZHANI (leaves) (Chattian) | 16.40-16.50°C | 24.70-25.20°C | 5.50-10.90°C | — | 1122-1187 mm | — |
| | KALE-TAVAS BASIN (Turkey) | | [7] KALE-TAVAS (palynomorphs) (Chattian) | 16.50-21.10°C | 27.30-28.20°C | 5.50-13.30°C | — | 1122-1355 mm | — |
| | THRACE BASIN (Turkey) | | [7] TAYFUR (palynomorphs) (Rupelian/Chattian) | 16.50-21.30°C | 27.30-27.90°C | 5.50-13.30°C | — | 887-1623 mm | — |

**Fig. 10.** Comparison of several paleoclimatic estimates from Chattian (late Oligocene) fossil floras from Europe, using different quantitative techniques. Data using regression models from (1) Wolfe (1979); (2) Mosbrugger et al. (2005); regression model from (3) Traiser et al. (2005); (4) Uhl et al. (2007); (5) Utescher et al. (2009); (6) Barrón et al. (2010); (7) As Pontes (Casas-Gallego, 2017), Balchik (Ivanov et al., 2007), Brezhani (Bozukov et al., 2009), Kale-Tavas (Akgün et al., 2007), Tayfur (Akgün et al., 2013); (8) Tosal et al. (2019); (9) Tanrattana et al. (2020).

interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2021.110302.

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