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General Palaeontology, Systematics, and Evolution (Palaeobotany)

Influence of short- and long-term climatic cycles on floristic change across the Eocene–Oligocene boundary in the Ebro Basin (Catalonia, Spain)

Influence des cycles climatiques de longue et courte périodes sur les changements floristiques de la limite Éocène–Oligocène dans le bassin de l'Èbre (Catalogne, Espagne)

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ABSTRACT

The Eocene–Oligocene transition (EOT) climatic turnover is modelled in the Ebro Basin using CLAMP and analysing the Sarral (Priabonian) and the Cervera (Rupelian) floras. The results show a drop of temperature and an increase in seasonality and precipitation. The changes in temperature and seasonality follow the trend described for the EOT in southern Europe; however, the increase in precipitation is the opposite of what would be expected. This increase might be related to the stratigraphic location of the Sarral Priabonian leaf bed within a dry stage of a precession cycle, whereas the Cervera Rupelian leaf bed would be located within the wet stage of a similar cycle. CLAMP combined with sedimentology, taphonomy and palaeoecology reveals that precession cycles would produce a shift in the habitat of certain plants during the EOT, with the Lauraceae being limited to riparian communities during the Priabonian of Sarral to grow in small laurisilvas during the Rupelian of Cervera.

Mots clés :
Cénozoïque
Grande Coupure
Végétation
Dépôts lacustres
Forçage orbitaire

RÉSUMÉ

Le bouleversement climatique de la transition Éocène–Oligocène (EOT) est modélisé en utilisant la méthode CLAMP et à partir de l'analyse des flores du Priabonien de Sarral et du Rupélien de Cervera (bassin de l'Èbre). Les résultats montrent une diminution de la température et une augmentation de la saisonnalité et des précipitations. Les changements de température et de saisonnalité suivent les tendances décrites pour l'EOT en Europe du Sud; contrairement à l'augmentation des précipitations. Cette dernière serait à mettre en

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relation avec la position stratigraphique du niveau à feuilles de Sarral dans le stade sec d'un cycle de précession, tandis que le gisement de Cervera appartiendrait à un stade humide. CLAMP, combiné avec la sédimentologie, la taphonomie et la paléoécologie, montre que les cycles de précession auraient induit un déplacement de l'habitat de certaines plantes durant l'EOT. Ainsi, les Lauracées seraient limitées aux communautés riveraines durant le Priabonien de Sarral, pour ensuite former de petites laurisylves durant le Rupélien de Cervera.

1. Introduction

The Eocene–Oligocene transition (EOT) constitutes a major climate change event during the Cenozoic. The boundary was marked by the Antarctic glaciation (Oi-1), which modified global atmospheric and thermohaline circulation patterns and tipped the Earth towards a new climate regime in the Oligocene (Liu et al., 2009). Following the EOT, the oceans' mean temperature fell and seasonality and aridity increased (Zachos et al., 2001). However, precise regional climatic evolution across the EOT is still poorly known. Records of the Oi-1 event in the Southern Ocean, close to the Antarctic continent, indicate a sharp change (Coxall et al., 2005; Escutia et al., 2011; Galeotti et al., 2016; Goldner et al., 2014). Conversely, continental records for mid to high latitudes in the Northern Hemisphere suggest stepwise cooling during the late Eocene (Cramwinckel et al., 2018). In Eurasia, a major faunal turnover, the Grande Coupure event, occurred during the EOT (Akhmetiev and Beniamovski, 2009; Hooker et al., 2004; Prothero, 1994). In parallel, the Oligocene Eurasian plant communities show a marked latitudinal distribution and increased regional heterogeneity compared with the Eocene vegetation (Mai, 1989, 1995; Pound and Salzmann, 2017), suggesting a less efficient longitudinal heat distribution than during the late Eocene.

Palaeoclimatic studies have been used to model the EOT climate-driven turnover based on leaf floras and pollen from non-marine European deposits, mostly in the northern and central parts of the continent (Akhmetiev et al., 2017; Eldrett et al., 2009; Mosbrugger et al., 2005; Roth-Nebelsick et al., 2004). These have generally employed the coexistence approach (CA) method, which consists in interpreting climatic indicators of the past based on the climatic requirements of the nearest living relatives of a fossil plant (Mosbrugger and Utescher, 1997; Utescher et al., 2000). Alternatively, the CLAMP method (Wolfe, 1993) can be used to interpret palaeoclimatic parameters based on leaf physiognomy data. We selected this method because it does not rely on the taxonomic affinities of fossil species.

EOT climate-driven turnover is relatively poorly known in Southern Europe, especially as regards the Iberian Peninsula (Barrón et al., 2010; Cavagnetto and Anadón, 1996; Fernández-Marrón, 1973a; Sanz de Siria, 1996a). For most of the Eocene, the European flora was homogeneously composed of broadleaf evergreen forests comprised of Lauraceae, Myrtaceae, and Sapindales, among others. In contrast, the flora became more heterogeneous during the Oligocene, showing a marked latitudinal distribution and increased local to regional taxonomic differences (Collinson and Hooker, 2003; Mai, 1995; Pound and Salzmann, 2017). However, while northern Europe was occupied by broadleaf deciduous forests composed of trees such as *Quercus*, *Corylus, Betula* or *Alnus* (Wolfe, 1980), evergreen plants prevailed in Southern Europe, including plants adapted to seasonal drought such as *Zizyphus* or *Comptonia*, which started to play an important ecological role (Kvaček, 2010).

Here, we present palaeoclimatic parameters from two well-dated floral records of the Ebro Basin, a terminal Eocene locality (Sarral) and a lowermost Oligocene locality (Cervera). This covers the EOT and provides valuable data concerning the floral consequences of the EOT in southern Europe. The two floras are analysed separately using the CLAMP method, and the palaeoclimatic indicators obtained are subsequently compared. These results are combined with previous sedimentological, taphonomic, and palaeoecological studies to shed light on the floristic change in southern Europe across the EOT. We then discuss the possible influence of orbital forcing on the evolution of Iberian plant communities across the EOT.

2. Geological, stratigraphic, and sedimentological settings

The fossil floras studied here are located in the Ebro Basin, which constitutes the South Pyrenean foreland basin (Fig. 1A). The Pyrenean compression gradually reduced the Ebro Basin's connection with the Atlantic and the Tethys oceans until eventually, during the late Eocene (*ca.* 36 Ma), the basin became endorheic (Costa et al., 2010). After isolation of the basin, lacustrine environments prevailed in the distal parts of the fluvial and alluvial sedimentary systems. The emplacement of the lacustrine systems was largely governed by Pyrenean orogenic flexure, which controlled subsidence rates and the lateral distribution of lakes (Gómez-Paccard et al., 2012; Vergés et al., 1995). Nevertheless, the spreading of these lacustrine systems was forced by astronomical cycles at all temporal ranges (Valero et al., 2014). According to these authors, the classical Palaeogene and Neogene lacustrine units of the Ebro Basin described by Anadón et al. (1989) would represent episodes of greater lacustrine extension, related to 2.4 Myr eccentricity cycles. In turn, expansion of these lacustrine units was internally modulated by the 400 kyr and 100 kyr eccentricity cycles. Among the units defined by Anadón et al. (1989) in the Ebro

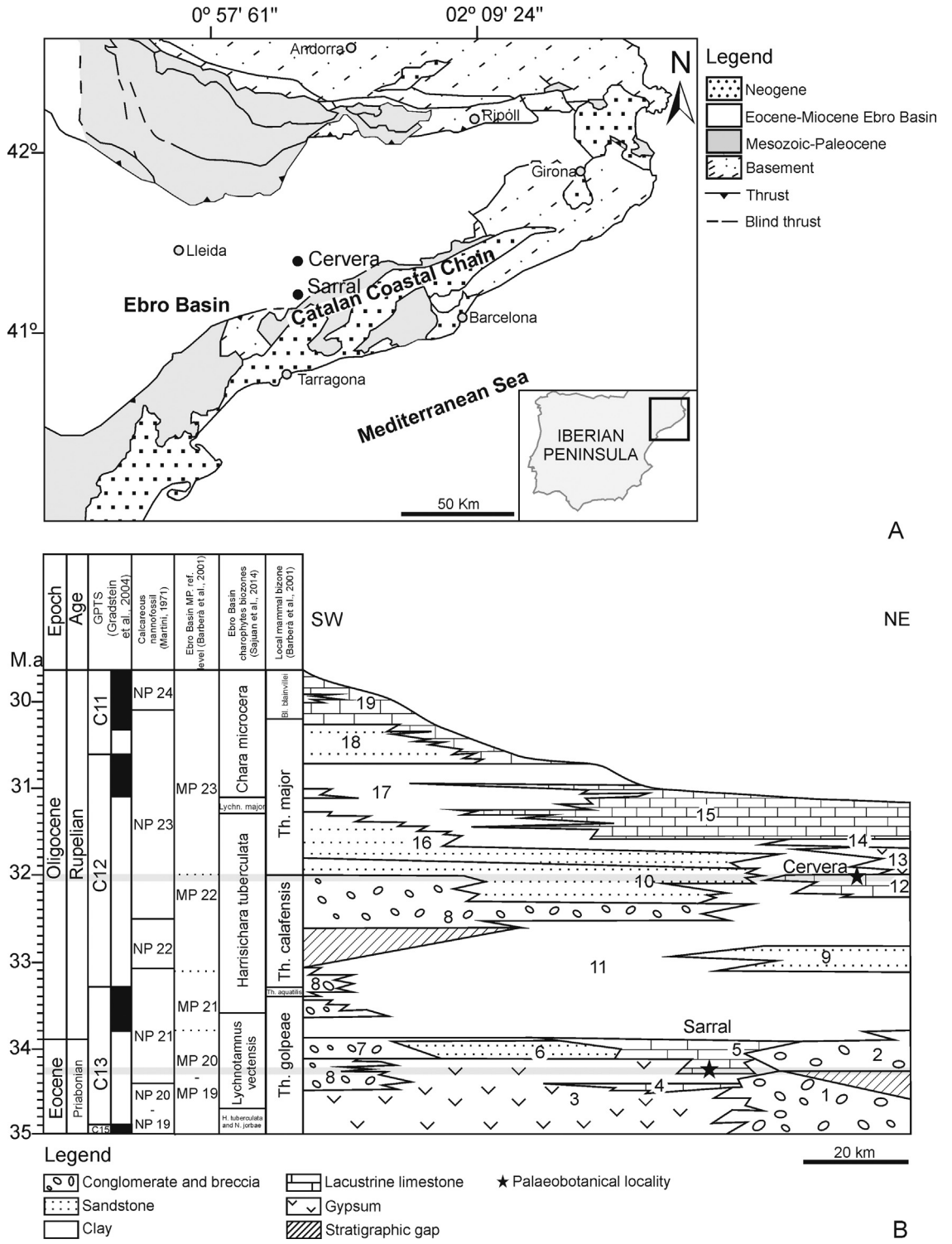

Fig. 1. Geological setting of the two plant localities studied. A. Geological map of the Ebro foreland basin with location of the study areas, modified from Vergés et al. (1998). B. Chronostratigraphy of the Cenozoic in the Ebro Basin (modified from Martini, 1971 and Barberà, 1999). Lithostratigraphic units: Sant Miquel de Montclar Formation (1), Bellprat Member (2), Pira Formation (3), Rocafort Member (4), Sarral Formation (5), Riu Francolí Member (6), Espluga Formation (7), Montsant Formation (8), Rauric Member (9), Gavatxa Formation (10), Blancafort Formation (11), Montmaneu Formation (12), Talavera Formation (13), Solsona Formation (14) Tàrrega Formation (15), Margalef Formation (16), Albi Formation (17), Cogul Formation (18), Marqueses Formation (19).

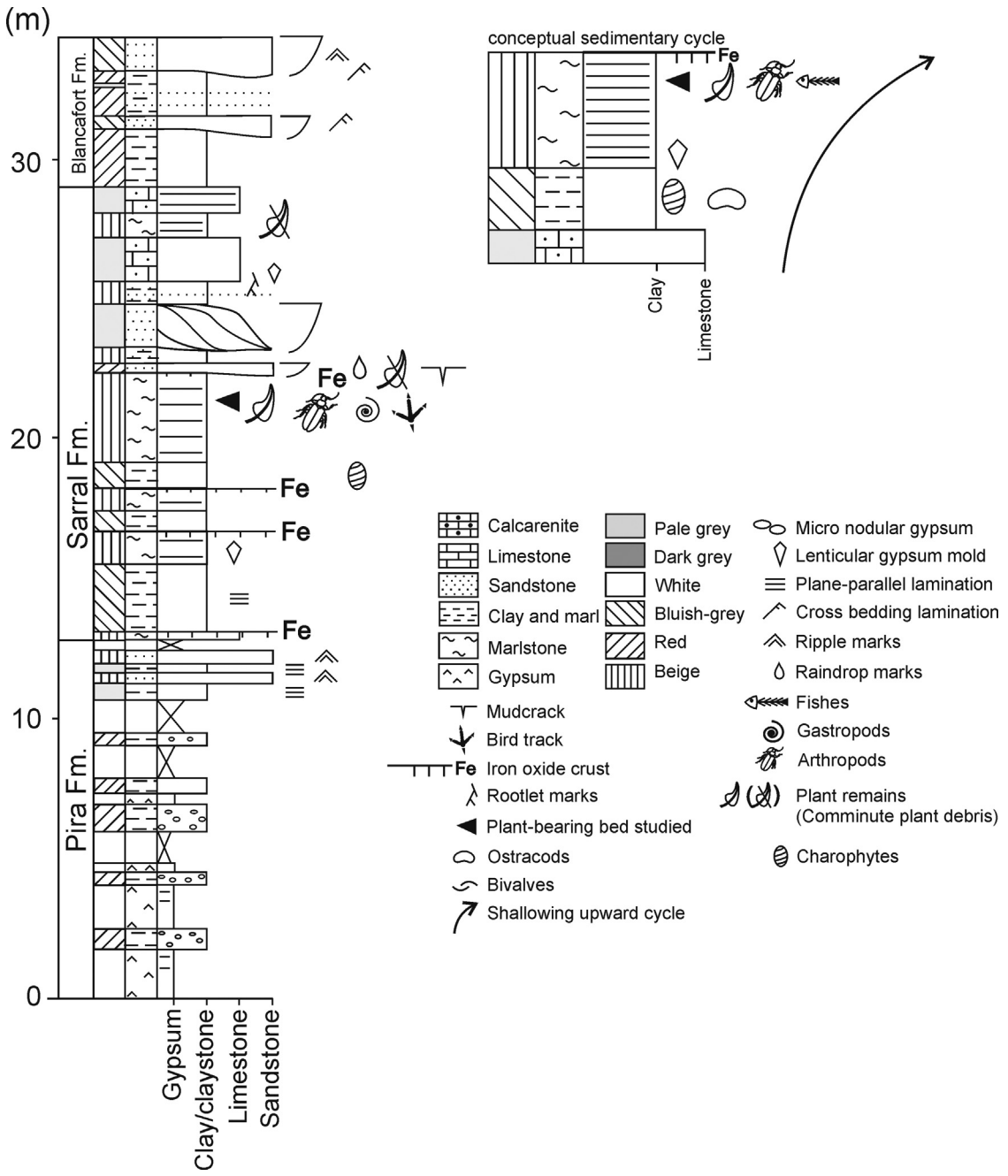

Fig. 2. Stratigraphic section studied in the Priabonian of Sarral with indication of the small, climatically-driven sedimentary cycles which controlled the origin of the leaf bed. Modified from Tosal et al. (2018).
Fig. 2. Section stratigraphique étudiée dans le Priabonien de Sarra, avec indication des petits cycles sédimentaires, influencés par le climat, qui ont contrôlé la formation du niveau à feuilles. D'après Tosal et al. (2018), modifié.

Fig. 1. Cadre géologique des deux localités paléobotaniques étudiées. A. Carte géologique du bassin d'avant-pays de l'Èbre avec situation de la zone étudiée (modifié d'après Vergés et al., 1998). B. Chronostratigraphie du Cénozoïque du bassin de l'Èbre (modifié d'après Martini, 1971; et Barberà, 1999). Unités lithostratigraphiques: formation Sant Miquel de Montclar (1), membre Bellprat (2), formation Pira (3), membre Rocafort (4), formation Sarral (5), membre Riu Francolí (6), formation Espluga (7), formation Montsant (8), membre Rauric (9), formation Gavatxa (10), formation Blancafort (11), formation Montmaneu (12), formation Talavera (13), formation Solsona (14) formation Tàrrega (15), formation Margalef (16), formation Albi (17), formation Cogul (18), formation Marqueses (19).

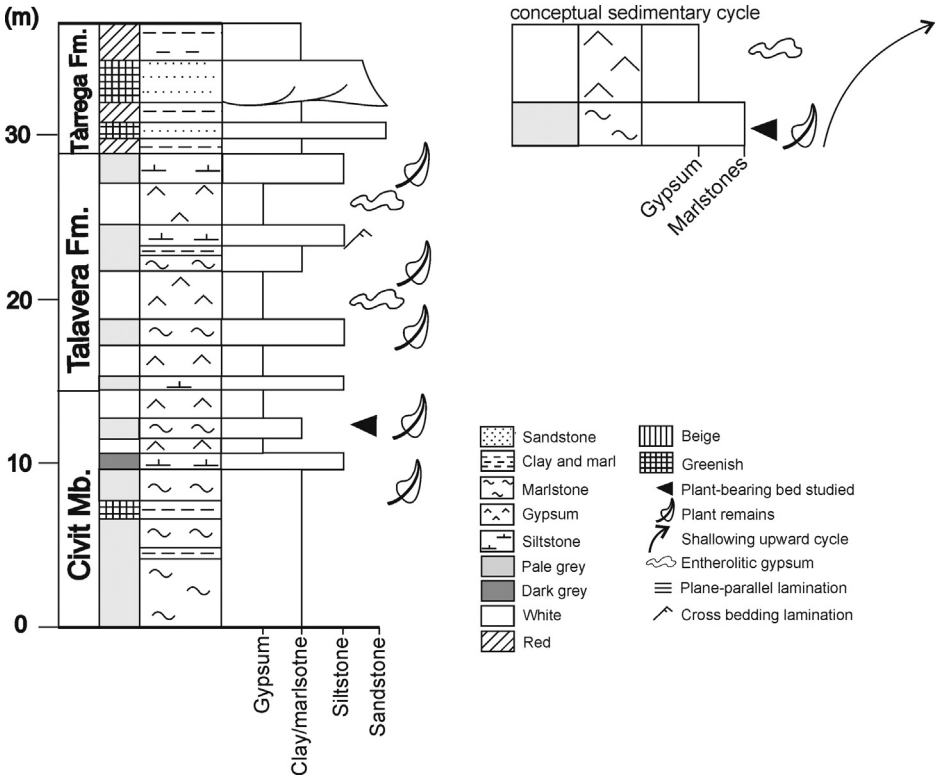

Fig. 3. Stratigraphic section studied in the Rupelian of Cervera with indication of the small, climatically-driven sedimentary cycles which controlled the origin of the leaf bed. Modified from Tosal and Martín-Closas (2016).
Fig. 3. Section stratigraphique étudiée dans le Rupélien de Cervera, avec indication des petits cycles sédimentaires, influencés par le climat, qui ont contrôlé la formation du niveau à feuilles (D'après Tosal et Martín-Closas 2016, modifié).

Basin, we focus here on the Anoia and Segarra lacustrine systems that encompass the Eocene–Oligocene boundary (Fig. 1B).

The Anoia lacustrine system includes the Sarral Formation, 17 m in thickness in the Sarral quarry, where the flora studied here was found (Fig. 2). Magnetostratigraphic constraints place Sarral within chron C13r, with an age of 34.5–34.4 Ma (Barberà et al., 2001; recalibrated to GPTS 2012, Vandenberghe et al., 2012). Available biostratigraphy relates the Anoia lacustrine system to the *Theridomys golpeae* (MP19–20) local mammal reference level (Agustí et al., 1987; Anadón et al., 1987) and the European Lychnothamnus pinguis charophyte biozone (Riveline, 1986; modified by Sanjuan and Martín-Closas, 2015).

From a sedimentological perspective, the Sarral Formation is mainly composed of calcarenites, marls and marlstones, interpreted as very shallow lacustrine environments. The sedimentation at Sarral is dominated by small-order, shallowing-upward lacustrine parasequences of about 1.5 m in thickness (Fig. 2). The basal part of the parasequence is characterised by tabular and massive calcarenites interpreted as having been deposited under low-energy sheet flows that represent the first stages of persistent floods in distal fluvial plains. The calcarenites are overlaid by bluish grey marls and limestones rich in remains of lacustrine benthic organisms such as charophytes, ostracods, and gastropods. This facies is interpreted as a shallow, alkaline, and oligotrophic permanent lake. According to Tosal et al. (2018), these facies would represent the wetter stages of the shallowing-upward cycle. The top of the cycle is composed of beige, finely laminated marlstones, rich in the well-preserved plant remains studied here. Locally, isolated vertical lenticular gypsum casts occur at the bottom of some of the marlstone beds, indicating solute concentration due to increased evaporation. This part of the sedimentary cycle would represent its drier stages. The marlstone beds culminate in a thin ferruginous crust with ripple lamination, raindrop marks and mud-cracks, indicating the terminal stages of lake development, eventually leading to subaerial exposure of the lake bottom. Overall, the lacustrine parasequences at Sarral show a gradual increase in water salinity linked to evaporation excess.

The Segarra lacustrine system lies stratigraphically above the Anoia lacustrine system and is early Oligocene (Rupelian) in age. Within this system, the Civit Member of the Montmaneu Formation includes the flora

Table 1
Magnoliopsids from the Priabonian of Sarral.
Tableau 1
Magnoliopsides du Priabonien de Serral.

Magnoliopsids from the Priabonian of Sarral	
Cl. Magnoliopsida Brongniart	Or. Rosales Brechtold and Presl
Or. Laurales Berchtold and Presl	Fam. Rhamnaceae Jussieu
Fam. Lauraceae Jussieu	*Zizyphus zizyphoides* (Unger) Weyland [Mft.44]
Daphnogene sp. indet. 1 [Mft. 1]	
Laurophyllum sp. indet. 1 [Mft.3]	Or. Fagales Enler
Or. Proteales Brechtold and Presl	Fam. Fagaceae Du Mortier
Fam. Proteaceae Jussieu	*Quercus weberi* Heer [Mft.45]
Banksia deikeana Heer [Mft.11]	*Quercus* sp. indet. 1 [Mft.47]
Or. Malpighiales Martius	Fam. Myricaceae Richard ex Kunth
Fam. Salicaceae Mirbel	*Myrica arenesi* Arenes et Depape [Mft.45]
Salix lavateri Al. Br. [Mft.13]	*Comptonia schrankii* (Sternb.) Berry [Mft.52]
Salix sp. indet. 2 [Mft.15]	
Or. Fabales Bromhead	Or. Caryophyllales Takhtadjan
Fam. Fabaceae Lindley	Fam. Nyctaginaceae Jussieu
Dalbergia bella Heer [Mft.16]	*Pisonia eocenica* Ettingshausen [Mft.61]
Podocarpium podocarpum (A.Braun) Herendeen [Mft.17]	Or. Ericales Brechtold and Presl
Fabales sp. indet. 1 [Mft.20]	Fam. Sapotaceae Jussieu
Fabales sp. indet. 2 [Mft.21]	*Bumelia minor* Unger [Mft.62]
Fabales sp. indet. 3 [Mft.22]	
Fabales sp. indet. 4 [Mft.23]	**Incertae sedis**
Fabales sp. indet. 5 [Mft.24]	Magnoliopsida sp. indet. 1 [Mft.63]
Fabales sp. indet. 6 [Mft.25]	Magnoliopsida sp. indet. 2 [Mft.64]
Fabales sp. indet. 7 [Mft.26]	Magnoliopsida sp. indet. 3 [Mft.65]
Fabales sp. indet. 8 [Mft.27]	Magnoliopsida sp. indet. 4 [Mft.66]

Table 2
Magnoliopsids from the Rupelian of Cervera.
Tableau 2
Magnoliopsides du Rupélien de Cervera.

Magnoliopsids from Rupelian Cervera	
Or. Laurales Berchtold and Presl	Or. Rosales Brechtold and Presl
Fam. Lauraceae Jussieu	Fam. Rosaceae Jussieu
Daphnogene sp. indet. 1 [Mft. 1]	*Crataegus bilinica* Ettingshausen [Mft. 42]
Daphnogene sp. indet. 2 [Mft. 2]	Fam. Rhamnaceae Jussieu
Laurophyllum sp. indet. 1 [Mft. 3]	*Rhamnus aizoon* Unger [Mft. 43]
Laurophyllum sp. indet. 2 [Mft. 4]	
Laurophyllum sp. indet. 3 [Mft. 5]	Or. Fagales Enler
Laurophyllum sp. indet. 4 [Mft. 6]	Fam. Fagaceae Mortier
Laurophyllum sp. indet. 5 [Mft. 7]	*Quercus drymeja* Unger [Mft. 46]
Laurophyllum sp. indet. 6 [Mft. 8]	*Quercus* sp. indet. 2 [Mft. 48]
Laurophyllum sp. indet. 7 [Mft. 9]	Fam. Myricaceae Richard ex Kunth
Laurophyllum sp. indet. 8 [Mft. 10]	*Myrica arenesi* Arenes et Depape [Mft. 49]
	M. faya [Mft. 50]
Or. Proteales Brechtold and Presl	*M. oligocenica* Boulay [Mft. 51]
Fam. Proteaceae Jussieu	*Comptonia schrankii* (Sternb.) Berry [Mft. 52]
Grevillea sp. [Mft. 12]	
Or. Malpighiales Martius	Or. Sapindales Brechtold and Presl
Fam. Salicaceae Mirbel	Fam. Anacardiaceae (Brown) Lindley
Salix lavateri Al. Br. [Mft. 13]	*Rhus asymmetrica* Tosal, Sanjuan et Martín-Closas [Mft. 53]
Salix sp. indet. 1 [Mft. 14]	*Toxicodendron* sp. [Mft. 54]
Salix sp. indet. 2 [Mft. 15]	Fam. Sapindaceae Jussieu
Or. Fabales Bromhead	*Acer* sp. indet. 1 [Mft. 55]
Robinia sp. [Mft. 18]	*Acer* sp. indet. 2 [Mft. 56]
Mimosites segarrensis [Mft. 19]	*Acer* sp. indet. 3 [Mft. 57]
Fabales sp. indet. 1 [Mft. 20]	*Acer* sp. indet. 4 [Mft. 58]
Fabales sp. indet. 9 [Mft. 28]	*Acer* sp. indet. 5 [Mft. 59]
Fabales sp. indet. 10 [Mft. 29]	Fam. Simaroubaceae Candoll
Fabales sp. indet. 11 [Mft. 30]	*Ailanthus cerverensis* Depape [Mft. 60]
Fabales sp. indet. 12 [Mft. 31]	
Fabales sp. indet. 13 [Mft. 32]	
Fabales sp. indet. 14 [Mft. 33]	Or. Ericales Brechtold and Presl
Fabales sp. indet. 15 [Mft. 34]	Fam. Sapotaceae Jussieu
Fabales sp. indet. 16 [Mft. 35]	*Bumelia minor* Unger [Mft. 62]
Fabales sp. indet. 17 [Mft. 36]	**Incertæ sedis**
Fabales sp. indet. 18 [Mft. 37]	Magnoliopsida sp. indet. 5 [Mft. 67]
Fabales sp. indet. 19 [Mft. 38]	Magnoliopsida sp. indet. 6 [Mft. 68]
Fabales sp. indet. 20 [Mft. 39]	Magnoliopsida sp. indet. 7 [Mft. 69]
Fabales sp. indet. 21 [Mft. 40]	Magnoliopsida sp. indet. 8 [Mft. 70]
Fabales sp. indet. 22 [Mft. 41]	Magnoliopsida sp. indet. 9 [Mft. 71]
	Magnoliopsida sp. indet. 10 [Mft. 72]
	Magnoliopsida sp. indet. 11 [Mft. 73]
	Magnoliopsida sp. indet. 12 [Mft. 74]
	Magnoliopsida sp. indet. 13 [Mft. 75]

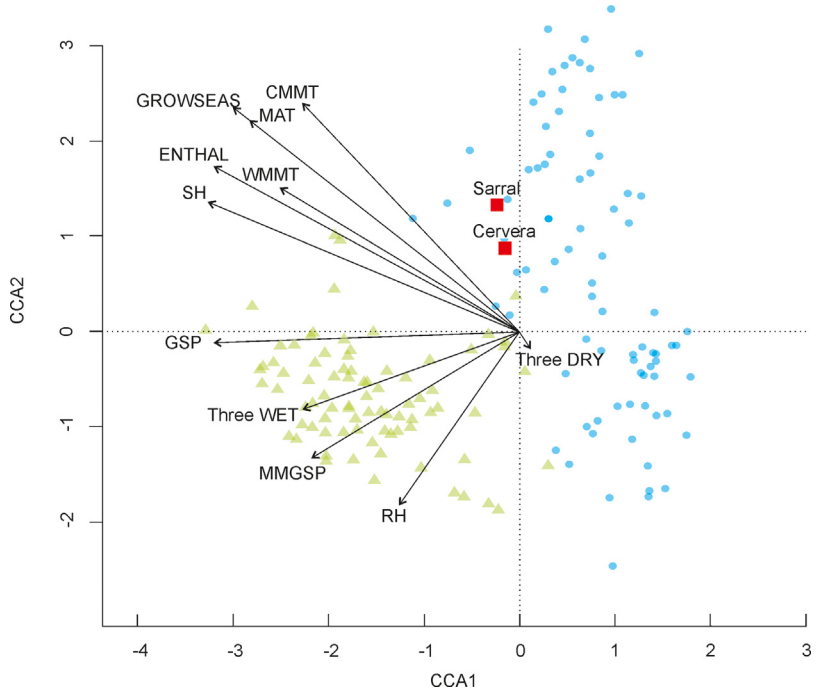

Fig. 4. CCA graph provided by CLAMP with the position of extant localities in comparison with the two palaeobotanical sites studied (squares). The triangles correspond to the present sites with a monsoonal climate. The dots correspond to the present localities with a non-monsoonal climate. The sites plotted by CLAMP without providing a precise geographical situation were not represented in this figure.
Fig. 4. Graphique CCA fourni par CLAMP, avec la position des localités actuelles, comparées à celles des deux localités paléobotaniques étudiées (carrés). Les triangles représentent les localités actuelles avec un climat de mousson. Les points correspondent aux localités actuelles avec un climat sans mousson. Les localités utilisées par CLAMP sans fournir de situation géographique précise n'ont pas été représentées sur cette figure.

from Cervera studied here. Based on lithostratigraphic and biostratigraphic correlations, the Cervera palaeobotanical site is *ca.* 33.2–32 Ma, and is ascribed to the *Lychnothamnus major* charophyte biozone (Sanjuan and Martín-Closas, 2016; Sanjuan et al., 2014) and to the *Theridomys calafensis* local mammal reference level (MP22).

The Civit Member at Cervera is 14 m in thickness and consists of tabular-bedded marlstones with a characteristic centimetric intercalation of pale and dark grey intervals. Pale grey marlstones display plane-parallel lamination and are rich in well-preserved leaf remains, which form the Cervera palaeobotanical site. This deposit is attributed to a distal lake with anoxia prevailing in the lake bottom. In contrast, dark grey marlstones show ripple lamination and poorly preserved plant remains, representing low-energy marginal lake environments. Gradually, nodular and enterolithic gypsum is intercalated within the pale grey marlstones (Fig. 3), representing the progressive onset of the overlaying Talavera Formation. Based on the models of subaqueous evaporite sedimentation provided by Kendall (1988), the nodular and enterolithic gypsum represents sabkha environments with 75% evaporation of the total water volume. As a consequence, the intercalations of pale grey marlstones and gypsum have been interpreted as lake evaporation cycles (Anadón et al., 1989; Tosal and Martín-Closas, 2016) where the pale grey marlstones containing the studied flora would represent the wetter stage of the sedimentary cycle, while gypsum would represent the drier stage (Tosal and Martín-Closas, 2016). In summary, the Priabonian flora from Sarral represents the vegetation that grew during the drier periods of small-order climate cycles, whereas the Rupelian flora from Cervera includes vegetation that grew during the wetter periods of similar cycles.

3. Materials and methods

CLAMP (Climate Leaf Analysis Multivariate Program, http://www.clamp.ibcas.ac.cn) is a statistical technique


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introduced by Wolfe (1993) and subsequently improved by Wolfe and Spicer (1999), Kovach and Spicer (1995), Spicer (2000, 2007, 2008), Spicer et al. (2004, 2009), and Yang et al. (2015). CLAMP models climatic parameters of the geological past based on the physiognomy of leaves from woody dicot angiosperms (class Magnoliopsida), relating 36 physiognomic leaf characters of living species to the climate in which they grow. Living dicots selected to build the CLAMP dataset are related to meteorological stations that have been collecting climatic data for more than thirty years (Spicer et al., 2009). Using CLAMP, these results can be compared with those obtained from the study of fossil leaves, providing quantitative climatic parameters for the past. This method typically yields 11 such parameters: mean annual temperature (MAT), warmest month mean temperature (WMMT), coldest month mean temperature (CMMT), length of growing season (GROWSEAS), growing season precipitation (GSP), three consecutive driest months (3-DRY), three consecutive wettest months (3-WET), mean month growing season precipitation (MMGSP), relative humidity (RH), specific humidity (SH), and enthalpy (ENTHAL). The latter two parameters do not provide palaeoclimatic information, since they are related to the modelling of palaeoaltitude. CLAMP uses the canonical correspondence (CANOCO) method to analyse the data (Yang et al., 2015).

At least 20 morphotypes are required for each plant bed studied in order to obtain robust and reliable palaeoclimatic parameters using CLAMP (Wolfe, 1993). The CLAMP online software provides a score sheet with the physiognomic characters required to obtain the palaeoclimatic parameters. Data are entered in a binary-like system where number 1 indicates the presence of a leaf character and 0 indicates absent or missing features. Species showing polymorphic leaves, i.e. those that display more than one leaf character, are scored 1 in the different character positions. The physiognomic characters of leaflets from Fabales or *Rhus asymmetrica* are entered in the CLAMP matrix as belonging to only one species. Both localities were analysed individually to obtain two data matrices (Supplementary material, Tables 1 and 2), which were used to run the CLAMP free online software (accessed on 19th May 2019). In the present study, we completed the score sheet with physiognomic data for floras from two palaeobotanical sites.

The CLAMP dataset consists of ca. 400 localities from all continents except Antarctica, and encompasses many climates and physiognomic leaf forms. For this reason, CLAMP provides some calibrations to adjust the palaeoclimatic results. To determine which of the calibration sets is the most appropriate, the global calibration algorithm (PhysgGlobal) was used for initial exploration (http://www.clamp.ibcas.ac.cn). The two localities studied were then plotted in non-monsoonal sites (Fig. 4). These results are in line with the palaeoclimatic knowledge of the Eocene and Oligocene in the Ebro Basin based on pollen (e.g., Cavagnetto and Anadón, 1996; Cavagnetto and Guinet, 1994). Within non-monsoonal calibration, the Physg3brcAZ_Calibration algorithm has been selected, assuming the probable absence of freezing temperatures during the Eocene and Oligocene in the Ebro Basin (e.g., Cavagnetto and Anadón, 1996; Cavagnetto and Guinet, 1994). The Physg3brcAZ_Calibration algorithm is built from 144 vegetation sites in the Northern Hemisphere with a temperate climate. Localities with an alpine climate that present extremely cold temperatures are therefore excluded from the algorithm's database. Two types of meteorological files can be selected in Physg3brcAZ_Calibration. For climates with a well-contrasted seasonality in terms of precipitation, such as those described in the Eocene and Oligocene eastern Ebro Basin (Cavagnetto and Anadón, 1996), raw data calibration (MET3brcAZ file) is preferred. This calibration avoids flattening off the signal of local intense storms (Spicer et al., 2009), which are characteristic of such climates.

Leaf physiognomic data from the Eocene–Oligocene boundary of the Ebro Basin were obtained from two well-known palaeobotanical sites from this palaeogeographic area. The first of these is Priabonian in age and corresponds to the Sarral plant locality (41°27′02″N, 01°14′17″E). The leaf collection from this site contains about 850 specimens obtained from a 50 cm-thick bed of well-laminated marlstone during several excavation campaigns undertaken from 1991 to 1995 by the staff of the Conca de Barberà County Museum (Museu Comarcal de la Conca de Barberà, MCCB), where the fossil plant remains are stored. The museum repository numbers for these fossil leaves are SA-1001 to SA-1837. From the entire collection, 55 specimens of woody dicots were selected to run CLAMP and 26 morphotypes were identified. The second site is Rupelian in age and corresponds to the Cervera palaeobotanical site (41°38′53″N, 01°19′35″). The collection from this locality consists of almost 400 specimens from plant-bearing bed No. 2 of the section studied by Tosal and Martín-Closas (2016), which yielded up to 56 leaf morphotypes. These specimens will be housed in the Natural History Museum of Barcelona (Museu de Ciències Naturals de Barcelona), where the specimens illustrated here were already stored with catalogue numbers MGB-88871–MGB-88923.

Fig. 5. Magnoliopsida morphotypes from the localities studied. 1: MFT 1from Sarral (SA-1049). 2: MFT 2 from Cervera (MGB-88872). 3: MFT 3 from Cervera (MGB-88873). 4: MFT 4 from Cervera (MGB-88874). 5: MFT 5 from Cervera (MGB-88875). 6: MFT 6 (MGB-88876) from Cervera. 7: MFT 7 (MGB-88877) from Cervera. 8: MFT 8 from Cervera (MGB-88878). 9: MFT 9 from Cervera (MGB-88879). 10: MFT 10 from Cervera (MGB-88880). Scale bar: 1 cm.
Fig. 5. Morphotypes de Magnoliopsida des localités paléobotaniques étudiées. 1 : MFT 1 de Sarral (SA-1049). 2 : MFT 2 de Cervera (MGB-88872). 3 : MFT 3 de Cervera (MGB-88873). 4 : MFT 4 de Cervera (MGB-88874). 5 : MFT 5 de Cervera (MGB-88875). 6 : MFT 6 de Cervera (MGB-88876). 7 : MFT 7 de Cervera (MGB-88877). 8 : MFT 8 de Cervera (MGB-88878). 9 : MFT 9 de Cervera (MGB-88879). 10 : MFT 10 (MGB-88880) de Cervera. Échelle : 1 cm.

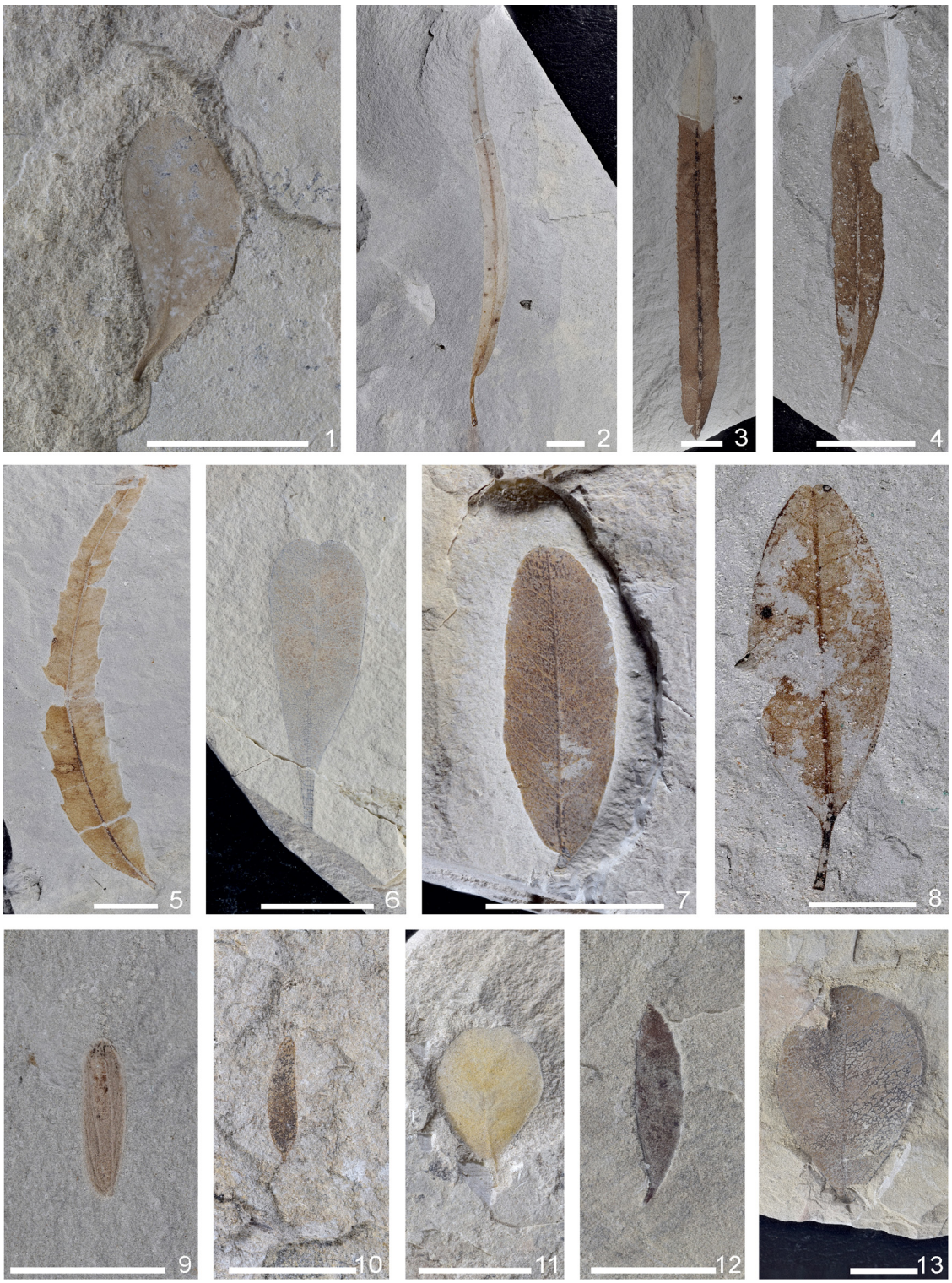

Fig. 6. Magnoliopsida morphotypes from the localities studied (continued). 1: MFT 11 from Sarral (SA-1259). 2: MFT 12 from Cervera (MGB-88881). 3: MFT 13 (MGB-88882) from Cervera. 4: MFT 14 from Cervera (MGB-88883). 5: MFT 15 from Cervera (MGB-88884). 6: MFT 16 from Sarral (SA-1066). 7: MFT 17 from Sarral (SA-1071). 8: MFT 18 from Cervera (MGB-88885). 9: MFT 19 from Cervera (MGB-88886). 10: MFT 20 from Sarral (SA-1007). 11: MFT 21 from Sarral (SA-1041). 12: MFT 22 from Sarral (SA-1273). 13: MFT 23 from Sarral (SA-1400). Scale bar: 1 cm.

Fig. 6. Morphotypes de Magnoliopsida des localités paléobotaniques étudiées (continuation). 1 : MFT 11 de Saral (SA-1259). 2 : MFT 12 de Cervera (MGB-88881). 3 : MFT 13 de Sarral (MGB-88882). 4 : MFT 14 de Cervera (MGB-88883). 5 : MFT 15 de Cervera (MGB-88884). 6 : MFT 16 de Sarral (SA-1066). 7 : MFT 17 de Sarral (SA-1071). 8 : MFT 18 de Cervera (MGB-88885). 9 : MFT 19 de Cervera (MGB-88886). 10 : MFT 20 de Sarral (SA-1007). 11 : MFT 21 de Sarral (SA-1041). 12 : MFT 22 de Sarral (SA-1273). 13 : MFT 23 de Sarral (SA-1400). Échelle: 1 cm.


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At both palaeobotanical sites studied, excavations were conducted in accordance with taphonomic criteria in order to characterise the degree of autochthony/allochthony of the plant remains and identify the potential biases of ancient collections from the same sites (Tosal and Martín-Closas, 2016; Tosal et al., 2018). Plant remains from both sites frequently show excellent preservation of the leaf physiognomy, including well-preserved leaf apexes and bases, leaf margins and the lowest-order venation pattern. Nevertheless, cuticles are absent or poorly preserved. At both palaeobotanical sites, leaf preservation mainly consists of a thin limonite crust that was probably formed by the biodegradation activity of sulphate-reducing bacteria growing upon the leaves deposited in the anoxic lake bottom as Spicer (1977) experimentally observed (i.e. authigenic preservation in the terms of Stewart and Rothwell, 1993).

In this study, the taxonomy of the Priabonian flora from Sarral is largely based on Fernández-Marrón (1971a, 1971b, 1973b), and Hably and Fernández-Marrón (1998). A revised taxonomic list of the Sarral flora based on these studies is provided in Table 1. Furthermore, the taxonomy of the Rupelian flora from Cervera is provided in Table 2 and is based on studies by Sanz de Siria (1992, 1996b). An example of the morphotypes used to run CLAMP is given in Figs. 5–11. A taxonomic revision of these fossil leaf floras is urgently required. For instance, a recent study revealed that a leaf morphotype from Cervera that had formerly been related to *Rhus pyrrhae* Unger should in fact be attributed to the new species *Rhus asymmetrica* Tosal et al. (2019). Other genera described in the paleobotanical sites studied are also controversial, such as *Dalbergia* or *Acer*. However, a taxonomic revision is beyond the scope of the present study and the CLAMP method enables palaeoclimatic data to be obtained from leaf physiognomic characters independently from the taxonomic status of the leaf morphotypes used to build the database (Yang et al., 2015).

The leaves used for this study were photographed using a Nikon 5300 camera equipped with a 105-mm macro lens. About 50 pictures were taken of each taxon and subsequently compiled using Helicon focus 5.3 software (http://www.heliconsoft.com). The processed photographs were used to characterise foliar features. Leaf measurements were taken using the free software "ImageJ" (https://www.imagej.net/): leaf length was measured from the apex to the base, excluding the petiole or petiolule length (Supplementary material, Table 3), while leaf width was measured at the broadest part of the blade. In compound leaves, the measurements were taken individually for each leaflet but entered into CLAMP as a single species.

4. Results

Thirty-six leaf characters from seven categories based on the leaf physiognomic features selected by Wolfe (1993) were entered into the CLAMP score sheet. Both localities were analysed individually to obtain two data matrices (Supplementary material, Tables 1 and 2), which were used to run the CLAMP free online.

4.1. CLAMP results for the Priabonian flora from Sarral and comparison with previous data

Twenty-six morphotypes of dicots from the Priabonian bed of Sarral were used for palaeoclimate characterisation (Supplementary material, Table 1). The results indicated a warm mean annual temperature (MAT) of $19.46 \pm 2\,^{\circ}C$. However, a marked contrast was observed between the mean temperatures of the warmest and coldest months, whereby the warmest month mean temperature (WMMT) was hot, at $27.50 \pm 2.7\,^{\circ}C$, and that of the coldest month (CMMT) was much colder, at $11.78 \pm 3.4\,^{\circ}C$. Although this difference is considerable, the growth season (GROWSEAS) lasted practically all year round, i.e. 10.73 ± 1.1 months. Rainfall during this growth period was 174.24 ± 48.3 cm (GSP), corresponding on average to 15.77 ± 5.2 cm per month (MMGSP). However, a comparison between the three wettest (3-WET) and the three driest (3-DRY) months indicated that the rainfall presented a strong seasonal contrast. During the three wettest months (3-WET), it was about four times higher (74.64 ± 20.6 cm) than during the three driest months (22.94 ± 13.7 cm). Relative humidity (RH) throughout the year was $52.64 \pm 11.1\%$ (Supplementary material, Table 3).

These palaeoclimatic results allow for a comparison with a previous palaeoclimatic study from this locality by Fernández-Marrón (1973a). She provided a climate estimate for the Priabonian from Sarral based on leaf physiognomy and the closest extant relatives. This author concluded that the mean annual temperature was between

Fig. 7. Magnoliopsida morphotypes from the localities studied (continued). 1: MFT 24 from Sarral (SA-1675). 2: MFT 25 from Sarral (SA-1078). 3: MFT 26 from Sarral (SA-1316). 4: MFT 27 from Sarral (SA-1687). 5: MTF 28 from Cervera (MGB-88888). 6: MTF 29 from Cervera (MGB-88889). 7: MFT 30 (MGB-88890) from Cervera. 8: MFT 31 from Cervera (MGB-88891). 9: MFT 32 from Cervera (MGB-88892). 10: MFT 33 from Cervera (MGB-88893). 11: MTF 34 from Cervera (MGB-88894). Scale bar: 1 cm.

Fig. 7. Morphotypes de Magnoliopsida des localités paléobotaniques étudiées (continuation). 1 : MFT 24 de Sarral (SA-1675). 2 : MFT 25 de Sarral (SA-1078). 3 : MFT 26 de Sarral (SA-1316). 4 : MFT 27 de Sarral (SA-1687). 5 : MTF 28 de Cervera (MGB-88888). 6 : MTF 29 de Cervera (MGB-88889). 7 : MFT 30 de Cervera (MGB-88890). 8 : MFT 31 de Cervera (MGB-88891). 9 : MFT 32 de Cervera (MGB-88892). 10 : MFT 33 de Cervera (MGB-88893). 11 : MTF 34 de Cervera (MGB-88894). Échelle : 1 cm.


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20 and 25 °C, which is in line with the calculated MAT provided here (19.46 ± 2 °C). In terms of precipitation, Fernández-Marrón (1973a) suggested that the abundance of xerophytic plants with small leaf sizes would indicate a long season of drought. This hypothesis was supported by Cavagnetto and Anadón (1996), who carried out a palynological study in another locality of the Sarral Formation laterally equivalent to the leaf bed. They highlighted the prevalence of herbaceous plants indicating a strong precipitation seasonality. The results obtained based on CLAMP also show this climate behaviour with a well-contrasted precipitation regime between the three wettest months and the three driest months. However, the precipitation of the three driest months was 22.94 ± 13.7 cm, suggesting that drought was not as strong as proposed before.

4.2. CLAMP results for the Rupelian flora from Cervera and comparison with previous data

Fifty-six leaf morphotypes from the plant bed No. 2 of the palaeobotanical site of Cervera were used to characterise the palaeoclimate of the Ebro Basin during the Oligocene (Supplementary material, Table 2). The results indicated a mean annual temperature (MAT) of 16.81 ± 2 °C and a warmest month mean temperature (WMMT) of 26.04 ± 2.7 °C. In contrast, the coldest month mean temperature (CMMT) was 8.49 ± 3.4 °C. The plants grew for 9.65 ± 1.1 months of the year (GROWSEAS), during which precipitation (GSP) was 216.23 ± 48.3 cm, providing an average of 18.80 ± 5.9 cm rainfall per month (MMGSP). During the three wettest months (3-WET), precipitation was 88.40 ± 20.6 cm, dropping to 28.05 ± 13.7 cm during the three driest months (3-DRY). As a result, the seasonal contrast in precipitation was more than threefold. Relative humidity (RH) throughout the year was 46.61 ± 11.1% (Supplementary material, Table 3).

A good basis for comparison with the results obtained here from the Cervera leaf assemblage is provided by the study of Barrón et al. (2010) based on a Coexistence Analysis (Nearest Living Relative method, NLR). While the temperature parameters are similar to the value obtained from the CLAMP, the precipitation values diverge. The mean annual precipitation of 1255–1355 mm reported by Barrón et al. (2010) is well below the total rainfall for nine months of growth obtained using CLAMP (2162 mm). These contrasting results may be due to the different methodological approaches used. For instance, some taxa such as *Tetraclinis*, considered by Barrón et al. (2010) as a reliable climate indicator, is only represented in present times by relict survivors of one single species living in extremely arid environments (Farjon and Filer, 2013). An in-depth discussion of the limitations that the use of such relicts has for palaeoclimate reconstruction based in the nearest living relative method has been recently provided by Utescher et al. (2014) and Grimm et al. (2016).

5. Discussion

A palaeoclimatic analysis of two macroflora sites in the eastern Ebro Basin (Catalonia, Spain), conducted using CLAMP, sheds light on the climatic impact of the EOT in Southern Europe. Some of the differences observed between the climatic parameters obtained from these two sites are consistent with the general long-term climatic transition around the Eocene–Oligocene boundary (Zachos et al., 2001). However, other differences were unexpected, but are nevertheless in line with the sedimentary and climatic cycles already documented for the EOT in the Ebro Basin (Tosal et al., 2018; Valero et al., 2014).

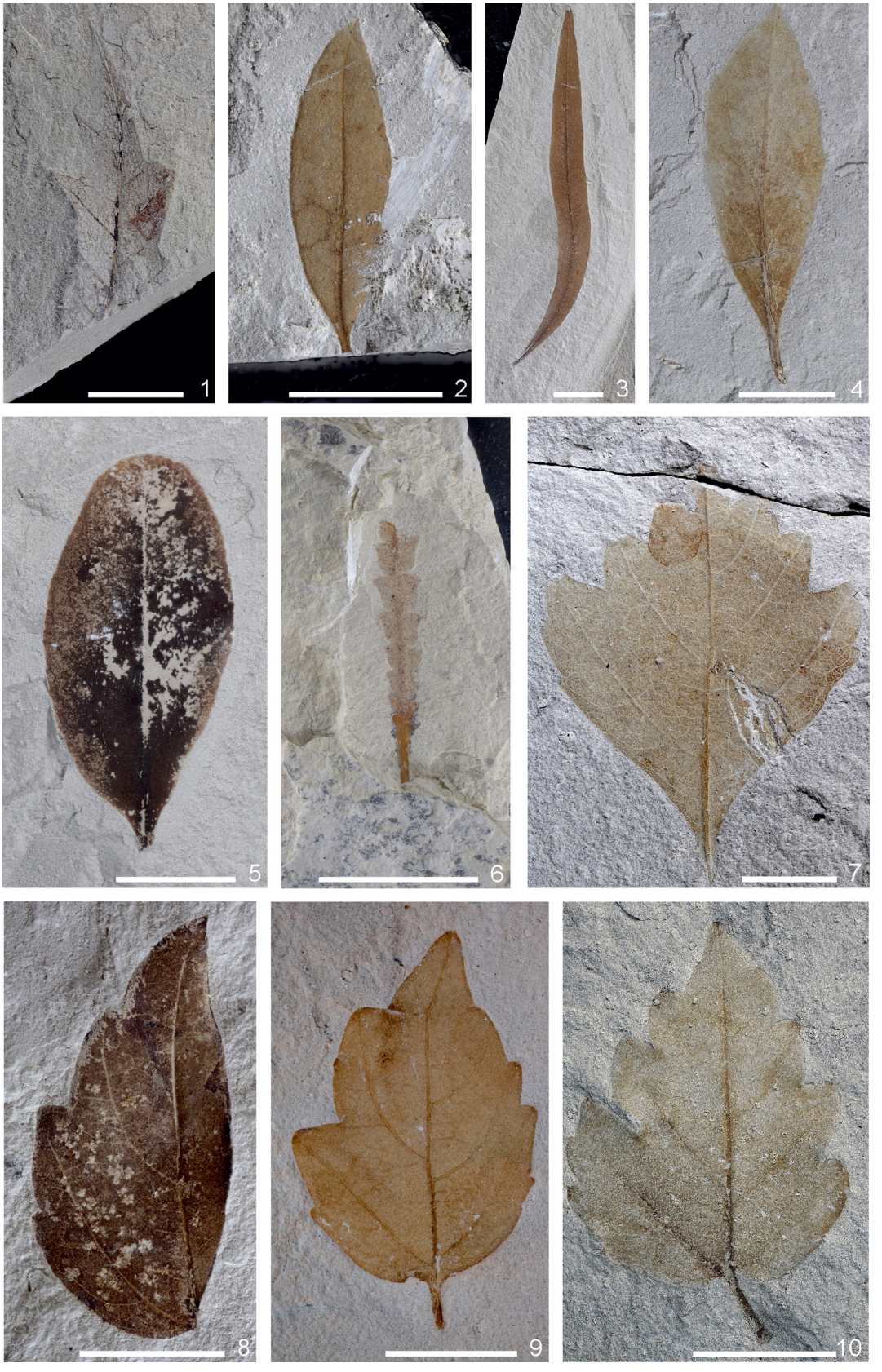
5.1. Influence of short-term climatic cycles on the evolution of the upper Eocene–lower Oligocene vegetation in the Ebro Basin

A climatic comparison between the latest Priabonian of Sarral and the Rupelian of Cervera based on CLAMP (Supplementary material, Table 3) evidences a drop of 3 °C in the mean annual temperature (MAT) and also in the CMMT (coldest month mean temperature). A similar pattern of lower winter temperatures has also been reported for central Europe after the EOT transition, where the MAT presents a decrease of 3.5 °C in the Oligocene (Mosbrugger et al., 2005; Roth-Nebelsick et al., 2004; Utescher et al., 2015).

This cooling event has also been recognised in Northern Hemisphere marine settings. Comprehensive isotopic analyses of benthic foraminifera tests revealed a drop of about 5 °C during an interval of 3–6 Myr encompassing the Eocene–Oligocene boundary (Liu et al., 2009; Miller et al., 1987; Zachos et al., 2001). In contrast, Sheldon et al. (2012) conducted a geochemical analysis of clay minerals in palaeosols from the Ebro Basin and proposed a mean annual temperature of 10 °C without variations across the Eocene–Oligocene boundary (33.3–34.2 Ma). These results

Fig. 8. Magnoliopsida morphotypes from the localities studied. 1: MTF 35 from Cervera (MGB-88895). 2: MTF 36 from Cervera (MGB-88896). 3: MTF 37 from Cervera (MGB-88897). 4: MTF 38 from Cervera (MGB-88898). 5: MTF 39 from Cervera (MGB-88899). 6: MTF 40 from Cervera (MGB-88900). 7: MTF 41 from Cervera (MGB-88901). 8: MTF 42 from Cervera (MGB-88902). 9: MTF 43 from Cervera (MGB-88904). 10: MTF 44 from Sarral (SA-1562). 11: MTF 45 from Cervera (MGB-88905). 12: MTF 46 from Sarral (SA-1061). Scale bar: 1 cm.

Fig. 8. Morphotypes de Magnoliopsida des localités paléobotaniques étudiées (continuation). 1 : MTF 35 de Cervera (MGB-88895). 2 : MTF 36 de Cervera (MGB-88896). 3 : MTF 37 de Cervera (MGB-88897). 4 : MTF 38 de Cervera (MGB-88898). 5 : MTF 39 de Cervera (MGB-88899). 6 : MTF 40 de Cervera (MGB-88900). 7 : MTF 41 de Cervera (MGB-88901). 8 : MTF 42 de Cervera (MGB-88902). 9 : MTF 43 de Cervera (MGB-88904). 10 : MTF 44 de Sarral (SA-1562). 11 : MTF 45 de Cervera (MGB-88905). 12 : MTF 46 de Sarral (SA-1061). Échelle : 1 cm.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challenge the available palaeobotanical and palynological data, which clearly point towards a subtropical climate. However, many factors could alter the original proportion of clay minerals, including diagenesis or weathering, and may result in a distorted view of the palaeotemperature (Passchier et al., 2013).

The increase in seasonality in the Ebro Basin across the upper Eocene–Oligocene boundary was equally significant. CLAMP analysis indicates that the plant growth period was shorter in the Oligocene of Cervera. Generally, plants stop growing at temperatures below 6 °C (Körner, 2016). Such low temperatures would be exceptionally rare in Sarral during the Priabonian, since the mean temperature was 11.78 ± 3.4 °C during the coldest months, allowing plants to grow almost all year round. In contrast, the coldest month mean temperature (CMMT) in the Rupelian of Cervera was 8.49 ± 3.4 °C, indicating that the 6 °C threshold was frequently reached. This decrease in temperature would halt plant growth and can be associated with the increasing seasonality across the Eocene–Oligocene boundary. Similar results have also been documented in Germany by Mosbrugger et al. (2005).

Precipitation also decreased substantially after the Eocene–Oligocene transition in many parts of the Northern Hemisphere, including North America (Sheldon, 2009). However, the record for the Ebro Basin provided by CLAMP indicates that precipitation was higher in the Rupelian of Cervera than in the Priabonian of Sarral. In addition, the Rupelian of Cervera benefitted from an evenly distributed precipitation, as shown by a relatively limited difference between the three wettest and the three driest months (3-WET *vs.* 3-DRY) in comparison with the Sarral site. These results are at variance with the general trend towards a more arid climate recognised from the late Eocene to the early Oligocene in the Ebro Basin (Cavagnetto and Anadón, 1996), other European basins (Utescher et al., 2015) and on other continents (Passchier et al., 2013 for Antarctica; Sun et al., 2014; Dupont-Nivet et al., 2007 for East Asia; Sheldon and Retallack, 2004 for North America).

The contrasting pluviometry of the two plant beds studied here might be the result of non-linear climatic behaviour during the EOT in the Ebro Basin, since both localities shared a very similar altitude and latitude. The lacustrine sequences hosting the floras studied show a cyclic architecture (Fig. 12), which we interpret as precession cycles, in agreement with the cyclostratigraphic studies carried out in similar environmental and chronostratigraphic settings in the Ebro Basin by Valero et al. (2014). Consequently, one plausible explanation for the anomalously high figures for precipitation in the Rupelian of Cervera is the location of this site closer to the high rainfall phase that eventually led to the spread of a palaeo-lake. This notion is supported by the sedimentary record, as pale grey marls rich in plant remains would represent relatively deeper and anoxic lacustrine facies corresponding to the wetter stages of such a cycle. Meanwhile, gypsum-rich intervals were deposited during the drier stage of the same cycle, evidencing evaporation exceeding precipitation (Tosal and Martín-Closas, 2016). In line with this rationale, asymmetry in the location of the palaeobotanical sites with respect to the precession cycle would also account for a slightly lower precipitation during deposition of the Sarral Priabonian leaf bed. This site is located in laminated marlstones from shallow saline lake facies, representing the drier part of a cycle. At the opposite extreme of the cycle, charophyte-rich marls and limestones represent permanent freshwater lakes (Tosal et al., 2018).

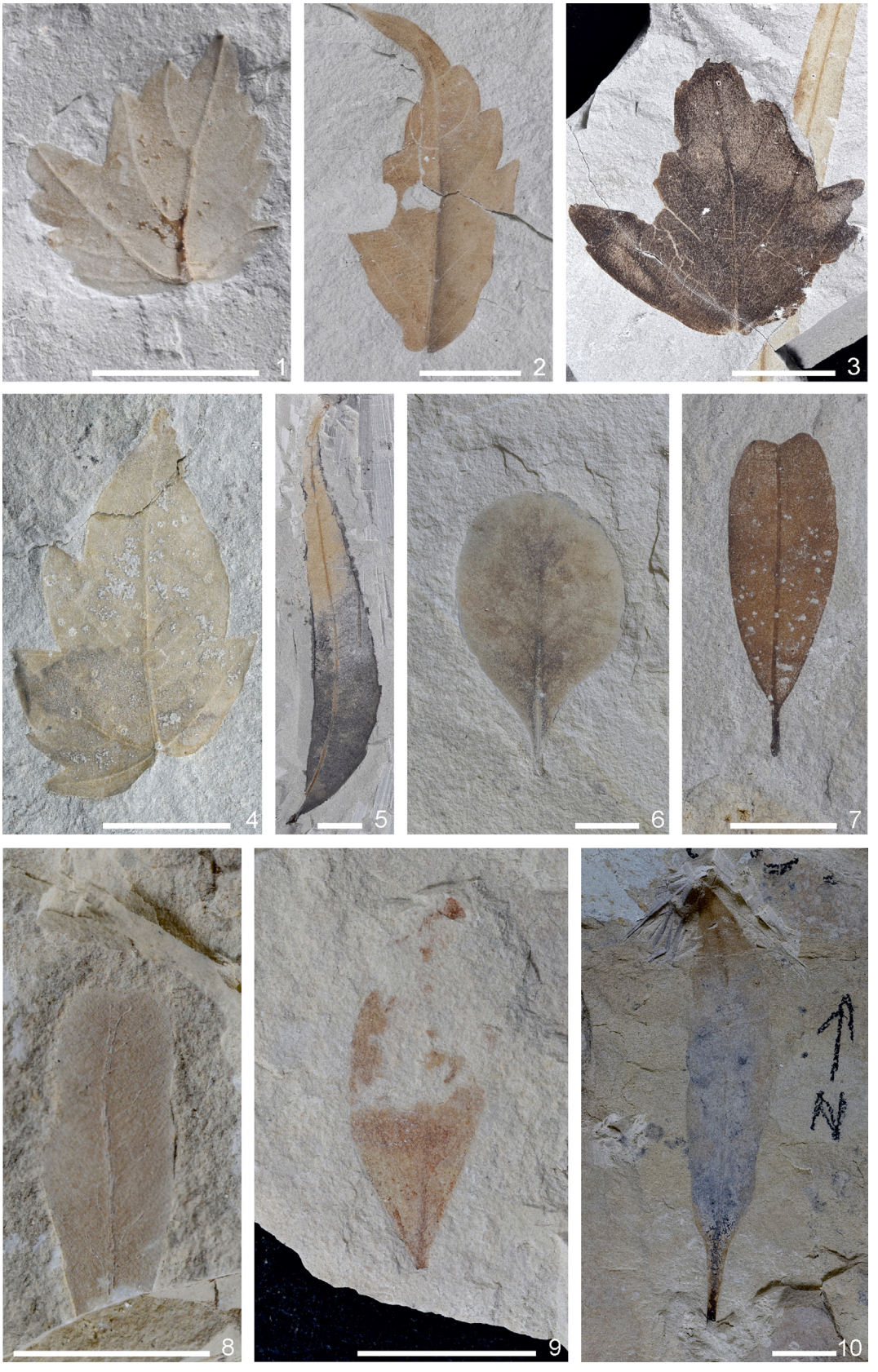
Both the Sarral and Cervera sites share identical phases of eccentricity, maxima of 400 kyr. Eccentricity maxima are linked to the main spreading phases of the Ebro Basin Paleogene lacustrine systems (Anadón et al., 1989; Valero et al., 2014). However, the exact location of these sites within the 400 kyr eccentricity maxima and the role of the 100 kyr eccentricity maxima are unknown, but may have had important consequences not only for the water budget but also as regards the seasonal contrast. A more detailed biocyclostratigraphic study, beyond the scope of this paper, would be necessary in order to fully understand the relationship between the studied fossil leaf floras and the phase of astronomical cycles. However, precession minima (summer insolation maxima) in the Northern Hemisphere are usually associated with an increase in precipitation at mid-latitudes, while precession maxima (summer insolation minima) represent less precipitation (Bosmans et al., 2015). Hence, the hypothesis is proposed that the Sarral palaeobotanical site would have been formed during a precession maximum, whereas the Cervera site represents the minimum of such a cycle.

5.2. Evolution of Ebro Basin plant biomes across the Eocene–Oligocene transition

A comparison of the distribution of flora from the Priabonian of Sarral (Tosal et al., 2018) and the Rupelian of Cervera (Tosal and Martín-Closas, 2016) can now be better understood in view of the palaeoclimatic results obtained from a CLAMP analysis (Fig. 13):

Fig. 9. Magnoliopsida morphotypes from the localities studied (continued). 1: MTF 47 from Sarral (SA-1690). 2: MTF 48 from Cervera (MGB-88906). 3: MTF 49 from Cervera (MGB-88908). 4: MTF 50 from Cervera (MGB-88909). 5: MTF 51 from Cervera (MGB-88910). 6: MTF 52 from Sarral (SA-1616). 7: MTF 53 from Cervera (MGB-85946). 8: MTF 53 from Cervera (MGB-85966). 9: MTF 54 from Cervera (MGB-85001). 10: MTF 55 from Cervera (MGB-85007). Scale bar: 1 cm.

Fig. 9. Morphotypes de Magnoliopsida des localités paléobotaniques étudiées (continuation). 1 : MTF 47 de Sarral (SA-1690). 2 : MTF 48 de Cervera (MGB-88906). 3 : MTF 49 de Cervera (MGB-88908). 4 : MTF 50 de Cervera (MGB-88909). 5 : MTF 51 de Cervera (MGB-88910). 6 : MTF 52 de Sarral (SA-1616). 7 : MTF 53 de Cervera (MGB-85946). 8 : MTF 53 de Cervera (MGB-85966). 9 : MTF 54 de Cervera (MGB-85001). 10 : MTF 55 de Cervera (MGB-85007). Échelle : 1 cm.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- *Vegetation in lakeshore and river bank zones.* According to Tosal et al. (2018), in the Priabonian of Sarral, the riparian community mainly consisted of species from the Salicaceae, Myricaceae (*Myrica arenesi* and *Comptonia schrankii*) and the Lauraceae (*Daphnogene* and *Laurophyllum*). In contrast, in the lower Oligocene of Cervera, only the Salicaceae (*S. lavateri* and *S. angusta*) and the Myricaceae, mainly *M. arenesi*, dominated in the riparian community (Tosal and Martín-Closas, 2016).

  The scarcity of *Comptonia schrankii* in Cervera contrasts with its abundance in Sarral and other Oligocene localities in Northern Europe (Utescher and Mosbrugger, 2009). The only living species of this genus, *C. peregrina*, shows significant edaphic control, growing in permanently moist sandy soils (Gleason and Cronquist, 1991). As the lakeshore deposits of Sarral are much more detrital than the equivalent carbonatic Cervera deposits (Tosal and Martín-Closas, 2016; Tosal et al., 2018), it might be that the occurrence of this species is related to edaphic conditions rather than to climatic variation.
- *Vegetation beyond the lakeshores and river banks.* In the Priabonian of Sarral, *Tetraclinis* dominated beyond riverine settings, forming open vegetation (Tosal et al., 2018). Although this cupressaceous genus persisted in the early Oligocene of Cervera, as indicated by rare remains reported by Sanz de Siria (1992), the Rupelian equivalent vegetation beyond the riverine biome was formed by a small laurisilva composed of *Daphnogene*, *Laurophyllum*, *Myrica* aff. *faya* and *M. oligocena* (Tosal and Martín-Closas, 2016).

  In a synthesis of the Cenozoic vegetation of Europe, Kvaček (2010) suggested that in the past, *Tetraclinis* was a sub-xerophytic element rather than a plant growing in extremely arid conditions, as does its extant representative. The palaeoclimatic results obtained using CLAMP for the Priabonian of Sarral support this hypothesis, showing that this plant would have preferred relatively semiarid conditions with a high seasonal precipitation regime. These palaeoclimatic conditions contrast with the largely wetter parameters and less seasonal variation in precipitation obtained for the Oligocene of Cervera. The latter conditions are consistent with the development of Lauraceae beyond the river banks (Tosal et al., 2018), and without the need for edaphic mediation in contrast to what Barrón et al. (2010) proposed based on the palaeoenvironmental model described by Mai (1989).
- *Vegetation in distal parts of the lake.* In both localities, this biome consisted of open savannah-like woodlands (Tosal et al., 2018). However, in the Priabonian of Sarral, it was mainly composed of abundant Fabaceae and *Zizyphus* (Tosal et al., 2018), growing beyond the *Tetraclinis* belt, while in the Rupelian of Cervera, it was dominated by other taxa such as *Rhus*, *Rhamnus*, *Mimosites*, and other Fabaceae (Tosal and Martín-Closas, 2016). The higher proportion of the Fabaceae in Sarral would be related to drier conditions. In contrast, the relatively more moderate temperatures associated with the higher, year-round precipitation characteristic of the Oligocene of Cervera would have facilitated higher diversity, including the Fabaceae but also *Rhamnus* or *Rhus*.

6. Conclusions

We studied the climate transition at the Eocene–Oligocene boundary, conducting a CLAMP analysis of two leaf floras from neighbouring palaeobotanical sites in the Ebro Basin (Iberian Peninsula): the latest Priabonian of Sarral and the Rupelian of Cervera. The results reveal a drop in temperatures and an increase in seasonality towards the Oligocene, in line with the global climatic trend observed in the Northern Hemisphere. Nevertheless, a coeval increase in the precipitation regime contrasts with the general trend towards aridity reported for this period in southern Europe.

The palaeoclimatic results presented here show that the long-term climate trend of the Eocene–Oligocene turnover can be punctuated by Milankovitch cycles, which may have a significant effect on precipitation and seasonality. Thus, the Priabonian flora from Sarral is located in the drier stage of a succession, which we suggest was a precession maximum, whereas the Rupelian flora from Cervera would reflect a wetter stage associated with a minimum of the precession cycle. These deviations highlight the importance of understanding the local impact of orbital cycles to contextualise palaeoclimatic studies based on flora.

The climatic change of the Eocene–Oligocene transition modified the plant biomes. Some authors suggested that this floristic change was non-linear and may have been influenced by palaeoclimatic fluctuations. The palaeoecological and palaeoclimatic results presented here would be consistent with this hypothesis and two types of vegetation response to short-term climatic changes are reported. The first of these is a change in plant habitats as represented by the Lauraceae, which in the Priabonian of Sarral were restricted to lakeshore, which provided the only scant moisture available. In contrast, during the Oligocene of Cervera, rainfall increased and the laurophyllous plants expanded beyond the river banks to form small laurisilva-type communities. The second response concerns variations in plant diversity within the savannah-like woodlands. As a result of the relatively low and irregular precipitation regime during the Priabonian, the Fabaceae were dominant in this biome, whereas higher and more regular rainfall combined with a drop in temperature during the Oligocene favoured the development of a more biodiverse community, including abundant *Rhamnus* and *Rhus*.

Fig. 10. Magnoliopsida morphotypes from the localities studied (continued). 1: MTF 56 from Cervera (MGB-88912). 2: MTF 57 from Cervera (MGB-88913). 3: MTF 58 from Cervera (MGB-85010). 4: MTF 59 from Cervera (MGB-85011). 5: MTF 60 from Cervera (MGB-88914). 6: MFT 61 from Sarral (SA-1117). 7: MFT 62 from Cervera (MGB-88915). 8: MFT 63 from Sarral (SA-1009). 9: MFT 64 from Sarral (SA-1156). 10: MFT 65 from Sarral (SA-1833). Scale bar 1: cm.
Fig. 10. Morphotypes de Magnoliopsida des localités paléobotaniques étudiées (continuation). 1 : MTF 56 de Cervera (MGB-88912). 2 : MTF 57 de Cervera (MGB-88913). 3 : MTF 58 de Cervera (MGB-85010). 4 : MTF 59 de Cervera (MGB-85011). 5 : MTF 60 de Cervera (MGB-88914). 6 : MFT 61 de Sarral (SA-1117). 7 : MFT 62 de Cervera (MGB-88915). 8 : MFT 63 de Sarral (SA-1009). 9 : MFT 64 de Sarral (SA-1156). 10 : MFT 65 de Sarral (SA-1833). Échelle: 1 cm.


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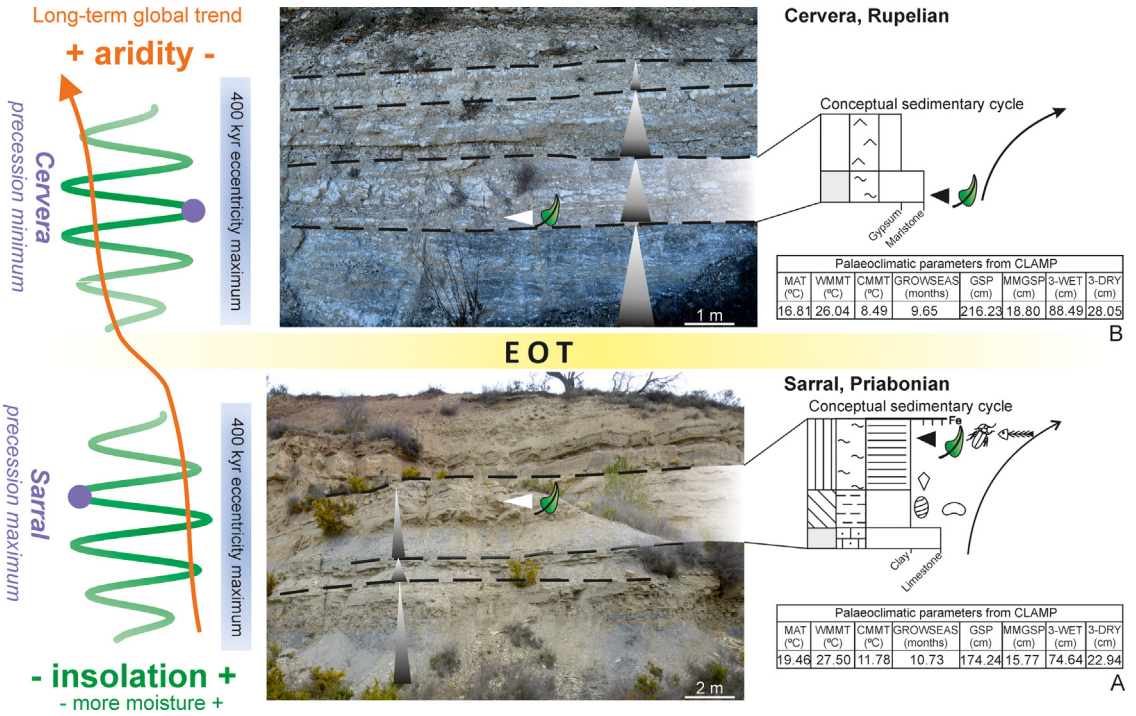

Fig. 12. Synthesis of sedimentary data, CLAMP palaeoclimatic results and cyclostratigraphic interpretations from the Priabonian of Sarral (A) and the Rupelian of Cervera (B). Conceptual graph of the 20kyr precession cycles and the relative position of the floras studied (left), sedimentary cycles on field pictures of the leaf beds (centre) and CLAMP palaeoclimatic data and conceptual sedimentary cycles (right). Symbols in the logs as in Figs. 2 and 3.
Fig. 12. Synthèse des données sédimentaires, résultats paléoclimatiques issus de l'analyse CLAMP et interprétations cyclostratigraphiques dans le Priabonien de Sarral (A) et le Rupélien de Cervera (B). Graphe conceptuel des cycles de précession de 20 kyr, avec la position des flores étudiées (gauche), cycles sédimentaires sur des photos des gisements à feuilles (centre) et résultats paléoclimatiques avec les cycles sédimentaires conceptuels (droite). Symboles des logs comme dans les Fig. 2 et 3.

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Fig. 11. Magnoliopsida morphotypes from the localities studied (continued). 1: MFT 67 from Cervera (MGB-88916). 2: MFT 68 from Cervera (MGB-88917). 3: MFT 69 from Cervera (MGB-88918). 4: MFT 70 from Cervera (MGB-88919). 5: MFT 71 from Cervera (MGB-88920). 6: MFT 72 from Cervera (MGB-88921). 7: MFT 73 from Cervera (MGB-88922). 8: MFT 74 from Cervera (MGB-88923). 9: MFT 75 from Cervera (MGB-88903). 10: MTF 75 from Cervera (MGB-88903). Scale bar: 1 cm.
Fig. 11. Morphotypes de Magnoliopsida des localités paléobotaniques étudiées (continuation). 1 : MFT 67 de Cervera (MGB-88916). 2 : MFT 68 de Cervera (MGB-88917). 3 : MFT 69 de Cervera (MGB-88918). 4 : MFT 70 de Cervera (MGB-88919). 5 : MFT 71 de Cervera (MGB-88920). 6 : MFT 72 de Cervera (MGB-88921). 7 : MFT 73 de Cervera (MGB-88922). 8 : MFT 74 de Cervera (MGB-88923). 9 : MFT 75 de Cervera (MGB-88903). 10: MTF 75 de Cervera (MGB-88903). Échelle : 1 cm.

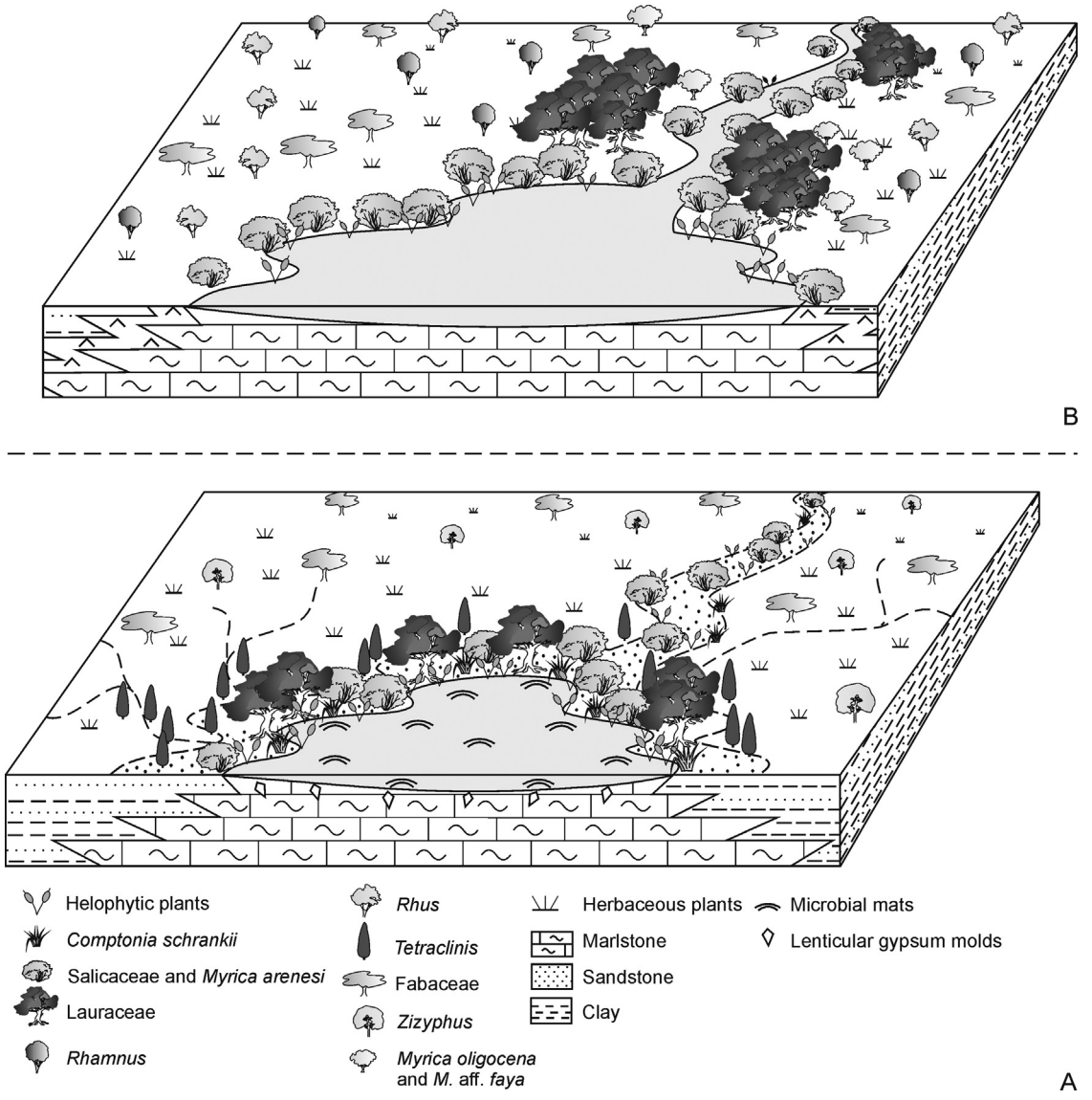

Fig. 13. Changes in the vegetation belts during the EOT in the Ebro Basin. A. Priabonian of Sarral. B. Rupelian of Cervera. A shift in the location of the lauraceous forest is highlighted. Modified from Tosal et al. (2018).
Fig. 13. Changements dans les ceintures de végétation durant l'EOT dans le bassin de l'Èbre. A. Priabonien de Sarral. B. Rupélien de Cervera. Un déplacement des forêts de lauriers est mis en évidence. Modifié d'après Tosal et al. (2018).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.crpv.2019.10.003.

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