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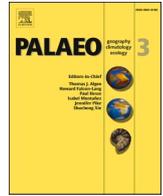
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# Plant palaeoecology of the latest Eocene flora from the Saint-Chaptes and Alès basins of Gard, southern France

Aixa Tosal<sup>a,b,c,\*</sup>, Mélanie Tanrattana<sup>b</sup>, François Fournier<sup>d</sup>, Dario De Franceschi<sup>b</sup>,  
Cédric Del Rio<sup>b</sup>, Carles Martín-Closas<sup>a,c</sup>, Alexandre Lettéron<sup>d</sup>, Nazim Semmani<sup>d</sup>, Anaïs Boura<sup>b</sup>

<sup>a</sup> Departament de Dinàmica de la Terra i de l'Oceà, Facultat de Ciències de la Terra, Universitat de Barcelona-UB, 08028 Barcelona, Catalonia, Spain

<sup>b</sup> UMR 7207 Centre de Recherche en Paléontologie-Paris (CR2P), MNHN - Sorbonne Université-CNRS, 43 Rue Buffon, 75005 Paris, France

<sup>c</sup> Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona-UB, 08028 Barcelona, Catalonia, Spain

<sup>d</sup> Aix Marseille Univ, CNRS, IRD, INRAE, Coll France, CEREGE, Aix-en-Provence, France

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## ABSTRACT

Rapid cooling during the Eocene-Oligocene transition resulted in a vegetation shift in southern France, from warm, humid vegetation to open savannah-like vegetation; however, the precise nature of this shift is uncertain. In this paper, we study the latest Eocene flora from the Saint-Chaptes and Alès basins (southern France) and compare it with other well-known southern European localities to evaluate vegetation changes near the Eocene-Oligocene boundary. Five plant communities are recognised: 1) hydrophytic vegetation dominated by water lilies and a *Limnobiophyllum*-like plant; 2) reeds that formed a palustrine belt around the lake; 3) ferns with *Osmunda* aff. *parschlugiana* and *Pronophrium stiriacum*, conifers with *Doliosirobus taxiformis*, a *Sequoia*-like plant, angiosperms with *Daphnogene* sp., *Bytneriopsis* sp., *Myrica* sp., *Comptonia difformis* and palms, which inhabited the lake shores and constituted the riparian vegetation; 4) *Tetraclinis*, which grew just behind the riparian vegetation but not far from watercourses, forming open landscapes and 5) *Zizyphus ziziphoides*, Fabaceae, and probably *Ailanthus* sp. and *Tetraclinis* forming an open woodland distal to the lake. The flora of the Saint-Chaptes and Alès basins resembles coeval floras from Sarral (Catalonia, Spain) that are characteristic of Southern Europe, although riparian vegetation is more diverse in the Saint-Chaptes and Alès basins, and Fabaceae diversity is higher at Sarral. We hypothesise that vegetation composition was mainly controlled by (1) basin architecture, allowing for a variety of wetland habitats and (2) climate. The coexistence of genera that are restricted to Central Europe (e.g., *Bytneriopsis* or *Doliosirobus*), together with genera more typical of Southern Europe (e.g., diversity of Fabaceae, *C. difformis* and *Z. ziziphoides*) suggests that the Saint-Chaptes and Alès basins contain latest Priabonian floras that are transitional between these two regions.

## 1. Introduction

The Eocene-Oligocene transition represents the most drastic climatic turnover of the Cenozoic era (e.g. Zachos et al., 2001). An abrupt shift in  $\delta^{18}\text{O}$  values of deep-marine carbonates at  $\sim 34$  Ma reflects the first glaciation of Antarctica and the beginning of a long-lasting trend in oceanic water cooling (Hutchinson et al., 2021). However, the terrestrial record of this major climatic event suggests that regional heterogeneities occurred (Hren et al., 2013; Sheldon, 2009). For instance, it is generally accepted that in Central Europe (Germany, Austria, the Czech Republic and Hungary), the decrease in temperatures triggered a migration of

broad-leaved deciduous plants (e.g. *Platanus* L., *Acer* L., *Alnus* Mill.) from higher latitudes (Mai and Walther, 1985; Collinson, 1992, 2000; Mihajlović and Ljubotenski, 1994; Collinson and Hooker, 2003). This flora differs from the contemporaneous vegetation of South Europe (Iberian Peninsula, South of France, Bulgaria and Macedonia) where subtropical elements (e.g. *Phoebe* Nees and *Daphnogene* Unger) prevailed according to Mai (1995), Knobloch et al. (1993), Kovar-Eder et al. (1996), Kvaček (2010) and Tosal et al. (2018).

Knowledge of the late Eocene flora of South Europe is still poor, in part due to the limited number of plant localities studied, i.e. Bourgas Basin (Bulgaria), Ovče Polje Basin (Macedonia), Alès and Saint-Chaptes

\* Corresponding author at: Departament de Dinàmica de la Terra i de l'Oceà, Facultat de Ciències de la Terra, Universitat de Barcelona-UB, 08028 Barcelona, Catalonia, Spain.

E-mail address: [atosal@ub.edu](mailto:atosal@ub.edu) (A. Tosal).

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basins (France) and Ebro Basin (Catalonia, NE Spain). In this study, we focus on new Priabonian plant localities of the Saint-Chaptes and Alès basins. The historical plant collection from these basins has been studied from several viewpoints, including taxonomy (Marion, 1888; Laurent, 1899), palaeoecology (Laurent, 1899) and palaeoclimatology (Tanrattana et al., 2020), but not from that of plant taphonomy. As a result, nothing was known about fossilisation or collection biases of the assemblage, which may have led to imprecise palaeoenvironmental interpretations.

The aim of the present study is to characterise the vegetation distribution of the Priabonian flora from the Saint-Chaptes and Alès basins (southern France), combining taxonomical data, sedimentological studies and taphonomic analyses, conducted in new plant localities of these basins, during several days field-work. In addition, we compare the latest Eocene flora from the Saint-Chaptes and Alès basins with the coeval floras from Sarra (Ebro Basin, NE Spain) and of several Central European floras to better characterise regional changes in Southwest Europe over this time span. The results are also compared with the palaeoclimatic figures available for several localities from South and Central Europe, for a better understanding of vegetation dynamics close the Eocene-Oligocene boundary.

## 2. Palaeobotanical setting and history of the ‘Célas plant collection’

The Priabonian flora from the Saint-Chaptes and Alès basins is known in the literature as the ‘Célas flora’ because the fossil plant beds were discovered close to the village of Célas during railway construction. Marion (1888) first studied the genus *Doliosrobis* Marion, and some years later, Laurent (1899) carried out an exhaustive taxonomic study of the entire plant collection, providing the first insight into biodiversity in South Europe during the Priabonian. Laurent (1899) described 76 fossil-species (Table 1) and the specimens are now stored in the Natural History Museum in Marseille (Tanrattana et al., 2020). This plant assemblage was regarded by Kvaček (2010) as characteristic for the vegetation of South Europe during the Palaeogene. From a palaeoecological viewpoint, Laurent (1899) recognised four vegetation belts located at different altitudes. From lowland to upland, these are: aquatic plants, riparian vegetation, laurel forest and woodland.

Gruas-Cavagnetto (1973) and Gruas-Cavagnetto and Bui (1976) both performed palynological and taxonomic studies of the Saint-Chaptes and Alès basins, but it was the palynological study by Semmani et al. (2023), who recognised 122 taxa, which vastly increased knowledge of the plant palaeodiversity in the two basins. These studies indicated a mixture of species, some with affinities to temperate areas (e.g. *Carya* Nutt., *Platycarya* Siebold et Zucc, *Salix* L., *Tilia* L., Pinaceae) and others with affinities to tropical and subtropical climates (e.g. *Lygodium* Sw., *Sabal* Adans., *Jodes* Blume, Nyssaceae, Araliaceae, Sapotaceae).

In recent years, interest has grown in reconstructing the past climate of South Europe. Tanrattana et al. (2020) determined the climate corresponding to the fossil plants of the Célas flora (historical collection) using the CLAMP method (climate leaf analysis multivariate program). Semmani et al. (2023) provided new climatic data based on the pollen record from different outcrops in the Saint-Chaptes and Alès basins, analysed using the climate amplitude method (Fauquette et al., 1998). Both studies indicate a subtropical climate with warm temperatures, mild winters and high precipitation seasonality. This interpretation is in line with the results reported by Laurent (1899), who proposed a xeric regional vegetation for the basin, but contrasts with the abundance of *Doliosrobis taxiformis* (Sternb.) Kvaček, *Byttneriopsis* Kvaček & Wilde. and Lauraceae, which instead suggests the presence of permanently humid environments (Tanrattana et al., 2020).

**Table 1**

Taxonomic list of the specimens from the historical plant collection compared with the taxonomic identification by Laurent (1899).

Family	Taxonomic list of Laurent (1899)	Updated taxonomic list (this study)
Cystopteridaceae	<i>Cystopteris fumariacea</i> P. Wessel et C.O. Weber	<i>Cystopteris fumariacea</i>
Thelypteridaceae	<i>Lastraea (Goniopteris) stiriaca</i> (Unger) Heer	<i>Pronephrium stiriicum</i> (Unger) Erw. Knobl., Z. Kvaček
Pteridaceae	<i>Pteris parschlugiana</i> Unger	<i>Osmunda</i> aff. <i>parschlugiana</i>
Pteridaceae	<i>Chrysodium lanzaeanum</i> Vis.	<i>Acrostichum lanzaeanum</i> (Vis.) J. S. Gardner
Lygodiaceae	<i>Lygodium gaudinii</i> Heer	<i>Lygodium gaudinii</i>
Doliosrobaceae	<i>Doliosrobis sternbergii</i> Mar.	<i>Doliosrobis taxiformis</i> (Sternb.) Z. Kvaček
Arecaceae	<i>Sabal major</i> (Unger) Heer <i>Chamaerops celasensis</i> L. Laurent <i>Pandanus intermedium</i> L. Laurent	<i>Sabal major</i> The whereabouts of the specimens is unknown Monocot. indet.
Hydrocharitaceae	<i>Vallisneria saportana</i> L. Laurent	[?] <i>Vallisneria saportana</i>
Myricaceae	<i>Myrica saportana</i> Schimp.	<i>Myrica saportana</i>
Myricaceae	<i>Myrica banksiaefolia</i> Unger [nomen illegitimum]	<i>Myrica longifolia</i>
Myricaceae	<i>Myrica (Comptonia) dryandriifolia</i> (Brongn.) Saporta	<i>Comptonia difformis</i> (Sternberg) Berry (= <i>Paracomptonia schrankii</i> ) (Sternberg) Doweld
“Proteaceae”	<i>Hakea banksiiformis</i> L. Laurent	<i>Berberis</i> sp.
“Proteaceae”	<i>Grevillea dissecta</i> L. Laurent	Indet.
“Proteaceae”	<i>Grevillea haeringiana</i> Ettingsh.	<i>Berberis</i> sp.
Salicaceae	<i>Populus gaudinii</i> Fisch.-Oost. in Heer	[?] <i>Populus gaudinii</i>
Lauraceae	<i>Cinnamomum scheuchzeri</i> Heer	<i>Daphnogene</i> sp.
Moraceae	<i>Ficus marionii</i> L. Laurent	<i>Byttneriopsis daphnogenes</i> (Ettingsh.) Z. Kvaček & Wilde
Malvaceae	<i>Ficus goeppertii</i> Ettingsh.	<i>Byttneriopsis daphnogenes</i> (Ettingsh.) Z. Kvaček & Wilde
Malvaceae	<i>Ficus fraterna</i> L. Laurent	<i>Byttneriopsis</i> sp.
Malvaceae	<i>Ficus calophylla</i> L. Laurent	<i>Byttneriopsis</i> sp.
Malvaceae	<i>Ficus ambigua</i> L. Laurent	<i>Byttneriopsis daphnogenes</i> (Ettingsh.) Z. Kvaček & Wilde
Malvaceae	<i>Ficus irregularis</i> L. Laurent	<i>Byttneriopsis</i> sp.
Malvaceae	<i>Ficus rotunda</i> L. Laurent	<i>Byttneriopsis</i> sp.
Malvaceae	<i>Ficus diffusa</i> L. Laurent	<i>Byttneriopsis daphnogenes</i> (Ettingsh.) Z. Kvaček & Wilde
Malvaceae	<i>Ficus heckeli</i> L. Laurent	<i>Byttneriopsis</i> sp.
Vitaceae	<i>Ficus crenata</i> L. Laurent	Vitaceae?
Moraceae	<i>Ficus ovalis</i> L. Laurent	<i>Byttneriopsis</i> sp.
Moraceae	Fructus fici	Indet. fruit
Moraceae	<i>Artocarpus latifolia</i> L. Laurent	The whereabouts of the specimens is unknown
	<i>Viburnum oblongum</i> L. Laurent	Angiosperm indet.
Oleaceae	<i>Fraxinus grossedentata</i> L. Laurent	<i>Fraxinus</i> ?
Oleaceae	<i>Fraxinus grossedentata</i> L. Laurent	<i>Fraxinus</i> ?
Oleaceae	<i>Fraxinus grossedentata</i> L. Laurent	<i>Fraxinus</i> ?
Primulaceae	<i>Myrsine marioni</i> L. Laurent	Angiosperm indet.
Ericaceae	<i>Andromeda neglecta</i> Sap.	The whereabouts of the specimens is unknown
Ericaceae	<i>Rhododendron celasensis</i> L. Laurent	The whereabouts of the specimens is unknown
	<i>Aralia (Oreopanax) rigida</i> L. Laurent [nomen illegitimum]	Angiosperm indet.
	<i>Aralia antecedens</i> L. Laurent	Angiosperm indet.
Vitaceae	<i>Vitis dubia</i> L. Laurent [nomen illegitimum]	Angiosperm indet. [The specimens are on loan]

(continued on next page)

Table 1 (continued)

Family	Taxonomic list of Laurent (1899)	Updated taxonomic list (this study)
Annonaceae	<i>Annona incerta</i> L. Laurent	Angiosperm indet. [The whereabouts of the specimens is unknown]
Menispermaceae	<i>Cocculus intermedius</i> DC. <i>Clematis</i> (Tourn.) L.	<i>Cocculus intermedius</i> The whereabouts of the specimens is unknown
Nymphaeaceae	<i>Nymphaea</i> (Tourn.) L. <i>Pterospermites incrassatum</i> L. Laurent	<i>Nymphaea</i> "Pterospermites incrassatum"
Malpighiaceae	<i>Banisteria vasseuri</i> L. Laurent	? <i>Cedrelospermum kovaciae</i> Z. Kvaček & Wilde. [The whereabouts of the specimens is unknown]
Sapindaceae	<i>Sapindus falcifolius</i> (A. Braun in Unger) A. Braun in Stizenb.	Angiosperm indet. [The whereabouts of the specimens is unknown]
Sapindaceae	<i>Dodonaea saportana</i> L. Laurent	<i>Craigia europaea</i> (Bronn) Doweld
Rhamnaceae	<i>Ilex pachynervia</i> L. Laurent <i>Zizyphus paradisiaca</i> (Unger) Heer <i>Zizyphus propinquus</i> L. Laurent	Angiosperm indet. <i>Zizyphus ziziphoides</i> (Unger) Weyl. The whereabouts of the specimens is unknown
Rhamnaceae	<i>Rhamnus aizoon</i> Unger <i>Heterocalyx ungeri</i> (Saporta in Heer) Saporta [nomen illegitimum] <i>Rhus paucidentata</i> L. Laurent <i>Rhus juglandogene</i> Ettingsh.	"Rhamnus aizoon" <i>Trilobium ungeri</i> Saporta in Heer Angiosperm indet. Angiosperm indet.
Cupressaceae	<i>Rhus juglandogene</i> Ettingsh.	winged seed of <i>Tetraclinis</i>
Simaroubaceae	<i>Ailanthus prisca</i> Saporta	<i>Ailanthus prisca</i>
Myrtaceae	<i>Myrtus oceanica</i> Ettingsh.	"Myrtus oceanica"
Myrtaceae	<i>Myrtus oceanica</i> Ettingsh. <i>Pyrus elongata</i> L. Laurent	"Myrtus oceanica" The whereabouts of the specimens is unknown
Fabaceae	<i>Dalbergia leptolobiana</i> Saporta	<i>Leguminophyllum</i> A. Escalup-Bassi
Fabaceae	<i>Parkinsonia recta</i> L. Laurent	<i>Leguminophyllum</i> sp.
Fabaceae	<i>Parkinsonia recta</i> L. Laurent	<i>Leguminocarpum</i> Dotzler
Fabaceae	<i>Acacia servacensis</i> L. Laurent	"Acacia" <i>servacensis</i>
Fabaceae	Fructus leguminosae <i>Phyllites reticulata</i> <i>Phyllites tamarindiformis</i> <i>Phyllites cordiformis</i> <i>Phyllites dichotomus</i> <i>Crassulites</i> <i>Leguminosites celasensis</i> <i>Phyllites minutissima</i> <i>Phyllites herbacea</i> <i>Phyllites</i> diverse unidentified <i>Lignum</i> <i>Fructus</i> indet.	<i>Leguminocarpum</i> <i>Leguminophyllum</i> <i>Leguminophyllum</i> sp. Angiosperm indet. Angiosperm indet. Angiosperm indet. Angiosperm indet. Angiosperm indet. <i>Leguminophyllum</i> sp. <i>Leguminophyllum</i> sp. Angiosperm indet. Axis <i>Fructus</i> <i>Anoetomeria</i>
Cupressaceae	indet.	<i>Sequoia</i> -like foliage
Lemnaceae	indet.	<i>Limnobiophyllum</i> -like foliage
Arecaceae	indet.	Palm axis
Arecaceae	indet.	Axis of palm inflorescence

### 3. Materials and methods

#### 3.1. Re-examination of the historical plant collection

The historical megafossil plant collection from Célas housed in the Natural History Museum in Marseille consists of 593 specimens. This plant assemblage was first studied from the taxonomical viewpoint by Laurent (1899), An updated taxa list is provided in Table 1. Specimens of

the most representative fossil-species in the collection were photographed using a Nikon D5300 camera. Re-examination of the historical plant collection made it possible to reassign some of the genera and fossil-species to different taxa (Fig. 1 and Table 1). However, foliar details of some specimens described by Laurent (1899), mainly the delicate venation pattern, were no longer recognisable. This hindered taxonomic re-evaluation of some fossil-species, such as *Zizyphus paradisiaca* (Fig. 1) Laurent and *Z. propinquus* Laurent, which were differentiated on the basis of the intersecondary venation pattern (Laurent, 1899).

#### 3.2. The new plant localities studied

The original leaf-bearing beds that yielded the historical Célas flora are no longer accessible. However, stratigraphic and sedimentological analyses were carried out in three new Priabonian plant localities in the Saint-Chaptes and Alès basins, enabling determination of the depositional setting where the plant remains were buried. In these localities, three main stratigraphic sections were logged:

- 1) The Saint-Hippolyte-de-Caton section is situated in the northern part of the Saint-Chaptes Basin, close to the mammal fossil site of Monteils. This section is 48 m thick and follows the local D981 road (base coordinates 44°04'48"N; 04°11'59"E; top coordinates 44°05'07"N; 04°11'44"E). It is composed of intercalations of argillaceous limestones rich in plant remains, grey or ochre silts and clays.
- 2) The Saint-Jean-de-Ceyrargues section is 11.5 m thick and is located 400 km SE of the village of Saint-Jean-de-Ceyrargues, following the D7 road (base coordinates 44°02'47"N; 04°13'53"E; top coordinates 44°02'46"N; 04°13'50"E). A complementary section 7 m thick was logged at Saint-Maurice-de-Cazevielle and correlated with the former to complete the sedimentological framework. It is mainly constituted by brownish clays and sandstones with planar cross-bedding.
- 3) The Saint-Jean-de-Maruéjols section is situated on the north-eastern margin of the Alès Basin, in the vicinity of an abandoned asphalt mine. This section is 20 m thick (base coordinates 44°16'06"N; 04°17'50"E; top coordinates 44°16'07"N; 04°17'47"E). It is composed of argillaceous and bituminous marls with tabular stratification.

Selected lacustrine facies were sampled for microfacies analysis. Thin sections were prepared from selected limestone beds and are housed in the Muséum National d'Histoire Naturelle in Paris, France (provisional reference numbers SHC. 1, SHC. 1.2, SHC. 1×, SHC.5, SHC.5×).

The plant remains studied from these sections were collected during one-week field campaign in 2022 to elucidate taphonomic biases. They consist of 893 megaremaines now stored in the Muséum National d'Histoire Naturelle in Paris (France). Four plant-bearing beds and 271 specimens from the Saint-Hippolyte-de-Caton section were studied (Supplementary Table S1), of which 225 specimens corresponded to beds SHC. 1, 3 and 4 and 46 specimens to bed SHC.2. One plant-bearing bed and 445 specimens from the Saint-Jean-de-Ceyrargues section (Supplementary Table S2) and 174 specimens from one plant-bearing bed from the Saint-Jean-de-Maruéjols-et-Avéjan section (Supplementary Table S3) were also analysed.

Semi quantitative taphonomic data were obtained from leaf assemblages of selected leaf beds. However, comminuted plant debris and fossil-species represented by an insufficient number of specimens (1% of the total assemblage) were only considered from a qualitative viewpoint. The main taphonomic features considered were the size of leaves and shoots, their orientation and the type and degree of plant organ preservation and completeness.

### 4. Geological setting

The study area is located SE of the French Massif Central, close to



**Fig. 1.** Most important genera in the historical plant collection from the Alès Basin. A: *Tetrclinis articulata* winged seed. B: *Lygodium gaudini* pinnule. C: Palm stipe fragment. D: Palm leaf. E: *Limnobiophyllum*-like leaf (16,773.2). F: *Ailanthus prisca* seed (16,773.297). G: *Comptonia difformis* leaf (16,773.385) H: *Populus gaudini* leaf (16,773.160). I: *Zizyphus paradisiaca* leaf (16,773.68). J: *Rhamnus aizoon* leaf (16,773.214).

Alès (Gard, Occitanie, France), and belongs to the Palaeogene lacustrine system of Alès-St. Chaptès-Issirac (ASCI), which consists of three narrow, elongated basins (Fig. 2A). The largest corresponds to the Alès Basin, which is 55 km long and 6 km wide and runs in a NE-SW direction. The other two basins are located E to SE from the former and are almost perpendicular to it. They correspond to the Issirac Basin (ca 15 km long and 5 km wide) located NE of the lacustrine system, and the Saint-Chaptès Basin (ca. 25 long and 10 km wide) located to the SE (Sanchis and Séranne, 2000).

Recent studies have reassessed the tectonic setting of the Priabonian Languedoc basins and concluded that they resulted from left-lateral strike-slip movements of the Cévennes and Nîmes major regional faults, thus encompassing both the Western European Rift System extension (ECRIS) and the still active N-S shortening of the Central and Western Pyrenees (Séranne et al., 2021). The resulting structure of the Alès Basin is a half-graben with an associated hanging wall rollover controlled by the Alès listric fault (Sanchis and Séranne, 2000). In the Saint-Chaptès and Issirac basins, and on the eastern margin of the Alès

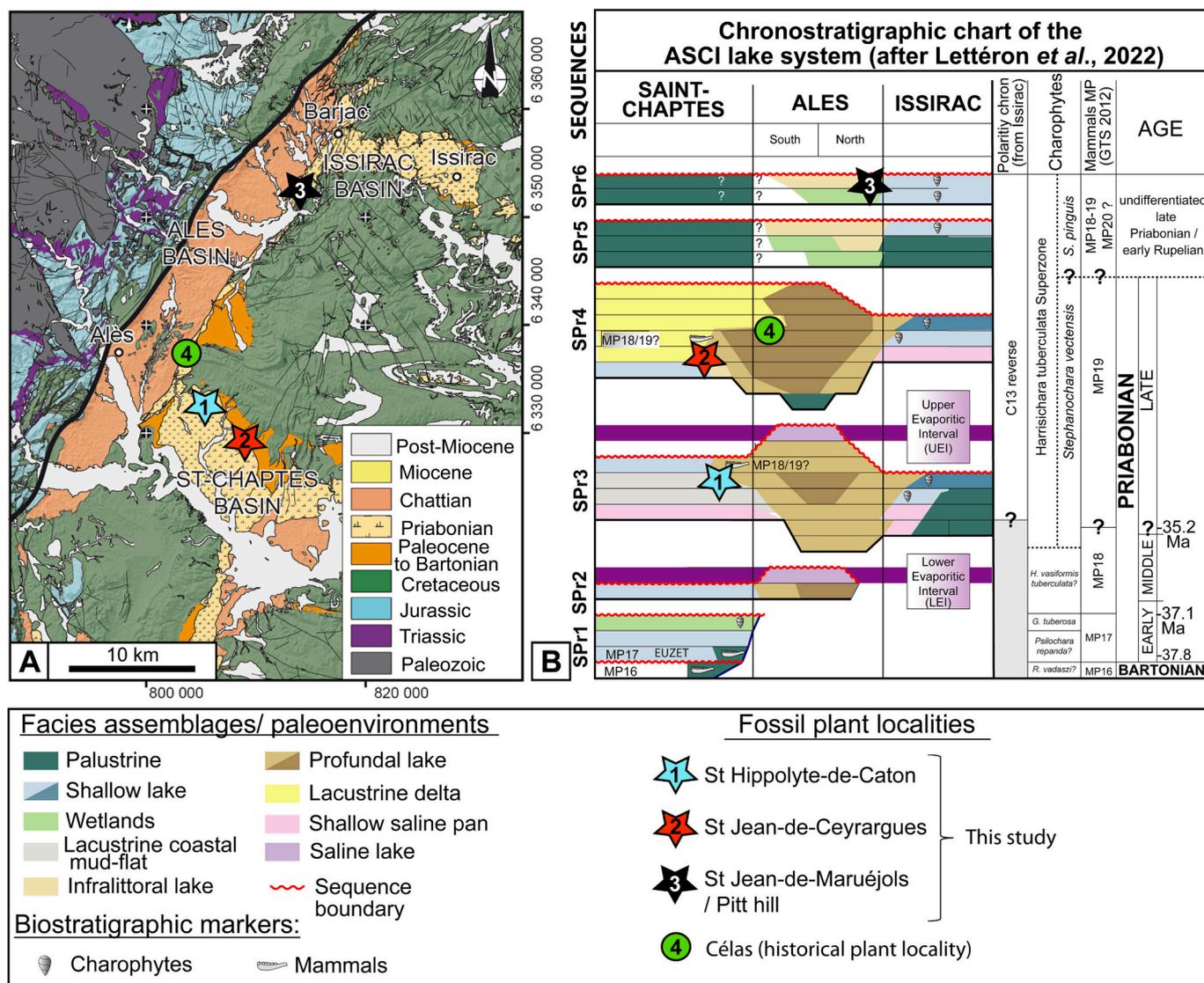


Fig. 2. Geological setting. A Geological map of the study area. B Lithostratigraphic diagram of the formations studied. Modified from Lettéron et al. (2022).

Basin, palustrine to shallow lacustrine deposits accumulated and are well exposed (Lettéron et al., 2017, 2018). In contrast, the lake depocentre, located along the Alès fault, is only accessible through cores in the Alès Basin (Lettéron et al., 2022).

The Priabonian deposits of ASCI have been exhaustively studied by Lettéron et al. (2017, 2018, 2022), who subdivided them into six parasequences (SPr1 to SPr6) separated by unconformities and interpreted as transgressive-regressive cycles. The Saint-Hippolyte-de-Caton and Saint-Jean-de-Ceyrargues fossil plant localities are situated in stratigraphic sequences SPr3 and SPr4 of the Saint-Chaptes Basin respectively, while the Saint-Jean-de-Maruéjols-et-Avéjan site is located on the north-eastern margin of the Alès Basin, representing the SPr6 sequence (Lettéron et al., 2017, 2018).

The age of the Priabonian deposits containing the palaeobotanical localities studied here is well constrained based on vertebrate (Remy, 1994, 1999, 2015) and charophyte biostratigraphy (Feist-Castel, 1971; Lettéron et al., 2017) and magnetostratigraphic analyses (Lettéron et al., 2022). The results indicate that the flora from Saint-Hippolyte-de-Caton (SPr 3 sequence) is 35.4–34.8 Ma old; the flora from Saint-Jean-de-Ceyrargues (SPr4 sequence) was deposited 34.4–34 Ma ago and the Saint-Jean-de-Maruéjols-et-Avéjan flora (SPr6 sequence) is 34–33.8 Ma old (Fig. 2B).

## 5. Results

Integration of sedimentological and taphonomic analyses carried out at Saint-Hippolyte-de-Caton, Saint-Jean-de-Ceyrargues and Saint-Jean-de-Maruéjols-et-Avéjan has made it possible to propose a testable hypothesis regarding plant distribution in the Alès and Saint-Chaptes basins during the Priabonian. The facies and facies association features are summarised below, and more details are given in Table 2.

### 5.1. Facies, facies associations and depositional model

#### 5.1.1. Saint-Hippolyte-de-Caton

Six facies and facies associations were recognised (Fig. 3, Table 2):

**Facies 1 description.** Brownish-ochre silts with plane-parallel lamination and devoid of plant remains (Fig. 4A). The silts from the upper part of the succession are massive and rich in brackish bivalves (Table 2).

**Interpretation.** The brownish silts were interpreted by Lettéron et al. (2018) as deposited by decantation into a very shallow, oxygenated brackish environment. The occasional preservation of lamination suggests that anoxia occurred locally in the water-sediment interface and below, hindering the development of infauna. In contrast, the massive beds from the upper part of the succession were intensively bioturbated by benthic invertebrates such as bivalves.

**Table 2**  
Summary of the facies described in the Priabonian of the Alès and Saint-Chaptes basins.

Facies	Code	Description	Interpretation	Parasequence ( Lettéron et al., 2022)	Locality
Brownish-ochre silts	F1	Brownish-ochre silts 0.2–2 m thick with locally plane-parallel lamination. At top, massive silts rich in the brackish bivalve <i>Polymesoda</i> .	Suspended load deposited by decantation in a shallow lacustrine environment with oxygenated bottom conditions. Local lamination suggests anoxic water-sediment interface. Massive beds from the upper part of the sequence are intensely bioturbated.	Upper part of the regressive parasequence SPr3	Saint-Hippolyte-de-Caton
Finely laminated beige argillaceous limestones	F2	Beige argillaceous limestones 0.5–1.5 m thick, ca. 100 m lateral extension. Millimetre-thin undulated lamination. Alternating horizons of light and dark brown limestones. Bed surface with irregular polygons. Abundant gastropods, i.e. <i>Potamides</i>	Finely undulated lamination attributed to cyanobacterial mats (stromatolites) probably growing in shore lake areas. Water table was oxygenated and brackish conditions as indicated the benthic fauna.		
Pale grey limestones or argillaceous limestones	F3	Pale grey tabular limestones or argillaceous limestones 0.20–1.5 m thick. Base with packstone-wackestone fabrics. Abundant brackish molluscs ( <i>Polymesoda</i> sp. <i>Potamides</i> sp.) and ostracods. Top limestones with mudstone-wackestone fabrics, 5–10 cm thick and plane parallel lamination. Scarce molluscs and ostracods.	Massive limestones rich in infaunal-epifaunal organisms indicates shallow oxygenated lake. Laminated limestones at top indicate anoxia in sediment-water interface.		
Beige grainstone limestones	F4	Beige tabular grainstone limestones 0.2 m thick. Low-angle cross stratification. Well-sorted peloidal/oncoidal grains (1–3 mm across). Intraclasts, 2–3 cm across.	Energetic nearshore lake. Intraclasts represent reworking of the lake bottom deposits after compaction.		
Dark grey silts	F5	Dark grey silts 0.5–1 m thick grading to clays with plane-parallel lamination. Occasionally, lignite horizons (0.5 cm thick) without rootlet marks at top.	Deposition by suspended load in a lake ( Lettéron et al., 2018). Plane-parallel lamination indicates oxygen-poor conditions. Lignites devoid of root marks at the base represent detrital accumulation of plant remains.		
Brownish-black silts, silty clays and clays	F6	2 m-thick brownish-black silts, silty clays and clays with plane-parallel lamination with a lateral extension of 100 m.	Sedimentation by decantation in an oxygen-poor lake with high content in organic matter	Lower part of SPPr4 parasequence	Saint-Maurice-de-Cazeville
Sandstones with sigmoidal large-order stratification	F7	Orange medium to coarse grained sandstones 0.50–1.5 m thick, sigmoidal stratification and planar cross bedding. Laterally passes to coarse-grained sandstones with symmetric ripples covered by grey silts (15 cm thick)	Unidirectional low-medium energetic flows probably corresponding to river mouth areas at the lake margins.		Saint-Jean-de-Ceyrargues and Saint-Maurice-de-Cazeville
Laminated argillaceous and bituminous limestones	F8	Grey to beige tabular, laminated argillaceous and bituminous limestones (5–10 cm thick), rich in brackish molluscs and ostracods.	Deposition in moderately deep lake with anoxia in the sediment-water interface allowing for the preservation of bituminous organic matter.	Upper part of SPPr 6 parasequence	Saint-Jean-de-Maruéjols-et-Avéjan

**Facies 2 description.** Beige argillaceous, finely-laminated limestones. Millimetre-thin undulating lamination shows alternating horizons of light and dark brown limestones (Table 2). The bed surface shows irregular polygons (Fig. 4B). This facies contains abundant megaplant remains that were studied in bed SHC. 2, palynomorphs (Semmani et al., 2023), brackish fishes and gastropods, as well as insects (Lettéron et al., 2018).

**Interpretation.** This facies is attributed to the growth of planar stromatolites (Lettéron et al., 2018), which commonly occur in the shallowest areas of the lake shore (Dean and Fouch, 1983). Microbial biofilms may have trapped the plant remains and other organisms deposited on the lake bottom, sealing them under poorly oxygenated conditions (e.g. Guerrero et al., 2016). The polygonal shape of the bed surface is characteristic of biofilms growing under space-limited conditions (e.g. Lokier et al., 2017). The composition of the water was brackish and oxygenated as indicated by the ochre sediment colour and the occurrence of brackish epifaunal organisms (Table 2).

**Facies 3 description.** Pale grey limestones or argillaceous limestones of variable thicknesses and fabrics (Fig. 4C), but consistently rich in ostracod carapaces (Fig. 4D), gastropods (Fig. 4E) and bivalves, including brackish genera (Table 2). The base of these limestones is massive, displays packstone-wackestone fabrics and contains scarce plant remains, while towards the top the fabrics changes to mudstone-wackestone, the bed displays plane-parallel lamination and contains abundant plant remains (plant beds SHC-1, 3 and 4), insects and fishes.

**Interpretation.** The two types of limestones indicate opposite lake bottom conditions as regards oxygenation. Massive limestones at the base indicate significant biogenic activity on well-oxygenated lake bottoms, while finer-grained fabrics and the preservation of lamination at the top suggest anoxia at the sediment-water interface. The water salinity would remain constantly brackish. This frequent association of the two types of limestone is compatible with deposition in a deepening-upwards shallow lake, according to the Platt and Wright (1991) sedimentary model.

**Facies 4 description.** Beige grainstone limestone beds with a tabular shape and low-angle cross-stratification. The grains are spheroidal (1–3 mm across), well sorted and predominantly internally laminated, corresponding to small oncoids or peloids (Fig. 4F, Table 2). Intraclasts and comminuted plant debris occasionally occur (Table 2).

**Interpretation.** Grainstone fabrics, low-angle cross-stratification and the well-sorted spheroidal shape of the oncoids and peloids indicate relatively high hydrodynamism in a lacustrine context (Platt and Wright, 1991). Grainstone facies may dominate the nearshore of low-gradient lake margins (Clausing, 1990; Arp, 1995). Intraclasts indicate reworking of the lake bottom deposits after compaction and subaerial exposure (Freytet and Plaziat, 1982).

**Facies 5 description.** Dark grey silts that pass vertically to clays. They display plane-parallel lamination and are devoid of plant remains. Locally, lignite horizons without rootlet marks at the base occur (Table 2).

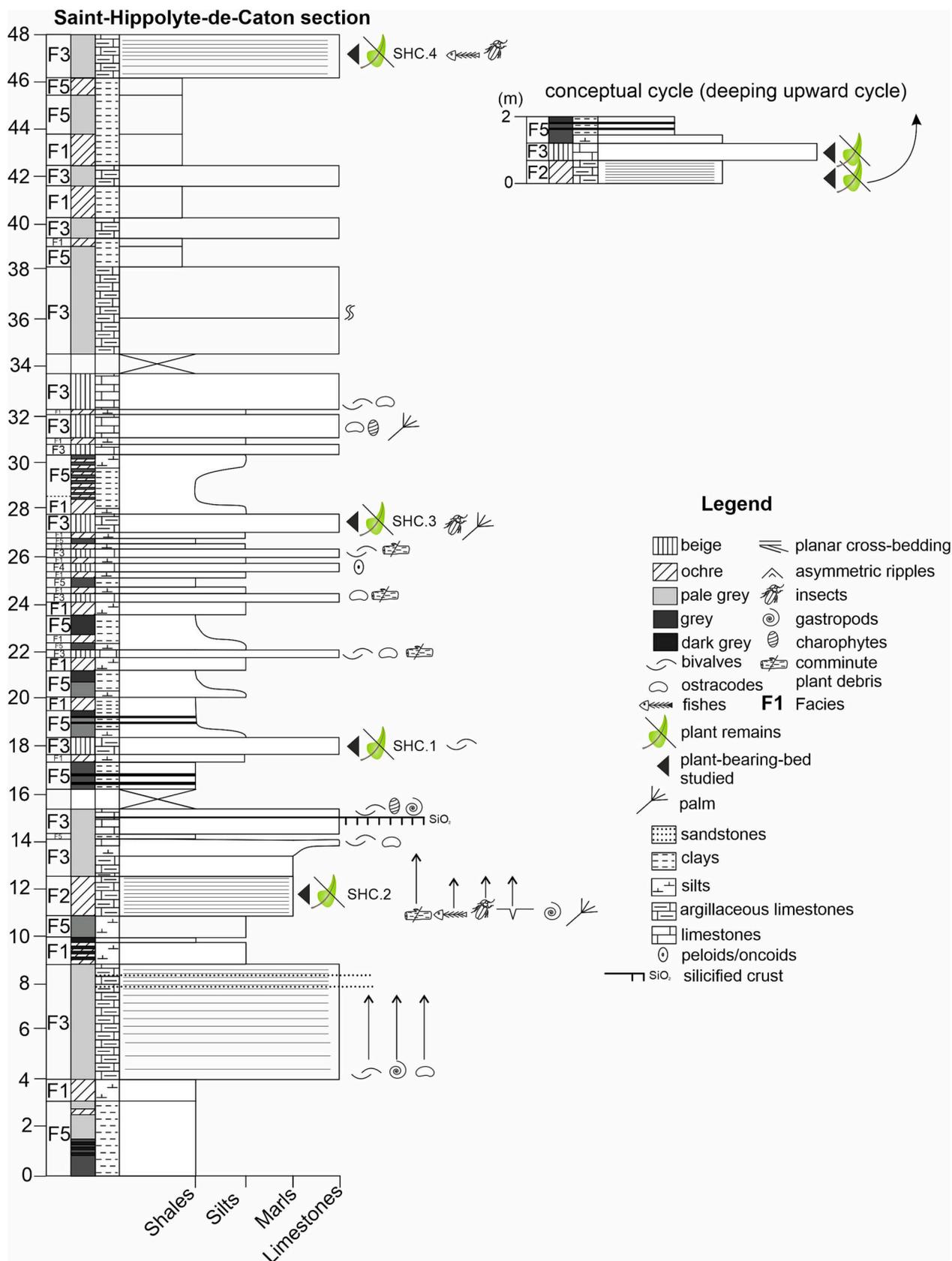


Fig. 3. Stratigraphic section of Saint-Hippolyte-de-Caton with the position of the plant beds studied.



**Fig. 4.** Lithofacies from the Alès and Saint Chaptes basins. A to F are facies described from Saint-Hippolyte-de-Caton, G corresponds to north of Saint-Maurice-de-Cazevielle and H Saint-Jean-de-Maruéjols-et-Avéjan. A: Laminated brownish silts and clays from facies 1. B: Surface of argillaceous limestones showing irregular polygons (facies 2). C: Argillaceous pale grey limestones (facies 3). D: Ostracod from facies 3 (SHC.1.X). E: Gastropod from facies 3 (SHC.1.2). F: Peloidal/oncolidal grainstone, facies 5 (SHC.5). G: Coarse- to medium-grained orange sandstones, epsilon cross-stratification and cross-bedding from facies 7. H: Bituminous grey marlstones from facies 8. Hammer for scale: 28 cm.

*Interpretation.* Silts and clays represent deposition of suspended load in the lake (Lettéron et al., 2018). The dark grey colour together with the preserved plane-parallel lamination indicate significant organic matter accumulation on an oxygen-poor lake bottom (Table 2). The absence of root marks at the base of lignite horizons suggests that an allochthonous detrital accumulation of plant remains formed a peat precursor of lignite.

*5.1.1.1. Depositional model of Saint-Hippolyte-de-Caton.* The facies described are vertically organised following the succession of (1) brownish-ochre silts (facies 1) or stromatolitic argillaceous limestones rich in plant remains (facies 2; plant bed SHC-2) at the base; (2) argillaceous limestone with plant remains (plant beds SHC-1, SHC-3 and SHC-4) and brackish benthic molluscs (facies 3) in the middle. Sporadically, this environment was affected by currents allowing the deposition

of peloidal/oncoidal grainstones (facies 4). The succession is topped (3) by laminated dark grey silts and clays with occasional intercalations of detritic lignite (facies 5), indicating anoxic lake bottoms and a relatively deeper lake. The sedimentary cycle of 0.5–1.5 m thickness recognised here represents a deepening-upwards cycle of a lake, which is consistent with the stacking pattern of the entire sequence SP3, related to a transgressive sedimentary cycle (Lettéron et al., 2022).

### 5.1.2. Saint-Jean-de-Ceyrargues

The section studied belongs to the Célas Sandstone Formation (Fig. 5) and is complemented by the Saint-Maurice-de-Cazeville outcrop, with laterally equivalent facies (Fig. 4G). Based on the notes made by Laurent (1899), these sections correspond to the area where the historical plant collection from Célas was obtained, now housed in the Natural History Museum in Marseille. The lower part of the unit is better developed at Saint-Maurice-de-Cazeville, while its upper part crops better at Saint-Jean-de-Ceyrargues. Two lithofacies are recognised:

**Facies 6 description:** Brownish-black silts and silty clays and clays with plane-parallel lamination. This facies is rich in well-sorted comminute plant debris but is devoid of identifiable megaplant remains.

**Interpretation.** Silts and silty clays were deposited by decantation of suspended load at a lake margin (Lettéron et al., 2018). The dark colour indicates high organic matter input. The well-sorted comminute plant debris suggests that it was transported by low-energy flows and eventually deposited on the lake margin.

**Facies 7 description:** Medium-grained, orange sandstone beds with sigmoidal large-order stratification forming angles of 15° – 20° with the base (Fig. 4G). These bodies display planar cross-bedding, contain abundant comminute plant debris and are topped by thin beds of grey silts. Laterally and vertically, this facies passes to medium- to coarse-grained orange sandstones with symmetric ripple lamination and abundant plant remains at the top, including the plant bed studied at Saint-Jean-de-Ceyrargues.

**Interpretation:** The sandstone beds represent low to medium unidirectional energetic flows in fluvial channels or river mouth areas at the lake margins (e.g. Pollard et al., 1982; Olariu et al., 2021). This succession was attributed by Lettéron et al. (2018) to a perennial sub-aqueous environment belonging to a lake margin area close to a fluvial inlet.

**5.1.2.1. Depositional model of Saint-Jean-de-Ceyrargues.** The entire succession of the Célas Sandstone Formation studied at Saint-Jean-de-Ceyrargues and Saint-Maurice-de-Cazeville follows a coarsening-upwards trend. The finest-grained deposits are limited to Saint-Maurice-de-Cazeville (facies 6) and represent the deposition of mud and organic matter in a shallow lake environment. Northwards, at Saint-Jean-de-Ceyrargues, these beds are laterally equivalent to facies 7, showing an upwards increase in grain size of sigmoidal sandy beds that may correspond to the mouth bar deposits of a fluvial delta prograding northwards (Lettéron et al., 2022).

### 5.1.3. Saint-Jean-de-Maruéjols-et-Avéjan

Saint-Jean-de-Maruéjols-et-Avéjan outcrop is a well-known asphalt mine. The section is composed of a single facies (Fig. 4H).

**Facies 8:** Grey to beige well-laminated argillaceous and bituminous marl with tabular stratification, rich in bivalves, ostracods, gastropods and plant remains.

**Interpretation.** Laminated strata correspond to deposition in moderately deep lacustrine environments, with limited disruption by waves (e.g. Anadón et al., 1989; Norsted et al., 2015). The lake bottom would have been relatively well-oxygenated, permitting the biogenic activity of epibenthic fauna. However, the sediment-water interface would have been anoxic, allowing for the preservation of organic matter.

## 5.2. Plant taphonomic analyses

### 5.2.1. Saint-Hippolyte-de-Caton

Three of the plant beds studied here (SHC.1,3,4) belong to beige argillaceous limestones of facies 3, which Lettéron et al. (2018) interpreted as having been deposited in a shallow brackish lake, while one plant bed (SHC.2) belongs to finely-laminated argillaceous limestones related to the growth of microbial mats (facies 2).

#### 1) Plant taphonomy in beige argillaceous limestones (Facies 3)

**Description.** Most of the plant remains correspond to reed stems, i.e. *Typha* sp., *Phragmites* sp. and rarely *Equisetum* sp. (Table 3). Also abundant are the well-articulated shoots of *Doliosstrobilus taxiformis* (Fig. 6A), in association with isolated but well-preserved bract scales of ovuliferous cones attributed to the same fossil-species (Table 3, Fig. 6B). These plant beds also contain complete but isolated pinnules of *Osmunda* aff. *parschlugiana* Unger and *Pronephrium stiriacum* (Unger) Erw. Knobloch et Kvaček (Fig. 6C) and terrestrial angiosperm leaves characterised by whole *Myrica* sp. and *Comptonia difformis* leaves, isolated Fabaceae leaflets (Table 3), *Daphnogene* Unger leaves with damaged margins and torn *Byttneriopsis* sp. leaves. Aquatic angiosperms are represented by *Nymphaea* L. leaves and rhizomes (Fig. 6D, E respectively). Comminute plant debris and seeds are locally abundant. Rarely, slightly damaged *Sabal major* Unger palm leaves (Fig. 6F) and inflorescence axes (Fig. 6G) presumably belonging to the same fossil-species occur in the assemblage

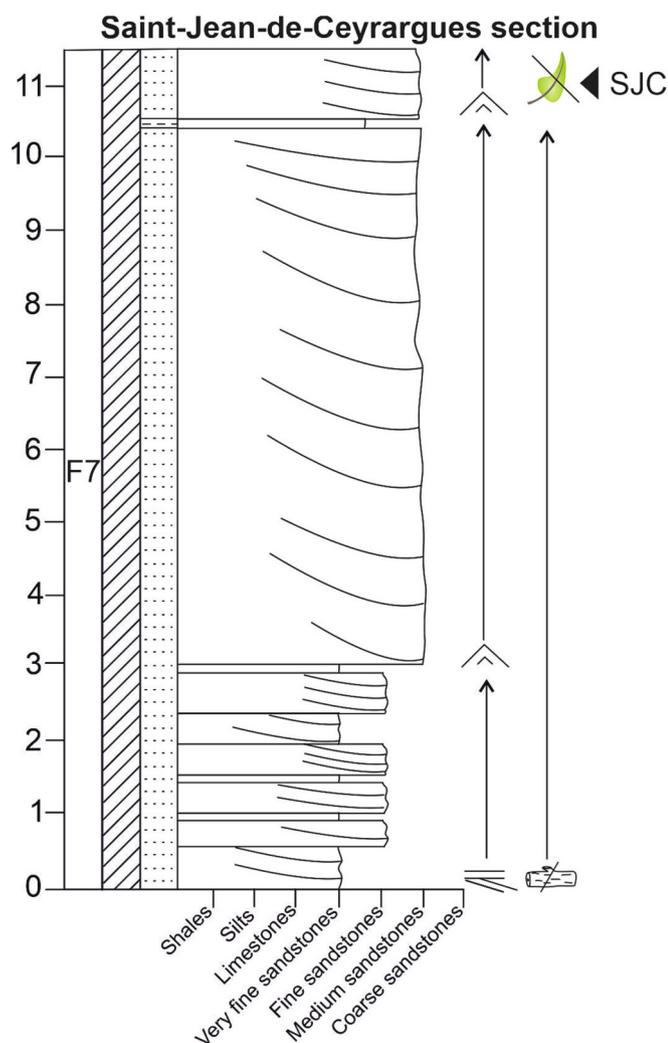


Fig. 5. Stratigraphic section of Saint-Jean-de-Ceyrargues with the position of the plant bed studied. Legend as in Fig. 4.

**Table 3**  
Main plant taphonomic features from the leaf beds studied in the Alès and Saint-Chaptes basins.

Lithofacies	Interpretation of depositional setting	Locality	Plant taphonomy	Palaeoecological interpretation
Beige argillaceous limestones (Facies 3)	Shallow lake	Saint-Hippolyte-de-Caton	17–48% stems of reeds, up to 13 cm long. 16%, fern pinnules (3.5–9 cm long), whole leaves of <i>Myrica</i> (2–7 cm long), damaged leaves of <i>Daphnogene</i> and <i>Comptonia</i> and torn leaves of <i>Byttneriopsis</i> . 12%, whole leaves and rhizomes of <i>Nymphaea</i> . 9–10.5%, articulated shoots of <i>D. taxiformis</i> up to 18 cm long. 4% <i>D. taxiformis</i> ovuliferous bract-scales. Rare leaves of <i>Sabal major</i> and inflorescence axes, comminute plant debris (1–3 mm long) and seeds (1–2 mm across)	Autochthonous <i>Nymphaea</i> . Parautochthonous, ferns, <i>D. taxiformis</i> , reeds, <i>Sabal major</i> , Lauraceae and Myricaceae Allochthonous <i>Byttneriopsis</i> and Fabales comminute plant debris and seeds
Finely laminated limestones with alternating light and dark brown horizons (Facies 2)	Shallow lake with microbial mats	Saint-Hippolyte-de-Caton	28% of the assemblage articulated shoots and ovuliferous bract-scales of <i>Doliosstrobos</i> . 12% stems of reeds 20–30 cm long with the rootlets still attached. 12% leaves and rhizomes (0.3–4.5 cm long) of <i>Nymphaea</i> . 9% whole leaves of <i>Myrica</i> sp. and <i>Daphnogene</i> sp. 2–7 cm long and isolated leaflets of Fabales up to 2 cm long. Rare whole fern pinnules and squashed palm leaves	Autochthonous <i>Nymphaea</i> and reeds. Parautochthonous ferns, <i>D. taxiformis</i> , Lauraceae Myricaceae and <i>Sabal major</i> Allochthonous Fabales
Sandstone beds with sigmoidal large-order cross-stratification. Internally asymmetric ripple lamination (Facies 7)	Fluvial inlet channels or river mouth delta lobes	Saint-Jean-de-Ceyrargues	47% torn leaves of <i>Daphnogene</i> , <i>Laurophyllum</i> , <i>Byttneriopsis</i> , reeds and palm leaf hastula. 53% complete leaves of <i>Byttneriopsis</i> , <i>Daphnogene</i> and <i>Laurophyllum</i> (5 to 10 cm long and with the petiole preserved). Rarely, longer <i>Byttneriopsis</i> leaves up to 17 cm long and 5 cm wide occurred. Finely comminute plant debris occur	Parautochthonous to allochthonous <i>Daphnogene</i> , <i>Laurophyllum</i> , <i>Byttneriopsis</i> , reeds. Allochthonous palm remains and comminute plant debris
Bituminous marls (Facies 8)	Relatively deeper lake	Saint-Jean-de-Maruéjols-et-Avéjan	42% <i>D. taxiformis</i> articulated shoots (2–23 cm long) and ovuliferous bract-scales. 3% shoots of <i>Tetraclinis</i> (fragmented) and <i>Sequoia</i> -like species. 9% <i>Daphnogene</i> sp. Leaves, margin damaged, 3% water lily leaves with biodegradation, 4% <i>Zizyphus</i> leaves 4 cm long, and isolate leaflets of Fabales, 2–4 cm long. Rarely whole leaves of <i>Comptonia difformis</i> , 5 m long occur.	Autochthonous-parautochthonous water lilies Parautochthonous <i>D. taxiformis</i> , <i>Sequoia</i> -like plant <i>Comptonia difformis</i> , Allochthonous <i>Tetraclinis</i> , <i>Daphnogene Zizyphus</i> , Fabales

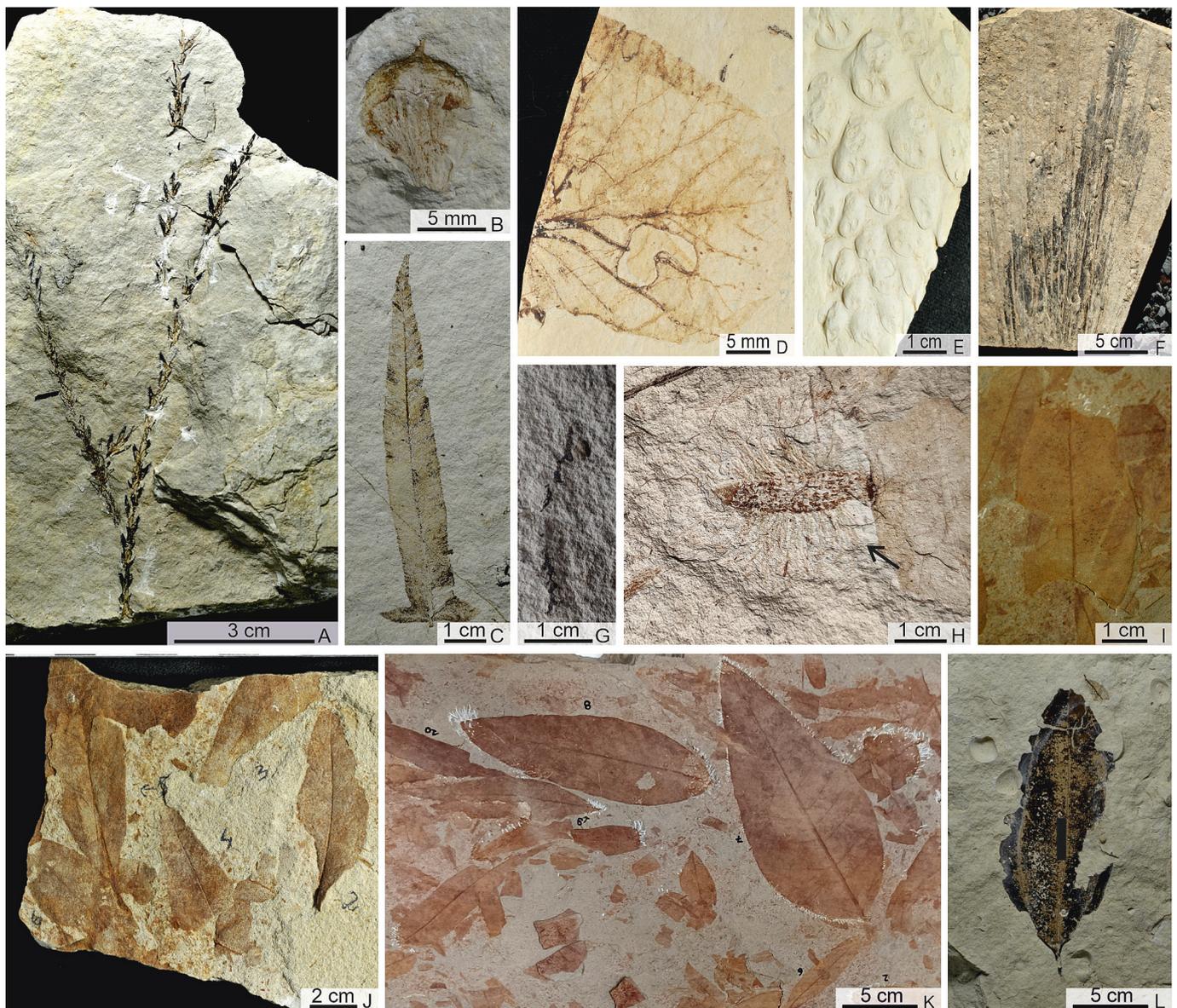
(Table 3).

**Interpretation.** The reed and *Equisetum* sp. stems most probably fell into the lake by natural physiological abscission, forming a parautochthonous assemblage. The well-articulated *D. taxiformis* shoots associated with bract scales would be directly supplied from the plant to the lake, also indicating parautochthony. Water lily rhizomes (*Nymphaea* sp.) indicate in situ burial. Complete delicate pinnules of *Osmunda parshchlugiana* and *Pronephrium stiriacum* suggest minimal transport and direct supply to the lake. As with most of the living ferns, the pinnules remain attached to the plant long after their death and become fragile (Martín-Closas and Gomez, 2004), suggesting that the Priabonian fern species from the Alès Basin were supplied after traumatic loss rather than by physiological abscission. In addition, intact angiosperm *Myrica* sp. leaves without size selection indicate that they were directly supplied to the lake. In contrast, based on the laboratory experiments conducted by Ferguson (1985) and the actotaphonomic observations of Spicer (1981), the damaged leaf margins of *Daphnogene* and *Comptonia difformis* suggest that they were transported by low-energy flow regimes before sinking in the lake, while the torn *Byttneriopsis* leaves suggest a longer and/or a more turbulent flow transport and allochthony. The rare but almost complete coriaceous leaves of *Sabal major* possibly associated with their inflorescence axes suggest that this plant would have grown close to the lake, with a consequently direct supply indicating parautochthony. As with ferns, many palm leaves are not abscised after death, and decay while still attached to the plant; thus, traumatic loss is the most plausible cause in this case, explaining why they are rare in the assemblage. Furthermore, the size sorting of comminute plant debris and small coriaceous seeds indicates long transport by traction in river inlets (e.g. Ferguson, 1985). A different sort of transport is suggested by isolated, size-selected and relatively undamaged Fabaceae leaflets. In accordance with the actotaphonomic observations of Spicer and Wolfe (1987), Gastaldo (1988) and Spicer (1981, 1989), these features would be compatible with wind transport, suggesting allochthony.

## 2) Plant taphonomy in finely-laminated argillaceous limestones (Facies 2)

**Description.** Articulated *Doliosstrobos taxiformis* shoots and well-preserved ovuliferous bract scales prevail in this assemblage, whereas *Doliosstrobos* cones are rarer (Table 3). Associated with *Doliosstrobos*, stems and rhizomes with the delicate rootlets attached of reeds may locally be abundant (Fig. 6H, Table 3). Also significant in the assemblage are whole leaves and rhizomes bearing numerous adventitious root scars of *Nymphaea* (Table 3). Whole leaves of woody dicotyledonous plants (*Myrica* sp., Lauraceae including *Daphnogene* sp.) and isolated complete Fabaceae leaflets also occur in a lower proportion (Table 3). More rarely, damaged apical areas of *Sabal major* leaves and complete fern pinnules occur.

**Interpretation.** The occurrence of rhizomes of reeds with the fragile roots still attached, associated with water lily rhizomes, indicate null transport, and therefore these form an autochthonous assemblage. Production of abundant and complete *D. taxiformis* shoots may result from a similar ecological behaviour to some recent Araucariaceae, such as *Agathis australis* (D. Don) Loudon, which loses complete shoots under adverse conditions (Wilson et al., 1998). Bract scales of ovuliferous cones related to the same fossil-species would have been abscised at maturity, as suggested by Tanrattana et al. (2020). Thus, the different plant organs of *D. taxiformis* would be directly supplied from the plant to the lake, again indicating parautochthony. The whole, non-size-selected leaves from Lauraceae and Myricaceae found in this bed indicate a direct supply to the lake by gravitational fall, suggesting that they were parautochthonous. Parautochthony is also suggested for the whole fern pinnules supplied to the lake following trauma and for the damaged coriaceous leaves of *Sabal major*. The isolated and presumably size-selected Fabaceae leaflets indicate that they were blown off and eventually deposited in the shallow marginal lake area as allochthonous elements.



**Fig. 6.** Taphonomic features of the plant assemblages studied. A: Articulated *Doliostrubus taxiformis* shoot from Saint-Hippolyte-de-Caton, plant bed SHC. 1 (SHC.4). B: Isolated *Doliostrubus* bract scale from Saint-Hippolyte-de-Caton, plant bed SHC. 1 (SHC.2.2022). C: Whole *Osmunda* aff. *pardschlugiana* pinnule from Saint-Hippolyte-de-Caton, plant bed SHC. 2 (SHC. 17). D: *Nymphaea* leaf from plant bed SHC. 4 (SHC.4.5). E: *Nymphaea* rhizome bearing adventitious root scars, plant bed SHC. 1 (SHC.9.2). F: An almost complete palm leaf from Saint-Hippolyte-de-Caton that shows a partial biodegradation of costal tips, suggesting drying and biodegradation while still attached to the stipe (field picture). G: inflorescence axes of a palm from Saint-Hippolyte-de-Caton, plant bed SHC. 3 (SHC.3.2022.51). H: Roots still attached to a reed rhizome from Saint-Hippolyte-de-Caton, plant bed SHC. 2 (SHC.3.41a.2022). I: Broken leaf of *Byttneriopsis* from Saint-Jean-de-Ceyrargues (field picture). J: Torn Lauraceae leaves and other undetermined angiosperms from Saint-Jean-de-Ceyrargues (SJC.62). K: Whole, long *Byttneriopsis* leaves from Saint-Jean-de-Ceyrargues (field picture). L: Torn Lauraceae leaf from Saint-Jean-de-Marujols-et-Avéjan (SJM.44).

### 5.2.2. Plant taphonomy at Saint-Jean-de-Ceyrargues (facies 7)

**Description.** The plant bed studied belongs to coarse sandstones of facies 7, interpreted as fluvial inlets or river mouth areas at the lake margins. Most of the plant remains are poorly preserved and only 40% of the leaves could be determined. These belong to *Daphnogene* sp., *Laurophyllum* sp., *Byttneriopsis* sp., reed stems, *Doliostrubus taxiformis* and *Sabal major* palm leaves. From the taphonomic viewpoint, almost half of the specimens of *Daphnogene*, *Laurophyllum*, *Byttneriopsis* and reed stems are torn (Table 3, Figs. 6I–J). A higher degree of fragmentation is observed in the palm leaves, which only preserve their lignified base (hastula). In contrast, the other half of the assemblage corresponds to complete leaves from *Byttneriopsis*, *Daphnogene* and *Laurophyllum* (Table 3). Rarely, longer *Byttneriopsis* leaves up to 17 cm long (Fig. 6K) and comminuted plant debris occur (Table 3).

**Interpretation.** The significant fragmentation of many *Daphnogene*, *Laurophyllum* and *Byttneriopsis* leaves, reed stems and palm leaves indicates transport by turbulent water flows before sinking, as demonstrated experimentally with dicot leaves by Ferguson (1985) and observed in the nature Spicer and Wolfe (1987) and Spicer (1981, 1989). In addition, the plant remains underwent prolonged traction transport until becoming comminuted. An allochthonous occurrence of these remains is compatible with the energetic deltaic environment proposed for the plant bed. This contrasts with a few complete and well-preserved *Daphnogene*, *Laurophyllum* and *Byttneriopsis* leaves, suggesting direct supply to the delta mouth bars from the surrounding vegetation. This is especially evident for the long, whole *Byttneriopsis* leaves. Similar taphonomic features were noted by Spicer (1981) in the extant Silwood Park lacustrine delta (England) or by Gastaldo et al. (1987) in a

Holocene delta in Alabama (USA). Based on these field observations, only the complete leaves found at Saint-Jean-de-Ceyrargues would constitute a parautochthonous assemblage.

5.2.3. Plant taphonomy at Saint-Jean-de-Maruéjols-et-Avéjan (facies 8)

**Description.** The plant assemblage found in the bituminous marl of facies 8 is dominated by *Doliosrobis taxiformis*, represented by shoots and ovuliferous bract scales. A few shoots from a *Sequoia*-like plant are also recognised. The conifer shoots are generally articulated but some leaves are often missing. *Tetraclinis* Mast. remains are rare and composed of a few whorls (Table 3). Angiosperms are mainly represented by *Daphnogene* sp. leaves and in a lower proportion by *Nymphaea* rhizomes and leaves. The blade margin of most of the *Daphnogene* sp. leaves is damaged (Fig. 6L). Moreover, the water lily leaves show evidence of biodegradation i.e., rounded small holes and some areas with skeletonization. Rarely, whole *Comptonia difformis* leaves, small *Zizyphus* leaves and isolated Fabaceae leaflets occur.

**Interpretation.** The well-articulated *Doliosrobis taxiformis* shoots and isolated bract scales from the same plant found in the plant bed suggest that they fell directly into the lake. Some leaves from the *Sequoia*-like shoots are missing, which suggests they were transported before sinking

in the lake. The water lily leaves probably degraded in situ before sinking. In contrast, angular breaks in the angiosperm laminas in *Daphnogene* sp. and other undetermined angiosperm fossil-species indicate significant mechanical fragmentation during fluvial transport, forming part of the allochthonous assemblage. *Tetraclinis* shoots are rare and consist of a low number of whorls. This contrasts with the well-articulated specimens from the same genus found in some coeval plant localities in France and Hungary (e.g. Kvaček et al., 2000), suggesting a significant disarticulation of these remains in the Alès Basin. Therefore, *Tetraclinis* remains probably underwent longer transport before reaching the lake, forming part of the allochthonous assemblage. Lastly, the small size of the *Zizyphus* leaves contrasts with the longer leaves (7 cm long) of the same genus in the historical plant collection. Field investigations by Spicer (1981) showed that the wind can transport the lightest and smallest plant leaves for relatively long distances. The biased size of the *Zizyphus* leaves from the plant bed studied here strongly suggests this sort of transport, which indicates allochthony. The complete, small Fabaceae leaflets from the plant assemblage may also be the result of air dispersal before reaching the lake.

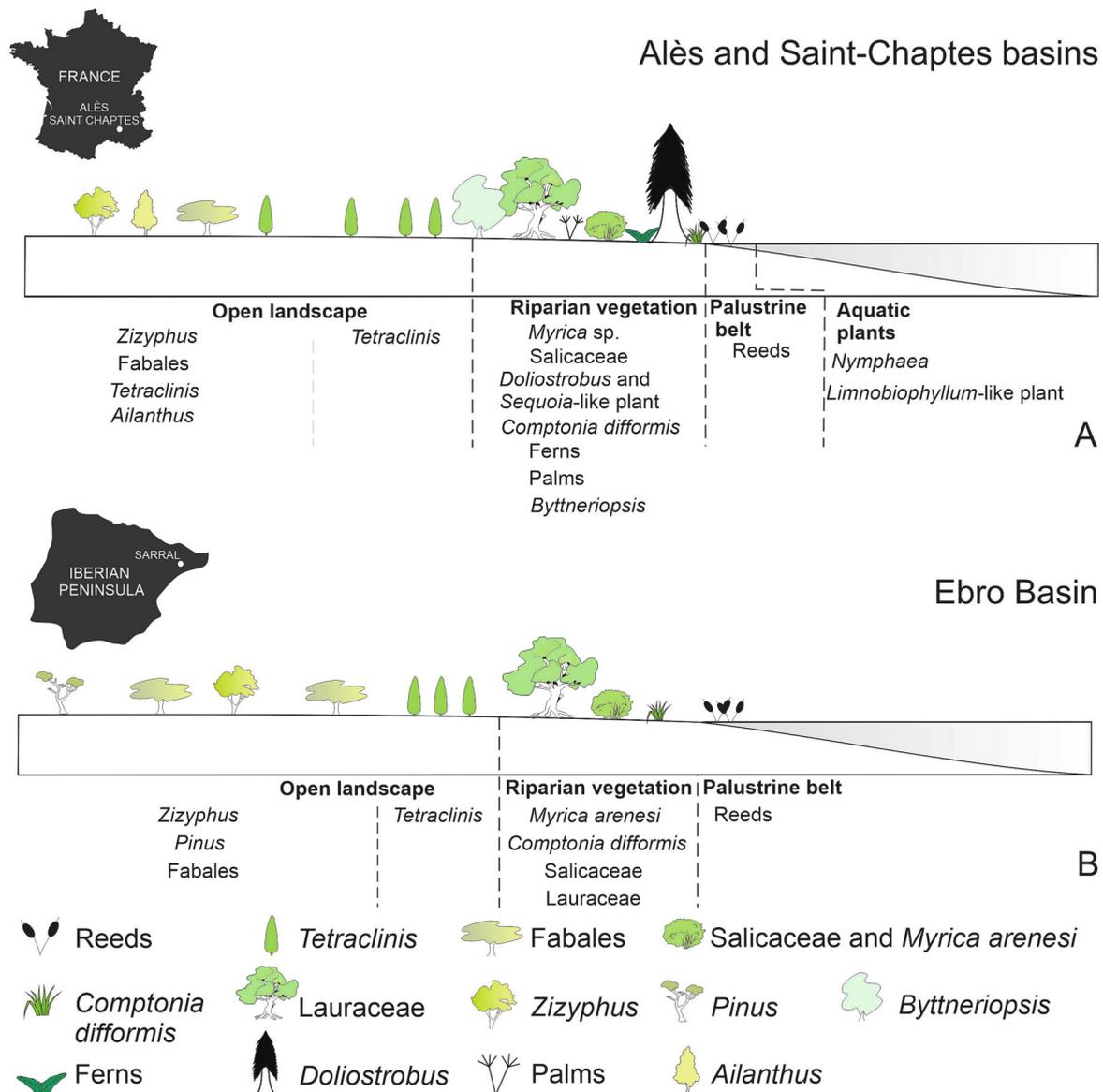


Fig. 7. Comparison of vegetation belts in the late Eocene in (A) the Alès and Saint-Chaptes basins and (B) Sarral, Ebro Basin.

## 6. Discussion

### 6.1. Palaeoenvironmental reconstruction of the late Eocene flora of the Saint-Chaptes and Alès basins

The sedimentological study revealed that two depositional environments in the Saint-Chaptes and Alès basins allowed for plant preservation: a lacustrine environment has been interpreted for the outcrops studied at the Saint-Hippolyte-de-Caton and Saint-Jean-de-Maruéjols-et-Avéjan sites, whereas a deltaic environment has been interpreted for the plant beds studied at Saint-Jean-de-Ceyrargues. Fossil-species composition in the two settings varies in some respects, but this can be explained by taphonomic processes. When combined, the sedimentological and plant taphonomic data distinguish five vegetation belts (Fig. 7A):

- Aquatic plants: this plant community was dominated by water lilies (*Nymphaea*), their leaves and rhizomes being frequent remains in the plant beds studied. *Limnobiophyllum*-like leaves occurred in association with water lilies, although this macrophyte was considerably less abundant since it is only known from a single isolated leaf in the historical collection.
- Palustrine belt: Stems of reeds are common in all plant beds studied, especially in the finely-laminated limestones at Saint-Hippolyte-de-Caton (plant bed SHC. 2), where rhizomes occur with the roots still attached, representing the lake margin (Fig. 7A).
- Riparian forest: this assemblage consists of the ferns *Osmunda* aff. *parschlugiana* and *Pronephrium stiriaticum*, angiosperms (i.e. *Comptonia difformis*, *Bytneriopsis*, *Daphnogene* and *Laurophyllum*), palms and conifers (i.e. *Doliosobus taxiformis* and a *Sequoia*-like plant). These plants indicate that ferns and *Comptonia difformis* formed part of the understory, while the remaining assemblage would have formed the canopy.

In riverbank and deltaic facies, the riparian vegetation was mainly composed of Lauraceae (i.e., *Laurophyllum*, *Daphnogene*) and Malvaceae i.e., *Bytneriopsis*. Lauraceae growing close to river margins have also been reported in coeval localities in the Weipfelster Basin in Germany Staré Sedlo in the Czech Republic (Kunzmann et al., 2016) and in the Sarral in Catalonia (Tosal et al., 2018), which suggests that lauraceous plants were recurrent riparian elements in the European Palaeogene. In contrast, *Doliosobus taxiformis* remains are rare and fragmented in fluvial facies, indicating that this plant rarely inhabited watercourses, as noted previously by Kvaček (2002) in Bohemian basins in the Czech Republic. An exception to this rule would be the Weipfelster Basin (Germany), where this plant was interpreted to grow in fluvial environments (Mai and Walther, 2000), suggesting a broadening of its palaeoecological tolerance close to the species extinction.

Open landscape vegetation. Two vegetation belts have been distinguished:

(1) *Tetraclinis* would have dominated an open woodland immediately behind the riparian vegetation, with an indirect supply of remains to the lake. The remains of these plants are rare and fragmentary, but contain several organs from the same plant. Rare *Tetraclinis* shoots found in the Alès Basin can be supplemented with winged seeds and an isolated bract scale from the historical collection. A similar habitat was interpreted in coeval plant localities in Bohemia (Kvaček, 2002) and Catalonia (Tosal et al., 2018).

(2) *Zizyphus* and Fabaceae would represent a small part of the total diversity of a more distal open woodland. The complete but size-biased leaves and leaflets of these plants suggest lengthy wind-borne transport before reaching the lake. *Zizyphus* and Fabaceae populations in the late Eocene of Kučlin, Hungary, would have grown in a similar habitat (Kvaček, 2002). This assemblage may be enriched with *Ailanthus*, only represented by a winged seed, i.e. *Ailanthus prisca* from the historical plant collection (Fig. 1F), suggesting strong selection of an organ

adapted to wind dispersal. This plant community was probably much more diverse, and it is possible that some winged *Tetraclinis* seeds would also have belonged to this community.

### 6.2. Comparison with a previous palaeoecological interpretation of the flora from the Alès and Saint-Chaptes basins

Taphonomic analyses of the plant assemblages revealed that the plants represented five main vegetation belts: an aquatic (hydrophytic) belt, a palustrine belt, a riparian forest and two open woodland belts. Similar vegetation belts were reported by Laurent (1899). Nevertheless, significant differences arise in the location and composition of the plant communities. Based on extant representatives, Laurent (1899) concluded that the riparian belt was composed of *Populus* and *Fraxinus*; however, these genera were not found in the plant beds sampled here, and the specimens in the historical plant collection (one *Populus* leaf and three *Fraxinus* leaves) are not only poorly preserved, but also—in the case of *Fraxinus*—of difficult taxonomic attribution. It seems that these elements were rare and that their leaves only reached the lake under exceptional circumstances.

Laurent (1899) interpretation was that *Bytneriopsis* (that he attributed to *Ficus*) grew behind the riparian vegetation, forming extensive forests. This plant is considered an iconic element of the Alès Basin due to its abundance in the historical collection. However, the results obtained here support the hypothesis that *Bytneriopsis* leaves were only abundant in deltaic facies at Saint-Jean-de-Ceyrargues, which belong to the same terrigenous beds where the historical collection was obtained.

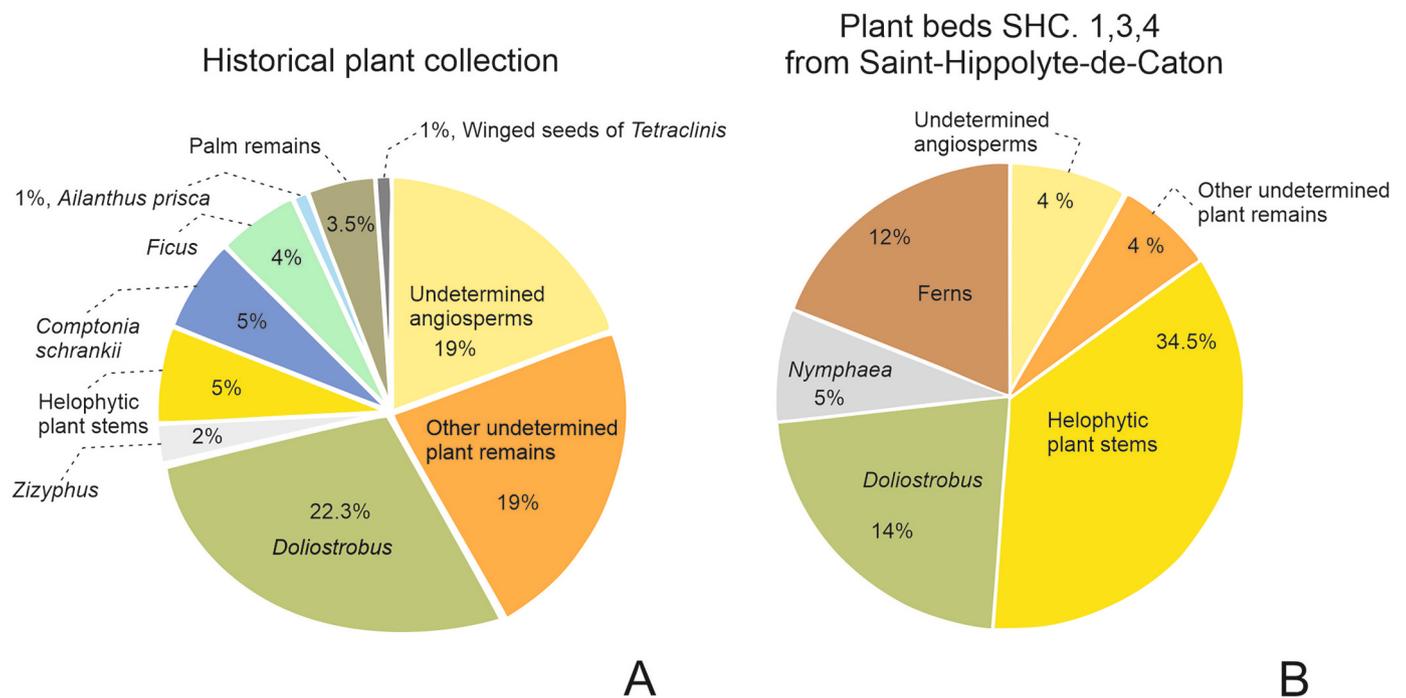
Another difference with previous studies is the habitat of the Lauraceae. Based on Laurent (1899) interpretations, these plants grew in highlands surrounding the basin, as is the case of the well-known present-day laurel forests on the Canary Islands and Madeira (e.g. Florencio et al., 2021). However, this palaeotopographic setting is unrealistic for the latest Eocene Alès Basin, when the closest mountains were located about 200 km north of the study area, in the French Massif Central.

### 6.3. Comparison with the historical plant collection

Most of the 'Célas flora' plant remains that are housed in the historical plant collection in Marseille were collected from facies similar to the argillaceous limestones of Saint-Hippolyte-de-Caton (facies 3). The plant assemblage from the Natural History Museum from Marseille is similar to that obtained after sampling the new plant beds following taphonomic criteria (Fig. 8). Most of the plant remains correspond to *Doliosobus* (31.5%) followed by *Comptonia difformis* (Sternberg) Berry (4.8%), stems of reeds (4%), *Bytneriopsis* leaves (4%), palms (3.5%) and *Zizyphus* Mill. (2%). However, the abundance of each plant group differed in each locality. For instance, in facies similar to those of the historical plant collection sampled at Saint-Hippolyte-de-Caton, *C. difformis* presented a relative abundance of up to 9%, while Fabaceae leaflets ranged from 1–17% of total plant specimens, contrasting with their low percentage in the historical plant collection (<0.5%).

In addition, the historical plant collection contains a highly diverse flora that contrasts with the much poorer assemblages found here, rendering the Célas historical collection very useful for taxonomic studies. However, despite these differences, the assemblages in both collections are dominated by Doliosobaceae, Malvaceae, Myricaceae, Rhamnaceae, Poaceae and Typhaceae, although Areaceae (palms) are abundant in the historical plant collection but not in the assemblage sampled here, and the relative abundance of these families is also slightly different when comparing both collections.

Furthermore, most of the plant remains in the historical plant collection (mainly leaves) are large, complete and well preserved. This contrasts with the plant remains recovered here from Saint-Hippolyte-de-Caton, which show leaf tearing, varying degrees of fragmentation or a broader range of size. This suggests the existence of collection bias (selection of only the larger, best-preserved specimens) when forming



**Fig. 8.** Comparison of relative abundances of the most characteristic plant remains. A Values for the historical ‘Célas’ plant collection. B Average figures for beds SHC 1,3,4 at Saint-Hippolyte-de-Caton.

the historical collection, as is the case for the majority of leaf collections created at the late 19th and early 20th centuries. Said bias is responsible for considerable confusion in Laurent (1899) palaeoecological interpretation.

#### 6.4. Comparison with pollen data from the Alès Basin

Palynological studies by Gruas-Cavagnetto (1973) and Semmani et al. (2023) indicate that conifers were represented by pollen from *Pinus*, *Taxodium*, *Glyptostrobus* and undetermined Taxodiaceae-Cupressaceae genera. Of this group, only *Tetraclinis* and cf. *Sequoia* were recognised in the macroremain assemblage, and Pinaceae was absent. As regards the angiosperm record, the pollen assemblages found by Gruas-Cavagnetto (1973) and Semmani et al. (2023) coincide with the macrofossils in the occurrence of Fabales, mainly Fabaceae, Lauraceae, *Populus*, *Myrica* and *Salix*. Nevertheless, other genera represented in the pollen assemblage, such as *Quercus*, *Palaeocarya*, *Carya* and *Platycarya* are absent in the macrofloral assemblages.

One plausible explanation for these differences is the different pollen production and dispersal capacities of the taxa. Hence, anemophilous plants such as conifers and some angiosperms (e.g. *Quercus*, *Palaeocarya*, *Carya*, *Platycarya*) produce an enormous quantity of pollen, and their pollen grains can be transported dozens of kilometres before being buried, providing a regional signal rather than representing the local flora (e.g., Traverse, 2008).

Of particular note is the absence of araucariaceous pollen, such as that produced by *Araucarites europeus*, which Kvaček and Teodoridis (2011) related to *Doliosrobos*. However, some of the pollen grains of unknown taxonomic attribution figured by Gruas-Cavagnetto (1973), (e.g. Plate I Figs. 1–4) share several features with araucariaceous pollen and might correspond to *Doliosrobos*.

Based on the pollen assemblage, Gruas-Cavagnetto (1973) distinguished two environments, which would have co-existed in the basin: 1) a warm, humid environment, which allowed Lauraceae, Menispermaceae and Araliaceae to grow and 2) an environment with relatively cold winters and marked precipitation seasonality, which permitted the Fagaceae, Betulaceae and Juglandaceae to develop. These results were

re-interpreted by Lettéron et al. (2018), who concluded that the pollen beds studied by Gruas-Cavagnetto (1973) would represent two facies (i. e. lignite and limestones) corresponding to different phases of short-term climatic cycles. These authors suggested that during wet stages, represented by lignite-rich facies, swampy areas would have developed, leading to a predominance of *Doliosrobos* and the Sapotaceae, while during the drier periods, recorded in limestones, *Bytneriopsis*, Pinaceae, Fagaceae and Areaceae would thrive.

Although these climatic cycles may have influenced the vegetation studied, the taphonomic and sedimentological analyses presented here indicate that some taxa (e.g. *Bytneriopsis* and *Doliosrobos*) grew in different habitats in the Alès and Saint-Chaptes basins, presumably co-habiting under the same climatic conditions. In fact, the two sources of information—macro- and microflora—are compatible and complement each other when they are analysed from a taphonomic perspective. Hence, the vegetation from the Alès and Saint-Chaptes basins was mainly composed of *Doliosrobos*, *Tetraclinis*, Lauraceae (*Laurophyllum* and *Daphnogene*), palms, leguminous plants and *Zizyphus*. Meanwhile, *Pinus* L., *Taxodium* Rich., *Glyptostrobus* Endl. and thermophilous angiosperms grew beyond the basin, but only the pollen grains would reach the depositional areas. This interpretation is more compatible with the palaeoclimatic reconstruction by Tanrattana et al. (2020) based on fossil dicot leaves, which attests to a warm subtropical climate with high precipitation seasonality and mild winters in this palaeogeographic area during the late Eocene.

#### 6.5. Comparison with other South and Central European coeval floras

Biogeographic subdivision of the late Eocene European floras has been attempted by several authors. Mai (1995) proposed a subdivision in bioprovinces by comparison with faunal biogeography and distinguished within them the so-called floral complexes (“Florenkomplexe”), some of them diachronous. The flora of Célas was representative of one such complexes. Later, Popov et al. (2001), carried out a synthesis of the World late Eocene biogeography and proposed somewhat different bioprovinces (“Phytogeographic Zones”) than Mai (1995). Again, the Célas flora stands out as a representative vegetation in this case of the

South European bioprovince. More recently, Kvaček (2010) updated Mai (1995) bioprovincial subdivision and “Florenkomplexe”, mentioning again the Célas flora or “unit” as characteristic for the ‘Tethys Phytogeographical Province’. He stressed also that a review and redefinition of such provinces is urgently needed. Whenever such a revision will be undertaken, the Célas flora will be clearly a key locality in European plant biogeography.

Comparison with other localities from South Europe is best undertaken with the strictly coeval Catalan plant locality of Sarral (Ebro Basin). Both localities share quite a large deal of taxa, such as the Lauraceae (*Daphnogene* and *Laurophyllum*), leguminous plants, *Comptonia difformis*, *Zizyphus ziziphoides* and *Tetraclinis*. The distribution of these plants in the Alès and Saint-Chaptes basins is also similar to that found in Sarral (Tosal et al., 2018), with lauraceous plants and *Comptonia difformis* forming part of the riparian vegetation (Fig. 7B), *Tetraclinis* open woodlands growing just behind this community, while the Fabaceae and *Zizyphus* formed an open woodland distal to the lake (Fig. 7B). However, certain differences distinguish the two assemblages. The riparian vegetation was much more diverse in the Alès and Saint-Chaptes basins, with conifers (i.e. *Doliosobus*, *Sequoia*-like plants) and ferns (i.e. *Osmunda* aff. *parschlugiana* and *Pronephrium striacum*, Fig. 7B), growing in association with palms, *Byttneriopsis*, *Comptonia difformis* and

the Lauraceae. One plausible explanation for these differences is the contrasting basin palaeogeography. Lettéron et al. (2018) showed that the Saint-Chaptes and Issirac basins were compartmented in several horsts and grabens that favoured the development of permanent areas of stagnant water, which would facilitate the growth of ferns, *Doliosobus* and *Byttneriopsis* (Kvaček, 2002). In contrast, the lacustrine system of Sarral developed on an almost flat palaeo-topography, corresponding to the distal part of a foreland basin, with intermittent wetlands that depended on orbital cycles (Valero et al., 2014). These latter conditions would have prevented the growth of plants with high hydric requirements.

Furthermore, climatic conditions may have also played an important role in the distribution of latest Eocene plants in South Europe. The results reported by Tanrattana et al. (2020) based on CLAMP (climate leaf analysis multivariate program) using the historical plant collection from the Alès and Saint-Chaptes basins indicate similar temperature parameters than the values obtained by the same method in Sarral by Tosal et al. (2019), i.e., 20.5 °C Mean Annual Temperature; 15.6 °C Coldest Month Mean Temperature and 25.9 °C Warmest Month Mean Temperature. However, precipitation was higher in the French localities (2237 mm during plant growth season in Alès and Saint-Chaptes vs. 1328 mm in Sarral). These paleoclimatic figures based on CLAMP

**Table 4**

Comparison of data from the main Priabonian European palaeobotanical sites, significant from the viewpoint of plant palaeoecology and biogeography.

Locality	Country	Plant organ	Plant taxonomy (main taxa)	Depositional setting	Age	Reference
1 Alès and Saint-Chaptes basins	France	Leaf	Ferns, <i>Tetraclinis</i> , <i>Doliosobus</i> , <i>Sequoia</i> -like, palms <i>Daphnogene</i> , <i>Laurophyllum</i> , <i>Zizyphus</i> , Fabales (>4 fossil-species), <i>Myrica</i> , <i>Comptonia</i> , <i>Salix</i> , <i>Byttneriopsis</i> .	Lacustrine	Late Eocene	Present study
2 Sarral	Catalonia, Spain	Leaf	<i>Tetraclinis</i> , <i>Pinus</i> <i>Daphnogene</i> , <i>Laurophyllum</i> , <i>Zizyphus</i> , Fabales (>4 fossil-species), <i>Myrica</i> , <i>Comptonia</i> , <i>Salix</i> , <i>Sabal</i> .	Lacustrine	Latest Eocene	Tosal et al. (2018)
3 Ovče Polje	Macedonia	Leaf	cf. <i>Protosequoia hardtii</i> , <i>Daphnogene cinnamomea</i> , <i>D. lanceolata</i> <i>Eotrigonobalanopsis jurcinervis</i> , <i>Trigonobalanopsis</i> , <i>Dryophyllum</i> , <i>Quercus Equisetites</i> sp., cf. <i>Laurophyllum acutumontanum</i> , <i>Trachycarpus rhapijolia</i> , cf. <i>Sequoia couttsiae</i> , <i>Zizyphus</i>	Marine-Coastal	Late Eocene	Mihajlović and Ljubotenski (1994)
4 Staré Sedlo Kučlín	Czech Republic	Leaf	<i>Osmunda lignitum</i> , <i>Pronephrium striacum</i> , <i>Lomariopsis bilinca</i> , <i>Acrostichum</i> , <i>Rumohra recentior</i> , <i>Tetraclinis salicornioides</i> , <i>Doliosobus</i> , <i>Anoetomeria brongiarti</i> , <i>Nymphaea polyrhiza</i> , <i>Magnolia longipetiolata</i> , <i>Liriodendrom</i> , <i>Laurophyllum</i> , <i>Daphnogene</i> , <i>Nitophyllites bohemicus</i> , <i>Smilax</i> , <i>Sabal</i> , <i>Berberis</i> , cf. <i>Mahonia</i> , <i>Palatanus neptuni</i> , cf. <i>Ampelopsis</i> , <i>Sloanea</i> , <i>Leguminosites</i> , <i>Zizyphus</i> , <i>Cedrelopermum</i> , <i>Tremophyllum</i> , <i>Ulmites</i> , <i>Eotrigonobalanus</i> , <i>Trigonobalanus</i> , <i>Engelhardtia</i> , <i>Hooleya hermis</i> , <i>Raskya</i> , <i>Byttneriopsis</i> , <i>Acer</i> , <i>Sterculina</i> , <i>Hemitrapa</i> , <i>Chaneya</i> , <i>Ailanthus</i> , <i>Hydoangea</i> , <i>Palaeohosiea</i> , <i>Apocynophyllum</i> , <i>Pungiphyllum</i> , <i>Craspedromophyllum</i> <i>Rhodomyrtophyllum</i> , <i>Pasaniopsis</i> , <i>Fagopsis</i> , <i>Quercus</i> (?), <i>Dryophyllum</i> , <i>Sterculia</i> , ferns	Fluviatile-lacustrine	Late Eocene  Late Eocene	Knobloch et al. (1996) Kvaček and Teodoridis (2011)
5 Häring	Austria	Leaf	<i>Daphnogene</i> , cf. <i>Eotrigonobalanus furcinervis</i> , <i>Lauraceae</i> , <i>Cedrelopermum flichei</i> , <i>Myrica longifolia</i> , <i>Myrica</i> sp., <i>Comptonia difformis</i> , Fabaceae (<4 fossil-species), <i>Zizyphus</i> , <i>Sloanea</i> , <i>Berberidaceae</i> , <i>Smilax</i> .	Lacustrine-palustrine	Late Eocene to lowermost Oligocene	Erdei and Rákosi (2009)
6 Bourgas; Hvoyna; Eleshnita	Bulgaria	Pollen	Ferns, palms, <i>Pinus</i> , <i>Doliosobus</i> , <i>Libocedrites</i> , Lauraceae, <i>Myrica</i> , <i>Nyssa</i> , <i>Acer</i> , <i>Bumelia</i> , <i>Platanus</i> , <i>Populus</i> , <i>Juglans</i> , <i>Pterocarya</i> , <i>Cyclocarya</i> , <i>Dodonea</i> , Magnoliaceae, Ulmaceae, Sabiaceae, Aquifoliaceae, Ebenaceae, Araliaceae, Celastraceae, Apocynaceae., <i>Chamaecyparis Sciadopitys</i> , <i>Dryophyllum</i> , <i>Eotrigonobalanus</i> , <i>Celastrophyllum</i> , <i>Rumohra</i> , <i>Cyclosorus</i> , « <i>Acacia</i> », « <i>Caesalpinites</i> », <i>Cassiophyllum</i> , <i>Myrtus</i> , <i>Zizyphus</i> , <i>Rosa</i> , <i>Rubus</i> , <i>Pyrus</i> , <i>Boehmeria</i> , <i>Punica</i> , and <i>Olea</i> .	Lacustrine-palustrine	Late Eocene-early Oligocene	Bozukov et al. (2009)
7 Henisbury	England	Leaf	Ferns, palms, <i>Doliosobus</i> , <i>Pinus</i> , <i>Pityospermum</i> , <i>Quaseisequoia</i> , <i>Daphnogene Neolitsea</i> , <i>Palaeocarya</i> , <i>Hooleya Quercus</i> sp.? <i>Fagus</i> sp.?, <i>Raskya</i> , <i>Zanthoxylum</i> , <i>Zizyphus</i> , <i>Dipelta</i> ,? <i>Byttneriopsis</i>	Lacustrine-palustrine	Latest Eocene	Hayes and Collinson (2014)
8 Sambian peninsula Kaliningrad district	Russian	Flower, fruits and leaves	<i>Pinus</i> , Taxodiaceae, Lauraceae, Anacardaceae, Hamamelidaceae, Araliaceae	Coastal?	Late Eocene	Akhmetiev (2010)
9 Tatra Mountains	Poland	Leaf	<i>Eotrigonobalanus</i> , <i>Daphnogene</i> , <i>Nypa</i> , <i>Quercus</i>	Coastal	Latest Eocene	Worobiec et al. (2015)

indicate a temperate climate, fully humid and with hot summers (Cfa Köppen climate classification) for the Alès and Saint Chaptes basins, while Sarral would be at the boundary between the former type and a temperate climate with a dry season and a hot summer (Csa type). The higher precipitation figures in the Alès and Saint-Chaptes basins would have allowed development of trees with high hydric requirements, such as *Doliosirobus*. In contrast, frequent lake water table fluctuations in the latest Eocene Ebro Basin would have favoured more drought-tolerant plants such as the Fabaceae, with twice the number of fossil-species represented in the Alès and Saint-Chaptes basins (Table 1).

The differences in precipitation between these two basins may be related to proximity to the Tethys Sea. The Alès and Saint-Chaptes basins were intermittently connected with the sea (Lettéron et al., 2017, 2018, 2022; Semmani et al., 2022), which would have provided regular moisture and a higher possibility of rain, as occurs nowadays on the Mediterranean coast. In contrast, the latest Eocene Ebro Basin was an isolated endorheic basin located about 80 km away from the coast and with a more continental precipitation regime.

Comparison of the flora from the Alès and Saint-Chaptes basins is also possible with coeval plant localities from Central Europe (Table 4, Fig. 9). Examples of taxa that are shared between Central European plant localities and Alès and Saint Chaptes basins include *Populus* L in Bourgas, Hvoyna and Eleshnita (Bozukov et al., 2009), *Doliosirobus* in Kučlín (Kvaček and Teodoridis, 2011) and Staré Sedlo, both in the Czech Republic (Knobloch et al., 1996), and Häring in Austria (Erdei and Rákosi, 2009), *Byttneriopsis* in Kučlín, Czech Republic

(Kvaček and Wilde, 2010) and presumably in the Isle of Wight, England (Hayes and Collinson, 2014). As matter of fact *Doliosirobus* and *Byttneriopsis* from Alès and Saint-Chaptes basins represent the most southern occurrence of these genera (Fig. 9; Table 4). Paleoclimatic data using CLAMP and CA (Coexistence Approach) methods from coeval plant localities from Germany i.e., Haselbach (Mosbrugger et al., 2005), Profen (Mosbrugger et al., 2005; Kunzmann et al., 2019) show similar climatic parameters than Saint Chaptes and Alès basins with mild-warm mean annual temperatures (16 °C–18 °C), hot summers (24 °C–18 °C), mild winters (5 °C–9 °C). The rainfall in central Europe (1000–1300 mm/year) is lower than in Alès and Saint Chaptes. Nevertheless, all these localities are characterised by the absence of a dry season (Cfa-type climate) unlike the South European locality of Sarral.

In sum, the Priabonian vegetation in the Alès and Saint-Chaptes basins shows intermediate features between South and Central Europe vegetation. This suggests that the Célas flora represents a transitional flora between these two main European vegetations (Fig. 9). Modified from Popov et al. (2004).

### 7. Conclusions

The Priabonian flora from the Saint-Chaptes and Alès basins (France) has yielded significant data about the plant ecosystems in South Europe close to the climatic turnover of the Eocene-Oligocene transition. Plants from these basins were distributed into five plant palaeocommunities: 1) aquatic plants dominated by water lilies and a *Limnobiophyllum*-like

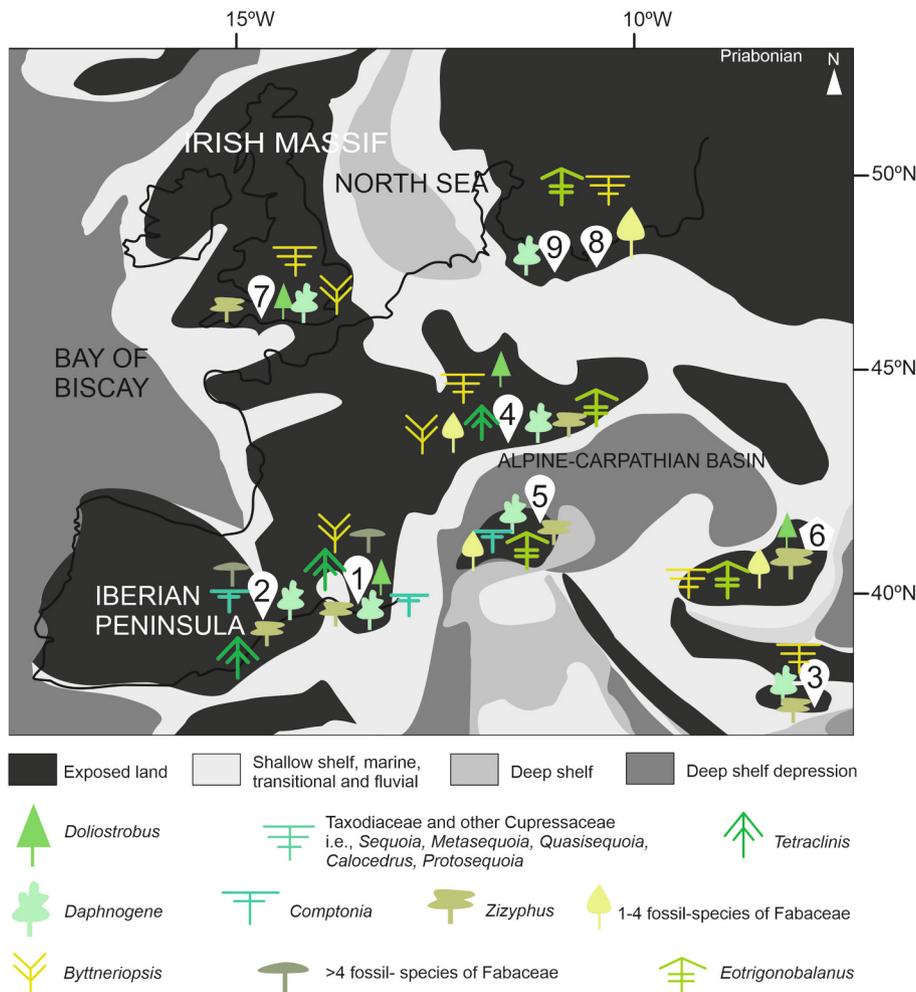


Fig. 9. Palaeogeographic map of Western Eurasia with representation of late Eocene plant genera with paleobiogeographic interest. Localities are numbered as in Table 4.

plant; 2) reeds on the lakeshore; 3) riparian vegetation formed by *Doliosstrobos taxiformis*, *Sequoia*-like plants, *Sabal major*, *Daphnogene* sp., *Byttneriopsis* sp., *Myrica* sp., *Comptonia difformis*, *Osmunda* aff. *parschlugiana* and *Pronephrium stiriacum*; 4) open woodlands with *Tetraclinis* growing not far from river inlets to the lake; and 5) *Zizyphus*, Fabales and probably *Ailanthus* also growing in open woodlands, more distal to the lake.

This flora bears some resemblance to the coeval assemblages from Sarral (Ebro Basin, Catalonia). However, the riparian vegetation is more diverse in the Alès and Saint-Chaptes basins, where the two main controlling factors proposed to explain these differences are: 1) the basin architecture, leading to the formation of stable stagnant waters or permanently humid soils, and 2) the climate, i.e. warm temperatures and a high precipitation regime. These environmental conditions would be favoured by proximity to the Tethys sea and might have contributed to the onset of uncommon plants in South Europe (e.g. *Doliosstrobos*). Future detailed taxonomic studies of those specimens with imprecise or uncertain taxonomic attribution (e.g. the *Sequoia*-like foliage, *Leguminophyllum* sp., *Byttneriopsis* sp. leaves) will enable better characterisation of floral diversity and will shed light on the influence of the sea moisture on plant diversity during this time span in south-west Europe.

The plant assemblage from the Alès and Saint-Chaptes shows that in these basins, taxa from Central Europe (i.e. *Doliosstrobos*, a *Sequoia*-like plant, *Byttneriopsis* or *Populus*) co-existed with sclerophyllous plants more characteristic from South Europe (e.g. leguminous plants, *Comptonia difformis* and *Zizyphus zizyphoides*). This suggests that the flora from the basins studied, traditionally known as 'Célas flora', is transitional between these two European regions. However, re-assessment of the European floras, following a detailed taxonomic study coupled with taphonomic and palaeoecological analyses, is needed before a progress in biogeographic studies can be undertaken.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2023.111740>.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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## References

- Akhmetiev, M.A., 2010. Paleocene and Eocene floristic and climatic change in Russia and Northern Kazakhstan. *Bull. Geosci.* 85 (1), 77–94.
- Anadón, P., Cabrera, L., Colldeforns, B., Sáez, A., 1989. Los sistemas lacustres del Eoceno superior y Oligoceno del sector oriental de la Cuenca del Ebro. *Acta Geol. Hisp.* 24 (3–4), 205–230.
- Arp, G., 1995. Lacustrine bioherms, spring mounds, and marginal carbonates of the Ries-impact-crater (Miocene, Southern Germany). *Facies* 33, 35–89.
- Bozokov, B., Utescher, T., Ivanov, D., 2009. Late Eocene to early Miocene climate and vegetation of Bulgaria. *Rev. Palaeobot. Palynol.* 153, 360–374.
- Clausing, A., 1990. Mikrofazies lakustriner Karbonat-horizonte des Saar-Nahe-Beckens (Unterperm, Rotliegend, SW-Deutschland). *Facies* 23, 121–140.
- Collinson, M.E., 1992. Vegetational and floristic changes around the Eocene/Oligocene boundary in western and central Europe. In: Prothero, D.R., Berggren, W.A. (Eds.), *Eocene-Oligocene Climatic and Biotic Evolution*. Princeton University Press, pp. 437–450.
- Collinson, M.E., 2000. Cenozoic evolution of modern plant communities and vegetation. In: Culver, S., Rawson, P. (Eds.), *Biotic Response to Global Change: The Last 145 Million Years*. Cambridge University Press, Cambridge, pp. 223–243.
- Collinson, M.E., Hooker, J.J., 2003. Paleogene vegetation of Eurasia: Framework for mammalian faunas. *Deinsea* (Rotterdam) 10, 41–83.
- Dean, W.E., Fouch, T.D., 1983. Lacustrine environment. In: Scholle, P.A., Bebout, D.G., Moore, C.H. (Eds.), *Carbonate Depositional Environments*, 33. American Association of Petroleum Geologists, pp. 98–130.
- Erdei, B., Rákosi, L., 2009. The middle Eocene flora of Csordakút (N Hungary). *Geol. Carpath.* 60 (1), 43–57.
- Fauquette, S., Guiot, J., Suc, J.-P., 1998. A method for climatic reconstruction of the Mediterranean Pliocene using pollen data. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 144, 183–201.
- Feist-Castel, M., 1971. Sur les charophytes fossiles du bassin Tertiaire d'Alès (Gard). *Geobios* 4, 157–172.
- Ferguson, D.K., 1985. The origin of leaf assemblages new light on an old problem. *Rev. Palaeobot. Palynol.* 46 (1–2), 117–188.
- Florencio, M., Patiño, J., Nogue, S., Traveset, A., Borges, P.A.V., Schaefer, H., Amorim, I. R., Arnedo, M., Ávila, S.P., Cardoso, P., de Nascimento, L., Fernández-Palacios, J.M., Gabriel, S.I., Gil, A., Gonçalves, V., Haroun, R., Illera, J.C., López-Darias, M., Martínez, A., Martins, G.M., Neto, A.I., Nogales, M., Oromí, P., Rando, J.C., Raposo, P.M., Rigal, F., Romeiras, M.M., Silva, L., Valido, A., Vanderpoorten, A., Vasconcelos, R., Santos, A.M.C., 2021. Macaronesia as a Fruitful Arena for Ecology, Evolution, and Conservation Biology. *Front. Ecol. Evol.* 9, 718169.
- Freytet, P., Plaziat, J.-C., 1982. Continental carbonate sedimentation and pedogenesis – Late Cretaceous and Early Tertiary of Southern France. In: Purser, B.H. (Ed.), *Contrib. Sedimentology*, 12. Schweizerbart'sche Verlag, Stuttgart, p. 217.
- Gastaldo, R.A., 1988. Conspectus of phytotaphonomy. In: Di Michele, W.A., Wing, S.L. (Eds.), *Methods and Applications of Plant Palaeoecology*. The Paleontological Society Special Publication 3 University of Tennessee, Tennessee, pp. 14–28.
- Gastaldo, R.A., Douglass, D.P., McCarroll, S.T., 1987. Origin, characteristics, and Provenance of plant macrodetritus in a Holocene crevasse splay, Mobile Delta, Alabama. *PALAIOS* 2, 229–240.
- Guerrero, M.C., López-Archilla, A.I., Iniesto, M., 2016. Microbial Mats and Preservation. In: Poyato-Ariza, F.J., Buscalioni, Á.D. (Eds.), *Las Hoyas: A Cretaceous Wetland. A Multidisciplinary Synthesis after 25 Years of Research on an Exceptional Fossil Lagerstätte from Spain*. Las Hoyas, Spain, pp. 220–228.
- Gruas-Cavagnetto, C., 1973. Première contribution à l'étude de la palynoflore de la formation de Célas. Bassin d'Alès, Gard, *Paléobiologie Continentale* 4, 1–14.
- Gruas-Cavagnetto, C., Bui, N.-S., 1976. Présence de pollen d'araliacées dans le Paléogène anglais et français. *Rev. Palaeobot. Palynol.* 22, 61–72.
- Hayes, P., Collinson, M., 2014. The Flora of the Insect Limestone (latest Eocene) from the Isle of Wight, southern England. *Earth Environ. Sci. Trans. R. Soc. Edinburgh* 104 (3–4), 245–261.
- Hren, M.T., Sheldon, N.D., Grimes, S.T., Collinson, M.E., Hooker, J.J., Bugler, M., Lohmann, K.C., 2013. Terrestrial cooling in Northern Europe during the Eocene-Oligocene transition, 110 (19), 7562–7567.
- Hutchinson, D.K., Coxall, H.K., Lunt, D.J., Steinthorsdottir, M., de Boer, A.M., Baatsen, M., von der Heydt, A., Huber, M., Kennedy-Asser, A.T., Kunzmann, L., Ladant, J.-B., Lear, C.H., Morawek, K., Pearson, P.N., Piga, E., Pound, M.J., Salzmann, U., Scher, H.D., Sijp, W.P., Śliwińska, K.K., Wilson, P.A., Zhang, Z., 2021. The Eocene-Oligocene transition: a review of marine and terrestrial proxy data, models and model-data comparisons. *Clim. Past* 17, 269–315.
- Knobloch, E., Kvaček, Z., Bůžek, Č., Mai, D.H., Batten, D.J., 1993. Evolutionary significance of floristic changes in the Northern Hemisphere during the late cretaceous and Palaeogene, with particular reference to Central Europe. *Rev. Palaeobot. Palynol.* 78 (1–2), 41–54.
- Knobloch, E., Konzalová, M., Kvaček, Z., 1996. Die obereozäne Flora der Staré Sedlo-Schichtenfolge in Böhmen (Mitteleuropa). *Rozpr. Česk. Geol. Ústavu* 49, 260.
- Kovar-Eder, J., Kvaček, Z., Zastawniak, E., Givulescu, R., Hably, L., Mihajlovic, D., Teslenko, Y., Walther, H., 1996. Floristic trends in the vegetation of the Paratethys surrounding areas during Neogene time –. In: Bernor, R., Fahlbusch, V., Mittmann, H.-W. (Eds.), *The Evolution of Western Eurasian Later Neogene Faunas*. Columbia University Press, pp. 399–409.
- Kunzmann, L., Kvaček, Z., Teodoridis, V., Müller, C., Morawek, K., 2016. Vegetation dynamics of riparian forest in Central Europe during the late Eocene. *Palaeontogr. Abt. B* 295, 69–89.
- Kunzmann, L., Morawek, K., Müller, C., Schröder, I., Wappler, T., Grein, M., Roth-Nebelsick, A., 2019. A Paleogene leaf flora (Profen, Sachsen-Anhalt, Germany) and

- its potentials for palaeoecological and palaeoclimate reconstructions. *Flora* 254, 71–87.
- Kvaček, Z., 2002. Late Eocene landscape, ecosystems and climate in northern Bohemia with particular reference to the locality of Kučlín near Břilina. *Bull. Geosci.* 77 (3), 217–236.
- Kvaček, Z., 2010. Forest flora and vegetation of the European early Palaeogene—a review. *Bull. Geosci.* 85 (1), 63–76.
- Kvaček, Z., Wilde, V., 2010. Foliage and seeds of malvacean plants from the Eocene of Europe. *Bull. Geosci.* 85 (1), 163–182.
- Kvaček, Z., Manchester, S.R., Schorn, H.E., 2000. Cones, seeds, and foliage of *Tetraclinis salicoides* (Cupressaceae) from the Oligocene and Miocene of western North America: a geographic extension of the European tertiary species. *Int. J. Plant Sci.* 161 (2), 331–344.
- Kvaček, Z., Teodoridis, V., 2011. The Late Eocene flora of Kučlín near Břilina in North Bohemia revisited. *Acta Mus. Natl. Pragae Ser. B Hist. Naturalis* 37 (3–4), 9–69.
- Laurent, L., 1899. Flore des calcaires de Célas. *Ann. Mus. d'hist. Naturelle de Marseille. Série II, Tome I.* Mouillot, Marseille 148.
- Lettéron, A., Fournier, F., Hamon, Y., Villier, L., Margerel, J.-P., Bouche, A., Feist, M., Joseph, P., 2017. Multi-proxy paleoenvironmental reconstruction of saline lake carbonates: Paleoclimatic and paleogeographic implications (Priabonian-Rupelian, Issirac Basin, SE France). *Sediment. Geol.* 358, 97–120.
- Lettéron, A., Hamon, Y., Fournier, F., Séranne, M., Pellenard, P., Joseph, P., 2018. Reconstruction of a saline, lacustrine carbonate system (Priabonian, St-Chaptes Basin, SE France): Depositional models, paleogeographic and paleoclimatic implications. *Sediment. Geol.* 367, 20–47.
- Lettéron, A., Hamon, Y., Fournier, F., Séranne, M., Pellenard, P., Joseph, P., 2022. Stratigraphic architecture of a saline lake system: From lake depocentre (Alès Basin) to margins (Saint-Chaptes and Issirac basins), Eocene–Oligocene transition, south-east France. *Sedimentology* 69, 651–695.
- Lokier, S.W., Andrade, L.L., Court, W.M., Dutton, K.E., Head, I.M., Van Der Land, C., Paul, A., Sherry, A., 2017. A new model for the formation of microbial polygons in a coastal sabkha setting. *Deposit. Record* 3 (2), 201–208.
- Mai, J.D., 1995. In: *Tertiäre Vegetationsgeschichte Europas*. Gustav Fischer, Jena, p. 691.
- Mai, D.H., Walther, H., 1985. Die obereozänen Floren des Weissesterbeckens und seiner Randgebiete. *Abhandlungen Staatlichen Mus. Mineral. Geol. Dresden* 33, 260.
- Mai, D.H., Walther, H., 2000. Die Fundstellen eozäner Floren des Weißelster-Beckens und seiner Randgebiete. *Altenburger Nat. Forschungen* 13, 220.
- Marion, A.F., 1888. *Doliosirobium sternbergii*. Nouveau genre de conifères fossiles. *Ann. Sci. Geol.* 20 (3), 1–20.
- Martín-Closas, C., Gomez, B., 2004. Taphonomie des plantes et interpretations paléocologiques. *Une synthèse*. *Geobios* 37, 65–888.
- Mihajlović, D., Ljubotenski, T., 1994. Upper Eocene Flora of Ovce Polje, Macedonia. *Geol. Carpath.* 45, 203–210.
- Mosbrugger, V., Utescher, T., Dilcher, D.L., 2005. Cenozoic continental climatic evolution of Central Europe. *Proc. Natl. Acad. Sci.* 102 (42), 14964–14969.
- Norsted, B.A., Carroll, A.R., Smith, M.E., 2015. Initiation of Eocene lacustrine sedimentation in the Greater Green River Basin: Luman Member of the Green River Formation. In: Smith, M.E., Carroll, A.R. (Eds.), *Stratigraphy and Paleolimnology of the Eocene Green River Formation*, Western USA. Springer, Berlin, Germany, pp. 13–30.
- Olariu, C., Zhou, C., Steel, R., Zhang, Z., Yuan, X., Zhang, J., Chen, S., Cheng, D., Kim, W., 2021. Controls on the stratal architecture of lacustrine delta successions in low-accommodation conditions. *Sedimentology* 68 (5), 1941–1963.
- Platt, N.H., Wright, V.P., 1991. Lacustrine carbonates: facies models, facies distributions and hydrocarbon aspects. *Lacustrine carbonates: facies models, facies distributions and hydrocarbon aspects*. In: Anadón, P., Cabrera, L., Kelts, K. (Eds.), *Lacustrine Facies Analysis*, 13. Special Publications of the International Association of Sedimentology, pp. 55–73.
- Pollard, J.E., Steel, R.J., Undersrud, E., 1982. Facies sequences and trace fossils in lacustrine/fan delta deposits, Hornelen Basin (M. Devonian), Western Norway. *Sediment. Geol.* 32, 63–87.
- Popov, S.V., Akmetiev, M.A., Bugrova, E.M., Lopatin, A.V., Amitrov, O.V., Andreeva-Grigorovich, A.S., Zherikhin, V.V., Zaporozhets, N.I., Nikolaeva, I.A., Krashenninnikov, V.A., Kuzmicheva, E.I., Sytchevskaya, E.K., Shcherba, I.G., 2001. Biogeography of the Northern Peri-Tethys from the Late Eocene to the Early Miocene: Part 1. Late Eocene. *Paleontol. J.* 35 (1), S1–S68.
- Popov, S.V., Rögl, F., Rozanov, A.Y., Steininger, F.F., Shcherba, I.G., Kovac, M., 2004. Lithological-paleogeographic maps of Paratethys. *Courier Forschungs institut Senckenberg* 250, 1–46.
- Remy, J.A., 1994. Une faunule de vertébrés sous la base des Grès de Célas (Éocène sup.) à Saint-Dézéry (Gard). *Palaeovertebrata* 23, 211–216.
- Remy, J.A., 1999. Deux nouveaux gisements de Vertébrés fossiles dans la formation de Célas (Éocène supérieur du Gard). *Bull. Soc. Sci. Nat. Nîmes Gard* 62, 16–22.
- Remy, J.A., 2015. Les Périssodactyles (Mammalia) du gisement Bartonien supérieur de Robiac (Éocène moyen du Gard, Sud de la France). *Palaeovertebrata* 39, 1–98.
- Sanchis, E., Séranne, M., 2000. Structural style and tectonic evolution of a polyphase extensional basin of the Gulf of Lion passive margin: the Tertiary Alès basin, southern France. *Tectonophysics* 322, 219–242.
- Semmani, N., Fournier, F., Léonide, P., Feist, M., Boularand, M., Borgomano, J., 2022. Transgressive-regressive cycles in saline lake margin oolites: paleogeographic implications (Priabonian, Vistrenque basin, SE France). *Earth Sci. Bull.* 193 (8), 1–28.
- Semmani, N., Fournier, F., Suc, J.-P., Fauquette, S., Godeau, N., Guihou, A., Popescu, S.-M., Melinte-Dobrinescu, M.C., Thomazo, C., Marié, L., 2023. The Paleogene continental basins from SE France: New geographic and climatic insights from an integrated approach, Palaeogeography, Palaeoclimatology. *Palaeoecology* 615, 111452.
- Séranne, M., Couffé, R., Husson, E., Baral, C., Villard, J., 2021. The transition from Pyrenean shortening to Gulf of Lion rifting in Languedoc (South France) – a tectonic sedimentation analysis. *BSGF - Earth Sciences Bull.* 192 (27), 1–29.
- Sheldon, H.D., 2009. Non-marine records of climatic change across the Eocene-Oligocene transition. In: Koeberl, C., Montanari, A. (Eds.), *The Late Eocene Earth: Hothouse, Icehouse and Impacts*, 452. The Geological Society of America Special Paper, pp. 241–248.
- Spicer, R.A., 1981. The sorting and deposition of allochthonous plant material in a modern environment at Silwood Lake, Silwood Park, Berkshire, England, 1143, 1–77.
- Spicer, R.A., 1989. The formation and interpretation of plant fossil assemblages. *Adv. Bot. Res.* 16, 95–19.
- Spicer, R.A., Wolfe, J.A., 1987. Taphonomy of Holocene deposits in Trinity (Clair Engle) Lake, Northern California. *Paleobiology* 13, 227–245.
- Tanrattana, M., Boura, A., Jacques, F.M.B., Villier, L., Fournier, F., Enguehard, A., Cardonnet, S., Voland, G., Garcia, A., Chaouch, S., De Franceschi, D., 2020. Climatic evolution in Western Europe during the Cenozoic: insights from historical collections using leaf physiognomy. *Geodiversitas* 42 (11), 151–174.
- Tosal, A., Sanjuan, J., Cartanyà, J., Martín-Closas, C., 2018. Taphonomy and palaeoecology of the uppermost Eocene flora from Sarrià (Eastern Ebro Basin): Palaeoclimatic implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 497, 66–81.
- Tosal, A., Valero, L., Sanjuan, J., Martín-Closas, C., 2019. Influence of short- and long-term climatic cycles on floristic change across the Eocene-Oligocene boundary in the Ebro Basin (Catalonia, Spain). *Compt. Rend. Palevol.* 18, 925–947.
- Traverse, A., 2008. *Paleopalynology*. In: second edition. Springer, Dordrecht, p. 813.
- Valero, L., Garcés, M., Cabrera, L.L., Costa, E., Sáez, A., 2014. 20 Myr of eccentricity paced lacustrine cycles in the Cenozoic Ebro Basin. *Earth Planet. Sci. Lett.* 408, 183–193.
- Wilson, V.R., Gould, K.S., Lovell, P.H., 1998. In vitro abscission of kauri (*Agathis australis*) branches. *N. Z. J. Bot.* 36, 495–501.
- Worobiec, G., Jach, R., Machaniec, E., Uchman, A., Worobiec, E., 2015. Eocene flora and trace fossils from the Hruby Regiel section in the Tatra Mountains (Poland): Taxonomic revision of the Wiktor Kuźniar fossil plant collection. *Acta Geol. Pol.* 65 (2), 203–226.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292 (5517), 686–693.