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# Plant palaeoecology of the latest Eocene flora from the Saint-Chaptes and Alès basins of Gard, southern 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 Pronephrium stiriacum, conifers with Doliostrobus taxiformis, a Sequoia-like plant, angiosperms with Daphnogene sp., Byttneriopsis 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., Byttneriopsis or Doliostrobus), 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  $\delta^{18}$ O values of deep-marine carbonates at ~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; Mihajlovič 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

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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 Sarral (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 *Doliostrobus* 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., *Iodes* 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 *Doliostrobus 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	Cystopteris fumariacea P. Wessel et C.O. Weber	Cystopteris fumariacea
Thelypteridaceae	Lastraea (Goniopteris) stiriaca (Unger) Heer	Pronephrium stiriacum (Unger) Erw. Knobl., Z. Kvaček
Pteridaceae	Pteris parschlugiana Unger	Osmunda aff. parschlugiana
Pteridaceae	Chrysodium lanzaeanum	Acrostichum lanzaeanum (Vis.) I
rtendaceae	Vie	Cordpor
	vis.	S. Gardiler
Lygodiaceae	Lygodium gaudinii Heer	Lygodium gaudinii
Doliostrobaceae	Doliostrobus sternbergii	Doliostrobus taxiformis (Sternb.)
	Mar.	Z. Kvaček
Arecaceae	Sabal major (Unger) Heer	Sabal major
	Chamaerops celasensis L.	The whereabouts of the
	Laurent	specimens is unknown
	Pandanus intermedius I	Monocot indet
	I auropt	Monocot. maet.
r		[2] <i>V</i> -11:
Hydrocharitaceae	Vallisneria saportana L.	[?] Vallisneria saportana
	Laurent	
Myricaceae	Myrica saportana Schimp.	Myrica saportana
Myricaceae	Myrica banksiaefolia Unger	Myrica longifolia
	[nomen illegitimum]	
Myricaceae	Myrica (Comptonia)	Comptonia difformis (Sterpherg)
minicaccae	dmandmifalia (Dron on )	Borry (_Daracemeteria
	aryunaryona (Brongn.)	berry (=Purucomptonia
	Saporta	schranku) (Sternberg) Doweld
"Proteaceae"	Hakea banksiiformis L.	Berberis sp.
	Laurent	
"Proteaceae"	Grevillea dissecta L.	Indet.
	Laurent	
"Proteaceae"	Grevillea haeringiana	Berberis sp.
	Ettingsh.	
Salicaceae	Populus gaudinii Fisch	[?] Populus gaudinii
	Oost, in Heer	
Lauraceae	Cinnamomum scheuchzeri	Danhnogene sp
Lauraceae	Hoor	Daphilogene sp.
		D
Moraceae	Ficus marionii L. Laurent	Byttheriopsis daphnogenes
		(Ettingsh.) Z. Kvaček & Wilde
Malvaceae	Ficus goeppertii Ettingsh.	Byttneriopsis daphnogenes
		(Ettingsh.) Z. Kvaček & Wilde
Malvaceae	Ficus fraterna L. Laurent	Byttneriopsis sp.
Malvaceae	Ficus calophylla L. Laurent	Byttnerionsis sp
Malvaceae	Ficus ambigua L. Laurent	Byttherionsis danhnogenes
vialvaceae	Ficus univigua L. Laurent	Byuneriopsis adpiniogenes
		(Ettingsh.) Z. Kväcek & Wilde
Malvaceae	Ficus irregularis L. Laurent	<i>Byttneriopsis</i> sp.
Malvaceae	Ficus rotunda L. Laurent	Byttneriopsis sp.
Malvaceae	Ficus diffusa L. Laurent	Byttneriopsis daphnogenes
	55	(Ettingsh.) Z. Kvaček & Wilde
Malvaceae	Ficus heckeli L. Laurent	Byttnerionsis en
Vite eeee	Figure anomata L. Laurent	Viteocool
vitaceae	Ficus crenata L. Laurent	vitaceae?
Moraceae	Ficus ovalis L. Laurent	Byttneriopsis sp.
Moraceae	Fructus fici	Indet. fruit
	Artocarpus latifolia L.	The whereabouts of the
	Laurent	specimens is unknown
	Viburnum oblongum I	Angiosperm indet
	Viburium obioligum L.	Angiosperin indet.
- 4	Laurent	
Oleaceae	Fraxinus grossedentata L.	Fraxinus?
	Laurent	
Oleaceae	Fraxinus grossedentata L.	Fraxinus?
	Laurent	
Oleaceae	Frazinus arossedentata I	Fraxinus?
cicucia	I auront	L. uxptus.
D.:	Laurent	A
runulaceae	myrsine marioni L. Laurent	Augiosperm indet.
Ericaceae	Andromeda neglecta Sap.	The whereabouts of the
		specimens is unknown
Ericaceae	Rhododendron celasensis L.	The whereabouts of the
	Laurent	specimens is unknown
	Analia (Oneon an and) mini 1-	Angiognorm indet
	Araua (Oreopundx) rigiaa	Angiosperin indet.
	L. Laurent [nomen	
	illegitimum]	
	Aralia antecedens L.	Angiosperm indet.
	Laurent	
Vitaceae	Vitis dubia L. Laurent	Angiosperm indet [The
, miccue	Fromon illogitimum	anosimona aro an loan]
	nomen megnunum i	specimens are on ioant

(continued on next page)

#### Table 1 (continued)

Family	Taxonomic list of Laurent (1899)	Updated taxonomic list (this study)	
Annonaceae	Annona incerta L. Laurent	Angiosperm indet. [The whereabouts of the specimens is unknown]	
Menispermaceae	Cocculus intermedius DC. Clematis (Tourn.) L.	<i>Cocculus intermedius</i> The whereabouts of the	
Nymphaeaceae	Nymphaea (Tourn.) L. Pterospermites incrassatum L. Laurent	specimens is unknown Nymphaea "Pterospermites incrassatum"	
Malpighiaceae	<i>Banisteria vasseuri</i> L. Laurent	? Cedrelospermum kovaciae 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	Dodonaea saportana L. Laurent	Craigia europaea (Bronn) Doweld	
Rhamnaceae	Zizyphus paradisiaca (Unger) Heer Zizyphus propinquus L.	Zizyphus ziziphoides (Unger) Weyl. The whereabouts of the	
Rhamnaceae	Laurent Rhamnus aizoon Unger Heterocalyx ungeri	specimens is unknown "Rhamnus aizoon" Trilobium ungeri Saporta in Heer	
	(Saporta in Heer) Saporta [nomen illegitimum] <i>Rhus paucidentata</i> L.	Angiosperm indet.	
	Rhus juglandogene Ettingsh.	Angiosperm indet.	
Cupressaceae	Rhus juglandogene Ettingsh.	winged seed of Tetraclinis	
Simaroubaceae	Ailanthus prisca Saporta	Ailanthus prisca	
Myrtaceae	Myrtus oceanica Ettingsh.	"Myrtus oceanica"	
Myrtaceae	Myrtus oceanica Ettingsn.	The whereabouts of the	
	r yrus eiongulu L. Laurent	specimens is unknown	
Fabaceae	Dalbergia leptolobiana Saporta	Leguminophyllum A. Escalup- Bassi	
Fabaceae	<i>Parkinsonia recta</i> L. Laurent	Leguminophyllum sp.	
Fabaceae	Parkinsonia recta L. Laurent	Leguminocarpum Dotzler	
Fabaceae	Acacia servacensis L. Laurent	"Acacia" servacensis	
Fabaceae	Phyllites reticulata	Leguminocarpum Leguminophyllum	
	Phyllites tamarindiformis	Leguminophyllum sp.	
	Phyllites cordiformis	Angiosperm indet.	
	Phyllites dichotomus	Angiosperm indet.	
	Crassulites	Angiosperm indet.	
	Leguminosites celasensis	Angiosperm indet.	
	Phyllites minutissima Phyllites herbacea	Leguminophyllum sp.	
	Phyllites diverse	Angiosperm indet.	
	unidentified	5 · · · · · ·	
	Lignum	Axis	
	Fructus	Fructus	
0	indet.	Anoectomeria	
Lemnaceae	indet.	Sequola-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. 11) 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:

- 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.  $1\times$ , SHC.5, SHC.5 $\times$ ).

The plant remains studied from these sections were collected during one-week field campaign in 2022 to elucidate taphonomic biases. They consist of 893 megaremains 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: *Tetraclinis 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. Chaptes-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-Chaptes 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 Nimes 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-Chaptes 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-Jeande-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 SPr4 parasequence	Saint-Maurice-de- Cazevieille
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- Cazevieille
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 SPr 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 deepeningupwards 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 lowgradient 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/oncoidal 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 SPr3, 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-Cazevieille 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-Cazevielle, 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.



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

*Facies 7 description*: Medium-grained, orange sandstone beds with sigmoidal large-order stratification forming angles of  $15^{\circ} - 20^{\circ}$  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 subaqueous 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-Cazevieille follows a coarseningupwards trend. The finest-grained deposits are limited to Saint-Maurice-de-Cazevieille (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 *Doliostrobus 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

#### 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 Nymphaea. Parautochthonous, ferns, D. taxiformis, reeds, Sabal major, Lauraceae and Myricaceae Allochthonous Byttneriopsis 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>Doliostrobus</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 D. taxiformis, Sequoia-like plant Comptonia difformis, Allochthonous Tetraclinis, Daphnogene Zizyphus, 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 actuotaphonomic 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 actuotaphonomic 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 *Doliostrobus taxiformis* shoots and wellpreserved ovuliferous bract scales prevail in this assemblage, whereas *Doliostrobus* cones are rarer (Table 3). Associated with *Doliostrobus*, 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 sizeselected 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 *Doliostrobus taxiformis* shoot from Saint-Hippolyte-de-Caton, plant bed SHC. 1 (SHC.4). B: Isolated *Doliostrobus* bract scale from Saint-Hippolyte-de-Caton, plant bed SHC. 1 (SHC.2.2022). C: Whole *Osmunda* aff. *parschlugiana* 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-Maruéjols-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, *Doliostrobus 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 *Doliostrobus 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 Doliostrobus 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 wellarticulated 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 Zizvphus 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.

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# 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 stiriacum*, angiosperms (i.e. *Comptonia difformis, Byttneriopsis, Daphnogene* and *Laurophyllum*), palms and conifers (i.e. *Doliostrobus 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, Daphonogene*) and Malvaceae i.e., *Byttneriopsis*. Lauraceae growing close to river margins have also been reported in coeval localities in the Weißelster 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, *Doliostrobus taxiformis* remains are rare and fragmented in fluviatile 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 Weißelster 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 *Byttneriopsis* (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 *Byttneriopsis* 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 *Doliostrobus* (31.5%) followed by *Comptonia difformis* (Sternberg) Berry (4.8%), stems of reeds (4%), *Byttneriopsis* 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 Doliostrobaceae, Malvaceae, Myricaceae, Rhamnaceae, Poaceae and Typhaceae, although Arecaceae (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-Hippolytede-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 *Doliostrobus*. 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 *Doliostrobus*.

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 *Doliostrobus* and the Sapotaceae, while during the drier periods, recorded in limestones, *Byttneriopsis*, Pinaceae, Fagaceae and Areaceae would thrived.

Although these climatic cycles may have influenced the vegetation studied, the taphonomic and sedimentological analyses presented here indicate that some taxa (e.g. Byttneriopsis and Doliostrobus) grew in different habitats in the Alès and Saint-Chaptes basins, presumably cohabiting under the same climatic conditions. In fact, the two sources ment each other when they are analysed from a taphonomic perspective. Hence, the vegetation from the Alès and Saint-Chaptes basins was mainly composed of Doliostrobus, 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. *Doliostrobus, Sequoia*-like plants) and ferns (i.e. *Osmunda* aff. *parschlugiana* and *Pronephrium stiriacum*, 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, *Doliostrobus* 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, Tetraclinis, Doliostrobus, Sequoia-like, palms Daphnogene, Laurophyllum, Zizyphus, Fabales (>4 fossil- species) Myrica Comptonia Saliy, Byttheriansis	Lacustrine	Late Eocene	Present study
2	Sarral	Catalonia, Spain	Leaf	Tetraclinis, Pinus Daphrogene, Laurophyllum, Zizyphus, Fabales (>4 fossil-species), Myrica, Comptonia, Salix, Sabal.	Lacustrine	Latest Eocene	Tosal et al. (2018)
3	Ovče Polje	Macedonia	Leaf	cf. Protosequoia hardtii, Daphogene cinnamomea, D. lanceolata Eotrigonobalanopsis jurcinervis, Trigonobalanopsis, Dryophyllum, Quercus Equisetites sp., cf. Laurophyllum acuümontanum, Trachycarpus rhapijolia, cf. Sequoia couttsiae, Zizyphus	Marine- Coastal	Late Eocene	Mihajlovič and Ljubotenski (1994)
4	Staré Sedlo	Czech Republic	Leaf	Osmunda lignitum, Pronephrium stiriacum, Lomariopsis bilinca, Acrostichum, Rumohra recentior, Tetraclinis salicornioides,	Fluviatile- lacustrine	Late Eocene	Knobloch et al. (1996)
	Kučlín	-		Doliostrobus, Anoectomeria brongiarti, Nymphaea polyrhiza, Magnolia longipetiolata, Liridodendrom, Laurophyllum, Daphnogene, Nitophyllites bohemicus, Smilax, Sabal, Berberis, cf. Mahonia, Palatanus neptuni, cf. Ampelopsis, Sloanea, Leguminosites, Zizyphus, Cedrelospermum, Tremophyllum, Ulmites, Eotrigonobalanus, Trigonobalanus, Engelhardtia, Hooleya hermis, Raskya, Byttneriopsis, Acer, Sterculina, Hemitrapa, Chaneya, Ailanthus, Hydoangea, Palaeohosiea, Apocynophyllum, Pungiphyllum, Craspedodromophyllum Rhodomyrtophyllum, Pasaniopsis, Fagopsis, Quercus(?), Drvophyllum, Sterculia, ferns		Late Eocene	Kvaček and Teodoridis (2011)
5	Häring	Austria	Leaf	Daphnogene, cf. Eotrigonobalanus furcinervis, Lauraceae, Cedrelospermum flichei, Myrica longifolia, Myrica sp., Comptonia difformis, Fabaceae (<4 fossil-species), Zizyphus, Sloanea, Berberidaceae, Smilax.	Lacustrine- palustrine	Late Eocene to lowermost Oligocene	Erdei and Rákosi (2009)
6	Bourgas; Hvoyna; Eleshnita	Bulgaria	Pollen	Ferns, palms, Pinus, Doliostrobus, Libocedrites, Lauraceae, Myrica, Nyssa, Acer, Bumelia, Platanus, Populus, Juglans, Pterocarya, Cyclocarya, Dodonea, Magnoliaceae, Ulmaceae, Sabiaceae, Aquifoliaceae, Ebenaceae, Araliaceae, Celastraceae, Apocynaceae, Chamaecyparis Sciadopitys, Dryophyllum, Eotrigonobalanus, Celastrophyllum, Rumohra, Cyclosorus, « Acacia », « Caesalpinites », Cassiophyllum, Myrtus, Zizyphus, Rosa, Rubus, Pyrus, Boehmeria, Punica, and Olea.	Lacustrine- palustrine	Late Eocene- early Oligocene	Bozukov et al. (2009)
7	Henisbury	England	Leaf	Ferns, palms, Doliostrobus, Pinus, Pityospermum, Quasisequoia, Daphnogene Neolitsea, Palaeocarya, Hooleya Quercus sp.? Fagus sp.?, Raskya, Zanthoxylum, Zizyphus, Dinelta.? Byttmerionsis	Lacustrine- palustrine	Latest Eocene	Hayes and Collinson (2014)
8	Sambian peninsula Kaliningrad district	Russian	Flower, fruits and leaves	Pinus, Taxodiaceae, Lauraceae, Anacardaceae, Hamamelidaceae, Araliaceae	Coastal?	Late Eocene	Akhmetiev (2010)
9	Tatra Mountains	Poland	Leaf	Eotrigonobalanus, Daphnogene, Nypa, Quercus	Coastal	Latest Eocene	Worobiec et al.

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 *Doliostrobus*. 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, Bulgaria (Bozukov et al., 2009), *Doliostrobus* in Kučlin (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 Kučlin, Czech Republic (Kvaček and Wilde, 2010) and presumably in the Isle of Wight, England (Hayes and Collinson, 2014). As matter of fact *Doliostrobus* 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 (Cfatype 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 *Doliostrobus taxiformis, Sequoia*-like plants, *Sabal major, Daphnogene* sp., *Byttneriopsis* sp., *Myrica* sp., *Comptonia difformis, Osmunda* aff. *pars-chlugiana* 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. *Doliostrobus*). 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. *Doliostrobus*, 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.

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#### **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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