Origin, evolution and decline of European mangroves: the Cenozoic paleobotanical record

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Abstract

This paper reviews available paleobotanical evidence (pollen and macrofossils) from 114 European sites to infer Cenozoic mangrove dynamics. European mangroves originated at the Paleocene/Eocene boundary in western Europe as relatively diverse communities comprising seven true-mangrove taxa, including the major mangrove-forming elements Rhizophoraceae, *Avicennia* and *Nypa*. Some taxa arrived from the Indo-West Pacific (IWP) via the Tethyan seaway, while others evolved locally. The occurrence of *Pelliciera*, the only element from the Atlantic–East Pacific (AEP) region, remains questioned. Maximum expansion and diversity occurred during the Early–Middle Eocene (Ypresian–Bartonian), coinciding with Cenozoic thermal and eustatic maxima. The European mangrove flora was completed following the arrival of seven additional true-mangrove and associate elements; however, four of these, including Rhizophoraceae, disappeared by the Lutetian. A first diversity crisis occurred during the Priabonian, when *Nypa* became the sole European mangrove component. This coincided with the cooling trend preceding the abrupt Eocene/Oligocene cooling and its associated eustatic drop, which restricted mangroves to southern refugia in Anatolia and Iberia. Following the definitive disappearance of *Nypa* during the Aquitanian, a mangrove recovery—in terms of geographical range but not diversity—culminated during the Middle Miocene Climatic Optimum. During this Langhian maximum, *Avicennia*-only mangroves formed an extensive arc across the northern proto-Mediterranean and Paratethys. A second crisis during the Messinian Salinity Crisis almost eradicated European mangroves, forcing *Avicennia* into a Black Sea refugium before its final disappearance during the Pliocene. Finally, pending uncertainties and knowledge gaps are identified, and further studies are proposed to address them.

Keywords

Mangroves, Europe, Cenozoic, biogeography, diversification, extinction, paleoclimates

1. Introduction

Mangroves are land–sea transitional, forested wetland ecosystems that form the distal continental fringe marking the reach of normal tides along tropical and subtropical coasts, between approximately 30° N and 30° S worldwide (Spalding et al., 2010) (Fig. 1). Mangroves play a key role in safeguarding coastlines and in maintaining continental and marine biodiversity and ecological dynamics (Nagelkerken et al., 2008), as well as in global biogeochemical cycles—with particular emphasis on the carbon cycle—as the major blue-carbon ecosystem that help mitigate global warming (Fest et al., 2022). Nevertheless, mangroves face significant threats as one of the most endangered ecosystems globally (Worthington et al., 2020).

Mangrove forests are structured around a few dominant species, known as mangrove-forming trees, which shape the physical structure of the community and without which mangrove ecosystems cannot exist. These mangrove-forming species, also referred as major true-mangrove elements, are exclusive to mangrove communities and usually form pure stands. Minor true-mangrove elements are likewise exclusive to mangrove ecosystems but are less conspicuous, tend to occupy marginal environments, and rarely form pure stands. Both major and minor true-mangrove elements possess specialized morphological and physiological adaptations that enable them to survive in intertidal environments characterized by soft, anoxic substrates and variable water levels and salinity. A third category of mangrove elements are mangrove associates or species that commonly occur within mangrove communities but are not exclusive to them, and lack specialized adaptations to intertidal environments (Tomlinson, 2016).

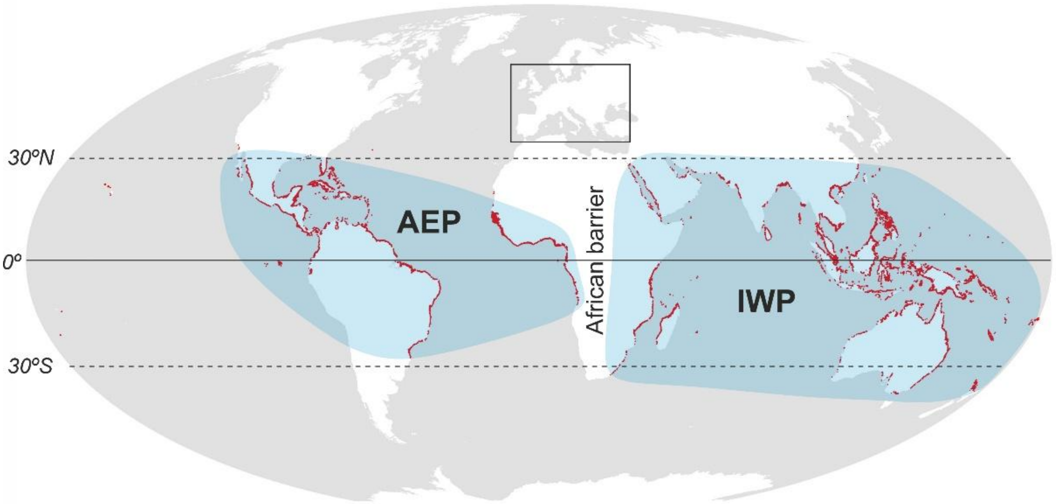

Figure 1. World map showing mangrove distribution (red coastal fringes), the major Atlantic–East Pacific (AEP) and Indo–West Pacific (IWP) biogeographic regions, and the African barrier that separates them. The study area of this paper is highlighted by a box. Modified from Rull (2023a).

Among mangrove-forming elements, only *Rhizophora* and *Avicennia* are globally distributed, although their species exhibit a disjunct distribution across two main biogeographical regions: the Atlantic–East Pacific (AEP) and the Indo–West Pacific (IWP) regions, which are separated by the African barrier (Tomlinson, 2016; Duke, 2017) (Table 1, Fig. 1). The other mangrove genera are restricted to either the AEP or the IWP regions, except the fern genus *Acrostichum*, which is also cosmopolitan. The origin of these global biogeographical patterns has been linked to either dispersalist or vicarianist processes. Dispersalists have suggested that the ancestors originated in the more diverse IWP region and dispersed to the AEP region (Van Steenis, 1962), whereas vicarianists proposed that mangroves evolved during the Late Cretaceous along the coasts of the pantropical Tethys Sea and later diversified following the closure of this sea by the African barrier (McCoy & Heck, 1976; Ellison, 1999). The timing of the IWP–AEP divergence varies among authors, ranging from the Late Cretaceous to the Oligocene (Sowunmi, 1986; Ellison et al., 1999; Plaziat et al., 2001; Duke, 2017; Srivastava & Prasad, 2019).

Table 1. Genera of true-mangrove and associate elements and their global biogeographical distribution. Based on Tomlinson (2016) and Duke (2017). Genera occurring in the European fossil record (this work) are indicated with an asterisk.

Type	**Atlantic-East Pacific (AEP)**	**Indo-West Pacific (IWP)**
Major (mangrove-forming)	*Rhizophora* (Rhizophoraceae)* *Avicennia* (Acanthaceae)* *Laguncularia* (Combretaceae)	*Rhizophora* (Rhizophoraceae)* *Avicennia* (Acanthaceae)* *Nypa* (Arecaceae)* *Lumnitzera* (Combretaceae) *Bruguiera* (Rhizophoraceae)* *Ceriops* (Rhizophoraceae)* *Kandelia* (Rhizophoraceae)* *Sonneratia* (Sonneratiaceae)*
Minor	*Acrostichum* (Pteridaceae)* *Conocarpus* (Combretaceae) *Pelliciera* (Tetrameristaceae)*	*Acrostichum* (Pteridaceae)* *Excoecaria* (Euphorbiaceae)* *Pemphis* (Lythraceae) *Camptostemon* (Malvaceae) *Xylocarpus* (Meliaceae)* *Osbornia* (Myrtaceae) *Aegialitis* (Plumbaginaceae)* *Aegiceras* (Primulaceae)* *Scyphiphora* (Rubiaceae)*
Associates	*Tabebuia* (Fabaceae) *Mora* (Fabaceae) *Muellera* (Fabaceae) *Crenea* (Lythraceae) *Pavonia* (Malvaceae)	*Brownlowia* (Malvaceae)* *Heritiera* (Malvaceae)* *Acanthus* (Acanthaceae) *Dolochandrone* (Bignoniaceae) *Cynometra* (Fabaceae) *Diospyros* (Ebenaceae) *Barringtonia* (Lecythidacae)

Rhizophora has been used as a guide genus to study the origin and evolution of mangroves through molecular phylogenetics and phylogeography. These studies have revealed that both vicariant and dispersalist processes are required to explain the current biogeographical pattern of *Rhizophora* (Lo et al., 2014; Takayama et al., 2021). However, the timing of speciation remains unresolved, with estimates ranging widely from the Eocene to the Miocene. Duke (2017) proposed the occurrence of two radiations: the first, in the Oligocene, would have caused the initial split into two *Rhizophora* lineages (AEP and IWP), whereas the second, in the Mio–Pliocene, would have produced the extant species. While allopatric diversification following the closure of the Tethys Sea is a classical biogeographical explanation commonly accepted for a wide range of plant and animal taxa (e.g., Celâl Şengör & Saniye, 2009; Zhao et al., 2022), the role of long-distance dispersal, especially across the Atlantic Ocean, is often overlooked. However, Van der Stocken et al. (2019) showed that global-scale dispersal is actually an effective diversification mechanism for mangroves and reconstructed dispersal routes both between and within the AEP and IWP regions.

Mangrove communities are typically arranged in a land–sea zonal pattern as a result of species-specific (idiosyncratic) environmental requirements related to meso-topography, flooding regime, water salinity, substrate type and disturbance intensity, as well as intra-community biotic interactions, notably facilitation and competition (Lugo & Snedaker, 1974; Rabinowitz, 1978; Woodroffe, 1982; Smith, 1992; Sousa et al., 2007; Dangremond et al., 2015). Generally, mangrove-forming trees—particularly *Avicennia* and *Rhizophora*—occupy the seaward fringe that is regularly flooded by marine waters, whereas minor true-mangrove elements, especially *Excoecaria, Nypa* and *Acrostichum*, prefer back-mangrove environments inundated by brackish waters (Thanikaimoni, 1987). Within the seaward zone, internal zonation is also observed, with *Avicennia* occupying more external positions and *Rhizphora* more internal ones (Giesen et al., 2006). *Pelliciera* typically thrives beneath the *Rhizophora* canopy, where it is protected from direct sunlight and highly saline substrates (Dangremond et al., 2015). A typical land–sea zonal pattern within the more diverse IWP region, may be described as follows: a seaward zone with *Rhizophora*, *Sonneratia*, *Avicennia* and *Bruguiera*; a middle zone with *Xylocarpus*, *Excoecaria*, *Ceriops*, *Heritiera* and *Lumnitzera*; and a landward zone, or back-mangrove, with *Acrostichum* and *Nypa* (Piyakarnchana, 1980; Giesen et al., 2006). Minor internal variations may exist depending on local features. Continental environments beyond the back-mangrove swamp are usually freshwater-influenced and are dominated by mangrove associates and non-mangrove flora.

Currently, Europe is devoid of mangroves due to its latitude (>35° N) and associated environmental constraints, notably temperature. However, these ecosystems were present during earlier Cenozoic times, particularly during warmer intervals such as the Paleocene/Eocene Thermal Maximum (PETM; 56 Ma), the Early Eocene Climatic Optimum (EECO; 54-49 Ma) and the Middle Miocene Climatic Optimum (MMCO; 17-14 Ma) (Popescu et al., 2021). During the PETM and the EECO, European mangroves were diverse and included the mangrove-forming elements *Avicennia*, Rhizophoraceae, *Sonneratia*-type and *Nypa*, along with minor true-mangrove components such as *Aegialitis*, *Excoecaria*, *Pelliciera* and *Xylocarpus*, as well as associate taxa including *Brownlowia* and *Heritiera*. These mangroves extended as far north as 65° N. In contrast, MMCO mangroves were restricted to latitudes below 35° N along the proto-Mediterranean and Paratethyan coasts and were dominated by a single mangrove-forming tree, *Avicennia*, with no minor true-mangrove elements or associated flora.

Other records are available within global Cenozoic reconstructions that focus on specific European regions or time slices, or emphasize particular mangrove taxa that have become iconic, notably *Nypa* (e.g., Tralau, 1964; Ellison et al., 1999; Plaziat et al., 2001; Collinson & Hooker, 2003; Jiménez-Moreno & Suc, 2007; Kayseri-Özer, 2013; Biltekin et al., 2015; Duke, 2017; Suc et al., 2018; Srivastava & Prasad, 2019; Popescu et al., 2021; Pocknall et al., 2023). However, many mangrove records have not been included in these syntheses and remain as local reports that have not been integrated into broader biogeographical or biostratigraphical frameworks. In addition, intervals between the better-known global warming phases – notably the Mid-Late Eocene to Oligocene and the Late Miocene to Pliocene – have received little attention and have not been incorporated into continental-scale reconstructions. Consequently, the European Cenozoic mangrove record is taxonomically and spatiotemporally fragmented, and a comprehensive synthesis has yet to be attempted.

This paper reviews Cenozoic mangrove records from the European continent based on original research literature, with an emphasis on pollen and plant macrofossils. Previous investigations of Paleogene and Neogene mangroves worldwide have shown that reliance solely on reviews and syntheses may lead to biogeographical and evolutionary inconsistencies (Rull, 2025). The primary aim of this study is to assemble the available evidence and provide a comprehensive and continuous spatiotemporal overview of mangrove evolution, biostratigraphy and biogeography throughout the Cenozoic. It is hoped that this synthesis will pave the way toward a more precise and detailed understanding of the origin, evolution and declines of European mangroves and will help identify promising avenues for future research. Previous analyses using the same methodology in other mangrove regions have proven effective in advancing knowledge of mangrove dynamics, providing valuable insights to inform conservation strategies (Rull, 2024).

2. The dataset

The geographical scope of this review encompasses the part of the present-day European continent that contains fossil records of mangrove vascular plants, approximately bounded between 34° and 52° N and 10° W to 35° E (Fig. 1). For biogeographical consistency, this area includes the Anatolian Peninsula (currently Turkey), irrespective of current political boundaries.

Data for this analysis were obtained from the original references rather than from existing syntheses. Searches were conducted within these syntheses as well as in standard bibliographic databases, mainly Web of Science (https://clarivate.com/), Scopus (https://www.scopus.com/), Google Scholar (https://scholar.google.com/), OpenAlex (https://openalex.org/), The Lens (https://www.lens.org/) and BASE (https://www.base-search.net/). Papers published in the grey literature – proceedings, local journals, theses, internal reports, etc. – or in journals that have since been discontinued were identified through the reference lists of syntheses and other papers citing them, as well as through additional searches in Google Scholar. In a number of cases, especially in older literature, the original papers were not available or very difficult to obtain, and the data were retrieved from other papers, provided that full information on the corresponding records was available (e.g., Tralau, 1964 for *Nypa*). The data were not reinterpreted, and the original information on age, location and taxonomy was reported. The dataset obtained is not necessarily exhaustive, especially with respect to older references, but is sufficiently representative to provide a spatiotemporally comprehensive view of mangrove origin and evolution across the present European continent.

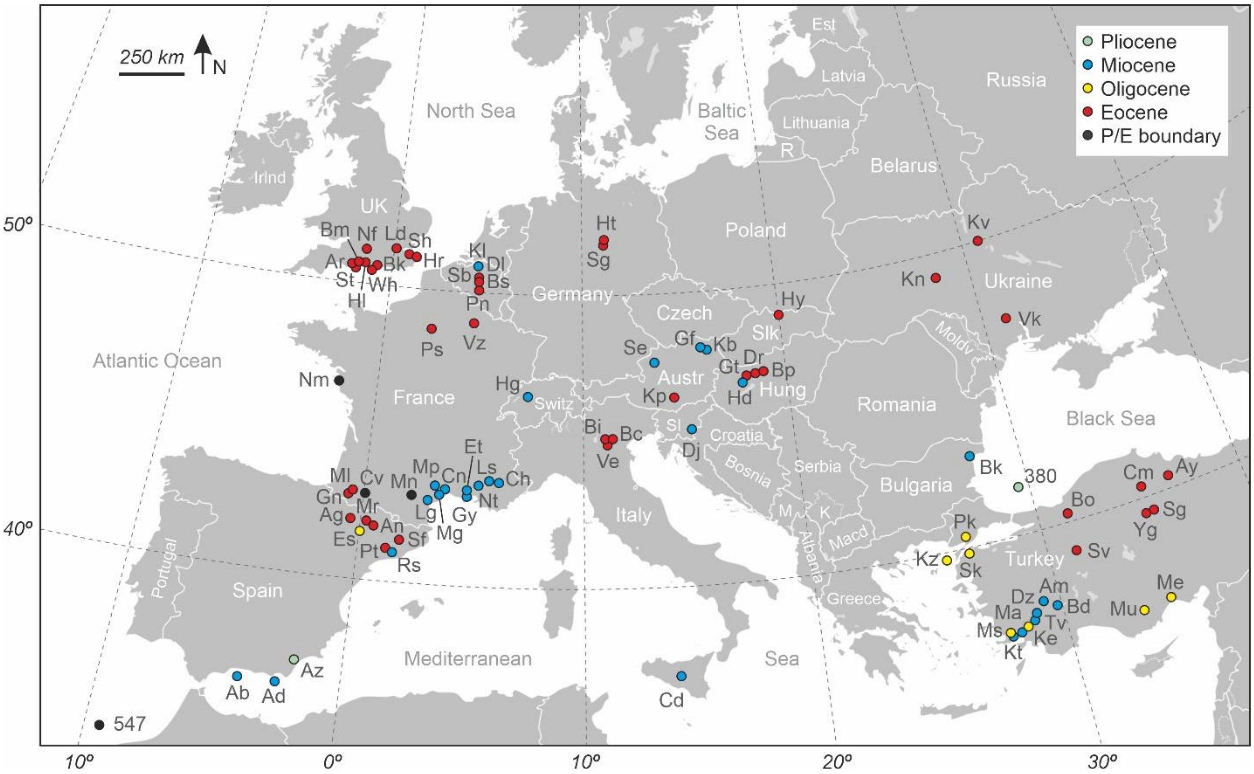

Figure 2. Map showing the area covered by this study and the localities with fossil mangrove records, indicating the geological epoch to which they correspond (abbreviations as in Table 2).

When geographical coordinates were not provided in the original references, the locality was determined using Google Earth. When two or more localities were in close proximity and shared the same mangrove taxa, the name and location of one site were provided, and the others were listed below in Table 2 (e.g., Paris, Issy, Vanves).

The fossils considered include pollen and macroremains (e.g., roots, wood, leaves, fruits), or their corresponding impressions or molds, from vascular plants whose nearest living relatives (NLRs) belong to the genera listed in Table 1 as major and minor true-mangrove elements and their associated taxa. In some cases, fossils were identified in the original literature by their NLRs (e.g., *Avicennia*), whereas in others the fossil form-genus was used (e.g., *Spinizonocolpites* for *Nypa*). In this review, the NLR names are used for consistency and to improve accessibility for non-specialists.

A number of pollen records lack descriptions and images that would allow verification of their taxonomic identity, which has been considered a drawback in mangrove data compilations (Rull, 2025). In contrast, for macroremains, the provision of morphological descriptions and images of the identified material is more common. Quantitative data (e.g., pollen percentages) are seldom available, especially in older records, where only presence/absence data are reported. This limitation hampers community-level reconstructions, particularly for mangroves (Rull, 2022), and reduces the interpretative value of presence/absence data, especially in the case of single-grain records, from which the occurrence of mangrove communities cannot be inferred. Therefore, the dataset compiled here should be considered evidence for the occurrence of mangrove taxa rather than of mangrove communities as a whole. Qualitative evidence is considered a reliable proxy for the presence of mangrove communities when several mangrove taxa coexist, especially if they are mangrove-forming tree taxa.

The latest version of the International Chronostratigraphic Chart (Cohen et al., 2013; v. 2024-12) was used. Numerical radiometric dates are provided only in the most recent papers; hence, ages in Ma could not be used to compare or group fossil records. The minimum geochronological unit available in most references is the Age (e.g., Ypresian, Chattian, Messinian). Therefore, this unit was selected to homogenize the entire dataset. In the case of the Eocene, references to the Early, Middle and Late Eocene have been taken to correspond to the Ypresian, Lutetian–Bartonian and Bartonian–Priabonian, respectively. For the Miocene, the subdivisions encompass the Early (Aquitanian–Burdigalian), Middle (Langhian–Serravallian), and Late (Tortonian–Messinian) Miocene. In a few cases, more imprecise dating is reported (e.g., Eocene, Middle–Late Pliocene); these records have been included in the general map (Fig. 2) and the dataset (Table 2) but were not used in the biogeographical and diversity analyses. Epoch and age boundaries are indicated using a slash (e.g., Paleocene/Eocene, Thanetian/Ypresian), whereas age ranges are expressed with a dash (e.g., Burdigalian–Langhian).

Global paleoclimatic trends were taken from Westerhold et al. (2020). Pollen- and macrofossil-based local and regional paleoclimatic estimates were not used due to methodological issues and to avoid circular reasoning; see Rull et al. (2024) and Rull (2026) for more details. Global sea-level changes were taken from Miller et al. (2020).

3. General observations

A total of 114 sites (83 when grouped by proximity) containing fossil evidence of mangrove vascular plants were identified (Fig. 2; Table 2). The most common evidence was pollen (65%), whereas macroremains represented 32% and the combination of pollen and macroremains accounted for only 4% of the records. A total of 12 mangrove taxa were identified, of which four (*Avicennia*, *Pelliciera*, Rhizophoraceae and Sonneratiaceae) are major true-mangrove elements; six (*Acrostichum*, *Aegialitis*, *Aegiceras*, *Excoecaria*, *Pelliciera* and *Xylocarpus*) are minor true-mangrove components; and two (*Brownlowia* and *Heritiera*) are associated members. The family Rhizophoraceae includes *Bruguiera*, *Ceriops* and *Rhizophora*, whereas the family Sonneratiaceae includes only *Sonneratia*-type. These taxa are considered at the family level because many papers report them in this form, owing to the difficulty of reliably distinguishing their genera using pollen morphology alone (Thanikaimoni, 1987). With the exception of the globally distributed genera *Avicennia* and *Rhizophora*, all other taxa belong to the present IWP biogeographical region, except *Pelliciera*, which is exclusive of the modern AEP flora.

A word of caution is pertinent regarding *Pelliciera*. This genus has traditionally been considered an exclusively Neotropical mangrove element (Rull, 2023b), and the occurrence of its fossil pollen outside the Neotropics during the Cenozoic has been called into question (Muller, 1981). A recent, careful revision of palynological evidence—using published pollen images and descriptions—concluded that European records of this pollen type, which occur mainly in the Paleogene, are unreliable or doubtful (Rull, 2025). Consequently, evolutionary and biogeographical interpretations based on these records remain questionable. This review includes several references previously used to dismiss the occurrence of *Pelliciera* in Europe; however, in other instances, verification was not possible due to a lack of pollen images and detailed descriptions. In these cases, the presence of *Pelliciera* cannot be unequivocally ruled out; consequently, these references were retained in the analysis. Nevertheless, interpretations based on the presence of this genus should be treated with caution.

The identified records ranged from the P/E boundary to the Pliocene, with the Eocene being the most represented epoch (52% of records), followed by the Miocene (30%), the Oligocene (10%), the P/E boundary (5%) and the Pliocene (2%). Geographically, the sites were distributed across the continent, showing three conspicuous SW–NE diagonals: a major trend crossing the entire continent from the Iberian Peninsula to Ukraine and two minor alignments—one extending from N France/S England to N Germany and another crossing the Anatolian Peninsula. A single record (Ypresian) was found outside this framework, in the Norwegian Sea at nearly 70° Lat N, between Norway and Iceland, containing pollen of *Avicennia*, *Excoecaria*, Rhizophoraceae, *Scyphiphora* and *Xylocarpus* (Popescu et al., 2021).

Table 2. European sites with paleobotanical records of Cenozoic mangroves (see Fig. 2 for location). Major true-mangrove elements, or mangrove-forming trees, are in boldM, macrofossils; P, pollen.

Map	Site	Country	Latitude	Longitude	Epoch	Age	Mangrove taxa	Fossil	References
Az	Cuevas de Almanzora	Spain	37°17’32”N	01°52’34”W	Pliocene	M-L Pliocene	***Rhizophora***	M	Sendra et al. (2020)
380	DSDP 380	Black Sea	42°05’56”N	29°36’49”E	Pliocene	Zanclean	***Avicennia***	P	Biltekin et al. (2015)
380	DSDP 380	Black Sea	42°05’56”N	29°36’49”E	Miocene	Messinian	***Avicennia***	P	Biltekin et al. (2015)
Cd	Capodarso	Italy	37°30’14”N	14°08’40”E	Miocene	Tortonian	***Avicennia***	P	Suc & Bessais (1999)
Bk	Balchik	Bulgaria	43°25’37”N	28°09’42”E	Miocene	Serravallian-Tortonian	***Avicennia***	P	Ivanov et al. (2007)
Ab	Alboran	Spain	36°38’00”N	04°13’23”W	Miocene	Serravallian-Tortonian	***Avicennia***	P	Jiménez-Moreno & Suc (2007)
Ad	Andalucia A1	Spain	36°38’00”N	04°13’23”E	Miocene	Serravallian-Tortonian	***Avicennia***	P	Jiménez-Moreno & Suc (2007)
Nt	La Motte d’Aigues	France	43°46'23"N	05°31'16"E	Miocene	Serravallian	***Avicennia***	P	Bessedik (1985)
Rs	La Rierussa	Spain	41°23’05”N	01°48’42”E	Miocene	Langhian-Serravallian	***Avicennia***	P	Bessedik (1985)
	Sant Pau d’Ordal		41°22'57"N	01°47'51"E					Jiménez-Moreno & Suc (2007)
	Vilobí del Penedès		41°23'20"N	01°39'43"E					
Dj	Dolnja Stara	Slovenia	45°53’49”N	15°17’33”E	Miocene	Langhian	*Xylocarpus?*	M	Koči et al. (2024)
380	DSDP 380	Black Sea	42°05’56”N	29°36’49”E	Miocene	Langhian	***Avicennia***	P	Billekin et al. (2015)
Lg	Lespìgnan	France	43°16'26"N	03°10'18"E	Miocene	L Burdigalian-Serravallian	***Avicennia***	P	Bessedik (1985)
	Saint-Gènies		43°20'39"N	03°12'57"E					
	Montady		43°20'02"N	03°07'23"E					
Ch	Châteaurédon	France	04°40’50”N	06°12’53”E	Miocene	L Burdigalian-Langhian	***Avicennia***	P	Châteauneuf et al. (2006)
Hd	Herend	Hungary	47°07’58”N	17°45’16”E	Miocene	L Burdigalian-Langhian	***Avicennia***	P	Nagy & Kókay (1991)
Ls	Les Mées	France	44°01’01”N	05°59’14”E	Miocene	L Burdigalian-Langhian	***Avicennia***	P	Jiménez-Moreno & Suc (2007)
Mp	Montpeyroux	France	43°41'43"N	03°30'23"E	Miocene	L Burdigalian-Langhian	***Avicennia***	P	Bessedik (1985)
Mg	Montagnac	France	43°28'51"N	03°29'01"E	Miocene	L Burdigalian-Langhian	***Avicennia***	P	Bessedik (1985)
	Loupian		43°26'54"N	03°36'53"E					
	Poussan		43°29'19"N	03°40'09"E					
	Montbazin		43°30'58"N	03°41'39"E					
	Issanka		43°28'44"N	03°41'57"E					
	Mèze		43°25'32"N	03°36'24"E					
Kt	Kultak	Turkey	37°04’42”N	27°56’24”E	Miocene	L Burdigalian-Langhian	***Avicennia***	P	Kayseri-Özer (2014)
							Acrostichum		
Et	Estagel	France	43°31’06”N	04°59’52”E	Miocene	Burdigalian-Langhian	***Avicennia***	P	Jiménez-Moreno & Suc (2007)
	Bayanne		43°31'39"N	04°57'15"E					
Gf	Göllersdorf	Austria	48°30’07”N	16°07’32”E	Miocene	L Burdigalian	***Avicennia***	P	Jiménez-Moreno et al. (2008)
Dl	Doel	Belgium	51°18’38”N	04°15’54”E	Miocene	Burdigalian	***Bruguiera***	M	Herman & Marquet (2007)
Kb	Korneuburg	Austria	48°20’41”N	16°19’53”E	Miocene	Burdigalian	***Avicennia***	P	Harzhauser et al. (2002)
Se	Strass	Austria	48°08’36”N	13°32’19”E	Miocene	Burdigalian	***Avicennia***	P	Jiménez-Moreno et al. (2008)
	Eberschwang		48°09'16"N	13°33'41"E					
Hg	Häutligen	Switzerland	46°51’26”N	07°36’19”E	Miocene	Burdigalian	***Avicennia***	P	Jiménez-Moreno (2005)
Gy	Pont-Gayé	France	43°24'20"N	04°59'09"E	Miocene	Burdigalian	***Avicennia***	P	Bessedik (1985)

	Les Tamaris		43°19'46"N	05°04'42"E					
Nt	Cap de Nautes Carry-le Rouet	France	43°46’22”N 43°19'51”N	05°31’16”E 05°09'08"E	Miocene	Aquitanian	***Avicennia***	P	Bessedik (1985)
Cn	Les Cévennes	France	43°36’49”N	03°50’52”E	Miocene	Aquitanian	***Avicennia***	P	Bessedik (1985)
Dz	Denizli Çardac	Turkey	37°46’59”N 37°49'30"N	29°05’47”E 29°40'06"E	Miocene	Aquitanian	*Acrostichum*	P	Kayseri-Özer (2014)
Ke	Kale	Turkey	37°27'05"N	28°48'47"E	Miocene	Aquitanian	*Acrostichum*	P	Kayseri-Özer (2014)
Tv	Tavas	Trukey	37°34'23"N	29° 4'17"E	Miocene	Aquitanian	*Acrostichum*	P	Kayseri-Özer (2014)
Bd	Burdur	Turkey	37°43’06”N	30°16’56”E	Miocene	Aquitanian	*Acrostichum*	P	Kayseri-Özer (2014)
Es	Estadilla	Spain	42°03’48”N	00°15’03”E	Oligocene	Chattian	*Acrostichum*	M	Moreno-Dominguez et al. (2016b)
Pk	Pullucku	Turkey	40°55’20”N	26°52’01”E	Oligocene	L Rupelian-Chattian	***Avicennia***	P	Isamoğlu et al. (2010)
Kz	Kuzu	Turkey	40°13’08”N	25°57’21”E	Oligocene	L Rupelian-Chattian	*Acrostichum* ***Nypa***	P	Akgün et al. (2013)
Sk	Şevketiye	Turkey	40°23’30”N	26°52’21”E	Oligocene	L Rupelian-Chattian	*Acrostichum* ***Nypa*** *Pelliciera*	P	Akgün et al. (2013)
Ms	Milas	Turkey	37°18’42”N	27°46’51”E	Oligocene	Rupelian	*Acrostichum* ***Avicennia*** *Pelliciera*	P	Kayseri-Özer (2013)
Ma	Muğla	Turkey	37°12’55”N	28°21’48”E	Oligocene	Rupelian	*Acrostichum* ***Avicennia*** *Pelliciera*	P	Kayseri-Özer (2013)
Me	Mersin	Turkey	36°38’43”N	34°38’29”E	Oligocene	Rupelian	***Nypa***	P	Kayseri-Özer (2013)
Mu	Mut	Turkey	36°38’43”N	33°26’13”E	Oligocene	Rupelian	***Nypa***	P	Kayseri-Özer (2013)
Bp	Budapest	Hungary	47°29’52”N	19°02’25”E	Eocene	Priabonian	***Nypa***	M	Trájer (2024)
Hy	Hruby Reigel	Poland	49°16’04”N	19°53’22”E	Eocene	Priabonian	***Nypa***	PM	Worobiec et al. (2015)
Nm	Noirmoutier	France	47° 00'40"N	02°13'11"W	Eocene	Bartonian-Priabonian	***Nypa***	M	Tralau (1964)
Bc	Bolca	Italy	45°35'46"N	11°12'16"E	Eocene	Bartonian-Priabonian	***Nypa***	M	Tralau (1964)
Bi	Breonio	Italy	45°37'26"N	10°54'12"E	Eocene	Bartonian-Priabonian	***Nypa***	M	Tralau (1964)
Ve	Verona	Italy	45°26'18"N	10°59'30"E	Eocene	Bartonian-Priabonian	***Nypa***	M	Tralau (1964)
Vk	Voznesensk	Ukraine	47°33'38"N	31°20'10"E	Eocene	Bartonian-Priabonian	***Nypa***	M	Kryshtofovich (1927) Tralau (1964)
Hl	Hordle	UK	50°45'42"N	01°37'19"W	Eocene	Bartonian-Priabonian	*Nypa*	M	Tralau (1964)
Pt	Pontils	Spain	41°28’39”N	01°23’14”E	Eocene	Bartonian	*Acrostichum* *Aegiceras* ***Avicennia*** *Brownlowia* *Heritiera* ***Nypa*** *Pelliciera*	P	Cavagnetto & Anadón (1995, 1996)

Ag	Arguis	Spain	42°18’53”N	00°26’21”W	Eocene	Bartonian	***Nypa***	M	Moreno-Dominguez et al. (2016a)
Sf	Sant Fruitós de Bages	Spain	41°35’03”N	01°52’29”E	Eocene	Bartonian	*Acrostichum* ***Nypa***	M	Biosca & Via (1988)
Gt	Gánt	Hungary	47°23’25”N	18°23’13”E	Eocene	Lutetian-Bartonian	*Pelliciera*	P	Bignot et al. (1985)
Bs	Brussels	Belgium	50°50'51"N	04°21'26"E	Eocene	Lutetian-Bartonian	***Nypa***	M	Tralau (1964)
Kv	Kiev	Ukraine	50°27’01”N	30°31’28”E	Eocene	Lutetian Bartonian	***Nypa***	M	Tralau (1964)
Bo	Bolu	Turkey	40°43’57”N	31°36’29”E	Eocene	Lutetian-Bartonian	*Acrostichum* ***Nypa***	P	Durak et al. (2025)
Bs	Brussels	Belgium	50°50'51"N	04°21'26"E	Eocene	Lutetian-Bartonian	***Nypa***	M	Tralau (1964)
Nf	New Forest	UK	51°25'00"N	1°42'31"W	Eocene	Lutetian-Bartonian	***Nypa***	M	Tralau (1964)
Bm	Bournemouth Hengistbury Head	UK	50°43'19"N 50°43'09"N	01°52'00"W 01°45'58"W	Eocene	Lutetian-Bartonian	***Nypa***	M	Tralau (1964)
Ps	Paris Issy Vanves	France	48°51’27”N 48°49'21"N 48°49'21"N	02°21’05”E 02°16'05"E 2°17'18"E	Eocene	Lutetian-Priabonian	***Avicennia*** ***Bruguiera****?* ***Nypa*** *Pelliciera*	P	Châteauneuf (1980) Tralau (1964)
Ht	Helmstedt	Germany	52°13’38”N	11°00’13”E	Eocene	Lutetian	***Avicennia*** ***Nypa*** ***Rhizophora***	P	Lenz & Riegel (2001) Lenz (2005) Lenz et al. (2021a)
Dr	Dudar	Hungary	47°18’23”N	17°56’32”E	Eocene	Lutetian	***Nypa***	M	Rásky (1948), Trájer (2024)
An	Arén	Spain	42°15’29”N	00°43’19”E	Eocene	Ypresian-Lutetian	***Nypa***	P	Haseldonckx (1973)
Sg	Schöningen	Germany	52°08’22”N	10°57’58”E	Eocene	Ypresian-Lutetian	***Rhizophora****?*	P	Riegel et al. (2012) Lenz et al. (2021b)
Bk	Bracklesham West Wittering	UK	50°46'03"N 50°46'50"N	00°52'04"W 00°53'45"W	Eocene	Ypresian-Lutetian	***Nypa***	M	Collinson & Cleal (2001)
Wh	Whitecliff Bay Portsmouth	UK	50°40'13"N 50°49'11"N	01°05'37"W 01°05'17"W	Eocene	Ypresian-Lutetian	***Avicennia*** ***Nypa***	PM	Collinson & Cleal (2001) Chandler (1964)
Sv	Sivrihisar	Turkey	39°27’05”N	31°32’16”E	Eocene	Ypresian-Lutetian	***Nypa***	P	Akkiraz et al. (2022)
Ar	Arne	UK	50°41'39"N	02°02'29"W	Eocene	Ypresian	*Acrostichum*	M	Collinson & Cleal (2001)
St	Studland	UK	50°38'31"N	01°57'10"W	Eocene	Ypresian	*Acrostichum*	M	Collinson & Cleal (2001)
Sh	Sheppey	UK	51°23'47"N	00°50'11"E	Eocene	Ypresian	***Ceriops*** ***Nypa***	M	Collinson & Cleal (2001)
Hr	Herne Bay	UK	51°22'15"N	01°07'40"E	Eocene	Ypresian	***Bruguiera****?* ***Nypa***	M	Collinson & Cleal (2001)
Ld	London Primrose Hill Highgate Archway Whetstone Haverstock Hill Clapham	UK	51°30'26"N 51°32'28"N 51°34'18"N 51°33'53"N 51°37'48"N 51°32'52"N 51°27'57"N	00°07'39"W 00°09'12"W 00°09'00"W 00°07'56"W 00°10'29"W 00°09'37"W 00°08'29"W	Eocene	Ypresian	***Avicennia*** ***Nypa***	PM	Chandler (1964) Tralau (1964)

Mr	Merli	Spain	42°20’32”N	00°29’05”E	Eocene	Ypresian	***Nypa***	P	Torricelli et al. (2006)
Vz	Verzenay	France	49°09’35”N	04°08’46”E	Eocene	Ypresian	*Acrostichum?* ***Bruguiera*** ***Nypa***	P	Gruas-Cavagnetto et al. (1980)
Kl	Kallo	Belgium	51°15'08"N	04°17'38"E	Eocene	Ypresian	***Avicennia*** ***Nypa*** **Rhizophoraceae** ***Sonneratia***-type	P	Popescu et al. (2021)
Ml	Morlaàs	France	43°19'42"N	00°14'17"W	Eocene	Ypresian	***Avicennia*** ***Nypa*** *Pelliciera* **Rhizophoraceae** ***Sonneratia***-type *Xylocarpus*	P	Popescu et al. (2021)
Gn	Gan	France	43°13'54"N	00°23'46"W	Eocene	Ypresian	*Aegialitis* ***Avicennia*** ***Nypa*** **Rhizophoraceae** ***Sonneratia****-type*	P	Popescu et al. (2021)
Kp	Krappfeld	Austria	46°50’34”N	14°29’00”E	Eocene	Ypresian	*Acrostichum* ***Avicennia*** ***Nypa***	P	Zetter & Hofmann (2001)
Sb	Schaerbeek Saint Gilles Saint-Josse-ten-Noode Melsbroek Uccle Jette	Belgium	50°51'51"N 50°49'37"N 50°50'59"N 50°54'55"N 50°47'54"N 50°53'07"N	04°22'24"E 04°20'40"E 04°22'23"E 04°28'43"E 04°22'33"E 04°19'02"E	Eocene	M-L Ecocene	***Nypa***	M	Tralau (1964)
Pn	Plancenoit	Belgium	50°39'43"N	04°25'43"E	Eocene	M-L Eocene	***Nypa***	M	Tralau (1964)
Yg	Yozgat	Turkey	39°49’16”N	34°48’31”E	Eocene	M-L Ecocene	***Avicennia*** *Pelliciera* ***Nypa***	P	Akkiraz et al. (2008)
Sg	Sorgun	Turkey	39°48’46”N	35°11’25”E	Eocene	M-L Eocene	***Avicennia*** ***Pelliciera*** ***Nypa***	P	Akkiraz et al. (2008)
Cm	Çorum	Turkey	40°32’59”N	34°57’13”E	Eocene	Eocene	*Acrostichum* ***Avicennia*** ***Nypa*** *Pelliciera*	P	Kayseri-Özer (2013)
Bs	Brussels	Belgium	50°50'51"N	04°21'26"E	Eocene	Eocene	***Nypa***	M	Tralau (1964)
Ay	Amasya	Turkey			Eocene	Eocene	*Acrostichum*	P	Kayseri-Özer (2013)

							Avicennia ***Nypa*** *Pelliciera*		
Dz	Denizli	Turkey	37°46’59”N	29°05’47”E	Eocene	Eocene	*Acrostichum* ***Pelliciera*** ***Nypa***	P	Kayseri-Özer (2013)
Am	Armutalani	Turkey	37°53'47"N	29°36'13"E	Eocene	Eocene	*Acrostichum* ***Pelliciera*** ***Nypa***	P	Kayseri-Özer (2013)
Bd	Burdur	Turkey	37°43’06”N	30°16’56”E	Eocene	Eocene	*Pelliciera*	P	Kayseri-Özer (2013)
Kn	Kalinovka	Ukraine	49°26'55"N	28°31'21"E	Eocene	Eocene	***Nypa***	M	Tralau (1964)
Nm	Noirmoutier	France	47° 00'40"N	02°13'11"W	P/E boundary	Thanetian/Ypresian	***Avicennia*** ***Nypa*** **Rhizophoraceae** *Xylocarpus*	P	Popescu et al. (2021)
Cv	Calavanté	France	43°12'31"N	00°10'59"E	P/E boundary	Thanetian/Ypresian	***Avicennia*** ***Nypa***	P	Popescu et al. (2021)
547	DSDP 547	Atlantic	33°46'50"N	09°20'59"W	P/E boundary	Thanetian/Ypresian	***Avicennia*** *Excoecaria* **Rhizophoraceae** ***Sonneratia*-type** *Xylocarpus*	P	Popescu et al. (2021)
Mn	Montaigne Noire	France	43°25’29”N	02°27’44”E	P/E boundary	Thanetian-Ypresian	***Nypa*** *Pelliciera* **Rhizophoraceae** **Sonneratiaceae**	P	Gruas-Cavagnetto et al. (1988)

4. Biogeographical patterns and diversity trends over time

The following sections describe the fossil records of Table 2 in chronological order by epoch and compare the geographical distribution of mangrove taxa with existing paleogeographical maps for each age. Paleogeographic maps were generated using GPlates v2.5.0, which reconstructs the past positions of present-day fossil sites for each geological age, using the Scotese (2016) PALEOMAP PaleoAtlas as the reference. Changes in diversity are expressed as the number of mangrove taxa (richness) recorded in each epoch.

4.1. First records

No reliable records of known mangrove components, as listed in Table 1, were found prior to the Paleocene/Eocene (P/E) boundary. Some authors have speculated about the possibility that certain Mesozoic fossils may correspond to plants living in environments similar to mangroves; however, no convincing evidence—or no evidence at all—has been provided. This is the case, for example, for some Jurassic and Cretaceous localities in France (Gomez et al., 2010; Peyrot et al., 2019), Poland (Kvaček et al., 2015; Chrząstowska et al., 2025), Germany (Schneider et al., 201), the Czech Republic (Uličny et al., 1997), Portugal (Guillaume et al., 2025) and Spain (Blain et al., 2010). Hofmann (1948) reported the occurrence of pollen and macrofossils of *Rhizophora*, *Avicennia* and *Xylocarpus* in the Upper Cretaceous Muntigl Flysch of Austria. However, the illustrations provided in support are of very poor quality, and the presence of mangrove communities cannot be reliably demonstrated based on this evidence.

Uncritical acceptance of these identifications may not only propagate the presumed occurrence of Cretaceous European mangroves but also support the interpretation of the Muntigl Flysch as having been deposited in mangrove environments (e.g., Just, 1951; Prey, 1952). Currently, however, this rock unit has been redescribed as the deep-water turbiditic Altlengbach Formation, and no mention is made of the occurrence of mangrove plant fossils (Egger, 1995; Egger & Schwerd, 2008; Egger & van Husen, 2009; Piller, 2022). Moreover, pollen analyses of other Upper Cretaceous sediments from Austria did not record any mangrove pollen or mention Hofmann's (1948) findings (Pavlishina et al., 2004; Mohamed & Wagreich, 2013). Finally, some *Nypa* records formerly attributed to the Cretaceous were reassigned to the Eocene by Tralau (1964), while other Cretaceous and Paleocene *Nypa* records were considered by the same author not to belong to this genus. Similarly, purported European fossil pollen records initially identified as *Rhizophora* or *Avicennia* were rejected due to morphological inconsistencies (Muller, 1981).

The oldest reliable records of known mangrove taxa roughly coincide with the PETM, near the Thanetian/Ypresian boundary (~56 Ma) (Gruas-Cavagnetto et al., 1988; Popescu et al., 2021). These records originate from France and an Atlantic marine borehole, all located in western Europe, and include most known mangrove-forming trees (*Avicennia*, *Nypa*, Rhizophoraceae, Sonneratiaceae), and three minor true-mangrove elements (*Pelliciera, Excoecaria* and *Xylocarpus*) (Table 2, Fig. 3). This assemblage strongly suggests the presence of typical mangrove communities in western Europe since the P/E boundary and represents the oldest reliable mangrove records available from this continent. These first mangroves emerged as already diverse communities, suggesting that their main components established themselves more or less simultaneously, rather than through a gradual colonization and community assembly process, such as that observed in other areas – for example the Neotropical region (Rull, 2024).

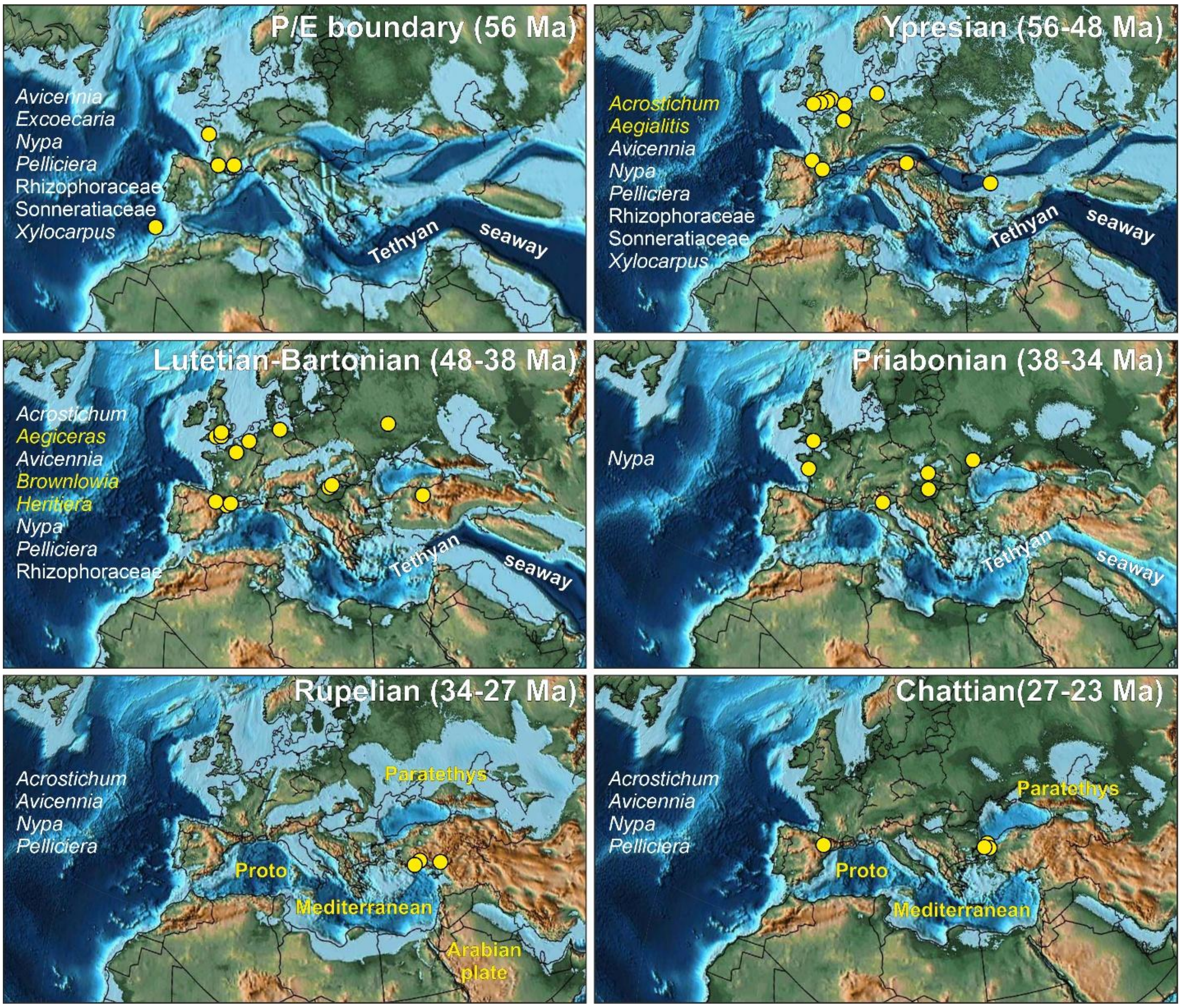

Figure 3. Paleogene records of European mangroves, sorted by geological age (see Table 2 for details), shown as yellow dots on palaeogeographical maps. Records with low-resolution dating (e.g., Eocene, Middle–Late Eocene) are not included. The mangrove taxa listed on the left correspond to those present during each age; newly appearing taxa are highlighted in yellow.

Geographically, these records occupy an intermediate position between the current AEP and IWP biogeographical regions (Fig. 1); however, most mangrove elements are characteristic of the IWP, with the exception of *Pelliciera*, which is currently restricted to the AEP (Table 1). As previously mentioned, *Rhizophora* and *Avicennia* are cosmopolitan genera, but the biogeographical origins of their European representatives are disparate, as demonstrated by phylogeographic studies. The ancestral *Rhizophora* clade originated in the IWP region, likely during the Paleocene, and dispersed westward to Europe before the Early Eocene along the Tethyan seaway, which connected the proto-Mediterranean Sea and the Indian Ocean, and remained open until the Late Eocene (Lo et al., 2014). The AEP species evolved by vicariance shortly after the closure of this passage, as the first Neotropical fossil records date from the Late Eocene (Rull, 2023b).

Avicennia followed a contrasting pattern, as its basal clade evolved in the central Tethys region—encompassing present-day Europe—and dispersed eastward to the IWP region. There, it diversified into the extant IWP species during the Late Miocene (Li et al., 2016). The fossil record suggests that the ancestral *Avicennia* clade has evolved locally in Europe and the Mediterranean area since the P/E boundary. As with *Rhizophora*, the AEP species of *Avicennia* evolved separately; however, this divergence occurred significantly later, as the first Neotropical records of the genus date from the Miocene (Rull, 2023c).

The oldest *Nypa* records date back to the Maastrichtian (Late Cretaceous) and appeared almost simultaneously in South America, Africa and Asia (Muller, 1981; Gee, 2001; Harley, 2006). Recent molecular phylogeographical studies date the differentiation of the *Nypa* clade to approximately 76 Ma (Wu et al., 2024). The closest early records to Europe were found in present-day Egypt during the Cretaceous/Paleocene transition (Gregor & Hagn, 1982; El-Soughier et al., 2015). Therefore, it can be inferred that European *Nypa* likely originated in the eastern proto-Mediterranean coasts before reaching the continent in the P/E boundary through the Tethyan seaway.

Regarding Sonneratiaceae, Duke (2017) places the first appearance of the *Sonneratia* precursor in the Early-Mid Eocene (55–40 Ma), whereas Muller (1981) situates the first *Sonneratia* species in the Early Miocene, both within the IWP region. A recent molecular phylogeographic study suggests that the genus *Sonneratia* emerged slightly after 40 Ma (Middle Eocene) (He et al., 2020). This situation mirrors that of *Rhizophora*; specifically, the precursor would have originated in the IWP region during the Early Eocene and subsequently dispersed to Europe via the Tethys seaway. Similar biogeographical and evolutionary patterns appear to hold for *Xylocarpus* and *Excoecaria*, with extant species emerging during the Early Miocene (Guo et al., 2018a, b; He et al., 2020).

In summary, some elements of the first European mangroves, or their precursors, evolved locally (*Avicennia*) in Europe, or within the neighbor Tethys coasts (*Nypa*), while others originated in the current Indo-West Pacific (IWP) region and migrated westward via the Tethys Seaway (Rhizophoraceae, Sonneratiaceae, *Xylocarpus*, *Excoecaria*) (Fig. 4). The case of *Pelliciera* is fundamentally distinct, as its oldest fossil records originate from the AEP region, specifically the Caribbean Basin and possibly Western Africa, during the Early to Mid-Eocene (Rull, 2022, 2023b, 2025). As noted previously, the occurrence of this genus in the European Cenozoic remains pending confirmation; consequently, any explanation regarding its potential origin remains speculative.

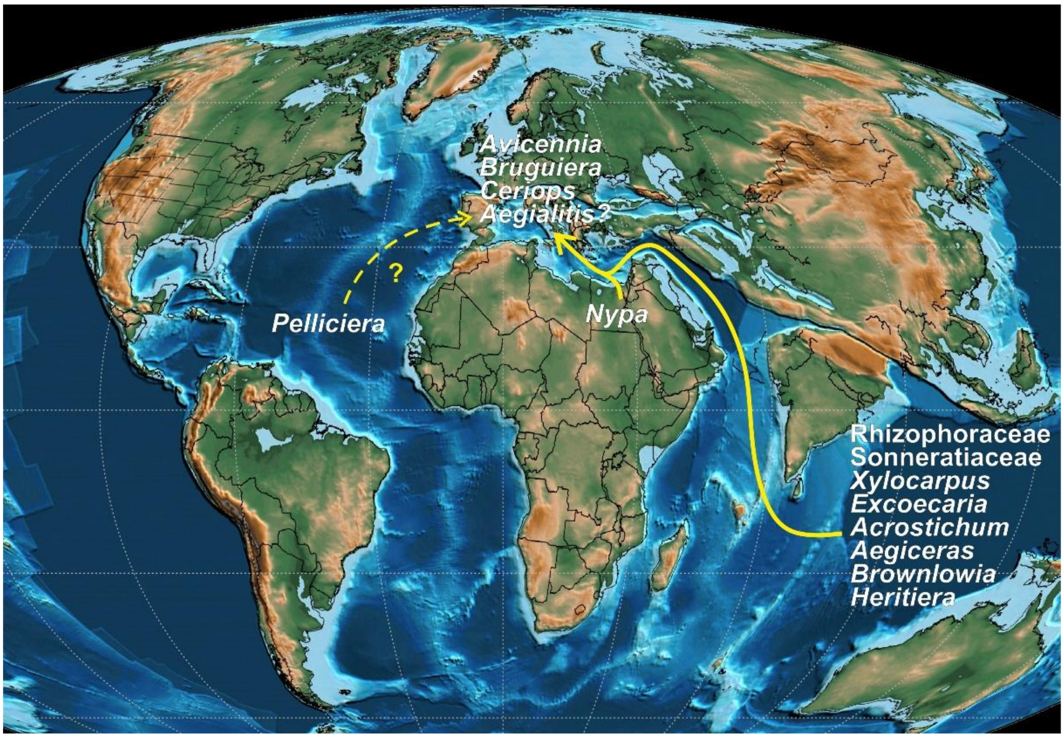

Figure 4. Early-Middle Eocene paleogeography (50-45 Ma) showing the most likely origin of the European mangrove elements and the potential dispersal routes (yellow arrows).

Mangrove diversity was nearly at its peak, with the highest richness of mangrove-forming elements such as Rhizophoraceae, *Avicennia*, *Nypa* and Sonneratiaceae coinciding with the PETM, when Cenozoic temperatures reached their maximum. The PETM was a short-lived warming event of approximately 200 ka duration during which global temperatures increased by 5–8 °C as a result of a massive release of carbon dioxide of volcanic origin into the oceans and the atmosphere and the subsequent greenhouse effect. This resulted in extinctions in a few groups of marine organisms, whereas in others the effects consisted of compositional turnovers and range shifts. Terrestrial organisms, especially vegetation, did not suffer mass extinctions but rather biogeographic rearrangements, notably range shifts toward the poles, changes in species composition and evolutionary change (McInerney & Wing, 2011). The occurrence of diversified mangroves in Europe during the PETM has been interpreted as part of this poleward extension of tropical species and communities (Popescu et al., 2021). During the PETM, global sea levels underwent a significant drop, from approximately 50 m to 0 m relative to present-day levels (Fig. 5).

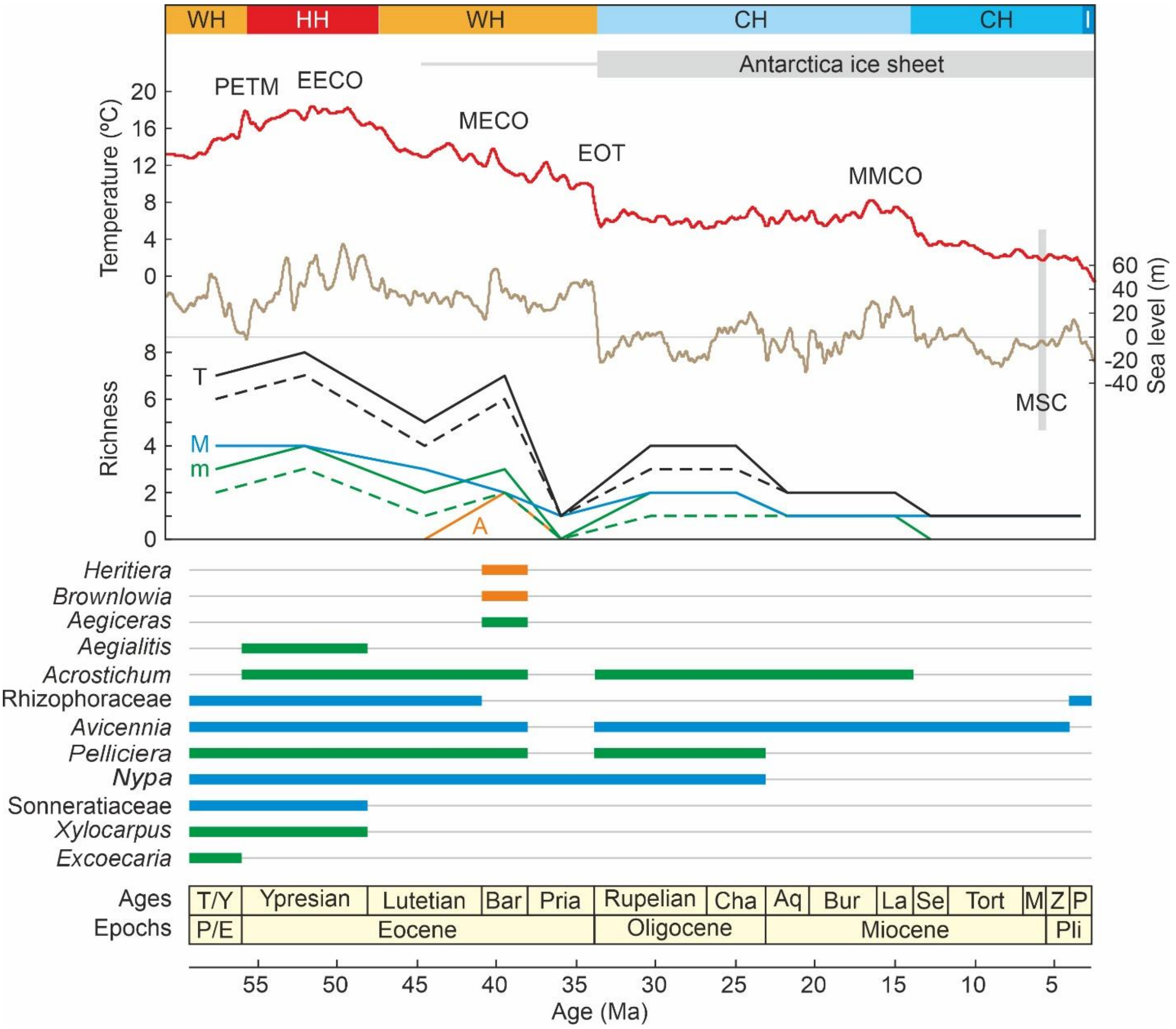

Figure 5. Geochronological ranges and richness shifts of total (T; black), major (M; blue), minor (m; green) and associate (A; orange) mangrove elements compared with global paleoclimatic (red) and eustatic (brown) trends. Broken lines are the richness trends excluding *Pelliciera*. WH, warmhouse; HH, hothouse; CH, coolhouse; I, icehouse. PETM, Paleocene/Eocene Thermal Maximum; EECO, Early Eocene Climatic Optimum; MECO, Middle Eocene Climatic Optimum; EOT, Eocene/Oligocene Transition; MMCO, Middle Miocene Climatic Optimum; MSC, Messinian Salinity Crisis. T/Y, Thanetian/Ypresian; P/E, Paleocene/Eocene; Bar, Bartonian; Pria, Priabonian; Cha, Chattian; Aq, Aquitanian; Bur, Burdigalian; La, Langhian; Se, Serravallian; Tort, Tortonian; M, Messinian; Z, Zanclean; P, Piacenzian; Pli, Pliocene. Temperature data from Westerhold et al. (2020) and sea-level data from Miller et al. (2020), both smoothed and expressed as anomalies with respect to the present (pre-industrial) values.

4.2 Eocene

4.2.1. Early

During the Ypresian, European mangrove communities were enriched by two rhizophoraceous mangrove-forming genera (*Bruguiera*? and *Ceriops*, which are recognizable using macrofossils) and two minor true-mangrove elements (*Acrostichum* and *Aegialitis*). In this way, European mangroves reached their maximum diversity during the Ypresian (Fig. 5). Of these new elements, only the fern *Acrostichum* has a cosmopolitan distribution. Its earliest known fossil occurrence is from the Maastrichtian (Late Cretaceous) of India (Bonde & Kumaran, 2002), but its IWP and AEP lineages diverged more recently, at the Eocene/Oligocene boundary (Zhang et al., 2016). This suggests that the Early Eocene European colonization was carried out by the IWP lineage, likely via westward Tethyan dispersal, similar to *Rhizophora* (Fig. 4).

Since *Bruguiera* and *Ceriops* belong to the family Rhizophoraceae and are currently restricted to the IWP region, colonization patterns similar to those of *Rhizophora* could be assumed a priori. However, the earliest fossil records of these genera are the Early Eocene (Ypresian) European occurrences listed in Table 2. Consequently, based on currently available data, these two genera may have originated and evolved in situ on the European continent. According to Muller (1981), the first fossil occurrences of *Aegialitis* are from the Middle Miocene of Borneo, whereas Duke (2017) places the origin of the genus in the modern-day Middle East between 40 Ma (Middle Eocene) and 25 Ma (Late Oligocene). A recent phylogeographical study suggests that this genus appeared during the Late Eocene (He et al., 2022). These findings contrast with the Early Eocene records from Europe compiled in this work. If these records are accepted, *Aegialitis* could have also originated in the study area, similar to *Bruguiera* and *Ceriops*.

Geographically, mangroves progressed toward the north (presently the UK, Belgium, and Germany) and the east (Austria and Anatolia) (Fig. 3). Climatically, the Ypresian was the warmest sustained age of the entire Cenozoic, defining a hothouse, ice-free Earth state that lasted for several million years, known as the EECO (Fig. 5). During the EECO, not only were global average temperatures ~18 °C higher than modern (pre-industrial) levels, but the latitudinal equator-pole gradient was also significantly reduced—a situation referred to as global climate equitability or an equable climate. For example, Greenwood & Wing (2011) estimated mean annual temperature (MAT) equator-pole gradients of approximately 30 °C to 10 °C for the EECO, compared to modern gradients of approximately 25 °C to -20 °C. The noted expansion and diversification of tropical mangroves in Europe is therefore consistent with this scenario, as previously observed by Popescu et al. (2021), who recorded mangrove communities near the North Pole at 80° latitude. According to these authors, a mangrove gradient existed at that time in the Northern Hemisphere, which they classified into three latitudinal belts: diversified and well-developed mangroves (<35° N), diversified but scrawny mangroves (35°–65° N), and impoverished *Avicennia*-only mangroves (70°–80° N). The EECO European mangroves fell within the second category. Sea levels remained consistently above modern values, reaching a peak of nearly 80 m during the EECO maximum (Fig. 5).

4.2.2. Middle

In the Middle Eocene (Lutetian–Bartonian), new taxa emerged—at that time belonging to IWP true mangroves (*Aegiceras*) and mangrove associates (*Brownlowia*, *Heritiera*)—while three other true-mangrove elements (Sonneratiaceae, *Xylocarpus*, *Excoecaria*) permanently disappeared from the study area (Fig. 5). The first records of *Brownlowia* correspond to the Paleocene of Borneo (Muller, 1981). The genera *Aegiceras* and *Heritiera* appeared in the Early Miocene (~20 Ma), though their precursors date from the Early to Mid-Eocene (55–40 Ma), also within the IWP region (Duke, 2017; He et al., 2020). Consequently, the arrival of these mangrove elements in Europe during the Middle Eocene was likely due to westward dispersal from the IWP via the Tethys Seaway, a pattern consistent with that of Rhizophoraceae, Sonneratiaceae, *Xylocarpus*, and *Excoecaria*.

Following these arrivals, the European Cenozoic mangrove flora was complete, as no further additions were recorded (Fig. 5). Therefore, three main groups of European mangrove elements can be identified according to their geographical origin (Fig. 5): the autochthonous component (*Avicennia*, *Bruguiera*, *Ceriops*, and possibly *Aegalitis*), the IWP component (Rhizophoraceae, Sonneratiaceae, *Xylocarpus*, *Excoecaria*, *Acrostichum*, *Aegiceras*, *Brownlowia*, and *Heritiera*), and the EAP component (*Pelliciera*). Given the questionable occurrence of *Pelliciera*, the IWP elements constitute the primary component of the European mangrove flora, followed by the autochthonous component.

Total diversity did not undergo significant changes, especially among true-mangrove elements (*Rhizophoraceae*, *Avicennia*, *Nypa*), which were accompanied by *Acrostichum* and *Pellicera*. These taxa ensured the continuity of mangrove communities across the continent. Geographical patterns remained similar to those of the Ypresian (Fig. 3), with the exception of a single incursion into eastern Europe (present-day Ukraine) under apparently continental conditions. Only *Nypa*, which is able to live in freshwater environments (Zhang et al., 2024), was recorded at this locality. Therefore, the occurrence of well-developed mangrove communities is unlikely. The same could be true for the continental Anatolian record, represented by *Nypa* and *Acrostichum*, which is another element typical of back-mangrove settings flooded by low-saline or fresh waters.

Some differences exist between the Lutetian and the Bartonian in terms of biodiversity, as the aforementioned true-mangrove elements disappeared during the former, while the associated genera emerged during the latter. The disappearance of *Sonneratia*, *Xylocarpus* and *Excoecaria* could be related to the declining temperature trend following the EECO, whereas the appearance of *Aegiceras*, *Brownlowia*, and *Heritiera*—which were restricted to the Bartonian—coincided with the short warming event known as the Middle Eocene Climatic Optimum (MECO) (Fig. 5). Global sea levels persisted consistently above modern values (~20–60 m) and the Tethyan seaway remained open during the Middle Eocene, favoring the immigration of IWP mangrove elements.

4.2.3. Late

The Late Eocene (Priabonian) represented a bottleneck for European mangroves, particularly regarding diversity. Indeed, all mangrove components disappeared except for *Nypa* (Fig. 5). While its geographical range experienced a minor reduction, it was not as significant as the depletion of diversity. The Tethyan connection with the IWP region remained open (Fig. 3), yet no new incorporations of mangrove elements were recorded. As a result, European mangroves were reduced to a latitudinal band of *Nypa*-only mangroves, stretching between the southern UK and the Alps.

Currently, pure *Nypa* stands occupy some back-mangrove environments flooded by brackish to nearly fresh water on the landward side of the mangrove. These stands can be very dense, forming true *Nypa* forests (Giesen et al., 2006). Another scenario in which *Nypa* may dominate is following a disturbance; as an aggressive invader, *Nypa* can replace previously diverse communities with monotypic forests, even at the mangrove forefront (Numbere, 2019). *Nypa* requires a salinity range of 0‰ to 10‰ for development, and salinities exceeding 10‰ inhibit germination (Zhang et al., 2024). Consequently, for *Nypa* to persist at the mangrove forefront, substantial freshwater input is required, such as in estuaries or regions with high precipitation. Current evidence is insufficient to decide which *Nypa*-only communities dominated the European Priabonian.

These patterns coincided with a progressive temperature decline that culminated in the global cooling and sea-level fall of the Eocene-Oligocene Transition (EOT) (Fig. 5). However, this decline is unlikely to have been a factor favoring *Nypa*'s survival while other mangrove taxa went extinct. Indeed, *Nypa* is considered a tropical megathermic element (Suc et al., 2018), less resistant to temperature drops than other mangrove taxa such as *Avicennia*, which is freeze-tolerant, or *Rhizophora*, which exhibits moderate chilling tolerance (Osland et al., 2017). With the available evidence, it would be premature to speculate about the potential causes of the Priabonian biodiversity crisis in the European mangroves.

The abrupt EOT cooling (~4 °C on average) and eustatic shift (~70 m on average) were global and intense; together with the establishment of permanent coolhouse conditions and the initiation of the Antarctic ice sheet (Fig. 5), they affected most planetary biomes. This led to significant biotic turnovers—driven by Late Eocene extinctions and Early Oligocene radiations—and biogeographical reorganizations (Coxall & Pearson, 2007; Hutchinson et al., 2021). Mangroves were significantly affected, as evidenced by the major Neotropical community turnover from *Pelliciera*-dominated Eocene mangroves to *Rhizophora*-dominated Oligocene mangroves (Rull, 2023a). In that case, the dominance shift from a megathermic (*Pelliciera*) to a more eurythermic (*Rhizophora*) element was consistent with the EOT cooling. However, no significant Late Eocene extinctions were recorded. This was also the case in Europe, as major disappearances had already occurred during the Priabonian. However, the disappearance of *Avicennia*, *Pelliciera* and *Acrostichum* was temporary, as these taxa reappeared in the Oligocene; in contrast, the Rhizophoraceae were absent until the Pliocene (Fig. 5). The impact of the EOT environmental shifts was more significant in biogeographical terms, as described in the following section.

4.3. Oligocene

The Oligocene (Rupelian and Chattian) witnessed a slight increase in diversity but a significant reduction in the geographical range of European mangroves. Indeed, the reappearance of *Avicennia*, *Pelliciera*, and *Acrostichum* was paralleled by the disappearance of mangrove communities from most of the continent, except for small areas primarily in the Anatolian Peninsula and NE Iberia (Fig. 3). The source for the reintroduction of these taxa after the Priabonian disappearance remains unknown; however, since the Tethyan connection with the IWP was closed by the collision between the Eurasian and the Arabian plates (Cai et al., 2021), it is possible they persisted unnoticed in areas lacking a fossil record. The general impression is that European mangroves were restricted to southern refugia during the Oligocene, likely due to EOT cooling. This pattern is consistent with the existence of Oligocene records from central Europe that are devoid of mangrove fossils (Maxwell et al., 2016).

The idea of the Anatolian region as a modern refugial area for Neogene tropical and subtropical plants in general was introduced by Biltekin et al. (2015). The distribution pattern of Oligocene mangroves reinforces the potential long-term refugial character of the region throughout the Cenozoic. During the Rupelian, all mangrove records were restricted to Anatolia, despite the occurrence of widespread shallow marine settings – such as the proto-Mediterranean and the Paratethys seas – across the present European continent (Fig. 3). This aligns with the idea of EOT cooling as the cause of mangrove contraction toward lower latitudes. In the Chattian, an Iberian locality was added for *Acrostichum*, which remains consistent with a latitudinal range shift. The possibility of the southern proto-Mediterranean coasts of Africa as potential mangrove refugia should not be disregarded, but no evidence is available to date.

4.4. Miocene

The most striking feature of Miocene European mangroves was the definitive disappearance of *Nypa* and *Pelliciera*. Consequently, Neogene mangroves were composed of *Avicennia* as the only mangrove-forming element accompanied in some sites by *Acrostichum*, a minor true-mangrove component (Fig. 5). *Avicennia* showed a continuous presence until the Pliocene, while *Acrostichum* disappeared in the Middle Miocene. The Tethyan passage, which had been closed during the Oligocene (Tofstein & Steiberg, 2020), remained so until the present.

During the Aquitanian, the biogeographical situation was very similar to the Oligocene, but with *Avicennia* and *Acrostichum* as the only mangrove components, growing in SE France and western Anatolia, respectively (Fig. 6). *Acrostichum* disappeared in the Burdigalian, while *Avicennia* dispersed into central Europe. During this same period, *Bruguiera* reached Belgium. At that time, global temperatures and sea levels tracked those of the Oligocene (Fig. 5).

During the Middle Miocene, The *Avicennia*-only European mangroves underwent a geographical expansion, forming an arc bordering the northern proto-Mediterranean-Paratethyan region (Fig. 6). A single *Acrostichum* record was found in Anatolia. This pattern was especially conspicuous during the Langhian, coinciding with the MMCO (Fig. 5). According to Popescu et al. (2021), these *Avicennia*-only mangroves marked the northernmost global Miocene mangrove boundary, reaching 35°N in Europe, and were similar to the impoverished mangroves that inhabited polar areas during the PETM-EECO under equable climatic conditions. However, evidence for similar mangroves outside Europe is not provided, which is insufficient to conclude that this was a global feature. Despite post-MMCO cooling, the situation remained similar during the Serravallian-Tortonian (Fig. 6), although the *Avicennia* range became more fragmented by the local extinction of central Europe representatives occurred between 18 and 14 Ma (Bitlekin et al., 2015). Global sea levels followed trends similar to temperature, with maximal values during the MMCO and a subsequent Serravallian decline (Fig. 5).

The Langhian *Avicennia*-only mangroves have sometimes been compared with modern Middle Eastern mangroves along the Red Sea and Persian Gulf coasts, which are also dominated by *Avicennia* with only occasional presence of *Rhizophora* (e.g., Jiménez-Moreno & Suc, 2007; Suc et al., 2018). However, these extant mangroves are an anomaly shaped by extreme environmental conditions—aridity, hypersalinity, and low sediment supply—rather than a latitudinal feature; therefore, they cannot be considered reliable modern analogues for the Middle Miocene European mangroves (Rull et al., 2025).

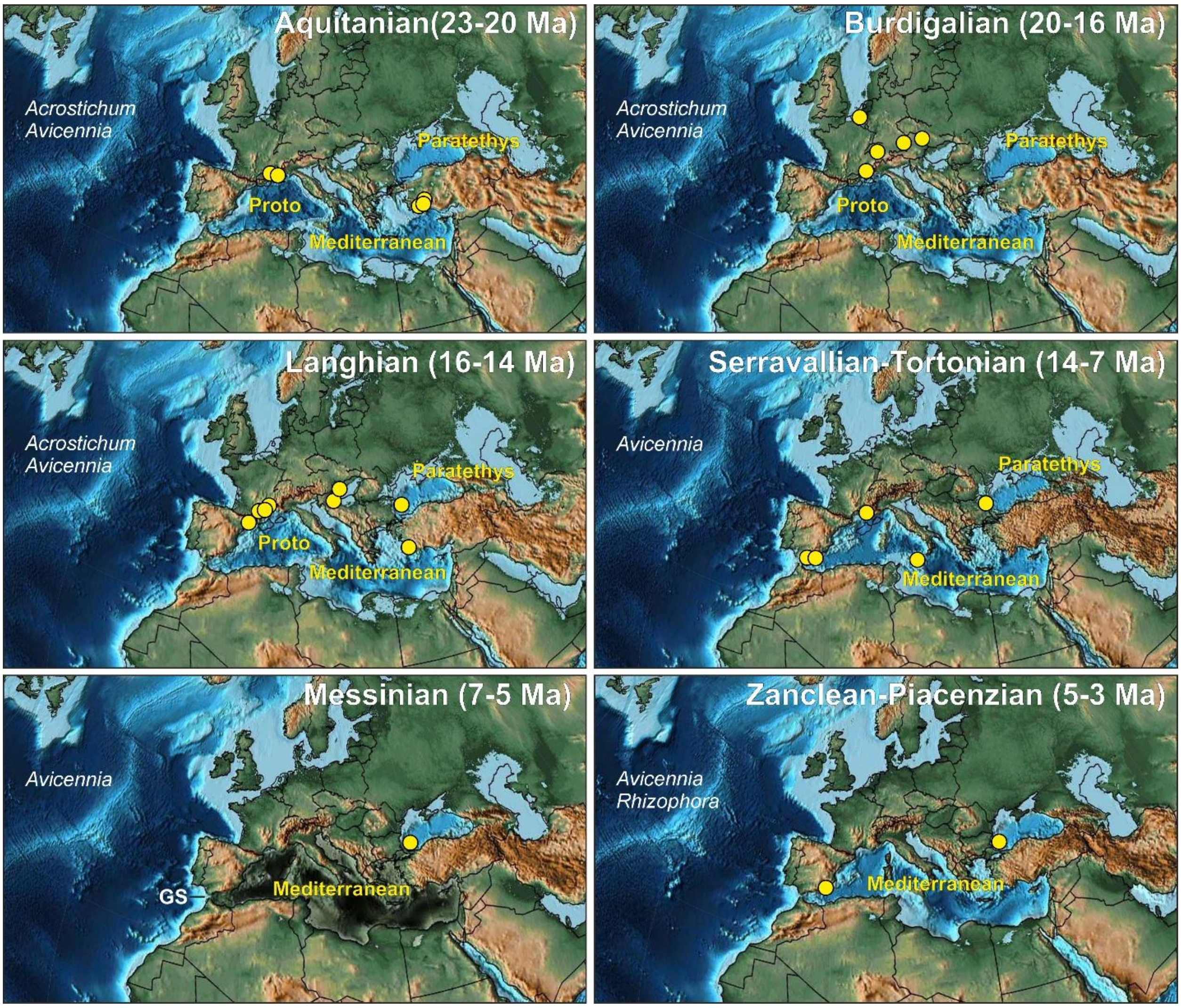

Figure 6. Neogene records of European mangroves, sorted by geological age (see Table 2 for details), shown as yellow dots on palaeogeographical maps.The mangrove taxa listed on the left correspond to those present during each age. GS, Gibraltar Straight.

The most drastic reduction of European mangroves occurred during the Messinian, when only a single record from the western Black Sea is available (Fig. 6). This coincided with the Messinian Salinity Crisis (MSC), during which the Mediterranean Sea became almost completely desiccated starting at approximately 6 Ma, following its disconnection from the Atlantic Ocean at the Strait of Gibraltar (Krijgsman et al., 1999). The MSC represented a regional anomaly within a period of sea-level values comparable to present-day levels. The consequences of this event for the marine biota were dramatic, resulting in a species turnover of nearly 70% and the survival of only ~90 endemic species, while approximately 700 other endemics disappeared (Agiadi et al., 2024). *Avicennia*, the only true-mangrove element existing at the time, disappeared from the continent and the Mediterranean region, but survived in a Black Sea refugium situated close to the Anatolian Peninsula (Biltekin et al., 2015). This is the minimum extent of European mangroves throughout their history, in both biogeographical and biodiversity terms.

4.5. Pliocene

During the Zanclean, the Mediterranean was replenished after reconnecting with the Atlantic Ocean (Krijgsman et al., 1999). The Black Sea refugium for *Avicennia* persisted, and a new record of *Rhizophora* appeared during the Piacenzian of SE Iberia (Figs. 5 and 6). This latter *Rhizophora* record is puzzling, as it represents a reappearance following its disappearance in the Lutetian. The mangrove-forming nature of *Rhizophora* suggests that communities dominated by this genus actually grew in the Iberian Pliocene. However, its biogeographical origin is difficult to ascertain. As with the *Pelliciera* pollen mentioned above, this record—based on macrofossil molds and impressions—must be carefully analyzed to confirm the taxonomic identification, given its potential impact on mangrove biogeography. It is difficult to explain how *Rhizophora* mangroves could have survived unnoticed along the Mediterranean coasts for ~40 Ma. Another possibility is that *Rhizophora* recolonized the western Mediterranean coasts from the AEP region via transatlantic dispersal through the newly opened Gibraltar passage, which is situated very near the fossiliferous locality (Fig. 6). However, with the available evidence, neither hypothesis can be substantiated.

The potential occurrence of *Avicennia* pollen during the Pleistocene was mentioned by Biltekin et al. (2015), who found a single grain at 1.6 Ma in a Black Sea site but considered the record questionable. Therefore, based on the available information, the last mangrove records found in Europe correspond to the Pliocene.

5. Conclusions

A synthetic view of the analyzed records allows for the definition of several phases and events in the rise and fall of European mangroves during the Cenozoic:

P/E origin. According to the available evidence, Cenozoic European mangroves originated at the P/E boundary (~56 Ma), in Western Europe, as relatively diverse communities comprising four major (mangrove forming trees) and three minor true-mangrove elements. Four of these mangrove taxa (Rhizophoraceae, Sonneratiaceae, *Xylocarpus* and *Excoecaria*) were from the IWP region and reached Europe through the Thethyan seaway, whereas other two (*Avicennia* and *Nypa*) evolved locally or at the near Tethyan coasts. The potential occurrence of *Pelliciera*, restricted to the AEP region, has been questioned due to pollen identification issues.

Eocene expansion. Maximum geographical expansion and diversity occurred during the Early and Middle Eocene (Ypresian to Bartonian), when seven new mangrove taxa—five true mangroves and two associates—became established in Europe. Of these, four (*Acrostichum*, *Aegiceras*, *Brownlowia*, and *Heritiera*) arrived from the IWP through the Tethyan connection, while the other three (*Bruguiera*, *Ceriops*, and possibly *Aegialitis*) evolved locally. This completed the European mangrove flora for the remainder of the Cenozoic. Four true-mangrove elements (*Rhizophoraceae*, *Sonneratiaceae*, *Xylocarpus*, and *Brownlowia*) were extirpated during the Middle Eocene (notwithstanding the Pliocene record for *Rhizophora*).

Envirnomental drivers. The origin and initial diversification of European mangroves occurred during the PETM and EECO, respectively, when global temperatures reached Cenozoic maxima and the latitudinal thermal gradient was significantly lower than today, allowing mangroves to reach polar areas. The expansion of European mid-latitude mangroves was characterized by global sea levels consistently above present-day levels, reaching values up to 80 m higher. This, combined with the persistence of the Tethyan seaway, likely facilitated westward colonization from the IWP region.

The first crisis. The first mangrove crisis occurred in the Late Eocene (Priabonian), when all mangrove taxa disappeared except *Nypa*, and the geographical range was slightly reduced latitudinally and longitudinally. This coincided with the temperature decline preceding the global EOT cooling and eustatic drop. The crisis intensified during the Oligocene, when mangroves—slightly more diverse than those of the Priabonian—were restricted mostly to an Anatolian refugial area, with an additional record in the Iberian Peninsula. Both were located at southern latitudes, coinciding with the onset of the "coolhouse" Earth state characterized by the formation of the Antarctica ice sheet. This situation extended into the Early Miocene (Aquitanian), by which time *Nypa* had definitively disappeared from Europe.

Miocene recovery. The Burdigalian (Early Miocene) represented a transitional phase characterized by the recolonization of Central Europe by *Avicennia*-only mangroves, culminating in the Langhian (Middle Miocene). During this interval, mangrove communities reached their Neogene maximum extent, forming a characteristic arc across the proto-Mediterranean and Paratethyan regions. These were taxonomically similar to the near-polar mangroves documented during the PETM-EECO. This Neogene maximum would have marked the northernmost boundary of mangroves at that time and coincided with the MMCO and a significant global sea-level rise.

Neogene decline and the second crisis. The Langhian mangrove arc was disrupted during the Serravallian–Tortonian (Middle to Late Miocene) by local *Avicennia* extinctions, coinciding with post-MMCO cooling. By this point, only *Avicennia* survived, as all other mangrove elements had already disappeared from Europe. A second crisis occurred during the Messinian (Late Miocene), specifically during the MSC, when *Avicennia*-only mangroves again took refuge near the Anatolian region—this time in the present-day Black Sea basin—where they persisted until the Pliocene before their final disappearance from the continent.

The *Rhizophora* mystery. An intriguing record is the finding of *Rhizophora* fossils in the Iberian Pliocene, as this taxon had disappeared from the European record in the Lutetian, nearly 40 Ma earlier. If confirmed, this record would necessitate a significant reconsideration of Cenozoic *Rhizophora* evolution and biogeography.

General trends. Overall, diversity trends tracked the long-term Cenozoic cooling of global temperatures—which remained consistently above present-day values—with the exception of the MMCO phase. During that interval, mangroves were dominated exclusively by a single tree genus (*Avicennia*) due to the region-wide extinction of all others. Sea levels remained consistently above present-day levels until the EOT, when they dropped abruptly and oscillated around modern values until the Pliocene, with significant increases during the Chattian and Langhian.

6. Further research

Beyond the synthesis of biogeographical and evolutionary patterns and processes provided here for European mangroves, several uncertainties and knowledge gaps remain to be addressed through future research. The following points represent a selection of relevant prospects derived from the preceding analysis of paleobotanical evidence, but others could be proposed.

Pre-Cenozoic mangroves. Although available evidence is insufficient to support their existence, the potential occurrence of Mesozoic mangrove communities remains an open question, and the possibility of eventually discovering unequivocal evidence should not be ruled out.

Initial mangrove establishment. The earliest mangrove records are from Western Europe, and a significant number of their components are of IWP origin. However, intermediate evidence for mangrove occurrence along the Tethyan seaway to substantiate progressive westward colonization is lacking.

Pelliciera. The potential occurrence of *Pelliciera* in Europe relies on pollen evidence that has been considered unreliable; however, the eventual discovery of macrofossils attributable to this AEP genus could resolve this uncertainty.

Priabonian diversity crisis. The disappearance of all Early–Middle Eocene mangrove elements except *Nypa* prior to the EOT remains to be explained in terms of environmental drivers. Furthermore, the specific environments in which *Nypa*-only mangroves developed during the Priabonian remain a pending issue.

Oligocene refugia. The hypothesis that mangroves persisted in southern refugia, or were displaced to lower latitudes following EOT cooling and the associated eustatic fall, could be tested by investigating additional localities along the present-day northern and southern Mediterranean coasts.

Avicennia mangroves. The Middle Miocene *Avicennia*-only mangroves have been well documented in Europe during the MMCO. Determining the presence or absence of similar mangroves at equivalent latitudes on other continents is required to test whether this was a global latitudinal feature.

Pliocene *Rhizophora*. The identification of Pliocene *Rhizophora* mangroves beyond those documented in SE Iberia is essential to fully understand the biogeography and evolution of this genus.

Quantitative approach. Generally, the use of quantitative studies and their comparison with modern analogues is recommended as the optimal methodology for community reconstruction. This approach is particularly effective when applied to the pollen record.

A final reflection that is often overlooked seems pertinent. As in any paleontological study based on literature-derived databases with a strong taxonomic component, the reliability of original fossil identifications is a paramount factor. Assessing this reliability is not always possible due to the lack of primary taxonomical evidence—notably images and descriptions—in many original studies. In some instances, a thorough review of this type reveals the main limitations of the gathered data. This is the case, for example, of *Pelliciera*, a characteristic Neotropical mangrove genus with purported Cenozoic fossil representatives in North America, Africa, and Europe. Only a small proportion of these records have withstood rigorous taxonomic analysis, especially in Europe, where none could be considered a reliable *Pelliciera* representative (Rull, 2025). Similar examples are not uncommon, especially in the case of pollen (e.g., Muller, 1981; Plaziat et al., 2001; Graham, 2006).

Performing a similar analysis for all taxa across all settings and geochronological units would be an overwhelming task, largely due to the scarcity of images and descriptions in the original literature. This is a drawback in this study and in most reviews and meta-analyses of this type, which must be kept in mind not only as a limitation but as an incentive to improve taxonomic databases. The use of original references is also recommended, as practiced in this work, to avoid relying on reviews and discussions that merely list taxonomic names. This is not a matter of a lack of trust, but rather of scientific rigor.

Despite these methodological constraints, it is hoped that this synthetic review helps set the foundation for a better understanding of the origin, development and decline of European mangroves during the Cenozoic. This work should be viewed as an attempt to establish an initial framework to be improved and refined by future research. As indicated in the title, this work reflects the current state of the published paleobotanical record. Its long-term validity depends on addressing the research gaps identified here, as well as any others that may arise in the future.

This is the second comprehensive and detailed regional synthesis of mangrove origin and evolution based on the compilation and critical evaluation of original paleobotanical records, following the study of the Neotropical Caribbean region (Rull, 2024). This strategy seems well suited to maintaining the reliability of taxonomic databases and identifying regional biogeographical and diversity patterns over time. If the same procedure were applied to other mangrove regions, an eventual global picture of mangrove dynamics since their origin would be much easier to assemble than by adopting a worldwide view from scratch, and the reliability of the resulting databases would be significantly enhanced. These compilations also provide the chronological basis for improving stratigraphic correlation and the calibration of molecular phylogenetic trees.

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References

Agiadi K, Hohmann N, Gliozzi E et al (2024) The marine biodiversity impact of the Late Miocene Mediterranean salinity crisis. Science 385:986-991

Akgün F, Akkiraz MS, Üçbaş SD et al (2013) Oligocene vegetation and climate characteristics in north-est Turkey: data from the sotuh-western part of the Thrace Basin. Turk J Erath Sci 22:277-303

Akkiraz MS, Kayseri MS, Akgün F (2008) Palaeoecology of coal-bearing Eocene sediments in Central Anatolia (Turkey) based on quantitative palynological data. Turkish J Earth Sci 17:317-360

Akkiraz MS, Nazik A., Özgen-Erdem N et al (2022) First micropalaeontological record from the early and middle Eocene Mamuca Formation of the Dümrek Basin, western central Anatolia, Turkey: biostratigraphy, depositional history and palaeoclimate. J Asian Earth Sci 224:105036

Bessedik M (1985) Reconstitution des environnements miocènes des regions nord-ouest méditerranéennes à partir de la palynologue. PhD thesis, Univ Montpellier

Bignot G, Blondeau A, Guernet C et al (1985) Age and characteristics of the Eocene transgression at Gánt (Vértes Mts, Transdanubia, Hungary). Acta Geol Hung 28:29-48

Biosca J, Via L (1988) El género *Nypa* (Palmae) en el Eoceno de la Depresión Central Catalana. Batalleria 1:7-23

Biltekin D, Popescu S-M, Suc J-P et al (2015) Anatolia: a long-time plant refuge area documented by pollen records over the last 23 million years. Rev Palaeobot Palynol 215:1-22

Bonde S, Kumaran K (2002) A permineralized species of mangrove fern *Acrostichum* L. from Deccan Intertrappean beds of India. Rev Palaeobot Palynol 120:285–299

Cai F, Ding L, Wang H et al (2021) Configuration and timing of collision between Arabia and Eurasia in the Zagros Collision Zone, Fars, southern Iran. Tectonics 40:e2021TC006762

Cavagnetto C, Anadón P (1995) Une mangrove complexe dans le Bartonien du Bassin de l'Ebre (NE de l'Espagne). Palaeontographica B 236:147-165

Cavagnetto C, Anadón P (1996) Preliminary palynological data on floristic and climatic changes during the Middle Eocene-Early Oligocene of eastern Ebro Basin, northeast Spain. Rev Palaeobot Palynol 92, 281-305

Celâl Şengör AM, Saniye A. (2009) The Permian extinction and the Tethys: an exercise in global geology. Spec Pap Geol Soc America 448:1-106

Chandler MEJ (1964) The Lower Tertiary Floras of Southern England. IV. A Summary and Survey of Findings in the Light of Recent Botanical Observations. British Mus Nat Hist, London

Châteauneuf JJ (1980) Palynostratigraphie et Paléoclimatologie de l'Éocène Superieur et de l'Oligocène du Basin de Paris. Bur Rech Géol Min 116, Paris

Châteauneuf J-J, Bauer H, Cojan I (2006) Présence d'une mangrove à *Avicennia* au Miocène moyen dans la région de Digne (Alpes-de-Haute-Provence, France): implications stratigraphiques el paléoclimatiques. C R Geoscience 338:197-205

Chrząstowska J, Dubicka Z, Barski M et al (2025) A micropalaeontological record of the Early Cretaceous marine-terrestrial interface in central Europe. Lethaia 58:1-17

Cohen KM, Finney SC, Gibbard PL et al (2013, v2024-12). The ICS International Chronostratigraphic Chart. Episodes 36: 199-204

Collinson ME, Cleal CJ (2001) Early and early middle Eocene (Ypresian-Lutetian) palaeobotany of Great Britain. In: Cleal CJ et al (eds) Mesozoic and Tertiary Palaeobotany of Great Britain. Joint Nature Conservation Committee, Peterborough, pp 187-226

Collinson ME, Hooker JJ (2003) Paleogene vegetation of Eurasia: framework for mammalian faunas. Deinsea 10:41-83

Coxall HK, Pearson PN (2007) The Eocene-Oligocene transition. In: Williams M et l (eds), Deep-Time Perspectives on Climate Change: Marrrying the Signal from Computer Models and Biological Proxies. The Geological Society, London, pp 351–387

Dangremond EM, Feller IC, Sousa WP (2015) Environmental tolerances of rare and common mangroves along light and salinity gradients. Oecologia 179:1187–1198

Duke NC (2017) Mangrove floristics and biogeography revisited: further deductions from biodiversity hot spots, ancestral discontinuities, and common evolutionary processes. In: Rivera-Monroy VH et al (eds) Mangrove ecosystems: a global biogeographic perspective. Springer, Berlin, pp 17–53

Durak SD, Akkiraz MS, Özgen-Erdem N et al (2025) Lutetian-Bartonian (Middle Eocene) micropalaeeontology, biostratigraphy and palaeoecology of the Mengen Coal Basin, Northwest Tükiye (Turkey). Palaeowotld 34:100871

Egger H (1005) Die lithostratigraphie der Altlengbach-Formation und der Anthering-Formation in Rhenodanubischen Flysh (Ostalpen, Penninikum). N Jb Geol Paläontol Abh 196:69-91

Egger H, Schwerd K (2008) Stratigraphy and sedimentation rates of Upper Cretaceous deep-water systems of the Rhenodanubian Group (Eastern Alps, Germany). Cretac Res 29:405-416

Egger H, van Husen D (2009) Geologische karte der Republik Österreich 1:50 000. Geol Bundessan, Wien

El-Soughier MI, Mehrotra RC, Zhou ZY et al (2011) *Nypa* fruits and seeds from the Maastrichtian–Danian sediments of Bir Abu Minqar, South Western Desert, Egypt. Palaeoworld 20:75–83

Ellison AM, Farnsworth EJ, Merkt RE (1999) Origins of mangrove ecosystems and the marine biodiversity anomaly. Glob Ecol Biogeogr 8:95–115

Fest BJ, Swearer SE, Arndy SK (2022) A review of sediment carbon sampling methods in mangroves and their broader impacts on stock estimates for blue carbon ecosystems. Sci Total Environ 816:151618

Gee CT (2001). The mangrove palm *Nypa* in the geologic past of the New World. Wetl Ecol Manag 9:181–194

Giesen W, Wulffraat S, Zieren M et al (2006) Mangrove Guidebook for Souheast Asia. FAO and Wetlands International, Bangkok

Gomez B, Cioffard C, Dépré E et al (2008) Diversity and histology of a plant litter bed from the Cenomanian of Archingeay-Les Mouillers (southwestern France. C R Palevol 7:135-144

Graham A (2006) Paleobotanical evidence and molecular data in reconstructing the historical biogeography of Rhizophoraceae. Ann Missouri Bot Gard 93:325-334

Greenwood DR, Wing SL (2011) Eocene continental climates and latitudinal temperature gradients. Geology 23:1044-1048

Gregor HJ, Hagn H (1982) Fossil fructifications from the Cretaceous–Palaeocene boundary of SW-Egypt (Danian, Bir Abu Munqar). Tertiary Res 4:121–147

Gruas-Cavagnetto C, Laurain M, Meyer R (1980) Un sol de mangrove fossilisé dans les lignites du Soissonnais (Yprésien) à Verzenay (Marne). Geobios 13:795-801

Gruas-Cavagnetto C, Tambareau Y, Villatte J (1988) Données paléoécologiques nouvelles sur le Thanétien et l’Ilerdien de l’avant-pays pyrénéen et de la Montaigne Noire. Inst fr Pondichéry, trav sec sci tech 25:219-235

Guillaume ARD, Puértolas-Pascual E, Moreno-Azanza M (2025) Revisiting the choristodere and stem-lepidosaur specimens of the Guimarota Beds (Kimmeridgian, Portugal): taxonomic implications. Acta Palaeontol Polon 70:77-96

Guo Z, Guo W, Wu H et al (2018a) Differing phylogeographic patterns within the Indo-West Pacific mangrove genus *Xylocarpus* (Meliaceae). J. Biogeogr 45:676-689

Guo W, Ng WL, Wu H et al (2018b) Chloroplast phylogeography of a widely distributed mangrove species, *Excoecaria agallocha*, in the Indo-West Pacific region. Hydrolobiologia 807:333-347

Harley MM (2006) A summary of fossil records for Arecaceae. Bot J Linn Soc 151:39–67.

Harzhauser M, Böhme M, Mandic O et al (2002) The Karpatian (Late Burdigalian) of the Koeneuburg Basin. A palaeoecological and biostratigraphical synthesis. Beitr Paläeontol 27:441-456

Haseldonckx P (1973) The palynology of some Palaeogene deposits between the Rio Esera and the Rio Segre, southeastern Pyrenees, Spain. Leidse Geol Mededel 49:145-165

He Z, Feng X, Chen Q et al (2022) Evolution of coastal forests based on a full set of mangrove genomes. Nature Ecol Evol 6:738-749

Herman J, Marquet R (2007) Observations paléontologiques réalisées dans les terrains néogènes belgues de 1971 à 2004 entre Kallo et Doel, Port d’Anvers, rive gauche (Flandre-Orientale, Belgique). Le Miocène du Deurganckdok à Doel. Mem Geol Surv Belgium 54:1-150

Hofmann E (1948) Das Flyschproblem im Lichte der pollenanalyse. Phyton 1:80-101

Hutchinson DK, Coxall HK, O’Regan M et al (2019) Arctic closure as a trigger for Atlantic overturning at the Eocene-Oligocene Transition. Nat Commun 10:3797

Isamoğlu Y, Harzhauser M, Gross M et al (2010) From Thethys to Eastern Paratatehys: Oligocene depositional environments, paleoecology and paleobiogeography of the Thrace Basin (NW Turkey). Int J Earth Sci 99:183-200

Ivanov D, Ashraf AR, Mosbrugger V (2007) Late Oligocene and Miocene climate and vegetation in the Eastern Paratethys area (northeast Bulgaria) based on pollen data. Palaeogeog Palaeoclimatol Palaeoecol 255:342–360

Jiménez-Moreno G (2005) Utilización del análisis polínico para la reconstrucción de la vegetación, clima y estimación de paleoaltitudes a lo largo del arco alpino europeo durante el Mioceno (21-8 Ma). PhD thesis, Univ Granada

Jiménez-Moreno G, Suc JP (2007) Middle Miocene latitudinal climatic gradient in Western Europe: Evidence from pollen records. Palaeogeog Palaeoclimatol Palaeoecol 253:224–241

Jiménez-Moreno G, Fauquette S, Suc JP (2008) Vegetation, climate and palaeoaltitude reconstructions of the Eastern Alps during the Miocene based on pollen records from Austria, Central Europe. J Biogeog 35:1638–1649

Just T (1951) Mesozoic plant microfossils and their geological significance. J Paleontol 25:729-735

Kayseri-Özer MS (2014) Spatial distribution of climatic conditions from the Middle Eocene to Late Miocene based on palynoflora in Central, Eastern and Western Anatolia. Geodin Acta 26:122–157

Koči T, Gašparič R, Buckeridge J et al (2024) The first record od a *Konservat-Lagenstätten* in which early post-settlement stages of fossils archaeobalanids (Cirripeda: Balanomorpha) are preserved. Integr Zool 19:200-2023

Krijgsman W, Hilgent FJ, Raffi I et al (1999) Chronology, causes and progression of the Messinian salinity crisis. Science 400:652-655

Kryshtofovich AN (1927) Remains of the palm (*Nipadites burtinii* Brongn.) from the Eocene near the city Voznesensk of Odessa Province. Proc Geol Comm 45:639–642

Kvaček J, Halamski AT, Sbobodová M et al (2015) Coniacian flora of the Sudetes (south-western Poland): palaeoecological and palaeoclimatic interpretations. Palaeogeog Palaeoclimatol Palaeoecol 436:178-187

Lenz OK (2005) Palynologie und Paläoökologie eines Küstenmoores aus dem Mittleren Eozän Mitteleuropas - Die Wulfersdorfer Flözgruppe aus dem Tagebau Helmstedt, Niedersachsen. Palaeontographica B 271:1-157

Lenz OK, Riegel W (2001) Isopollen maps as a tool for the reconstruction of a coastal swamp from the Middle Eocene at Helmstedt (Northern Germany). Facies 45:177-194

Lenz OK, Diekmeeier S, Wilde V (2021a) *Nypa* pollen diversity in middle Eocene mangroves at the edge on the southern Proto-North Sea (Helmstedt, northern Genrmany) – a statistical approach. Grana 60:97-118

Lenz OK, Riegel W, Wilde V (2021b) Greenhouse conditions in lower Eocene coastal wetlands? – Lesons from Schöningen, Northern Germany PLOS ONE 16:e0232861

Li X, Duke NC, Yang Y et al (2016) Re-evaluation of phylogenetic relationships among species of the mangrove genus Avicennia from Inod-West Pacific based on multilocus analyses. PLoS ONE 11:e0164453

Lo EYY, Duke NC, Sun M (2014) Phylogeographic pattern of *Rhizophora* (Rhizophoraceae) reveals the importance of both vicariance and long-distance oceanic dispersal to modern mangrove distribution. BMC Evol Biol 14:83

Lugo AE, Snedaker SC (1974) The ecology of mangroves. Ann Rev Ecol Syst 5:39–64

Maxwell EE, Alexander S, Bechly G et al (2016) The Rauenberg fossil Lagerstätte (Baden-Württemberg, Germany): a window into early Oligocene marine and coastal ecosystems of Central Europe. Palaogeog Palaeoclimatol Palaeoecol 463:238-260

McCoy ED, Heck KL (1976) Biogeography of corals, seagrasses, and mangroves: an alternative to the center of origin concept. Syst Zool 25:201–210

McInerney FA, Wing SL (2011) The Paleocene-Eocene Thremal Mazimum: a perturbation of carbon cycle, climate, and biosphere with implications for the future. Annu Rev Earth Planet Sci 39:489-516

Miller KG, Browning JV, Schmelz WJ et al (2020) Cenozoic sea-level and cryospheric evolution from deep-sea geochemical and continental margin records. Sci Adv 6:eaaz1346

Mohamed O, Wagreich M (2004) Organic-walled dinoflagellate cyst biostratigraphy of the Well Höflein 6 in the Cretaceous-Paleogene Rhenodanubian Flysh Zone (Vienna Basin, Austria). Geol Carpath 64:209-230

Moreno-Dominguez R, Cascales-Miñana B, Ferrer J et al (2016a) First record of the mangrove palm *Nypa* from the northeastern Ebro Basin, Spain: with taphonomic criteria to evaluate the drifting duration. Geol Acta 14:101-111

Moreno-Dominguez R, Cascales-Miñana B, Ferrer J et al (2016b) *Acrostichum*, a pioneering fern of floodplainareas from the Late Oligocene Sariñena Formation of the Iberian Peninsula. PLOS ONE 11:e0162334

Muller J (1981) Fosil pollen records of extant angiosperms. Bot Rev 47:1-140

Nagelkerken I, Blaver SJN, Bouillon S et al (2008) The habitat function of mangroves for terrestrial and marine fauna: a review. Aquat Bot 89:155–185

Nagy E, Kókay J (1991) Middle Miocene mangrove vegetation in Hungary. Acta Geol Hung 34:45–52

Numbere AO (2019) Impact of invasive *Nypa* palm (*Nypa fruticans*) on mangroves in coastal areas of the Niger Delta region, Nigeria. In: Makowski C, Finkl CW (eds) Impacts of invasive species on coastal environments. Springer Nature, Cham, pp 425–454

Osland MJ, Feher LC, Griffith KT et al (2017) Climatic controls on the global distribution, abundance, and species richness of mangrove forests. Ecol Monogr 87:341-359

Pavlishina P, Verreussel R, Leereveld H et al (2004) Palynological study of Gosau group deposits (Upper Cretaceous) of the northern calcareous Alps (Austria) Ann Naturhist Mus Wien 106A:67-90

Peyrot D, Barrón E, Polette F et al (2019) Early Cenomanian palynofloras and inferred resiniferous forests and vegetation types in Charentes (souhtwestern France). Cretac Res 94:168-189

Piller WE (2022) The lithostratigraphic units of Austria: Cenozoic Era(them). Abh Geol Bundesanst 76:1-357

Piyakarnchana T (1980) The Present State of Mangrove ecosystems in Southeast Asia and the Impact of Pollution – Thailand. FAO-UNEP, Rome

Plaziat J-C, Cavagnetto C, Koeniguer J-C et al (2001) History and biogeography of the mangrove ecosystem, based on a critical reassessment of the paleontological record. Wetl Ecol Manag 9:161–179

Pocknall DT, Clowes CD, Jarzen DM (2023) *Spinizonocolpites prominatus* (McIntyre) Stover & Evans: fossil *Nypa* pollen, taxonomy, morphology, global distribution, and paleoenvornmental significance. N Zealand J Geol Geophys 66:558-570

Popescu, S.-M., Suc, J.-P., Fauquette, S et al (2021) Mangrove distribution and diversity during three Cenozoic thermal maxima in the Northern Hemisphere (pollen records from the Arctic-North Atlantic-Mediterranean regions). J Biogeogr 48:2771–2784

Prey S (1952) Der obersenone Mutigler Flysch als Äquivalent der Mürbsandestein fürenden Oberkreide. Verh Geol Bundes-Anst 2:92-101

Rabinowitz D (1978) Early growth of mangrove seedlings in Panama and a hypothesis concernign the relationship of dispersal and zonation. J Biogeogr 5:113–133

Rásky K (1956) Fossil plants from the marl formationof the environs of Budapest. Földtani Közlöny 86:167-179

Riegel W, Wilde V, Lenz OK (2012) The early Eocene of Schöningen (N-Germany) – an interim report. Aust J Eartch Sci 105:88-109

Rull V (2022) The Caribbean mangroves: an Eocene innovation with no Cretaceous precursors. Earth-Sci Rev 231:104070

Rull V (2023a) Eocene/Oligocene global disruption and the revolution of Caribbean mangroves. Persp Plant Ecol Evol Syst 59:125733

Rull V (2023b) Taxon cycles in Neotropical mangroves. Plants 12:244

Rull V (2023c) The Neogene-Quaternary diversification trend in the shaping of modern Caribbean mangrove. Quat Sci Rev 300:107920

Rull V (2024) The Origin and Eolution of Caribbean Mangroves. Springer Nature, Cham

Rull V (2025) A critical evaluation of fossil pollen records from the mangrove tree *Pelliciera* beyond the Neotropics: biogeographical and evolutionary implications. Rev Palaeobot Palynol 335:105299

Rull V (2026) Challenges in using modern pollen analogues for Cenozoic palaeoecology: examples from the European Neogene. Lethaia, doi 10.18261/let.59.1.8

Rull V, Alba D, Casanovas-Vilar I (2024) Middle Miocene vegetation of the Vallès-Penedès Basin (NE Iberian Peninsula), as inferred from fossils pollen records: State of the art and future prospects. Rev Palaeobot Palynol 321:105042

Rull V, Vicente A, Bouchal JM et al (2025) On the use of extant Middle-East mangroves as modern analohues for Miocene Mediterranean-Paratethyan mangroves. Palaeobiodivers Palaeoenviron, doi 10.1007/s12549-025-00693-y

Schenider AC, Ulrich H, Carmen H et al (2018) From arid to humid – The Jurassic-Cretaceous boundary interval in northern Germany. Rev Palaeobot Palynol 255:57-69

Scotese CR (2016) PALEOMAP Paleoatlas for GPlates and the PaleoData Plotter Program, PALEOMAP Project. http://www.earthbyte.org/paleomap-paleoatlas-for-gplates/, doi 10.13140/RG2.2.34367.00166

Sendra J, Reolid M, Reolid J (2020) Paleoenvironmental interpretation of the Pliocene fan-delta system of the Vera Basin (SE Spain): fossil assemblages, ichnology and taphonomy. Palaeoworld 29:769-788

Smith TJ (1992) Forest structure. In: Robertson AI, Alongi DM (eds) Tropical Mangrove ecosystems. Am Geophys Union, Washington, pp 101–136

Sousa WP, Kennedy PG, Mitchell BI et al (2007) Supply-side ecology in mangroves: do propagule dispersal and seedling establishment explain forest structure? Ecol Monogr 77:53–76

Sowunmi MA (1986) Change of vegetation with time. In: Lawson GW (ed) Plant ecology in West Africa. Wiley, Chichester, pp 273–307

Spalding M, Kainuma M, Collins L (2010) World Atlas of Mangroves. Routledge, London

Srivastava J, Prasad V (2019) Evolution and paleobiogeography of mangroves. Mar Ecol 40:e12571

Suc J-P, Bessais E (1990) Pérennité d'un climat thermo-xérique en Sicile avant, pendant, après la crise de salinité messinienne. C R Acad Sci Paris 310:1701-1707

Suc J-P, Popescu S-M, Fauquette S et al (2018) Reconstruction of Mediterranean flora, vegetation and climate for the last 23 million years based on an extensive pollen dataset. Ecol Med 44:53-85

Takayama K, Tateishi Y, Kajita T (2021) Global phylogeography of a pantropical mangrove genus *Rhizophora*. Sci Rep 11:7228

Thanikaimoni G (1987) Mangrove Palynology. French Institute, Pondichéry

Tomlinson PB (2016) The botany of Mangroves. Cambridge University Press, Cambridge

Torfstein A, Steinberg J (2020) The Oligo-Miocene closure of the Tethys Ocean and evolution of the proto-Mediterranean Sea. Sci Rep 10:13817

Torricelli S, Knezaurek G, Biffi U (2006) Sequence biostratigraphy and paleoenvironmental reconstruction in the Early Eocene Figols Group of the tremp-Graus Basin (sotuh-central Pyrenees, Spain). Palaeogeog Palaeoclimatol Palaeoecol 232:1-35

Trájer AJ (2024) Reconstruction of palaeoenvironmental conditions that led to the formation of Eocene sub-bituminous coal sems in the Hungarian Paleogene Basin. Rev Palaeobot Palynol 323:105080

Tralau H (1964) The genus *Nypa* van Wurmb. K Sven Wetensk Acad Handl 10:1-29

Uličný D, Kvaček J, Svobodá M et al (1997) High-frequency sea-level fluctuations and plant habitats in Cenomanian fluvial to estuadrine succession: Pecínov quarry, Bohemia. Palaeogeog Palaeoclimatol Palaeoecol 136, 165-197

Van der Stocken T, Carroll D, Menemenlis D et al (2019) Global-scale dispersal and connectivity in mangroves. Proc Natl Acad Sci USA 116:915-922

Van Steenis CGGJ (1962) The distribution of mangrove plant genera and its significance for pal-aeogeography. Proc Kon Ned Akad Wetesnsch 65:164–169

Westerhold T, Marwan N, Drury AJ et al (2020) An astronomically dated record of Earth's climate and its predictability over the last 66 million years. Science 369:1383–1387

Woodroffe CD (1982) Mangrove swamp stratigraphy and Holocene transgression, Grand Cayman Island, West Indies. Mar Geol 41:271–294

Worobiec G, Jach R, Machaniec E et al (2015) Eocene flora and trace fossils from the Hruby Regiel section in the Tatra Mountains (Poland): taxonomic revision of the Wiktor Kuźniar fossil planr collection. Acta Geol Pol 65:203-226

Worthington TA, zu Ermgassen PSE, Fries DA et al (2020) A global biophysical typology of mangroves and its relevance for ecosystem structure and deforestation. Sci Rep 10:15652

Wu W, Feng X, Wang N et al (2024) Genomic analysis of Nypa fruticans elucidates its intertidal adaptations and early palm evolution. J Integr Plant Biol 66:824-843

Zhang M, Zhong C, Lv X et al (2024) Germplasm resource status and seed adaptability of *Nypa fruticans* Wurmb, and endangered species in China. Forests 15:1396

Zhang Z, He Z, Xu S et al (2016) Transcriptome analyses provide insights into the phylogeny and adaptive evolution of the mangrove fern genus Acrostichum. Scie Rep 6:35634

Zhao Z, Hou Z-E, Li S-Q (2022) Cenozoic Tethyan changes dominated Eurasian animal evolution and diversity patterns. Zool Res 43:3-13

Zetter R, Hofmann CC (2001) New aspects of the palynoflora of the lowermost Eocene (Krappfeld Area, Carinthia). In: Piller WE, Raser MW (eds) Paleogene of the Eastern Alps. Österr Akad Wiss, Shriftenr Erdwiss Komm 14:473-507