The evolution of West African Atlantic mangroves from the Late Cretaceous to the present: an evidence-based synthesis of the paleobotanical record

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Abstract

The paleobiogeographic and evolutionary history of tropical West African (WAF) mangroves has yet to be comprehensively reconstructed from the available paleobotanical evidence. This study presents the WAFMA (West AFrican MAngrove) dataset, the fourth regional compilation in an ongoing series aimed at reconstructing the origin and evolution of mangroves worldwide through standardized, evidence-based analyses of biogeographically coherent regions. Following the methodology previously applied to the Caribbean (CARMA), Europe (EURMA) and the Middle East (MESMA), WAFMA integrates all available original fossil records using rigorous taxonomic and bibliographic quality-control criteria, providing the most complete and reliable reconstruction of WAF mangrove history to date. The WAFMA dataset comprises 107 records spanning the Late Cretaceous to the Holocene. It shows that the earliest (Late Cretaceous-Paleocene) WAF communities containing modern mangrove elements consisted exclusively of *Nypa*, whereas present-like mangrove forests first appeared in the Early Eocene – coinciding with the Paleoceene-Eocene Thermal Maximum (PETM) and the Early Eocene Climatic Optimum (EECO) – and developed during the Middle Eocene with the establishment of *Pelliciera*-dominated communities accompanied by *Acrostichum* and *Nypa*, and the subsequent arrival of *Rhizophora* in the Late Eocene. The Eocene/Oligocene Transition (EOT) marked the disappearance of *Nypa* and the rise of *Rhizophora* as the dominant mangrove-forming tree, although, unlike in the Neotropics, *Pelliciera* remained an important component throughout the Neogene. *Avicennia* appeared during the Middle Miocene Climatic Optimum (MMCO), whereas *Conocarpus* and *Laguncularia* were incorporated during the Quaternary, when mangrove diversity reached its maximum. Comparison with the Caribbean demonstrates a coherent evolutionary history across the Atlantic-East Pacific (AEP) biogeographic region while revealing distinctive West African features, notably the prolonged persistence of *Pelliciera* and the absence of major diversity crises or compositional turnovers. WAFMA substantially refines the historical biogeography of Atlantic mangroves, provides a robust regional framework for future global syntheses of mangrove evolution, and identifies priorities for future research.

Keywords

Mangroves, West Africa, Late Cretaceous, Cenozoic, biogeography, evolution, paleogeography, paleoclimates, sea-level shifts, plant fossils

1. Introduction

Mangroves are iconic forested ecosystems that form a characteristic intertidal fringe along tropical and subtropical coasts worldwide, between approximately 30° N and 30° S (Spalding et al., 2010). Beyond the intrinsic value that each community possesses simply by virtue of its existence (Soulé, 1985), these ecosystems are important for several reasons. Geomorphologically, they protect coasts from erosion and foster progradation, thus facilitating the development of other coastal ecosystems. Ecologically, mangroves are ecotonal land-sea ecosystems that enhance and maintain coastal biodiversity by creating new habitats for terrestrial organisms and providing shelter for the early developmental stages of many marine species (Laegdsgaard & Johnson, 2001; Naglkerken et al., 2008). Economically, mangroves provide a variety of ecosystem services to humans that would otherwise be unavailable (Afonso et al., 2021). Mangroves are also the main blue-carbon ecosystems, contributing to the mitigation of global warming by sequestering carbon in their organic sediments (Nellemann et al., 2009; McLeod et al., 2011; Fest et al., 2022). Despite this, mangroves are among the most threatened forested ecosystems worldwide and require urgent conservation and restoration measures to ensure their persistence (Duke et al., 2017; Worthington et al., 2020).

Mangroves develop around a small, characteristic group of species from diverse phylogenetic origins that have evolved special morphological, physiological, and phenological adaptations to this ecosystem through convergent evolution, particularly to permanent flooding by saline or brackish waters and growth on soft, anoxic substrates. These species, which are exclusive to mangrove communities, are known as true-mangrove elements and have been subdivided into major and minor components. Major true-mangrove elements, or mangrove-forming trees, often develop pure stands and provide the main structural framework without which mangrove communities would not exist. Minor true-mangrove elements, although also restricted to these communities, rarely form pure stands and typically occupy more marginal habitats. Other species that can occur in mangrove communities but are not exclusive to them are known as associate elements (Tomlinson, 2016).

The geographic distribution of true-mangrove elements has allowed the subdivision of mangroves into two main biogeographic regions worldwide, namely the Atlantic-East Pacific (AEP) and the Indo-West Pacific (IWP) regions, which are separated by the African continental barrier (Fig. 1). These regions are characterized by markedly different biodiversity patterns, with 54 true-mangrove species (17 genera) in the IWP and 11 species (6 genera) in the AEP. Only two genera of mangrove-forming trees, *Rhizophora* (Rhizophoraceae) and *Avicennia* (Acanthaceae), are shared between these regions, although their species remain geographically disjunct. Among the minor true-mangrove elements, only *Acrostichum* (Pteridaceae) is cosmopolitan (Tomlinson, 2016; Duke, 2017).

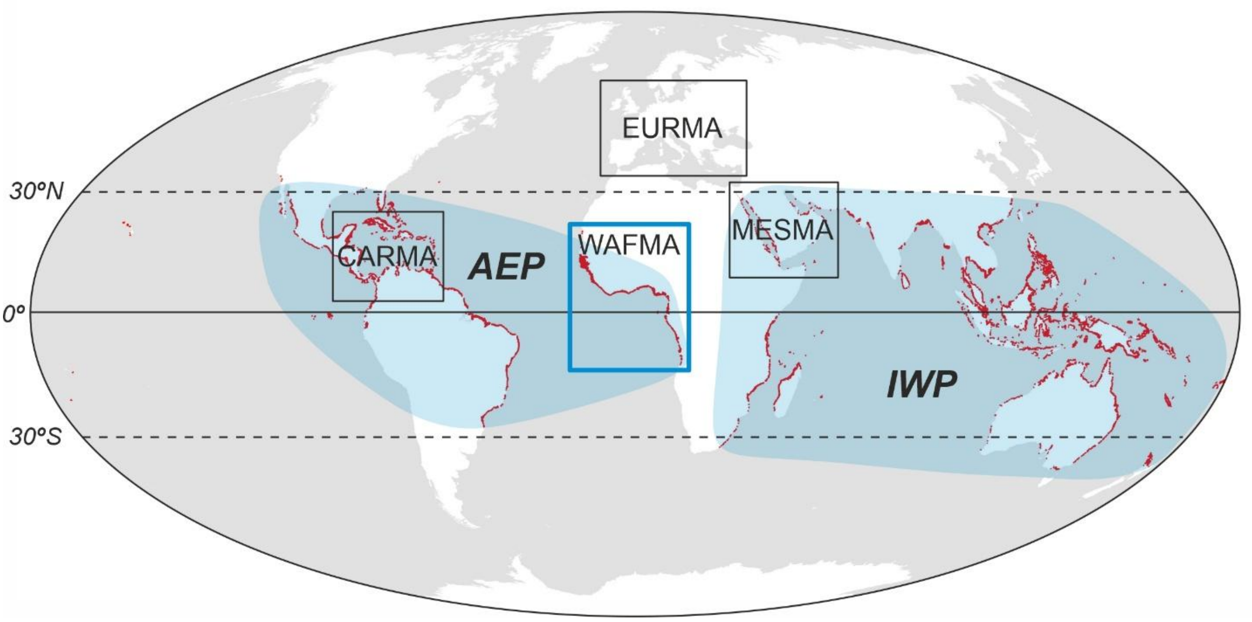

Figure 1. Worldwide mangrove distribution (red fringes) highlighting the Atlantic-East Pacific (AEP) and Indo-West Pacific (IWP) biogeographic regions (blue shading). The study area (WAFMA) is indicated by a blue box, while regions previously studied using the same methodology (EURMA, CARMA and MESMA) are denoted by black boxes. Base map from Rull (2022), downloaded from https://data.unep-wcmc.org/datasets/5 (last accessed April 15, 2026).

According to the dispersalist biogeographic paradigm, the higher biodiversity of the IWP would suggest that this region was the center of origin and dispersal of mangrove taxa worldwide (Van Steenis, 1962). However, the vicariance perspective favors an initial pantropical distribution of ancestral mangrove taxa along the former Tethyan coasts, followed by regional differentiation after the closure of the Tethys (McCoy & Heck, 1976; Ellison et al., 1999). Estimates of the timing of IWP-AEP divergence vary among authors, ranging from the Paleocene to the Oligocene (Ellison et al., 1999; Plaziat et al., 2001; Duke, 2017; Srivastava & Prasad, 2019). Recent molecular phylogenetic analyses using iconic cosmopolitan taxa, such as *Rhizophora* and *Avicennia*, suggest that elements of both vicariance and dispersal are needed to explain the biogeographic patterns of extant mangroves (Lo et al., 2014; Li et al., 2016; Takayama et al., 2021).

The mangroves of the tropical Atlantic coasts of Western Africa constitute a well-defined isolated spot that represents the only AEP mangrove subregion outside the American continent (Fig. 1). As in many other mangrove-bearing areas, comprehensive syntheses based on detailed, exhaustive, and critically assembled datasets are unavailable. Palynological research has a long tradition in this region, particularly in Nigeria, where pioneering work contributed to the development of palynology as a stratigraphic tool for oil exploration (Germeraad et al., 1968). However, comprehensive paleontological reconstructions of mangrove origin and evolution remain lacking. A recent critical review of the true-mangrove Neotropical element *Pelliciera* is available (Rull, 2025a), but it is taxon-centered and does not address the biogeographic and evolutionary history of West-African mangrove ecosystems as a whole.

Recently, an initiative has been launched to analyze mangrove dynamics through time by assembling regional datasets based exclusively on published original records from several biogeographically coherent regions worldwide, with the aim of achieving a more comprehensive, evidence-based understanding of mangrove origin and evolution. This regional-based approach ensures spatiotemporal coherence and can be readily scaled up to global perspectives without losing the resolution of the original studies. In addition, potential taxonomic and biogeographic inconsistencies are easier to identify, evaluate and revise before incorporation into the databases. Overall, this approach provides not only more comprehensive datasets but also higher-quality raw data for substantiating historical biogeographic inferences.

To date, this methodology has been applied to the Caribbean (CARMA dataset), Europe (EURMA), and the Middle East (MESMA), yielding previously unrecognized insights. For example, it was found that Neotropical mangroves originated de novo during the Middle Eocene, rather than through regional differentiation from presumed Cretaceous precursors (Rull, 2002), and acquired their present-like configuration after the Eocene/Oligocene global disruption (Rull, 2003). European mangroves, in turn, have a mixed origin, combining elements dispersed from the IWP region by the Paleocene/Eocene boundary with others that evolved in situ and a third group that originated in the southern Tethys (Rull, 2026a). As for the Middle East, this region emerged as an important center of mangrove origin and evolution, rather than merely serving as a dispersal corridor or barrier between other mangrove-bearing regions (Rull, 2026b).

This study applies the same methodology to the tropical Atlantic coasts of West Africa by assembling and analyzing the WAFMA (West-AFrican MAngrove) dataset (Fig. 1). As in previous regional analyses, consideration of the full published evidence will likely result in higher-quality datasets and previously unnoticed insights into regional mangrove evolution, which can be integrated into a more evidence-based and comprehensive understanding of the origin, paleobiogeography, and evolution of mangroves worldwide. In this case, the outcomes of WAFMA will be particularly useful for understanding mangrove development within the AEP region through comparison with their western Atlantic counterparts previously studied using the CARMA Neotropical dataset. This comparison will be especially valuable for assessing the role of the Atlantic Ocean and its progressive tectonic opening in mangrove development, given the significant floristic similarity between Neotropical and West African mangrove floras.

2. Study area

This review is centered on the tropical coasts of Western Africa (hereafter WAF), between approximately 19°50’N and 12°20’S, which correspond to the northernmost and southernmost occurrences of mangrove communities in the region (Saenger & Bellan, 1995) (Fig. 2). This includes the coasts of 19 countries, all of which contain mangrove ecosystems, with two major concentrations on the Upper Guinea coast (Senegal, Gambia, Guinea, Guinea-Bissau) and in the Gulf of Guinea (Nigeria, Cameroon, Gabon). By country, Nigeria has by far the largest mangrove extent, accounting for almost 39% of the total WAF area, followed by Guinea-Bissau and Guinea (10–12%), and Cameroon, Gabon, Sierra Leone and Senegal (5–9%) (Table 1). Countries with only scattered mangrove occurrences (<1% of the total each) are Liberia, Ghana, Ivory Coast, Benin, the Republic of Congo, Mauritania, Togo and São Tomé-Príncipe.

Table 1. Mangrove extent (Bunting et al., 2022) and true-mangrove genera (UNEP, 2007; Afonso et al., 2021; Naidoo, 2023) by countries.

Country	**Extent (km^2)**	**%**	***Rhizophora***	***Avicennia***	***Laguncularia***	***Acrostichum***	***Conocarpus***	***Nypa***
Nigeria	8442.43	38.88	X	X	X	X	X	X[1]
Guinea Bissau	2688.32	12.38	X	X	X		X	
Guinea	2211.45	10.18	X	X	X	X	X	
Cameroon	1970.01	9.07	X	X	X		X	
Gabon	1747.01	8.05	X	X	X	X	X	
Sierra Leone	1529.03	7.04	X	X	X		X	
Senegal	1269.74	5.85	X	X	X	X	X	
Gambia	609.72	2.81	X	X	X	X	X	
Angola	283.57	1.31	X	X	X		X	
E Guinea	255.95	1.18	X	X				
DR Congo	236.84	1.09	X	X	X	X	X	
Liberia	183.37	0.84	X	X		X	X	
Ghana	179.52	0.83	X	X	X	X	X	
Ivory Coast	54.48	0.25	X	X	X	X	X	
Benin	28.77	0.13	X	X	X	X	X	
R Congo	20.11	0.09	X	X	X	X	X	
Mauritania	3.44	0.02	X	X			X	
Togo	0.50	0.00	X	X			X	
S Tomé-Príncipe	0.48	0.00	X	X				
Total	**21,714.74**	**100.00**						

[1] Introduced from Singapore in 1906 (UNEP, 2007).

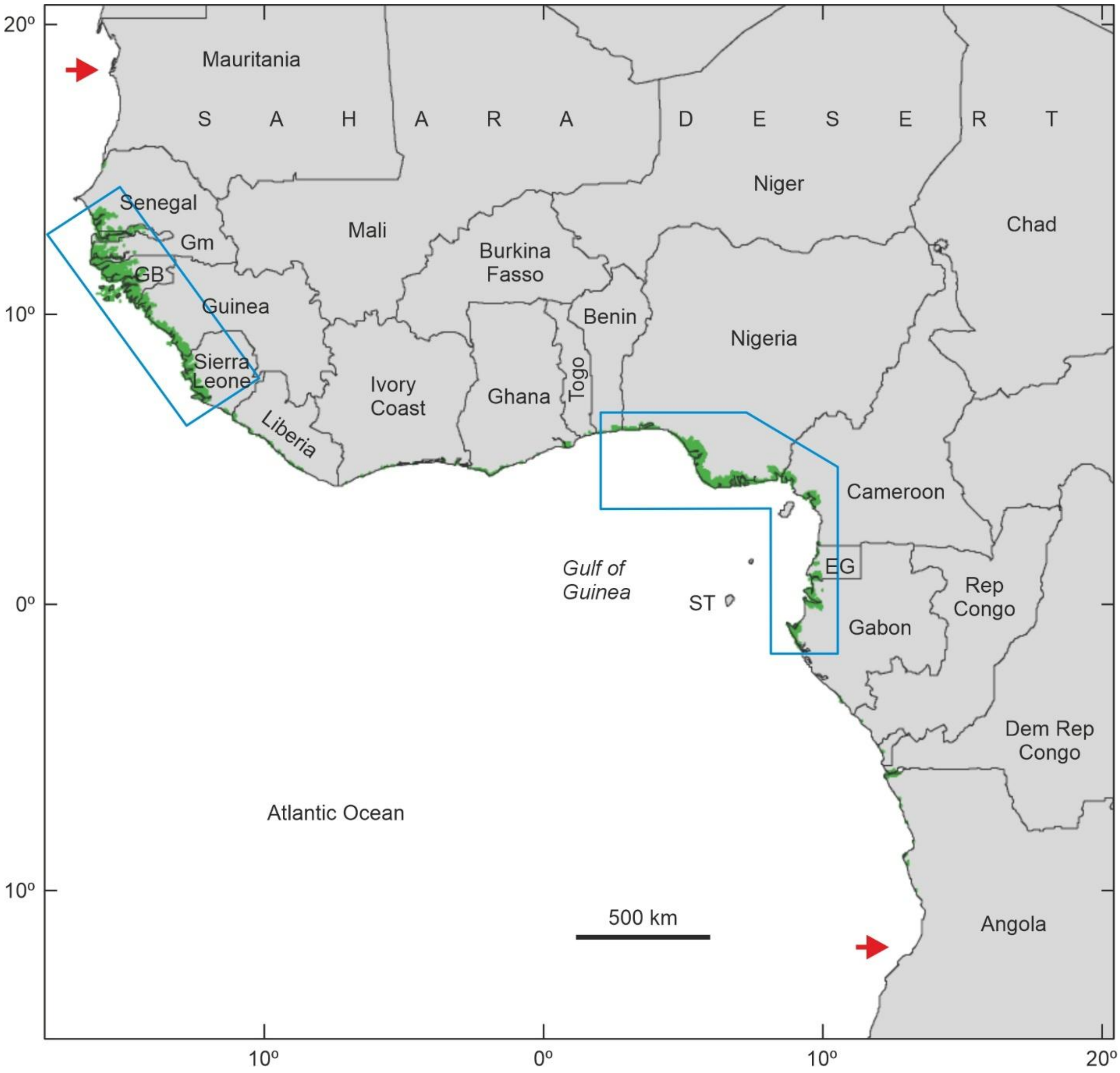

Figure 2. Map of Western African mangroves (green patches) indicating the northernmost and southernmost limits (red arrows). Areas of greater mangrove development (Senegal to Sierra Leone and Nigeria to Gabon) are highlighted with blue boxes. Base map from Bunting et al. (2022), laitutdinal boundaries after Saenger & Bellan (1995). EG, Equatorial Guinea; GB, Guinea Bissau; Gm, Gambia; ST, São Tomé-Príncipe.

The autochthonous WAF mangrove flora is represented by five mangrove-forming tree species belonging to three genera: *Rhizophora* (three species), *Avicennia germinans* and *Laguncularia racemosa*. Two minor true mangrove species, *Conocarpus erectus* and *Acrostichum aureum*, complete the list (Table 2). *Nypa fruticans* was introduced into Nigeria from Singapore in 1907 (UNEP, 2007). One of the *Rhizophora* species, *R. harrisonii*, has been considered a naturally occurring hybrid of *R. mangle* and *R. racemosa*, whereas *Avicennia africana* appears as a separate species in some publications but is currently treated as a synonym of *A. germinans* (Plants of the World Online; https://powo.science.kew.org/; last accessed 14 June 2026). Some of these taxa are represented in the fossil record by fossil form species listed in Table 2. Exceptions are *Avicennia*, *Laguncularia* and *Conocarpus*, whose fossils are reported as such. The Neotropical species *Pelliciera rhizophorae*, which is absent from the extant WAF flora, is also included because its fossil representatives have been reported from the WAF fossil record.

Table 2. Mangrove-forming tree genera from the AEP biogeographic region with extant and fossil representatives in the West African (WAF) record. Raw data from Kauffman et al. (2017) and Naidoo (2023) for extant species, and Germeraad et al. (1968),

Muller (1981), Frederiksen (1988) and Pocknall et al. (2023) for fossils. Chronostratigraphic ranges after Germeraad et al. (1968), Salard-Cheboldaeff (1990) and this study. NR, not recorded.

Type	**True-mangrove extant genera**	**Extant species**	**Fossil pollen representatives (M, macrofossils)**	**Range in WAF**
Major	*Rhizophora* (Rhizophoraceae)	*R. mangle* *R. racemosa* *R. harrisonii*[1]	*Zonocostites ramonae*	Eocene-present
	Avicennia (Acanthaceae)	*A. germinans* (=*A. africana*)	*Avicennia*	Miocene-present
	Laguncularia (Combretaceae)	*L. racemosa*	*Laguncularia*	Quaternary
	Nypa (Arecaceae)	*N. fruticans*[2]	*Spinizonocolpites baculatus* *S. prominatus* (= *S. echinatus*) *Nipadites/Nypa burtini* (M)	Maastrichtian-Eocene
Minor	*Acrostichum* (Pteridaceae)	*A. aureum*	*Deltoidospora adriennis*	Eocene-present
	Conocarpus (Combretaceae)	*C. erectus*	*Conocarpus*	Quaternary
	Pelliciera (Tetrameristaceae)	NR	*Psilatricolporites crassus* (= *Lanagiopollis crassa*)	Eocene-Pleistocene

[1] A naturally occurring hybrid of *R. mangle* and *R. racemosa*, according to the Plants of the World Online (POWO) database (https://powo.science.kew.org/; last accessed June 14, 2026).

[2] Introduced in Nigeria in the 20th century.

Rhizophora is the dominant mangrove-forming tree across the WAF coasts (Kauffman & Bhomia, 2017), except for some particular communities that are dominated by *Avicennia*, especially in the northernmost sector (Mauritania), which is under a desert climate, where *Avicennia* is the only mangrove-forming tree (Otero et al., 2016). A typical sea-to-land zonal pattern in WAF mangroves, extending from saline to brackish-water environments, is *Rhizophora–Avicennia–Acrostichum* (Marius & Lucas, 1991), with *Laguncularia* occupying intermediate positions and *Conocarpus* occurring in the most landward zones, either on dry soils or in areas flooded by freshwater. The WAF mangrove flora is very similar to its Neotropical counterpart, the main differences being the absence of *P. rhizophorae*, as already noted, and the presence of two additional *Avicennia* species, *A. bicolor* and *A. schaueriana*, in the Neotropics (Rull, 2024).

This is a general feature of the Late Cretaceous–Cenozoic floras of the equatorial marginal basins of West Africa, where most European taxa are absent and floristic affinities are instead with Gondwanan landmasses, such as South America and Australia (Boltenhagen, 1963; Castelain, 1966; Salard-Cheboldaeff, 1990). The West African sedimentary basins originated following the breakup of Gondwana and the progressive separation of Africa from South America during the opening of the Atlantic Ocean, which began in the Early Cretaceous. During this period, Africa was separated from present-day Europe by the pantropical Tethys Sea, and as the incipient Atlantic Ocean formed, all dispersal routes to and from the West African Atlantic coasts were open to marine and coastal organisms (Fig. 3).

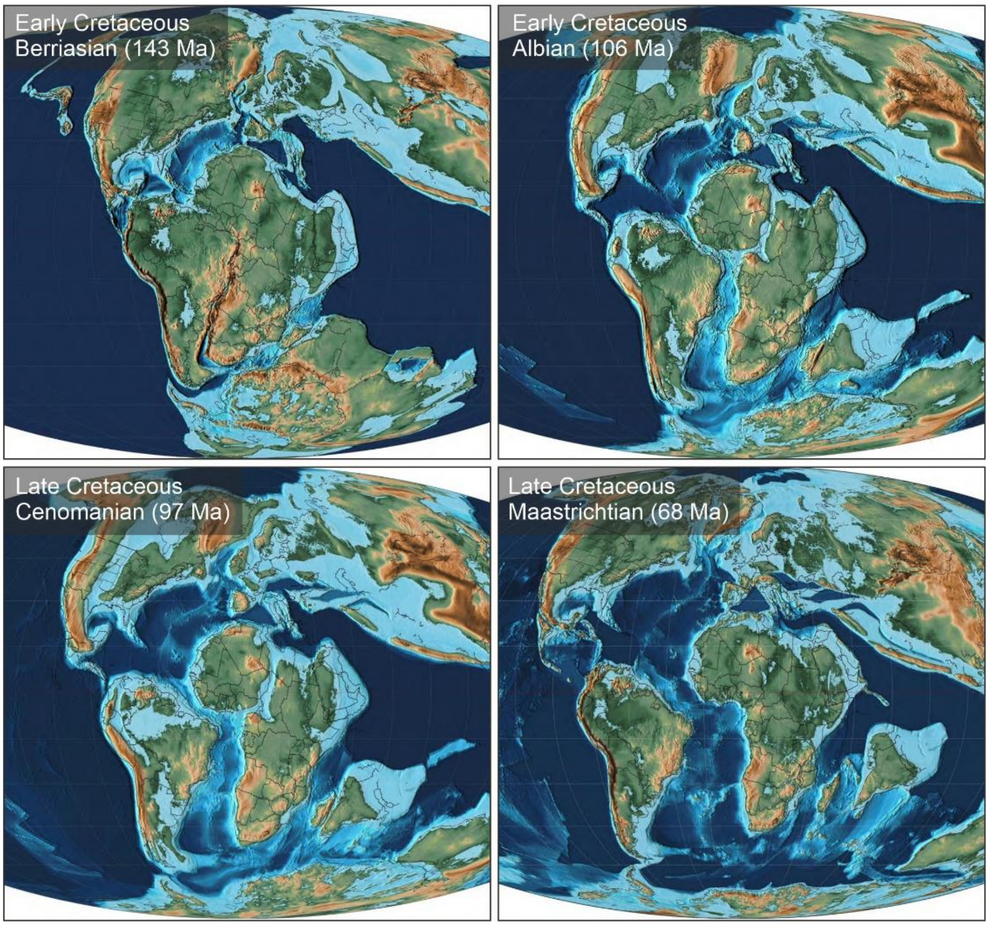

Figure 3. Global Cretaceous paleogeographic evolution showing the progressive opening of the Atlantic Ocean and the resulting separation of Africa and South America. Modified from Scotese (2014).

WAF mangroves are intensively used by humans, to the extent that some authors have described them as "veritable supermarkets" of goods and services (Feka & Ajonina, 2011). The main anthropogenic activities affecting WAF mangrove ecosystems are fish smoking, construction, cooking, salt production, rice farming, urbanization and petroleum exploration. These activities have caused significant mangrove losses, and conservation and restoration efforts are urgently needed to reverse this trend (Naidoo, 2023). According to the IUCN (International Union for Conservation of Nature) Red List of Mangrove Ecosystems, mangroves from Nigeria to Angola are classified as Vulnerable, whereas those from Mauritania to Benin are considered of Least Concern (https://iucn.org/node/33749/red-list-mangrove-ecosystems; last accessed June 15, 2026).

3. The WAFMA dataset

3.1. Methodological hints

The construction of the WAFMA dataset followed the same criteria as the CARMA, EURMA and MESMA datasets (Rull, 2024, 2026a, b). Mangroves are viewed as ecosystems rather than coastal sedimentary environments; therefore, taxonomy is a crucial consideration. To identify mangrove taxa, only extant taxa and their fossil ancestors (Table 2) were considered, whereas other taxa purported to have mangrove affinities based on unverified fossil morphological assumptions were excluded. Similarly, reports of presumed "mangrove peats" lacking independent taxonomic verification (e.g., Barusseau et al., 1988; Lézine & Chateauneuf, 1991) were not included. A biomarker study found that the triterpenoid taraxerol is significantly more abundant in *Rhizophora* leaves than in other higher plants and proposed its use as a proxy for mangrove occurrence (Versteegh et al., 2004). The authors tested this approach in a set of Late Pleistocene to Holocene marine cores off the Angolan coast and found good agreement between taraxerol content and *Rhizophora* pollen percentages. This information is included in the WAFMA dataset (Table 2).

Searches were carried out using major bibliographic databases, including Web of Science, Scopus, Google Scholar, OpenAlex, The Lens, BASE, and the comprehensive fossil pollen database PALYNODATA (White, 2008). Search queries combined geographic terms (countries, seas, gulfs), chronostratigraphic units (periods, epochs, ages), and extant and fossil taxonomic names listed in Table 2. Review papers and syntheses were used to trace the original publications containing the primary evidence, while recent studies were examined to identify additional older literature. Only original sources were included, reviews and syntheses were not used as primary sources of evidence. These original sources were subjected to further filtering in response to the recent proliferation of predatory publishing (sensu Beall, 2012) documented in the study region, especially in Nigeria (Omobowale et al., 2014; Shen & Björk, 2015; Nwagwu & Ojemeni, 2015; Macháček & Srholec, 2022).

This general trend toward questionable publishing prompted a critical assessment of the literature specifically on mangrove fossils. Using the indexing status of the corresponding source journals in Scopus as an objective filtering criterion, nearly 40 papers published during the last decade failed the screening, most of them authored by Nigerian researchers working on Nigerian localities. A significant proportion of the excluded journals were identified as potentially predatory or otherwise questionable according to Beall's List (https://beallslist.net/; last accessed 3 July 2026). Examples are *Elixir Geoscience, Greener Journal of Physical Sciences, Journal of Environment and Earth Science, International Journal of Scientific Invention Today, Biodiversity International Journal, IOSR Journal of Applied Geology and Geophysics* or *Journal of Geography, Environment and Earth Science International*, among others (see Rull, 2025a for a full list).

The same criterion was applied to the WAFMA dataset. Only journals indexed in Scopus and/or Web of Science (WoS) (type A journals), or peer-reviewed historical journals not covered by these modern databases but widely recognized as reliable sources – e.g., *AASP Contributions Series*, *Pollen et Spores*, *Revue de Micropaléontologie*, *Mémoires du Bureau de Recherches Géologiques et Minières*, *The Palaeobotanist*, *Revista Española de Micropaleontología* and *Proceedings of the Ocean Drilling Program*, among others (type B journals) – were included. Peer-reviewed chapters from books published by major scientific publishers were also included in the type B literature. It is important to clarify that the indexation in WoS and/or Scopus refers to the current versions of these databases. For example, the *Arabian Journal of Geosciences*, which contains some Nigerian papers potentially suitable for WAFMA and is published by a major scientific publisher (Springer), was recently removed from WoS and Scopus due to irregularities in editorial handling and peer review, among others (Al-Amri, 2023), and therefore is not eligible for the current version of WAFMA.

Journals not belonging to these categories, as well as gray literature – i.e., theses, working papers, occasional papers, technical reports, institutional reports, newsletters, conference proceedings, etc.) (Schöpfel, 2011) – were excluded from WAFMA. This conservative publication selection is aimed at maintaining rigor in evidence-based science and should not be regarded as a definitive classification. Indeed, if some of the excluded records are shown to be reliable in the future, they can be incorporated into the dataset through a procedure that is both easier and safer than building a database containing potentially unreliable records and subjecting it to repeated quality-control reviews.

In addition, each category (A or B) was assigned a "+" if the corresponding mangrove fossil records are accompanied by illustrations and/or descriptions suitable for taxonomic identification, or a "−" if they are not. Papers with illustrations/descriptions for part of the fossils considered in this study were designed as “+/-“. This is not considered a guarantee of correct identification but rather evidence that can be used to assess taxonomic reliability, as discussed in the text.

Table 3. The WAFMA dataset. Fossil localities compiled in this review and their main characteristics (see Fig. 4 for locations). Fossil types: B, biomarkers (taraxerol); F, fruits; P, pollen/spores. Literature sources: A, journals indexed in Web of Science (WoS) or Scopus; B, peer-reviewed journals not indexed in these databases but widely recognized as reliable sources; fossil illustrations/descriptions available (+) or unavailable (−). Qt, quantitative studies. ND, no data. See the methodological section for more details.

Map	Site	Country	Latitude	Longitude	Period	Epoch/Age	Mangrove taxa	Fossil	References	Source	Qt
Lo	St Louis	Senegal	16°02'00"N	16°29'00"W	Quaternary	L Holocene	*Rhizophora* *Avicennia*	P	Fofana et al. (2020)	A-	X
Rz	Lake Rkiz	Mauritania	16°55'06"N	15°09'26"W	Quaternary	E Holocene-Present	*Rhizophora*	P	Grouard & Lézine (2023)	A-	X
89	Core T89-16	RD Congo	05°42'12"S	11°14'06"E	Quaternary	M-L Holocene	*Rhizophora*	P/B	Marret et al. (1999)	A-	X
07	Core GeoB 1007	RD Congo	06°23'33"S	10°57'06"E	Quaternary	M-L Holocene					X
Ah	Ahanve	Nigeria	06°25'55"N	02°46'29"E	Quaternary	M-L Holocene	*Rhizophora*	P	Orijemie et al. (2024)	A-	X
Og	Ogudu	Nigeria	06°33'55"N	03°24'03"E	Quaternary	M-L Holocene	*Avicennia*				X
Ot	Otolu	Nigeria	06°24'11"N	04°09'14"E	Quaternary	M-L Holocene	*Acrostichum*				X
Ig	Ikorigho	Nigeria	05°57'26"N	04°55'51"E	Quaternary	M-L Holocene	*Laguncularia*				X
Yv	Yèvié	Benin	06°32'06"N	02°24'42"E	Quaternary	M-L Holocene	*Rhizophora*	P	Tossou et al. (2008)	A-	X
Dg	Dogla-Alago	Benin	06°36'25"N	02°35'43"E	Quaternary	M-L Holocene	*Avicennia*				X
Gh	Goho	Benin	06°26'35"N	02°34'45"E	Quaternary	M-L Holocene	*Acrostichum*				X
Ni	Niger Delta	Nigeria	04°33'00"N	06°26'00"E	Quaternary	M-L Holocene	*Rhizophora*	P	Sowunmi (1981)	A-	X
LS	Lac Sélé	Benin	07°09'00"N	02°26'00"E	Quaternary	E-L Holocene	*Rhizophora*	P	Salzamann & Hoelzmann (2005)	A-	X
G1	Core GC 1	Nigeria	04°49'43"N	05°20'20"E	Quaternary	L Pleistocene-Present	*Rhizophora*	P	Adojoh et al. (2023)	A-	X
G2	Core GC 2	Nigeria	04°05'08"N	06°33'30"E	Quaternary	L Pleistocene-Present	Avicenniaceae				X
G3	Core GC 3	Nigeria	04°11'59"N	07°21'29"E	Quaternary	L Pleistocene-Present					X
05	Core GEOB 4905	Cameroon	02°30'00"N	09°23'24"E	Quaternary	L Pleistocene-Present	*Rhizophora*	P	Marret et al. (2013)	A-	X
708	Core MD03-2708	Gabon	01°10'20"S	08°19'00"E	Quaternary	L Pleistocene-Present	*Rhizophora*	P	Kim et al. (2010)	A-	X
31	Core KW 31	Nigeria	03°31'01"N	05°34'01"E	Quaternary	L Pleistocene-Present	*Rhizophora*	P	Lézine et al. (2005)	A-	X
78	Core ODP 1078	Angola	11°55'00"S	13°24'00"E	Quaternary	L Pleistocene-Present	*Rhizophora*	P	Dupont et al. (2008)	A-	X
12	Core KS 12	Ghana	03°52'00"N	01°56'00"W	Quaternary	L Pleistocene-E Holocene	*Rhizophora* *Avicennia*	P	Lézine & Vergnaud-Grazzini (1993)	A-	X
23	Core KW 23	Gabon	03°46'05"S	09°17'05"E	Quaternary	M Pleistocene-Present	*Rhizophora*	P	Bengo & Maley (1991)	A-	X
96	Core V22-196	Senegal	13°50'00"N	18°57'00"W	Quaternary	M Pleistocene-Present	*Rhizophora*	P	Lézine (1991)	A-	X
56	Core GIK 16856	Nigeria	04°48'00"N	03°24'00"E	Quaternary	M Pleistocene-Present	*Rhizophora* *Avicennia* *Conocarpus*	P	Dupont & Weinelt (1996)	A-	X
16	Core GeoB 1016	Angola	11°46'00"S	11°40'00"E	Quaternary	M Pleistocene-Present	*Rhizophora*	P/B	Ning & Dupont (1997)	A-	X
67	Core GIK 16867	Gabon	02°12'00"S	05°06'00"E	Quaternary	M Pleistocene-Present	*Rhizophora*	P	Dupont et al. (1998)	A-	X
KZ	Core KZai 02	Angola	06°24'06"S	09°54'18"E	Quaternary	M Pleistocene-Present	*Rhizophora* *Avicennia*	P	Dalibard et al. (2014)	A-	X
76	Core GIK 16776	Liberia	03°44'00"N	11°23'50"W	Quaternary	M Pleistocene-Present	*Rhizophora*	P	Jahns et al. (1998)	A-	X
08	Core GeoB 1008	Angola	06°35'04"S	10°19'01"E	Quaternary	M Pleistocene-Present	*Rhizophora*	P/B	Jahns (1996)	A-	X
067	Core KS 84076	Ivory Coast	04°07'00"N	04°05'00"W	Quaternary	M Pleistocene-Present	*Rhizophora*	P	Frédoux (1994)	A-	X

							Avicennia				
							Acrostichum				
15	Core GIK 16415	Liberia	09°33'00"N	19°06'00"W	Quaternary	M Pleistocene-Present	*Rhizophora*	P	Hooghiemstra & Agwu (1988)	A-	X
		S Leone							Dupont & Agwu (1992)		
58	Core ODP 658	Mauritania	20°44'57"N	18°34'51"W	Quaternary	M-L Pleistocene	*Rhizophora*	P	Dupont et al. (1989)	A-	X
C	Well C	Nigeria	ND	ND	Quaternary	L Pliocene-Pleistocene	*Rhizophora*	P	Olayiwola & Bamford (2016a)	A+	X
							Pelliciera				
							Acrostichum				
Lb	Well Lubara Creek-2	Nigeria	04°39'58"N	07°31'02"E	Neogene	Miocene-Pleistocene	*Rhizophora*	P	Germeraad et al. (1968)	A+	X
BW	Well Benin West-1	Nigeria	06°21'57"N	04°46'42"E	Neogene	Miocene-Pleistocene	*Rhizophora*	P	Germeraad et al. (1968)	A+	X
A1	Well A-1	Nigeria	05°09'17"N	05°03'29"E	Neogene	L Miocene-E Pleistocene	*Rhizophora*	P	Adeonipekun & Sowunmi (2019)	A-	X
A2	Well A-2	Nigeria	04°57'18"N	05°02'43"E	Neogene	L Miocene-E Pleistocene	*Pelliciera*		Adeonipekun et al. (2016)		X
A3	Well A-3	Nigeria	05°04'43"N	05°05'35"E	Neogene	L Miocene-E Pleistocene	*Acrostichum*				X
Eb	Lagune Ebrié	Ivory Coast	05°41'10"N	03°54'48"W	Neogene	L Miocene	*Rhizophora*	P	Bacchiana et al. (1982)	A+	
							Pelliciera				
Tb	Well Tambacounda	Senegal	13°46'21"N	13°40'01"W	Neogene	L Miocene	*Rhizophora*	P	Médus (1975)	B+	X
							Pelliciera[1]				
Zg	Well Ziguinchor	Senegal	12°33'51"N	16°15'50"W	Neogene	L Miocene	*Rhizophora*	P	Médus (1975)	B+	X
							Pelliciera[1]				
S3	Well S3	Ivory Coast	ND	ND	Neogene	L Miocene	*Rhizophora*	P	Báldi-Beke et al. (1987)	A-	
							Pelliciera				
Bg	Well Bignona	Senegal	12°48'18"N	16°14'04"W	Neogene	L Miocene	*Rhizophora*	P	Médus (1975)	B+	X
A	Well A	Nigeria	ND	ND	Neogene	L Miocene-Pliocene	*Rhizophora*	P	Olayiwola & Bamford (2016b)	A+	X
B	Well B	Nigeria	ND	ND	Neogene	L Miocene-Pliocene	*Pelliciera*				X
							Acrostichum				
Ib	Well Igbomotoru-1	Nigeria	04°31'40"N	06°03'30"E	Neogene	M-L Miocene	*Rhizophora*	P	Oboh & Salami (1989)	A-	X
									Oboh et al. (1992)		
Ko	Kolo Creek Field	Nigeria	04°41'15"N	06°18'57"E	Neogene	M Miocene	*Rhizophora*	P	Oboh (1995)	B+	
M1	Well M1	Benin	ND	ND	Neogene	Middle Miocene	*Rhizophora*	P	Durugbo & Olayiwola (2017)	A+	X
							Avicennia				
							Pelliciera[1]				
							Acrostichum				
4	Well 4	Nigeria	ND	ND	Neogene	Miocene	*Rhizophora*	P	Bankole et al. (2014)	A+	X
6	Well 6	Nigeria	ND	ND	Neogene	Miocene	*Pelliciera*				X
8	Well 8	Nigeria	ND	ND	Neogene	Miocene	*Acrostichum*				X
KR	Well KR-1	Nigeria	ND	ND	Neogene	E Miocene	*Rhizophora*	P	Adebayo et al. (2016)	A-	X
							Pelliciera				
							Acrostichum				
UB	Umuahia-Bende	Nigeria	05°31'28"N	07°29'36"E	Paleogene	Oligocene-E Miocene	*Rhizophora*	P	Ikegwuonu & Umeji (2016)	A+	X
							Pelliciera		Ikegwuonu et al. (2020)		
B1	Well BN-1	Nigeria	ND	ND	Paleogene	Chattian-Aquitanian	*Rhizophora*	P	Ojenabor et al. (2026)	A+	X

Bb	Well Bambatenda	A2	13°31'16"N	15°34'22"W	Paleogene	Oligocene	*Rhizophora*	P	Médus (1975)	B+	X
KK	Well Kwa-Kwa	Cameroon	ND	ND	Paleogene	Oligocene	*Pelliciera*	P	Salard-Cheboldaeff (1981)	A-	
Ke	Well Kemar-1	Nigeria	ND	ND	Paleogene	L Eocene-E Miocene	*Rhizophora* *Pelliciera* *Acrostichum*	P	Aigbadon et al. (2024)	A+	
Ok	Well Olokonla-1	Nigeria	06°28'00"N	03°36'00"E	Paleogene	L Eocene-E Oligocene	*Nypa* *Rhizophora* *Pelliciera*	P	Olayiwola et al. (2022)	A+/-	X
Bd	Well Badore-1	Nigeria	06°26’00"N	03°51'00"E	Paleogene						X
Ep	Well Epe-1	Nigeria	06°27’00"N	03°26'00"E	Paleogene						X
Ik	Well Ikoyi-1	Nigeria	06°34'00"N	03°58'00"E	Paleogene						X
Az	Well Awaizombe-1	Nigeria	06°00'00"N	07°38'00"E	Paleogene	E Eocene-E Oligocene	*Rhizophora* *Pelliciera* *Nypa* *Acrostichum*	P	Chukwuma-Orji (2023)	A+	X
S5	Nnewi	Nigeria	06°00'38"N	06°54'37"E	Paleogene	L Eocene	*Nypa* *Pelliciera*		Jan du Chêne et al. (1978a)	B+	
S6	Oba Spring	Nigeria	06°04'20"N	06°49'48"E	Paleogene						
S0	Ihioma-Orlu	Nigeria	05°47'11"N	07°03'00"E	Paleogene						
KK	Well Kwa-Kwa	Cameroon	04°03'04"N	09°46'04"E	Paleogene	L Eocene	*Pelliciera*	P	Salard-Cheboldaeff (1976, 1979)	A+	
Nk	Well Nsukwa 1	Nigeria	06°00'00"N	06°50'00"E	Paleogene	L Eocene	*Nypa* *Pelliciera*		Jan du Chêne & Salami (1978a)	B-	
Lb	Well Lubara Creek-2	Nigeria	04°39'58"N	07°31'02"E	Paleogene	M Eocene-Pleistocene	*Pelliciera*[1]	P	Germeraad et al. (1968)	A+	X
BW	Well Benin West-1	Nigeria	06°21'57"N	04°46'42"E	Paleogene	M Eocene-Pleistocene	*Pelliciera*[1]	P	Germeraad et al. (1968)	A+	X
BM	Bargny M’bote	Senegal	14°41'55"N	17°13'42"W	Paleogene	M-L Eocene	*Nypa*	F	Fritel (1921) Tralau (1964)	A+	
Tm	Well Tambacounda	Senegal	13°46'21"N	13°40'01"W	Paleogene	M Eocene	*Nypa*	P	Médus (1975)	B+	X
Oj	Well Ojo-1	Nigeria	06°28'00"N	03°10'54"E	Paleogene	Eocene	*Pelliciera*	P	Jan du Chêne et al. (1978b)	B-	
KK	Well Kwa-Kwa	Cameroon	ND	ND	Paleogene	Eocene	*Nypa* *Pelliciera*	P	Salard-Cheboldaeff (1981)	A-	
B1	Well BN-1	Nigeria	ND	ND	Paleogene	Ypresian-Aquitanian	*Pelliciera* *Acrostichum*	P	Ojenabor et al. (2026)	A+	X
Mg	Well Moulongo	Cameroon	03°27'45"N	09°37'32"E	Paleogene	L Paleocene-E Eocene	*Nypa*	P	Mbesse et al. (2021)	A+	X
Ng	Well Ngata	Cameroon	03°24'21"N	09°52'13"E	Paleogene						X
Sg	Sagamu	Nigeria	06°49'56"N	03°37'55"E	Paleogene	L Paleocene-E Eocene	*Nypa* *Pelliciera*	P	Bankole et al. (2007)	B+/-	
IB	Well IB 10	Nigeria	ND	ND	Paleogene						
IL	Well IL 3	Nigeria	ND	ND	Paleogene						
Am	Ameke	Nigeria	05°34'07"N	07°29'54"E	Paleogene	L Paleocene-E Eocene	*Nypa* *Pelliciera*[1]	P	Mander et al. (2023)	A+	X
Ow	Okigwe	Nigeria	05°49'52"N	07°23'39"E	Paleogene						X
Oz	Ozuitem	Nigeria	05°38'43"N	07°36'34"E	Paleogene						X
B1	Well BN-1	Nigeria	ND	ND	Paleogene	Thanetian-Priabonian	*Nypa*	P	Ojenabor et al. (2026)	A+	X
UB	Umuahia-Bende	Nigeria	05°31'28"N	07°29'36"E	Paleogene	Paleocene-E Miocene	*Pelliciera*	P	Ikegwuonu et al. (2020)	A-	
Wa	Well Walalane	Senegal	14°35'00"N	16°07'00"W	Paleogene	Paleocene	*Nypa*	P	Caratini et al. (1991)	B+	X
NM	Northern Mine	Nigeria	07°00'04"N	03°01'412"E	Paleogene	Paleocene	*Nypa*	P	Bolagi et al. (2020)	A+/-	X

SM	Southwestern Mine	Nigeria	06°59'26"N	03°01'37"E	Paleogene		*Pelliciera*				X
UB	Umuahia-Bende	Nigeria	05°31'28"N	07°29'36"E	Paleogene	Paleocene-Eocene	*Nypa*	P	Ikegwuonu et al. (2020)	A+	
Mi	Missole	Cameroon	03°59'01"N	09°54'22"E	Paleogene	Paleocene-E Eocene	*Pelliciera*	P	Kwetche et al. (2018) Mfayakouo et al. (2021)	A/B+/-	
Iw	Ikpankwu	Nigeria	05°50'56"N	07°23'22"E	Paleogene	Danian	*Nypa*	P	Okeke et al. (2024)	A-	X
Oh	Ouinhi	Benin	07°05'41"N	02°30'51"E	Cretaceous	Maastrichtian-Eocene	*Nypa*	P	Bio-Lokoto et al. (1998)	B+	
Eg	Well Egoli-1	Nigeria	07°04'01"N	06°16'29"E	Cretaceous	Maastrichtian-Eocene	*Nypa*	P	Germeraad et al. (1968)	A+	X
Nn	Well Nani-1	Nigeria	ND	ND	Cretaceous	Maastrichtian-Paleocene	*Nypa*	P	Agharanya et al. (2022)	A-	
KK	Well Kwa-Kwa	Cameroon	ND	ND	Cretaceous	Maastrichtian-Paleocene	*Nypa*	P	Salard-Cheboldaeff (1981)	A-	
Op	Odukpani	Nigeria	05° 4'52"N	08°21'00"E	Cretaceous	Late Maastrichtian	*Nypa*	P	Edet & Nyong (1994)	A+	
Nz	Well Nzam-1	Nigeria	ND	ND	Cretaceous	Late Maastrichtian	*Nypa*	P	Bankole & Ola-Buraimo (2017)	A-	
M5	Well CM5	Senegal	ND	ND	Cretaceous	Maastrichtian	*Nypa*	P	Venkatachala et al. (1998)	B-	
Dk	Dakar	Senegal	14°43'00"N	17°28'03"W	Cretaceous	Maastrichtian	*Nypa*	P	Jardiné & Magloire (1965)	B+	X
S8	Well ST-8	Ghana	04°43'37"N	03°00'08"W	Cretaceous	Campanian-Eocene	*Nypa*	P	Atta-Peters & Salami (2004)	B+	
Bo	Bonoua	Ivory Coast	05°16'16"N	03°35'38"W	Cretaceous	Campanian-Paleocene	*Nypa*	P	Simon et al. (1984)	A-	
AB	Well AB-1	Nigeria	ND	ND	Cretaceous	Campanian-Paleocene	*Nypa*	P	Alege et al. (2025)	A-	X
BG	Well BG-1	Nigeria	ND	ND	Cretaceous						X
Mi	Missole	Cameroon	ND	ND	Cretaceous	Campanian-Maastrichtian	*Nypa*	P	Tchouatcha et al. (2025)	A+	
MF	Miang-Fiko	Cameroon	ND	ND	Cretaceous						
Ml	Mangoule	Cameroon	ND	ND	Cretaceous						
OO	Obi-Oshodi	Nigeria	06°57'48"N	05°49'46"E	Cretaceous	Campanian-Maastrichtian	*Nypa*	P	Ajidahun et al. (2025)	A-	X
D1	Well D1-1X	Ivory Coast	05°07'03"N	04°02'21"W	Cretaceous	Campanian-Maastrichtian	*Nypa*	P	Digbehi et al. (1996)	A-	

[1] Reliable identification (Rull, 2025a)

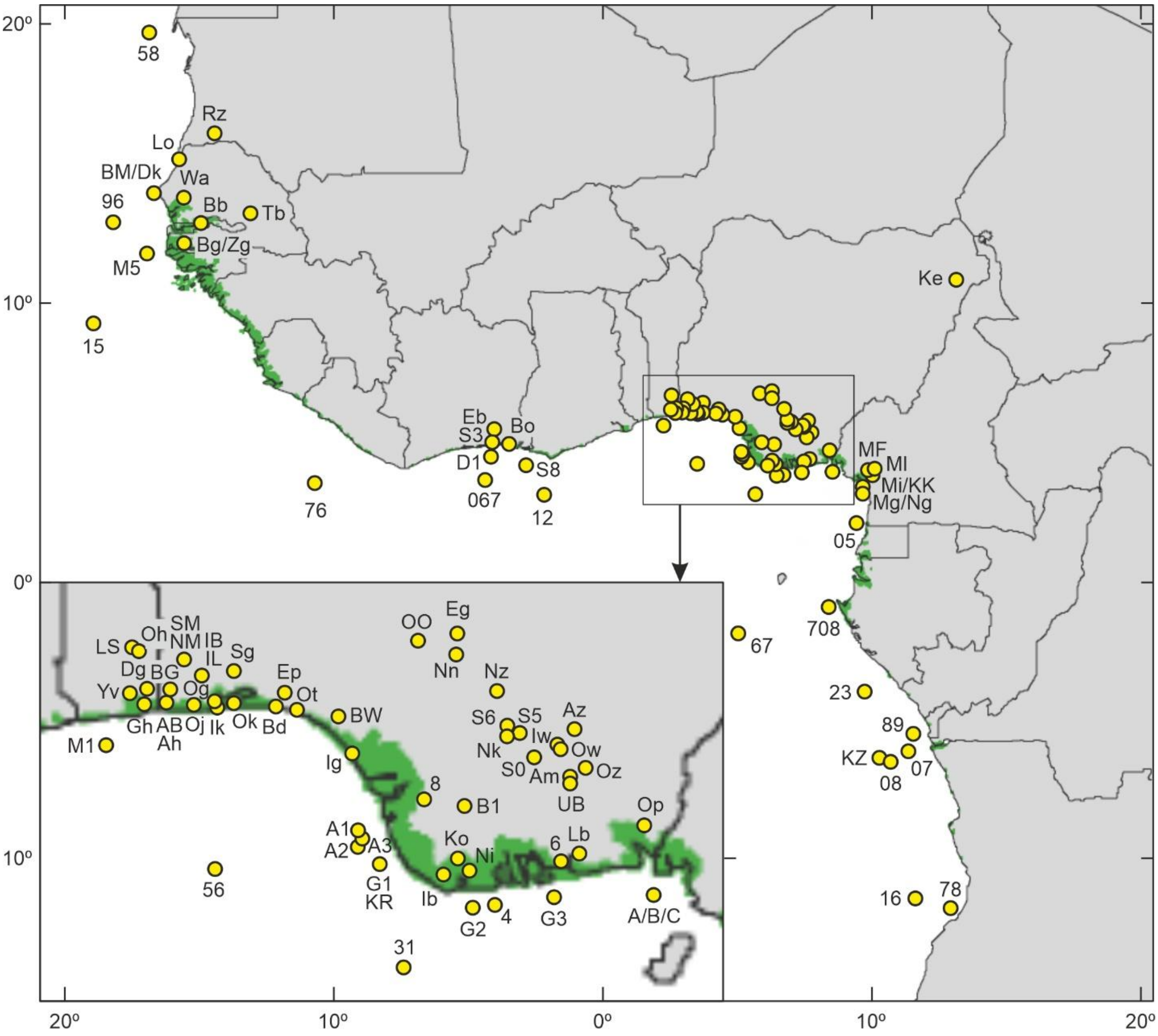

Figure 4. Localities with fossil mangrove records (yellow dots) considered in this study. The Nigerian coastal area is enlarged because of the high concentration of sites. See Table 3 for details.

When coordinates were not provided, localities were georeferenced using previous papers that reported their positions, fieldwork descriptions, nearby towns or other geographic landmarks identified with Google Earth. In some cases, especially for oil wells and other sites subject to confidentiality restrictions, the location of fossil sites is approximate and was inferred with the aid of maps provided in the original references. In a few cases, the locations of sites with fossil mangrove records were reported too imprecisely to be mapped with confidence (e.g., Durugbo et al., 2010).

Potential fossil representatives of *Pelliciera* have been shown to present identification concerns, with important implications for the global evolutionary and biogeographic history of the genus (Rull, 2025a). For this reason, special care has been taken to assess the reliability of its identification based on the information provided in the original references. Rull (2025a) distinguished three categories of publications reporting *Pelliciera* in the fossil record: (i) those that provide images and/or descriptions useful for assessing identification reliability, (ii) those that provide misleading information (e.g., unusable illustrations), and (iii) those that simply list *Pelliciera* fossils without providing sufficient information to verify the identification. The first category can be further subdivided into three groups: (ia) reliable, (ib) doubtful, and (ic) unreliable identifications. The criteria for these categories are detailed in Rull (2025a). Here, a conservative approach is adopted, and only publications of type (ia) are used to discuss the historical biogeography of *Pelliciera*. This does not invalidate other records but helps avoid overinterpretation. However, alternative views remain possible, provided they are evidence-based.

Notably, approximately 70% of the records contain quantitative data, usually expressed as percentages, which is remarkable compared with similar datasets, where qualitative presence/absence records are more common. This significantly improves paleocommunity reconstructions, a critical tool in fossil mangrove research (Rull, 2022).

The chronostratigraphic framework of this study was provided by latest version of the International Chronostrigraphic Chart (Cohen et al., 2013; v. 2024-12). Epochs and age boundaries are indicated using a slash (e.g., Paleocene/Eocene), whereas age ranges are expressed with a dash (e.g., Middle-Late Miocene). Global paleotermperature and paleoeustatic trends were taken from Westerhold et al. (2020) and Miller et al. (2020), respectively.

3.2. General observations

The WAFMA dataset consists of 107 records, of which 16% are Late Cretaceous, 36% Paleogene, 18% Neogene and 31% Quaternary. By country, Nigeria is the largest contributor, accounting for more than half of the records (55%), followed by Senegal and Cameroon (10% each), Benin (6%), Angola and Ivory Coast (4% each), Gabon (3%), Mauritania, the Democratic Republic of the Congo, Ghana and Liberia (2% each), and Gambia (1%). Regarding record type, nearly half of the records (47%) are from oil wells, approximately one-third (33%) are from outcrops and coastal peat cores, and the remaining 20% are from offshore cores. Notably, 74% of the records from oil wells are from Nigeria, particularly the Niger Delta petroleum system, which has been the dominant oil-producing region in the West-African Atlantic margin since the onset of large-scale commercial oil exploitation in the late 1950s (Watts, 2016; Okorobia & Olali, 2018). In contrast, Angola, the region's second-largest oil producer, is not represented by any oil well records.

Taxonomically, the similarity between the WAFMA and CARMA datasets (Rull, 2024)—with *Nypa*, *Rhizophora*, *Avicennia*, *Pelliciera*, *Laguncularia*, *Conocarpus* and *Acrostichum* as the main mangrove components—confirms the biogeographic coherence of the AEP region in the fossil record as well. The stratigraphic patterns of these mangrove elements, which are discussed in detail below, also support this interpretation and allow the extension of extant global mangrove biogeographic patterns back to the Late Cretaceous.

A significant shift in authorship patterns between foreign, notably French, and local researchers occurred in the 1990s, with a marked increase in local authorship and the near-disappearance of foreign-authored publications over the last two decades. This trend is particularly evident in pre-Quaternary studies and in Nigeria, and may reflect a progressive nationalization of research agendas and scientific capacity, together with confidentiality constraints associated with petroleum exploration datasets that may have favored the participation of locally based researchers. European (mostly French) contributions have remained concentrated mainly in offshore settings, where numerous short cores containing Pleistocene and Holocene sediments have been recovered and analyzed.

4. Spatiotemporal patterns in biogeography and diversity

4.1. Late Cretaceous

The oldest *Nypa* record corresponds to the Turonian of Ivory Coast (offshore well SWS5), but it remains unpublished, as it is only available in the form of a PhD thesis—therefore not eligible for WAFMA—with no illustrations or descriptions of the corresponding palynomorphs, in this case *Spinizonocolpites echinatus* (Tahi, 2022). The other Late Cretaceous records are from rocks dated to the Campanian–Maastrichtian or Maastrichtian and are mainly concentrated in the Gulf of Guinea, with a few representatives in Senegal (Fig. 5). This situation, in which *Nypa* is the only mangrove component, parallels that of the Caribbean region, represented by the CARMA dataset (Rull, 2024), and differs from Europe (EURMA), where no Cretaceous mangroves have been recorded (Rull, 2026a), and the Middle East (MESMA), where the *Nypa* lineage probably evolved from the Early Cretaceous (Albian) (Rull, 2026b). Other mangrove-bearing regions lack comparable comprehensive databases (although analogous studies are in progress), but *Nypa* is generally the oldest mangrove element recorded, dating back to the Late Cretaceous (e.g., Ellison et al., 1999; Plaziat et al., 2001; Duke, 2017; Srivastava & Prasad, 2019).

Currently, mangroves composed exclusively of *Nypa fruticans* are restricted to sheltered, low-energy estuarine environments with a strong freshwater influence. They typically occupy tidal rivers, upper and middle estuaries and protected tidal creeks, where they form dense monospecific stands on fine-grained muddy substrates subject to regular tidal inundation. These habitats are characterized by reduced salinity (typically 0 to 10‰), high sedimentation rates and limited wave energy. In contrast, open coastal fringes are generally dominated by tree mangroves such as *Rhizophora* and *Avicennia*, and monospecific *Nypa* communities are rarely found in such exposed settings. *Nypa* is also an aggressive invader of disturbed areas and can replace previously diverse communities with monotypic palm forests, even at the mangrove forefront (Giesen et al., 2007; Rahman et al., 2024; Zhang et al., 2024; Numbere, 2019).

Recent molecular phylogenetic studies suggest that the *Nypa* clade developed unique adaptive traits for living in intertidal habitats—most notably waterlogging tolerance and cryptovivipary—as early as 75 Ma, when it diverged from other palms of the *Phoenix–Cocos–Elaeis* complex (Wu et al., 2024). Accordingly, mangrove niche conservatism in *Nypa* could be traced back to the Late Cretaceous. However, the absence of mangrove tree genera such as *Rhizophora* and *Avicennia*, together with the ecological characteristics of *Nypa*, precludes the inference of Late Cretaceous mangrove ecosystems similar to those found today. Therefore, the mere occurrence of *Nypa*, despite its well-established intertidal affinity, is insufficient to infer the occurrence of present-like mangrove communities. This is also the case in the Caribbean region (Rull, 2022), and the same reasoning could be applied to the Middle East (Rull, 2026b) and possibly to the core IWP region.

In summary, the widespread Late Cretaceous communities in which *Nypa* was the only known mangrove component remain enigmatic, and their reconstruction could significantly contribute to our understanding of the origin and evolution of mangroves worldwide. Such reconstruction should be undertaken using quantitative approaches, including percentage data and modern-analog-independent statistical methods, such as fossil-community reconstruction (e.g., Rull, 1997, 1998, 1999, 2000, 2003, 2025c; Rull et al., 2024). This approach is worth pursuing and may lead to a major advance in mangrove research.

4.2. Paleocene

The Paleocene mangrove records show a similar but more restricted distribution (Fig. 5). *Nypa* was still the dominant element, but some records of *Pelliciera* began to emerge. Only one of these, a pollen record from southwestern Nigeria (Bolagi et al., 2020), was specifically dated as Paleocene, whereas the others are from strata assigned to the Paleocene–Eocene interval (Table 3). However, the Paleocene record has two main limitations. First, the strata were dated using pollen as chronostratigraphic markers, which may involve circular reasoning. Second, the presence of *Pelliciera* was inferred from *Psilatricolporites crassus*, but no descriptions or illustrations were provided to verify this identification. Therefore, the available evidence is insufficient to support the unequivocal presence of *Pelliciera* during the Paleocene, in agreement with previous detailed morphological studies of this taxon and its fossil representatives (Rull, 2025a).

4.3. Eocene

The Eocene witnessed the first diversification event with the arrival of *Pelliciera* and *Acrostichum*, coinciding with the Paleocene/Eocene Thermal Maximum (PETM) and the Early Eocene Climatic Optimum (EECO) (Figs. 5 and 6), and possibly *Rhizophora*. Although not all *Pelliciera* records reported for this epoch can be endorsed (Table 3), this mangrove tree was reliably identified in several Eocene intervals from Nigerian wells and outcrops. The earliest occurrences consisted of a few grains scattered throughout several Late Paleocene/Early Eocene samples, followed by a sudden increase during the Middle Eocene (Germeraad et al., 1968; Mander et al., 2023). The same trend was observed in the Caribbean region (Fig. 7), where the first present-like mangroves dominated by *Pelliciera* were recorded (Rull, 2022). This suggests that the first AEP mangroves may have originated more or less synchronously on both sides of the Atlantic Ocean during the Middle Eocene and persisted until the Late Eocene. As in the Neotropics, these mangroves were likely dominated by *Pelliciera* on the seaward side, with *Acrostichum* and *Nypa* occupying back-mangrove brackish environments. To date, *Pelliciera* has not been found anywhere outside the AEP region (Rull, 2025a); hence, it is most probably a species of Atlantic origin.

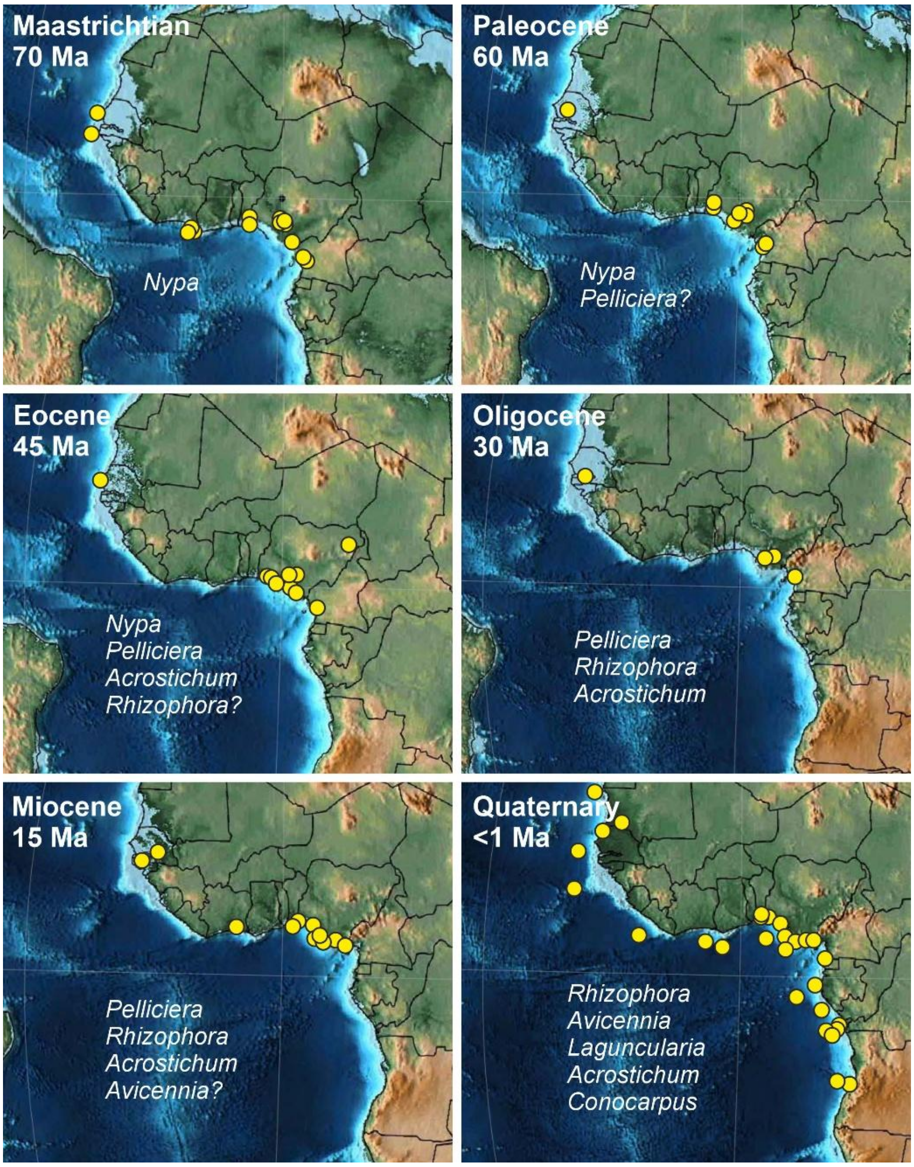

Figure 5. Biogeographic trends over time of major mangrove elements in the WAFMA dataset. Pleogeographic maps were generated with GPlates v2.5.0, which reconstructs the past position of present-day fossil sites for each geological age, using the Scotese (2016) PALEOMAP PaleoAtlas as the reference.

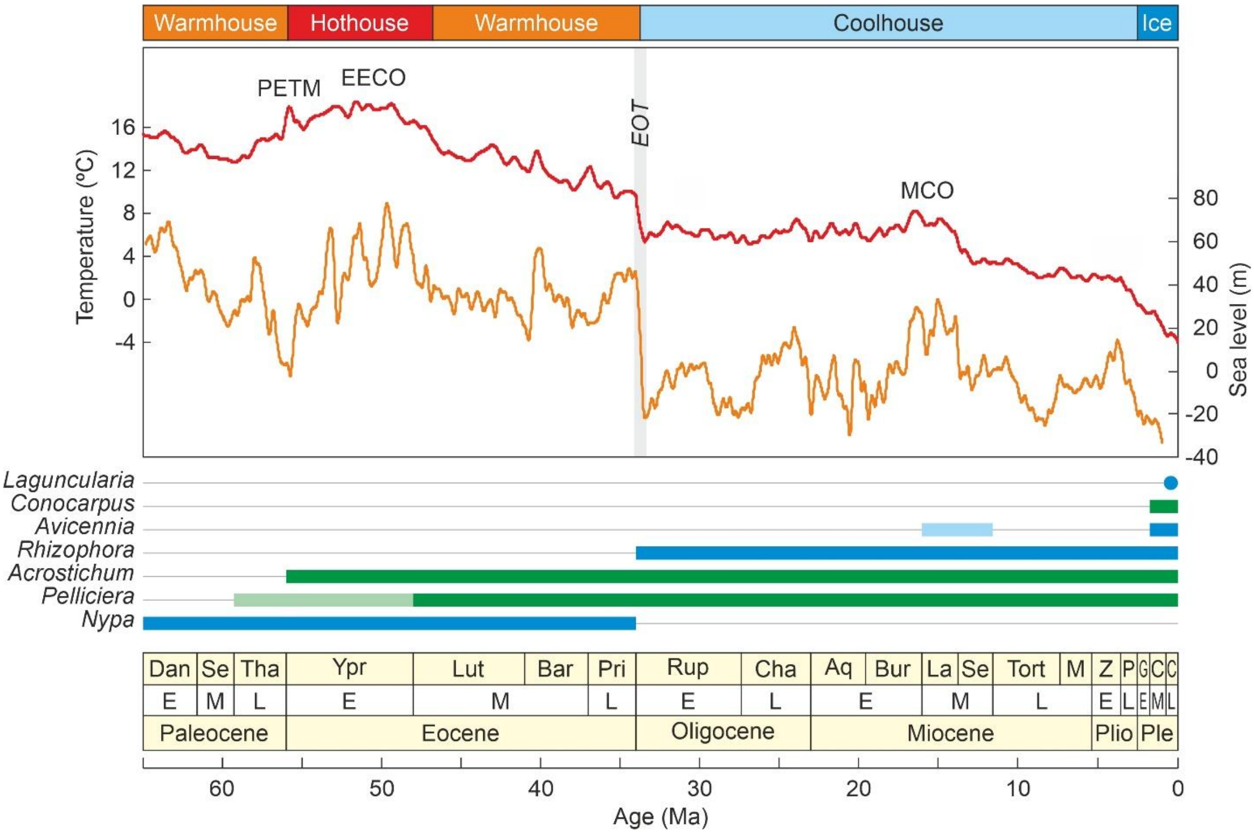

Figure 6. Geochronological ranges of major mangrove elements in the WAFMA dataset compared with global paleoclimatic (red) and eustatic (orange) trends. PETM, Paleocene/Eocene Thermal Boundary; EECO, Early Eocene Climatic Optimum; EOT, Eocene/Oligocene Transition; MMCO, Middle Miocene Climatic Optimum. 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.

Regarding *Rhizophora*, the first appearances were recorded in the Eocene, but they are doubtful owing to identification issues, as the photographies provided to illustrate *Zonocostites ramonae* do not correspond to this fossil form species (Chukwuma-Orji, 2023; Aigbadon et al., 2024), or no illustrations or descriptions are provided for verification (Olayiwola et al., 2022). In the Caribbean region, the first appearances of *Rhizophora* occurred in the Middle–Late Eocene (Fig. 7) and consisted of scattered occurrences, suggesting that *Pelliciera* was still the dominant mangrove tree (Rull, 2023a). Molecular phylogenetic studies suggest that *Rhizophora* originated in the IWP region and dispersed westward to the AEP region during the Early and Middle Eocene via the southern route around the African continent, the Tethys Seaway, or both (Takayama et al., 2021). The CARMA (Rull, 2024) and WAFMA (this study) datasets show that *Rhizophora* mangroves were not well developed throughout the Eocene in the AEP region, where mangroves were dominated by the autochthonous *Pelliciera* as the principal mangrove-forming tree.

4.4. Oligocene

The Eocene/Oligocene Transition (EOT), characterized by an abrupt global cooling and eustatic sea-level fall (Coxall & Pearson, 2007; Hutchinson et al., 2019) (Fig. 6), marked the last appearance of *Nypa* in West Africa. Some records are dated as Eocene to Early Oligocene but, again, these chronostratigraphic ranges do not necessarily include the Oligocene, and either no illustrations or descriptions, or only confusing, non-diagnostic photographs, were provided (Olayiwola et al., 2022; Chukwuma-Orji, 2023). The same situation occurred in the Caribbean (Fig. 7), confirming that *Nypa* disappeared from the AEP during the EOT, likely as a result of the global climatic change that initiated the coolhouse-Earth state characterized by the glaciation of Antarctica (Rull, 2024). The EOT also marked the emergence of *Rhizophora* as a major mangrove-forming tree in West African mangroves, together with *Pelliciera*. The situation was similar in the Caribbean, but there *Pelliciera* underwent a marked decline, leading to the dominance of *Rhizophora* from the Oligocene onward, which represented a major evolutionary turnover in Neotropical mangroves (Rull, 2023a). *Acrostichum* remained at similar abundances on both sides of the Atlantic as a minor true-mangrove element.

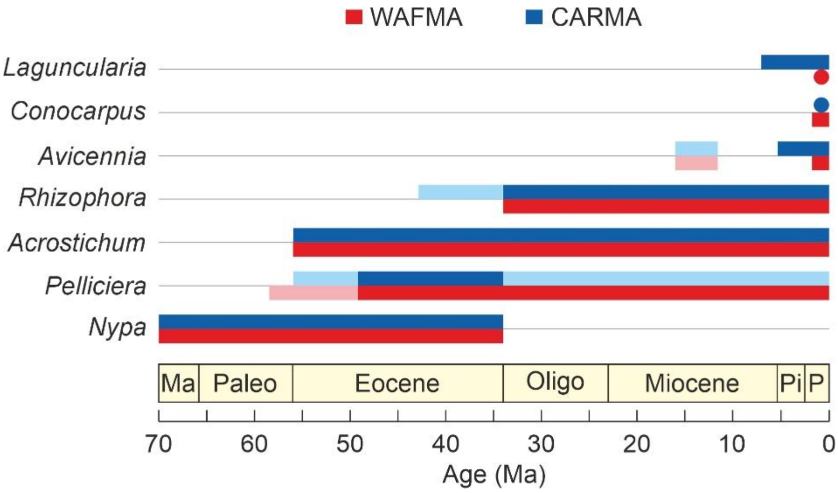

Figure 7. Comparison between the chronostratigraphic ranges of mangrove elements at both side of the Atlantic Ocean in the AEP biogeographic region using the WAFMA dataset for tropical West Africa (this study) and the CARMA dataset for the Caribbean (Rull, 2024).

The sustained importance of *Pelliciera* in West African Oligocene mangroves, in contrast with its replacement by *Rhizophora* in the Neotropics during the EOT, remains to be explained. The available evidence is still insufficient to provide a sound explanation, and the topic is worth exploring in future research, as *Pelliciera* fossils, notably *Psilatricolporites crassus*, have been unequivocally identified outside the Neotropics following a careful morphological analysis of the whole available evidence (see also Rull, 2025a). This means that the global historical biogeography of the AEP mangrove tree *Pelliciera* merits reconsideration.

4.5. Miocene

The Miocene record was similar to that of the Oligocene, with the addition of *Avicennia* during the Middle Miocene, roughly coinciding with the Middle Miocene Climatic Optimum (MMCO) (Figs. 5 and 6). However, this Miocene occurrence was mentioned only in the text of a study from the Niger Delta; *Avicennia* was neither shown in the pollen diagram nor illustrated in the accompanying pollen photomicrographs (Durugbo & Olayiwola, 2017). Therefore, this record should be treated with caution, particularly because it represents the only reported Neogene occurrence of this pollen type in the study area (Table 3). The same pattern was recorded in the Caribbean region (Rull, 2023b) (Fig. 7), providing consistency across the AEP region. If these *Avicennia* records are confirmed, this mangrove-forming tree may have been present, albeit at low abundances, in the Atlantic during the Middle Miocene, prior to its definitive Plio-Pleistocene inception.

The combination of fossil evidence (reviewed in Rull, 2026a, b) and molecular phylogenetic analyses (Li et al., 2016) suggests that *Avicennia* originated in the central Tethys region, between present-day Europe and the Middle East, around the Paleocene/Eocene boundary, and subsequently diverged into two major lineages, the IWP and the AEP clades. Molecular dating indicates that diversification within the IWP lineage occurred during the late Miocene, whereas the age of the split between the IWP and AEP lineages remains unconstrained. Consequently, the evolutionary history of *Avicennia* between its Paleogene origin and the Neogene diversification of its extant lineages remains poorly understood and requires further palaeobotanical and phylogenetic investigation.

To complicate the picture, an *Avicennia*-like pollen record was reported from the Eocene of Australia (Churchill, 1973). This record has propagated through the scientific literature and has often been regarded as convincing evidence of the presence of *Avicennia* in Australia during the Eocene. However, Muller (1981) noted that this pollen could instead belong to other genera of Verbenaceae (the family to which *Avicennia* was assigned at the time), such as *Gmelina* or *Peronema*.

4.6. Quaternary

This period represents the time of maximum mangrove diversity following the establishment of *Avicennia* in the Pleistocene and the addition of *Conocarpus* (Pleistocene) and *Laguncularia* (Holocene) (Figs. 5 and 6). This increase in mangrove diversity parallels the so-called Neogene–Quaternary Diversification Trend (NQDT) documented in the Caribbean region (Rull, 2023b), suggesting that it was a regional AEP phenomenon. The main difference is the persistence of *Pelliciera* in the Neotropics, although restricted to a relict area around the Isthmus of Panama (Duke, 2020). Considering only the reliable identifications (Table 3), *Pelliciera* could have disappeared from the West African fossil record during the Late Miocene. Although Germeraad et al. (1968) reported *Pelliciera* in high abundances until the Pleistocene, this is not supported by the numerous Pleistocene records compiled in the present study (Fig. 5). It is possible that the records reported by Germeraad et al. (1968) are predominantly of Early Pleistocene age, whereas most of those documented here are Middle to Late Pleistocene (700 ka onward). However, this interpretation remains to be confirmed. In any case, the available evidence suggests that the regional extinction of *Pelliciera* in West Africa, where the genus is now absent, occurred relatively recently.

The Pleistocene records documented changes in mangrove abundance, mainly of *Rhizophora*, across glacial-interglacial cycles. The longest of these records span the last 700 ka, encompassing the last seven glacial cycles, corresponding to marine isotope stages (MIS) 3 to 17. In these studies, *Rhizophora* pollen is considered *a priori* a proxy for wet climates, rather than a research target in its own right, and is sometimes grouped together with rainforest and freshwater swamp pollen (Dupont et al., 1989). This not only obscures mangrove dynamics as ecosystems and their potential relationships with other environmental factors (e.g., temperature or sea level), but also increases the risk of circular reasoning in paleoenvironmental reconstructions. When *Rhizophora* pollen curves are presented separately, no clear relationship between mangrove abundance and glacial and/or interglacial stages is observed (Dupont et al., 1998). In a couple of records spanning the last three-four glacial-interglacial cycles (400-300 ka onward), this relationship is clearer, with *Rhizophora* being more abundant during interglacials (especially MIS 5 and 7) and lower or absent during glacials (Ning & Dupont, 1997; Jahns et al., 1998). The last glacial cycle is represented in several cores, also with *Rhizophora* as the dominant or the only mangrove element. These records confirm the high mangrove abundances during the last interglacial (MIS 5), the marked decline throughout the last glacial, and the subsequent Holocene recovery (e.g., Dupont & Weinelt, 1996; Jahns, 1996; Dalibard et al., 2014), supporting the glacial–interglacial pattern suggested by earlier studies.

The proposed drivers of this cyclic pattern include a combination of climatic factors (temperature and moisture availability) and eustatic changes associated with glacial–interglacial cycles. In addition to temperature and moisture oscillations, which are well-known drivers of mangrove development (Quisthoudt et al., 2012; Osland et al., 2017), sea-level fluctuations could have played a significant role, as the continental shelf was largely exposed during glacials, greatly reducing the habitat available for mangroves. This was also the case in the Caribbean region, where mangroves were restricted to small refugial areas during the Last Glacial Maximum (LGM). They survived there until the Holocene sea-level rise inundated the continental shelf again, allowing Caribbean mangroves to re-expand to their present distribution and abundance (Rull, 2025b).

A major continental-scale Late Pleistocene–Holocene environmental shift, known as the African Humid Period (AHP), was detected in an offshore core off Mauritania and lasted approximately from 15 to 5.5 ka. The AHP was characterized by a significant increase in precipitation due to the astronomically driven strengthening of the African monsoon, which resulted in a fully vegetated Sahara with numerous perennial lakes (deMenocal et al., 2000). The termination of the AHP was abrupt and caused intense regional aridification, leading to the present-day desert conditions of the Sahara. In tropical West Africa, the effects were less pronounced and consisted of minor changes in rainforest composition (Lézine et al., 2005) and the local development of forest–savanna mosaics (Salzmann & Hoelzmann, 2005). However, this climatic shift did not significantly affect the extent or composition of mangrove communities.

4.7. Synthesis and AEP coherency

In contrast to other mangrove-bearing regions analyzed using the same methodology based on comprehensive regional datasets (CARMA, EURMA, and MESMA), where plate tectonics and continental drift led to the waxing and waning of biogeographic pathways and barriers for marine and coastal organisms, West African mangroves were subjected to comparatively minor paleogeographic changes. The main paleogeographic event was the progressive separation of Africa and South America during the opening of the Atlantic Ocean; however, these two continental masses were already far appart when the first mangrove elements appeared in the Late Cretaceous (Fig. 5). The most influential paleogeographic change was the closure of the Tethys Sea by the collision of the Arabian Plate with Eurasia, which occurred across the Oligocene–Miocene transition, approximately 27–21 Ma (Pirouz et al., 2017; Torfstein & Steinberg, 2020), thereby blocking the proto-Mediterranean connection between the IWP region and the European sector of the Tethys. Prior to this event, the Atlantic domain could have been colonized by IWP mangrove taxa, notably *Rhizophora*, via both the northern (Tethyan) and southern African dispersal routes (Fig. 3). From the Oligocene–Miocene transition onward, however, only the southern route remained available. In contrast, Tethyan elements such as *Avicennia* could have continued to disperse through the northern Atlantic. *Pelliciera* represents a special case because of its autochthonous Atlantic origin.

Some early studies, including the seminal work by Germeraad et al. (1968), suggested that IWP mangrove taxa could have reached the Atlantic through the Central American Seaway before the Pliocene closure of the Isthmus of Panama (O'Dea et al., 2016), a hypothesis that has subsequently been reiterated by several authors (e.g., Ellison, 1991). However, despite more than five decades of palaeobotanical research, this scenario remains unsupported by the fossil record. No Paleogene fossil evidence documents a trans-Pacific migration pathway for the major mangrove genera, whereas the Tethyan route is supported by numerous fossil occurrences extending from Europe to Southeast Asia. Consistent with this evidence, the global phylogeographic analysis of *Rhizophora* by Lo et al. (2021) interpreted the Central American Seaway as facilitating Neogene dispersal between the Atlantic and eastern Pacific sectors of the already established AEP lineage, rather than as the primary route by which that lineage originated. Regarding the potential role of southern African route, a regional EAFMA (East African MAngroves) study, similar to those developed for the Caribbean (CARMA), the Middle East (MESMA), Europe (EURMA) and West Africa (WAFMA), is in progress and will hopefully help clarify this issue.

An additional peculiarity of the WAF region is the absence of major diversity crises, bottlenecks or turnovers in mangrove biogeography and evolution, in contrast to other regions. For example, Caribbean mangroves experienced a major compositional turnover during the EOT, when *Rhizophora* mangroves replaced the primeval Eocene *Pelliciera* mangroves, paving the way for the establishment of the well-developed and diverse mangrove communities found today (Rull, 2023a). In Europe, mangroves flourished during the Paleogene and underwent major range and biodiversity crises during the EOT and the Messinian Salinity Crisis, culminating in the Pliocene extinction of these communities from the continent (Rull, 2026a). In the Middle East, mangroves were resilient to the global environmental disruption associated with the EOT but experienced two strong regional aridity crises, during the Miocene and the Holocene, that led to the present scarcity and low diversity of mangrove communities (Rull, 2026b).

By contrast, West African mangroves exhibited a slow and continuous increase in richness, interrupted only by the extinction of *Nypa* around the EOT, with no major geographic or diversity shifts. Further studies are required to understand the apparently greater stability of West African mangroves in relation to global and regional environmental changes. It is possible that the high paleogeographic stability has played a role in this long-term constancy. Indeed, the absence of major paleogeographic reorganizations linked to plate tectonics, such as those involving the Caribbean and Arabian plates, may have been an important contributing factor. In the WAF region, only minor coastal shifts have been documented since the Late Cretaceous (Fig. 5), with comparatively limited paleogeographic influence.

Comparisons between the WAFMA and CARMA datasets have supported the coherence of the AEP region in chronostratigraphic, paleobiogeographic and paleobiodiversity terms. Common features include the occurrence of *Nypa* as the only mangrove taxon during the Late Cretaceous and its extinction during the EOT, together with the Paleogene diversification following the emergence of *Pelliciera*, *Acrostichum* and *Rhizophora*, and the Neogene–Quaternary diversification driven by the arrival of *Avicennia* (Miocene), *Conocarpus* and *Laguncularia* (Plio-Pleistocene) (Fig. 7). The main difference has been the virtual disappearance of *Pelliciera* in the Caribbean region, where it persists in a relictual area, and its continuity as a significant mangrove element in West Africa until its recent (Pleistocene?) extirpation. These trends and patterns show that the AEP region is more than a biogeographic entity defined by extant taxonomic patterns, constituting instead a coherent unit within the global spatiotemporal context of mangrove biogeography and evolution.

5. Conclusions

<u>Origin</u>. The earliest West African communities with present-day mangrove elements emerged during the Late Cretaceous (Campanian–Maastrichtian) and were characterized solely by the palm *Nypa*. The absence of mangrove-forming trees such as *Rhizophora* and *Avicennia*, with their characteristic aerial root (pneumatophore) architecture, together with the known preference of *Nypa* and its ancestors for fresh to low-salinity floodwaters, precludes interpreting these communities as typical modern-like mangroves forming a coastal fringe inundated by marine waters. The same pattern has been documented in the Caribbean region, suggesting that it was widespread throughout the AEP region.

<u>Eocene diversification</u>. Similar to the Caribbean, the first characteristic mangrove trees emerged during the PETM–EECO warming interval and dominated coastal communities from the Middle Eocene onward. These Eocene mangroves were characterized by *Pelliciera* at the seaward fringe, with *Nypa* and *Acrostichum* occupying back-mangrove brackish environments. *Pelliciera* was absent from mangrove-bearing regions outside the Atlantic, reinforcing its status as an autochthonous AEP lineage. To date, it remains unknown whether *Pelliciera* originated in West Africa or the Caribbean, as it appeared almost simultaneously in both regions. The first scattered records of *Rhizophora* date to the Late Eocene, also mirroring the Neotropical pattern.

<u>EOT shifts</u>. The EOT global cooling and sea-level decline coincided with the regional AEP extinction of *Nypa* and the abrupt increase of *Rhizophora*, which became co-dominant with *Pelliciera* in West African mangroves. In the Neotropics, by contrast, *Rhizophora* replaced *Pelliciera* as the dominant canopy tree in post-Eocene mangroves. Therefore, the arrival of *Rhizophora*, likely from the IWP via the Tethyan Seaway, the southern African connection, or both, represented an enrichment of the seaward mangrove canopy in West Africa rather than a major community turnover, as occurred in the Neotropics.

<u>Continued Neogene enrichment</u>. The diversification of mangrove communities continued during the Neogene and the Quaternary with the addition of *Avicennia* (Miocene), *Laguncularia* and *Conocarpus* (Quaternary), following a trend similar to that observed in the Caribbean Neotropical region. *Avicennia* arrived from the central Tethys, where it originated during the Paleocene–Eocene, whereas *Laguncularia* and *Conocarpus* appear to be autochthonous AEP elements whose origin remains unknown.

<u>Quaternary reorganizations</u>. Following the completion of the Neogene enrichment of West African mangroves, the Pleistocene glacial–interglacial cycles led to the spatial reorganization of these communities, likely driven by climatic and eustatic changes. In general, mangrove communities, with *Rhizophora* as the dominant canopy tree, were more extensive during warm interglacial highstands and contracted during cold glacial lowstands. The end of the Late Pleistocene–Holocene African Humid Period (AHP), which was responsible for regional aridification and the onset of Saharan desertification, seems to have had a comparatively smaller effect on tropical West African mangroves.

<u>AEP coherency</u>. The analysis of the WAFMA dataset and its comparison with the CARMA dataset have emphasized the high degree of coherency within the AEP region, as defined not only by its present-day biogeographic patterns but also by its evolutionary history since the Late Cretaceous. Thus, the AEP may

be regarded as a biogeographic and evolutionary unit for mangroves, whose distinctive features have been established since its earliest history.

No apparent crises. A notable difference between West African mangroves and other mangrove-bearing regions studied to date using the same methodology is the apparent absence of significant demographic or diversity crises, bottlenecks or major outbreaks. Indeed, West African mangroves exhibited a modest but relatively continuous diversification trend from the Late Cretaceous to the present, with the only exception being the extinction of *Nypa* across the EOT. The long-term paleogeographic stability of the region may have played a key role in this process.

6. Further research and recommendations

The following is only a sample of the research topics suggested by the WAFMA dataset examined here. Hopefully, new evidence and its interpretation will generate additional avenues of inquiry, advancing our understanding of the evolutionary history and historical biogeography of West African mangroves, as well as their significance in a global context.

Nypa communities. This is a topic of general interest that transcends the West African context, as the occurrence of Late Cretaceous coastal communities characterized by *Nypa* as the only modern-like mangrove element is a widespread feature worldwide. As mentioned above, these communities must have differed from modern mangrove ecosystems because of the distinctive morphological and ecophysiological characteristics of this palm. Therefore, modern analogue methods do not appear to be appropriate for reconstructing such communities. Instead, fossil community inference based on quantitative statistical methods is likely to provide a more objective interpretation (Rull, 2025c). The use of pollen-independent paleoenvironmental proxies may also help to constrain the autecological traits of the reconstructed communities.

Pelliciera continuity and recent extinction. Within the general spatiotemporal homogeneity of the AEP region, *Pelliciera* represents the most notable difference between the eastern and western Atlantic sectors. Indeed, the EOT replacement of *Pelliciera* by *Rhizophora* in Caribbean mangroves and its subsequent restriction to a small equatorial range contrast with the co-dominance of *Pelliciera* and *Rhizophora* in West African mangroves throughout the Paleogene and Neogene, followed by the very recent (Pleistocene?) extinction of *Pelliciera*. This raises several questions regarding the evolution of *Pelliciera*, including its geographic origin, the ecological drivers of its biogeographic history and the causes underlying its persistence in the Neotropics, albeit as a relict, versus its extinction in Africa. In addressing this research topic, rigorous identification of fossil *Pelliciera* pollen is essential, as it represents one of the most critical aspects of mangrove research in West Africa and other extra-Neotropical areas, as discussed throughout this paper.

Avicennia temporal gap. The time lag between the Paleogene origin of *Avicennia* in the central Tethys and its first appearance in West Africa during the Miocene also demands further investigation. A similar temporal gap appears to exist worldwide, as the earliest records of *Avicennia* in the Neotropics and the IWP also date from the Miocene. Whether this gap is real or reflects sampling or preservation biases, or fossil taxonomic uncertainty, remains unknown.

Lack of crises. Unraveling the potential causes of the resilience of WAF mangroves in the face of environmental perturbations, compared with other mangrove-bearing regions that have experienced significant disruptions in range, abundance and diversity, may help identify the main external drivers of mangrove change and improve our understanding of how these ecosystems respond to global and regional environmental shifts.

Finally, the following recommendations have emerged from this review and may be applicable to fossil-based paleoecological research in general:

Literature reliability. The use of reliable sources of fossil evidence is essential in this context. Although no universally accepted procedure exists for selecting the literature, some general guidelines can help minimize the inclusion of potentially unreliable sources. The methodology adopted in this review is intentionally conservative, giving priority to journals indexed in the most widely recognized bibliographic databases and to books published by established academic publishers. Particular care has been taken to avoid so-called predatory journals and publishers, as well as gray literature whose peer-review procedures cannot be verified.

Taxonomic accuracy. This is another key aspect that strongly affects the reliability of the conclusions drawn. Incorrect or uncertain taxonomic identifications can only be evaluated when the original fossil evidence is explicitly presented in the form of illustrations and/or descriptions. Accordingly, only original references have been used in this review. In some cases, however, the actual fossil evidence is not presented and only taxon lists, textual mentions or pollen diagrams are provided. These references have been included for the sake of completeness, but their limitations have been explicitly noted whenever they are critical to a particular interpretation. This does not reflect a lack of confidence in the authors' expertise, but rather the fact that their taxonomic reliability cannot be independently verified.

Circularity avoidance. This is an often overlooked issue that should always be considered in paleoecological research. In the case of the WAFMA dataset, two main sources of potential circular reasoning have been identified: one chronostratigraphic, affecting mainly pre-Quaternary studies, and the other paleoenvironmental, primarily in a Quaternary context. Although this warning may seem trivial or unnecessary, circular reasoning is more common than generally acknowledged, and constant vigilance is warranted.

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