Scientific Research Publishing

Atmospheric and Climate Sciences, 2026, 16(2), 273-291
https://www.scirp.org/journal/acs
ISSN Online: 2160-0422
ISSN Print: 2160-0414

Climatic and Paleoenvironmental Changes in Central Africa over the Last 300,000 Years: Evidence from the Rhizophora/Podocarpus Pollen Ratio in a Marine Core from the Gulf of Guinea

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How to cite this paper: Bengo, M.D., de Dieu Nzila, J., Otongo, J. and Gomat, H.-Y. (2026) Climatic and Paleoenvironmental Changes in Central Africa over the Last 300,000 Years: Evidence from the Rhizophora/Podocarpus Pollen Ratio in a Marine Core from the Gulf of Guinea. *Atmospheric and Climate Sciences*, **16**, 273-291.
https://doi.org/10.4236/acs.2026.162015

Received: December 10, 2025
Accepted: February 8, 2026
Published: February 11, 2026

Abstract

This high-resolution study expands on the initial analysis of the KW 23 core, which only covered the last 135,000 years, going back up to 300,000 years, extracted off the coast of Congo in the Gulf of Guinea, to reconstruct climatic and paleoenvironmental fluctuations in Central Africa. Fifty-eight samples were analyzed, allowing the identification of more than 150 pollen taxa. Particular attention was paid to the bioindicator taxa *Rhizophora* and *Podocarpus*, whose ecological requirements are respectively associated with warm and humid littoral conditions and cooler montane environments. Pollen diagrams were constructed using two datasets, including or excluding spores, which are often dominant in the assemblages. Variations in the *Rhizophora*/*Podocarpus* pollen ratio reveal a marked alternation between warm and cold climatic phases. This curve shows strong correspondence with the benthic foraminiferal $\delta^{18}O$ record of *Melonis barleeanum*, as well as with Milankovitch orbital curves and isotopic and temperature reconstructions derived from the Vostok ice core. Nine climatic zones corresponding to marine isotope stages (MIS 1 to 9) were identified. Odd-numbered stages are characterized by a high abundance of *Rhizophora*, reflecting warm and humid conditions favorable to mangrove development, whereas even-numbered stages are dominated by *Podocarpus*, indicating cooler climates and a downslope expansion of montane vegetation. These results demonstrate that the *Rhizophora*/*Podocarpus* pollen ratio is a reliable proxy for reconstructing Quaternary climatic variations in Central Africa and provide new insights into the regional expression of major global climatic oscillations.

Keywords

Quaternary Climate Change, Marine Palynology, Central Africa, Gulf of Guinea, *Rhizophora*, *Podocarpus*, Paleoenvironment, Marine Isotope Stages

1. Introduction

Marine sedimentary archives are key recorders of Quaternary climatic and environmental variations because of their temporal continuity and their ability to integrate continental and oceanic signals at large spatial scales [1]-[3]. In Central Africa, marine cores recovered from the Gulf of Guinea, therefore, provide a particularly suitable framework for analyzing how tropical continental systems respond to major global climatic oscillations.

Continental pollen grains exported to the ocean by large rivers, especially the Congo River, represent robust tracers of vegetation dynamics and regional climatic conditions. In contrast to continental archives, which are often influenced by local effects related to basin morphology or hydrological conditions, deep-sea marine archives integrate a regional pollen signal at the scale of vast drainage basins [4] [5]. This integrative characteristic gives marine records particular value for reconstructing Central African paleoenvironmental changes over long-time scales.

Numerous palynological studies conducted in the Gulf of Guinea have demonstrated that marine pollen assemblages reliably reflect the major vegetation units of the Congo Basin, provided that fluvial transport processes and marine hydro sedimentary dynamics are taken into account [6] [7]. More recent studies have further refined these interpretations by highlighting the key role of coastal hydrodynamism and marine circulation in pollen dispersal, redistribution, and preservation on the Cameroonian continental shelf [8], as well as the sensitivity of marine pollen assemblages to climatic variations during the Late Pleistocène and the Holocene [9] [10].

Marine core KW23, recovered from the Congolese margin of the Gulf of Guinea, provides an exceptional record covering approximately the last 300,000 years. Previous sedimentological and isotopic studies have revealed a succession of warm and cold climatic phases that are well correlated with marine isotope stages [11] [12]. However, palynological investigations of this sequence have remained partial and were previously restricted to the uppermost levels.

This study aims to extend the palynological analysis of the KW23 marine core to reconstruct the climatic variations in Central Africa over the last 300,000 years. It is based on a rigorous assessment of the main pollen groups and indicator taxa, particularly those associated with mangroves and Afro-montane formations. Previous work has highlighted the importance of *Rhizophora* during high sea levels and the extension of low-altitude *Podocarpus* during cooler periods in equatorial and southern Africa [13]-[15]. The relative abundances of *Rhizophora and Podocarpus*, as well as the variations in their ratio, will serve as a climatic proxy to distinguish the warm and humid phases from the cooler periods. These two taxa, with contrasting ecological requirements, constitute excellent climatic bioindicators during glacial and interglacial periods: *Rhizophora* is typical of coastal mangroves in hot and humid climates, while *Podocarpus* characterizes montane forests associated with cooler conditions.

2. Materials and Methods

2.1. Geographical and Environmental Setting

2.1.1. Location and Geological Context

The study site is located in the Gulf of Guinea, on the Congolese margin of the equatorial Atlantic Ocean. Marine core KW23, recovered during the WALDA cruise aboard the R/V *Jean-Charcot*, was collected at a water depth of approximately 2300 - 2330 m, between coordinates 3˚12′S-9˚18′E and 3˚46′05″S-9˚17′05″E (**Figure 1**). The site lies about 250 km west of the Congolese coastline and 300 - 425 km offshore from the Congo River estuary.

This area belongs to a sedimentary basin formed during Mesozoic rifting associated with the opening of the South Atlantic Ocean [16] [17]. Its stratigraphic

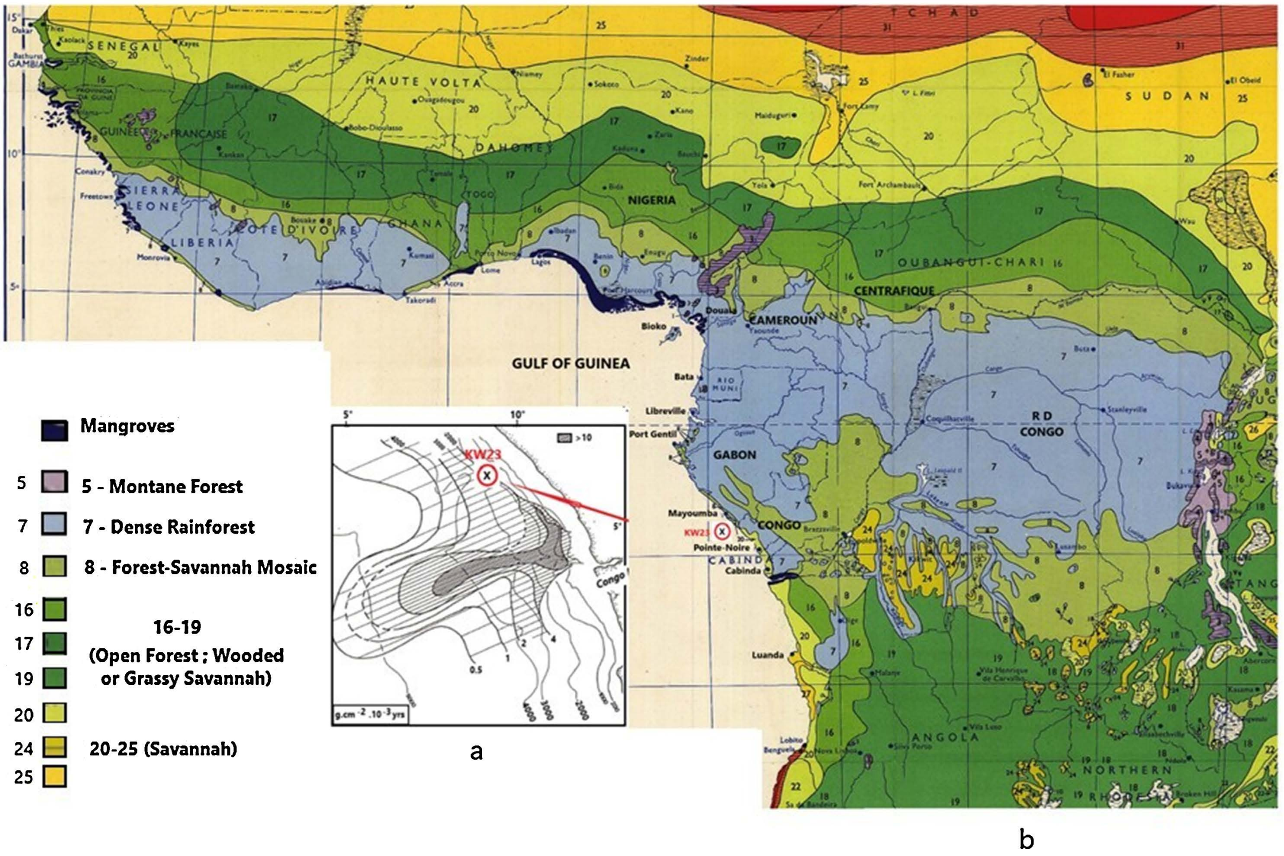

Figure 1. Location of core KW23 and vegetation. a: in Giresse et Barusseau (1989); b: in Aubreville *et al.* (1958).

succession includes pre-Albian continental deposits overlain by Upper Cretaceous and Cenozoic marine sediments. The distal position of core KW23, which is strongly connected to the Congo Basin (≈3.7×10^6 km^2), favors the recording of an integrated regional sedimentary and pollen signal dominated by continental terrigenous inputs [7] [18]-[20].

2.1.2. Terrigenous Inputs and Marine Dynamics

The Congo River represents the main source of terrigenous inputs to the Gulf of Guinea, with an average discharge of approximately 40,900 $m^3 \cdot s^{-1}$ and an annual suspended matter flux of 31 to 45 million tons, including sandy, pelitic, and organic fractions [21]-[23]. The fine fraction, dominated by kaolinite, smectites, and illite, results from the weathering of rocks and tropical ferrallitic soils within the Congo Basin [24], whereas the organic fraction notably includes pollen and spores produced by continental vegetation.

The dispersion and deposition of these materials are controlled by a complex system of currents, including the Guinea Current, the South Equatorial Current, the South Equatorial Countercurrent, the South Atlantic Current, and the Congo River outflow. Together, these circulation systems ensure water mass mixing and the transfer of sediments toward the deep basin [25] [26].

2.1.3. Atmospheric Circulation, Climate, and Vegetation

The climate of Central Africa is dominated by the seasonal latitudinal migration of the Intertropical Convergence Zone (ITCZ), which controls the alternation between a humid season characterized by oceanic monsoon influence and a dry season driven by continental trade winds [27]-[29]. The Congo Basin experiences a warm and humid equatorial climate, with annual rainfall ranging between 1500 and 2000 mm, favoring the development of dense and highly diversified vegetation [30] [31].

Lowland areas are dominated by Guineo-Congolian evergreen tropical rainforest, which transitions toward the basin margins into semi-deciduous forests, forest–savanna mosaics, and wooded savannas. Coastal zones host mangrove ecosystems dominated by *Rhizophora* [32] [33], while higher-altitude regions support montane forests where *Podocarpus* is a common component. These vegetation formations constitute the main sources of the pollen signal recorded in marine sediments from the Gulf of Guinea.

2.2. Material

Marine core KW23 was recovered using a Kullenberg coring system. Visual lithological observations reveal locally stratified layers, 1 to 2 cm thick, showing marked color variations, particularly olive to very dark olive lutite levels [11]. The sedimentary units, with thicknesses ranging from 10 to 250 cm, generally display gradual contacts, although sharp or bioturbated contacts are locally observed. Estimated sedimentation rates range between 3 and 8.5 $cm \cdot ka^{-1}$.

A standard analytical protocol was applied, including measurements of water content, $CaCO_3$ concentrations, and organic carbon and nitrogen contents, as well as detailed grain-size analyses at selected levels. Binocular microscope observations of the sandy fractions (>40 µm) allowed both quantitative and qualitative analyses of the main sedimentary components, including fecal pellets, foraminifera, diatoms, sponge spicules, quartz grains, and pyrite concretions.

In total, 58 samples, regularly distributed along the sequence and covering marine isotope stages 1 to 9, were analyzed.

2.3. Methods for Pollen Diagram Construction and Ecological Significance of Taxa

In long Quaternary marine sequences, the frequent overrepresentation of spores, as well as certain taxa such as *Rhizophora* and *Podocarpus*, requires a specific methodological approach for the construction and interpretation of pollen diagrams [6]. The data were processed using two distinct datasets. The first dataset includes all identified pollen taxa and allows the analysis of bioindicator taxa (*Rhizophora*, *Podocarpus*, and spores), whereas the second dataset excludes spores in order to improve the readability of relative variations in the other major taxa, following practices commonly applied in regional marine palynological studies [6] [10].

Pollen diagrams were constructed using percentage values calculated from each dataset. The ecological significance of the taxa is based on their modern ecology and on regional reference frameworks derived from previous palynological studies conducted in Central Africa, particularly for the interpretation of forest, savanna, littoral, and montane vegetation formations [34] [35]. Within this methodological framework, changes in the relative abundances of *Rhizophora* and *Podocarpus* are summarized by calculating the *Rhizophora/Podocarpus* pollen ratio, which is used as a quantitative indicator for analyzing paleoenvironmental and climatic variations throughout the sequence, in continuity with approaches developed in recent studies on the Cameroonian continental shelf [10].

3. Results

The main results of the geological study (lithology, mineralogy, and micropaleontology) of the biological and mineral components (**Figure 2**) are based on the work of Bonifay and Giresse (Bonifay, 1987; Bonifay and Giresse, 1992).

3.1. Biogenic Components

3.1.1. Foraminifera

Foraminifera constitute the main components of the calcareous tests in core KW23, with a general increase in carbonate content during warm isotope stages.

The species *Melonis barleeanum* (benthic) and *Globorotalia menardii* (planktonic) were used for oxygen isotope analyses and for biostratigraphic reconstruction. Benthic foraminifera tests are generally more resistant to dissolution processes than planktonic tests; a decrease in the value of P/B (planktonic foraminifera compared to benthics) is therefore linked to dissolution [36]. For each sample,

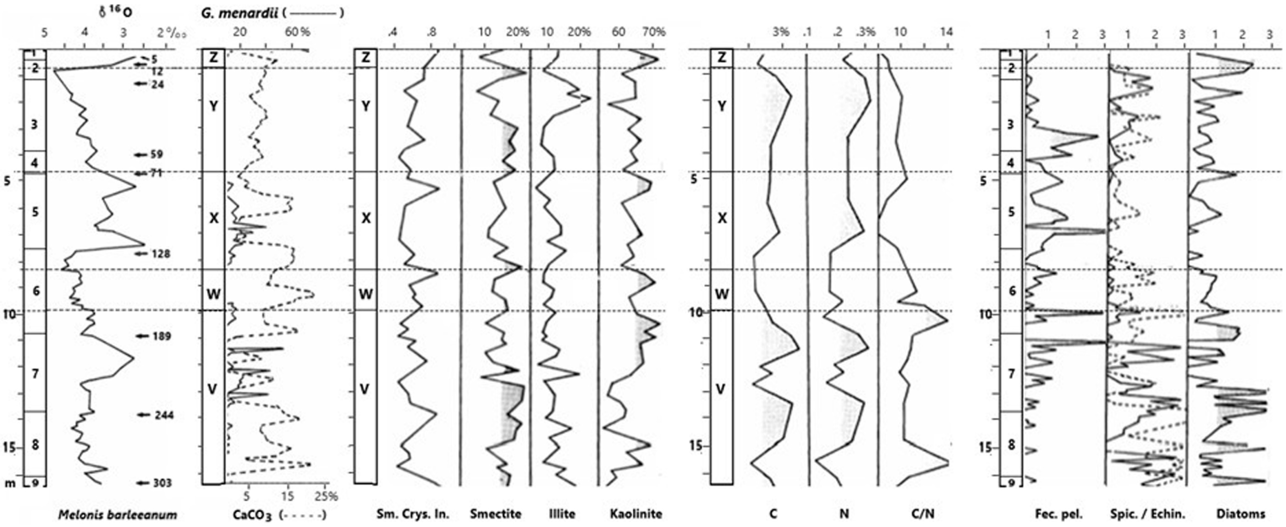

Figure 2. Lithostratigraphic section of core KW23 (Adapted from Extracts from the figures in Bonifay and Giresse, 1992).

15 to 20 specimens of *Melonis barleeanum* were selected for the determination of $\delta^{18}O$ values. The resulting isotopic curve allowed the sequence to be correlated with Marine Isotope Stages (MIS) 1 to 9 according to the chronology of [2], as revised by [3], with most stages displaying secondary fluctuations corresponding to substages. The top of the core is dated by radiocarbon (^{14}C) at approximately 5000 years BP, with the uppermost part of marine isotope stage 1 being poorly represented, whereas the base of the core, located at 16.40 m depth, corresponds to an age of about 303,000 years.

According to the ecostratigraphic zonation of Ericson and Wollin (1968), based on the relative abundance of *Globorotalia menardii*, its presence individualizes the warm biozones (Z, X and V), while its disappearance delimits the "cold" hypothermal biozones (Y and W). The top of biozone "X" is located at 460 cm; the disappearance of *G. menardii* at the top of isotopic stage 5 may be related to selective dissolution. The hypothermal biozone W, located between 820 and 970 cm, represents only a tiny fraction of MIS 6. Strong variations in the abundance of G. *menardii* within biozone V indicate significant climatic fluctuations.

3.1.2. Calcareous Tests

The P/B index generally follows the evolution of the carbonate curves. The cumulative curve of the carbonate particle flux (**Figure 2**) shows several marked decreases, mainly associated with warm Marine Isotopic Stages (MIS 5.0, 5.4, and 7), while smaller increases correspond to certain cold stages, particularly MIS 5.2 and 2. Lithological analysis reveals stratified sedimentary levels 1 to 2 cm thick, with varied colors. The chronostratigraphic framework of core KW23 allows estimating the periodicity of lamination formation between 116 and 330 years. Stages 3 and 5c are characterized by high sedimentation rates, whereas lower values indicate a greater distance from detrital input. These zones, distributed randomly throughout the stratigraphy, are mainly associated with biozones "V" and "Y".

3.1.3. Fecal Pellets and Siliceous Skeletons (Figure 2)

Fecal pellets and siliceous skeletons represent important biogenic components of core KW23. Their abundance reflects variations in oceanic primary productivity, with high concentrations generally associated with cold periods. Diatoms show maximum abundances during marine isotope stage 2, at the top of stage 3, as well as in the lower part of the sequence, whereas fecal pellets are particularly abundant during stages 3 and 5.4, at the base of stage 6, and at the top of stage 7. Sponge spicules, in turn, display increased abundances during marine isotope stages 2, 3, 7, and 8.

3.1.4. Organic Carbon and Nitrogen (Figure 2)

Profiles of total organic carbon and organic nitrogen display a closely correlated evolution throughout the sequence, indicating a predominantly marine origin of the organic matter. Carbon content, ranging between 2% and 3%, reflects high levels of organic matter. The C/N ratio, which is higher in the lower part of the core, highlights differences in the preservation state of organic matter within the sequence.

3.2. Mineral Components

3.2.1. Quartz

In the marine sediments of core KW23, the abundance and variations of coarse quartz (>50 μm) are directly related to terrigenous inputs and long-distance transport processes. Morphological observations indicate grains of multiple origins, including aeolian inputs attributed in particular to the Saharan and Chadian regions, as well as aquatic inputs linked to continental drainage. The highest quartz concentrations are mainly recorded during the cold and dry phases of the sequence (Figure 2).

3.2.2. Clay Minerals

Clay minerals are dominated by kaolinite, with proportions ranging between 40 and 75%, followed by smectites (15% - 30%) and illite (up to 10%). Kaolinite content decreases with increasing distance from the mouth of the Congo River. This clay fraction reflects substantial continental inputs, mainly derived from pedogenesis developed on adjacent land areas, with proportions varying along the sequence (Figure 2).

3.3. Pollen Identification, Abundance, and Taxonomic Diversity

The initial study carried out on 18 levels of the upper part of the nucleus (800 cm) and covering the last 135,000 years (Bengo and Maley, 1991), identified 152 types of pollen. Spores account for nearly half of the grains counted, followed by the main tropical families (Euphorbiaceae, Caesalpiniaceae, Rubiaceae), bioindicator taxa (Rhizophora and Podocarpus), taxa characteristic of open formations (Gramineae, Cyperaceae) and temperate taxa. For this follow-up study, the species richness remained similar, but a total of 17,262 pollen grains (53.5%) and 14,991 spores (46.5%) were recorded. The main taxa identified are Podocarpus (4246 grains; 24.60%), Rhizophora (3633; 21.05%), Gramineae (2511; 14.54%), Cyperaceae (2080; 12.05%), temperate taxa (1081; 6.26%), other taxa (2995; 17.35%), and indeterminate pollens (716: 4.15%). Detailed values for each level are presented in Table 1, corresponding to dataset 2.

Table 1. Counting table and percentages of the main taxa and plant groups.

	N°	*Profondeur (cm)*	*Rhizophora*	*Podocarpus*	*Gramineae*	*Cyperaceae*	*Temperate*	*Undetermined*	*Other*	*Total*	*Graminae + Cyperaceae*	*Rhizophora / Podocarpus*	*Dinocysts*
1		**20-22**	20,90	23,89	40,31	2,99	7,47	1,49	2,96	**100**	43,29	0,87	2 873
2	**12**	**40-42**	58,02	7,41	16,67	1,85	3,70	3,09	9,26	**100**	18,52	7,83	159
3		**40-54**	54,55	13,64	4,55	6,82	4,55	4,55	11,36	**100**	11,36	4,00	27
4		**54-56**	32,56	17,67	12,56	13,95	1,40	2,79	19,07	**100**	26,51	1,84	163
5		**62-64**	22,61	18,37	38,14	7,07	1,41	4,24	8,16	**100**	45,21	1,23	18
6		**72-74**	18,99	26,58	34,18	5,07	2,53	1,27	11,38	**100**	39,25	0,71	45
7		**82-84**	14,90	26,07	25,14	2,80	0,10	6,25	24,74	**100**	27,94	0,57	27
8		**92-94**	8,70	46,38	0,00	11,59	7,25	4,35	21,74	**100**	11,59	0,19	35
9	**24**	**112-124**	8,74	31,69	14,75	9,29	1,09	7,10	27,32	**100**	24,04	0,28	678
10		**150-152**	9,72	20,14	37,50	5,56	19,44	4,17	3,47	**100**	43,06	0,48	226
11		**160-162**	10,55	12,66	28,49	6,32	20,04	1,16	20,77	**100**	34,81	0,83	75
12		**175-177**	8,62	12,06	23,27	7,66	4,31	6,90	37,19	**100**	30,92	0,71	64
13		**190-192**	28,71	7,59	8,91	8,91	21,78	3,96	20,13	**100**	17,82	3,78	193
14		**210-222**	3,16	12,60	42,52	15,75	15,75	6,30	3,93	**100**	58,27	0,25	10
15		**250-252**	12,99	17,86	21,91	3,25	29,22	1,62	13,15	**100**	25,16	0,73	45
16		**270-282**	10,42	10,67	9,43	21,59	0,00	1,99	45,91	**100**	31,02	0,98	205
17		**290-292**	9,27	11,59	20,86	0,77	49,43	1,55	6,53	**100**	21,63	0,80	44
18		**331-342**	24,29	11,43	12,86	18,10	2,86	6,67	23,81	**100**	30,95	2,13	88
19		**360-362**	28,10	13,50	9,85	7,66	21,90	2,55	16,42	**100**	17,52	2,08	534
20	**59**	**393-395**	20,01	31,02	27,01	10,01	2,00	5,00	4,95	**100**	37,02	0,65	148
21		**423-435**	2,38	52,25	32,08	3,56	1,19	2,38	6,16	**100**	35,64	0,05	757
22	**71**	**463-475**	2,04	43,92	27,58	3,06	0,00	3,06	20,33	**100**	30,64	0,05	469
23		**487-489**	3,16	51,58	28,41	1,05	0,14	6,31	9,36	**100**	29,46	0,06	289
24		**513-515**	8,22	39,73	15,07	4,11	0,14	9,59	23,15	**100**	19,18	0,21	207
25		**530-532**	20,41	8,17	55,12	2,04	0,22	0,22	13,81	**100**	57,16	2,50	48
26		**540-552**	4,55	50,00	0,00	9,09	0,00	4,55	31,82	**100**	9,09	0,09	280
27		**580-592**	12,93	40,82	7,71	6,35	1,13	4,31	26,76	**100**	14,06	0,32	829
28		**600-612**	1,59	57,14	6,35	0,00	3,17	9,52	22,22	**100**	6,35	0,03	2 061
29		**619-631**	22,45	28,57	28,57	2,04	2,04	4,08	12,24	**100**	30,61	0,79	117
30		**646-648**	1,82	52,73	14,55	1,82	0,00	10,91	18,18	**100**	16,36	0,03	1 126
31		**656-658**	26,22	28,66	29,88	6,71	2,44	2,44	3,66	**100**	36,59	0,91	182
32		**686-696**	0,70	80,28	5,63	0,70	0,00	4,93	7,75	**100**	6,34	0,01	1 680
33		**696-698**	3,96	63,49	4,86	1,98	0,72	1,80	23,20	**100**	6,83	0,06	199
34		**716-718**	40,82	24,49	6,12	4,08	10,20	6,12	8,16	**100**	10,20	1,67	147
35		**726-728**	3,80	21,52	58,23	3,80	6,33	3,80	2,53	**100**	62,03	0,18	489
36		**736-738**	4,00	32,00	36,00	12,00	12,00	4,00	0,00	**100**	48,00	0,13	931
37	**128**	**756-758**	31,50	9,36	11,49	11,07	3,83	4,26	28,50	**100**	22,56	3,36	931
38		**766-768**	0,55	27,68	21,35	1,47	1,58	6,32	41,05	**100**	22,82	0,02	5 007
39		**796-798**	10,83	41,74	7,14	7,37	0,33	2,79	30,80	**101**	14,51	0,26	901
40		**815-817**	7,69	34,62	46,15	3,85	3,85	3,85	0,00	**100**	50,00	0,22	602
41		**875-877**	5,33	20,67	18,00	29,33	6,00	7,33	13,33	**100**	47,33	0,26	1 161
42		**891-893**	12,45	43,58	11,21	10,38	2,49	3,32	16,58	**100**	21,58	0,29	2 766
43		**911-913**	8,89	57,79	15,00	7,22	3,89	2,22	4,98	**100**	22,23	0,15	871
44		**941-943**	5,94	26,32	10,59	37,72	4,65	2,41	12,36	**100**	48,31	0,23	860
45		**991-993**	10,64	14,36	14,36	33,51	4,79	7,98	14,36	**100**	47,87	0,74	1 504
46		**1001-1003**	23,65	13,30	13,30	13,30	6,40	3,45	26,60	**100**	26,60	1,78	643
47		**1021-1023**	29,41	8,82	15,88	17,65	4,12	3,53	20,59	**100**	33,53	3,33	2 043
48		**1061-1063**	33,59	17,58	10,55	17,97	3,52	2,73	14,06	**100**	28,52	1,91	364
49		**1071-1073**	29,03	10,48	10,89	18,88	6,05	8,06	16,61	**100**	29,77	2,77	185
50	**189**	**1080-1082**	1,67	68,33	25,00	0,00	0,00	5,00	0,00	**100**	25,00	0,02	91
51		**1150-1152**	23,16	13,90	31,26	5,79	15,05	8,10	2,73	**100**	37,06	1,67	383
52		**1160-1162**	3,05	47,72	27,41	0,17	7,10	4,07	10,47	**100**	27,59	0,06	876
53		**1246-1248**	0,18	73,27	19,40	0,02	0,72	2,87	3,54	**100**	19,41	0,00	5 547
54	**244**	**1366-1368**	62,09	3,27	17,65	3,92	5,23	1,31	6,53	**100**	21,57	18,99	550
55		**1424-1426**	34,32	6,86	26,47	16,67	0,98	8,82	5,88	**100**	43,14	5,00	739
56		**1484-1486**	39,78	6,45	14,52	13,98	2,15	5,91	17,20	**100**	28,49	6,17	316
57		**1534-1536**	35,17	20,69	18,62	12,41	2,07	3,45	7,59	**100**	31,03	1,70	102
58	**300**	**1574-1576**	62,96	8,64	11,11	9,47	1,65	4,12	2,06	**100**	20,58	7,29	212
		Total	**21,05**	**24,59**	**14,54**	**12,05**	**6,26**	**4,15**	**17,35**	**100**			**42 121**

🟨 ***(Yellow color) Levels analyzed in the preliminary study***

3.4. Variations in Pollen Climatic Bioindicators during the Late Pleistocene

The pollen diagram of climatic bioindicators, constructed from dataset 1, highlights significant variations throughout the Late Pleistocene (**Figure 3**). Spectra derived from this dataset show a strong dominance of spores, whose proportions locally reach nearly 80%. Diagrams constructed from dataset 2, in which spores are excluded, allow clearer visualization of the relative variations of *Podocarpus* and *Rhizophora*.

These two taxa exhibit marked fluctuations, often opposite or alternating, along the sequence. These variations are summarized by changes in the *Rhizophora/Podocarpus* pollen ratio (**Figure 3**), which shows values lower than 1 during phases dominated by *Podocarpus* and distinctly higher than 1 during phases characterized by *Rhizophora* dominance.

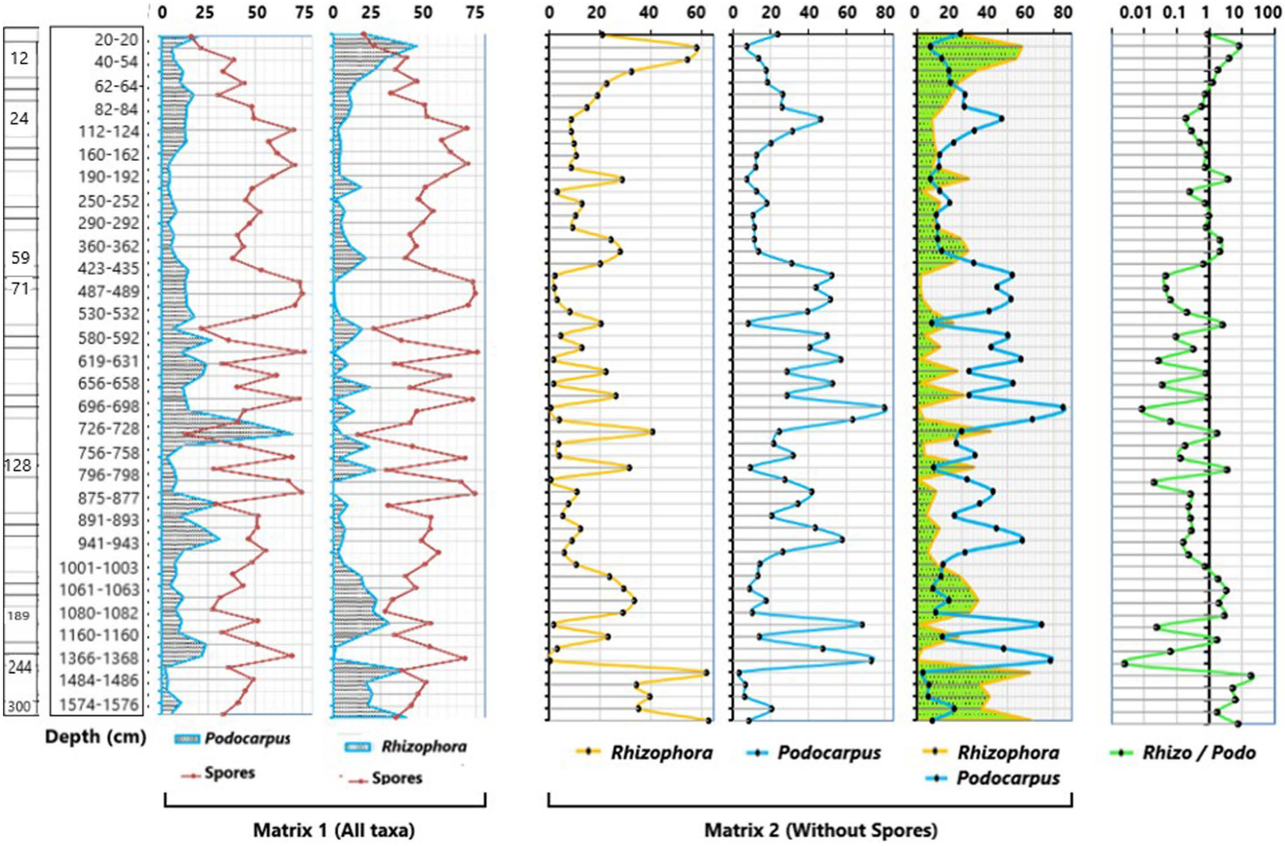

Figure 3. Pollen diagram (1): ecological bioindicators.

3.5. Variations in Vegetation Formations Inferred from Major Pollen Taxa

The spectrum of the *Rhizophora/Podocarpus* pollen ratio and of open savanna-type formations, represented by the taxa *Gramineae* and *Cyperaceae*, is shown in **Figure 4**. It highlights the contrast between savanna formations and forest formations, the latter being grouped under the category of “other taxa” in dataset 2,

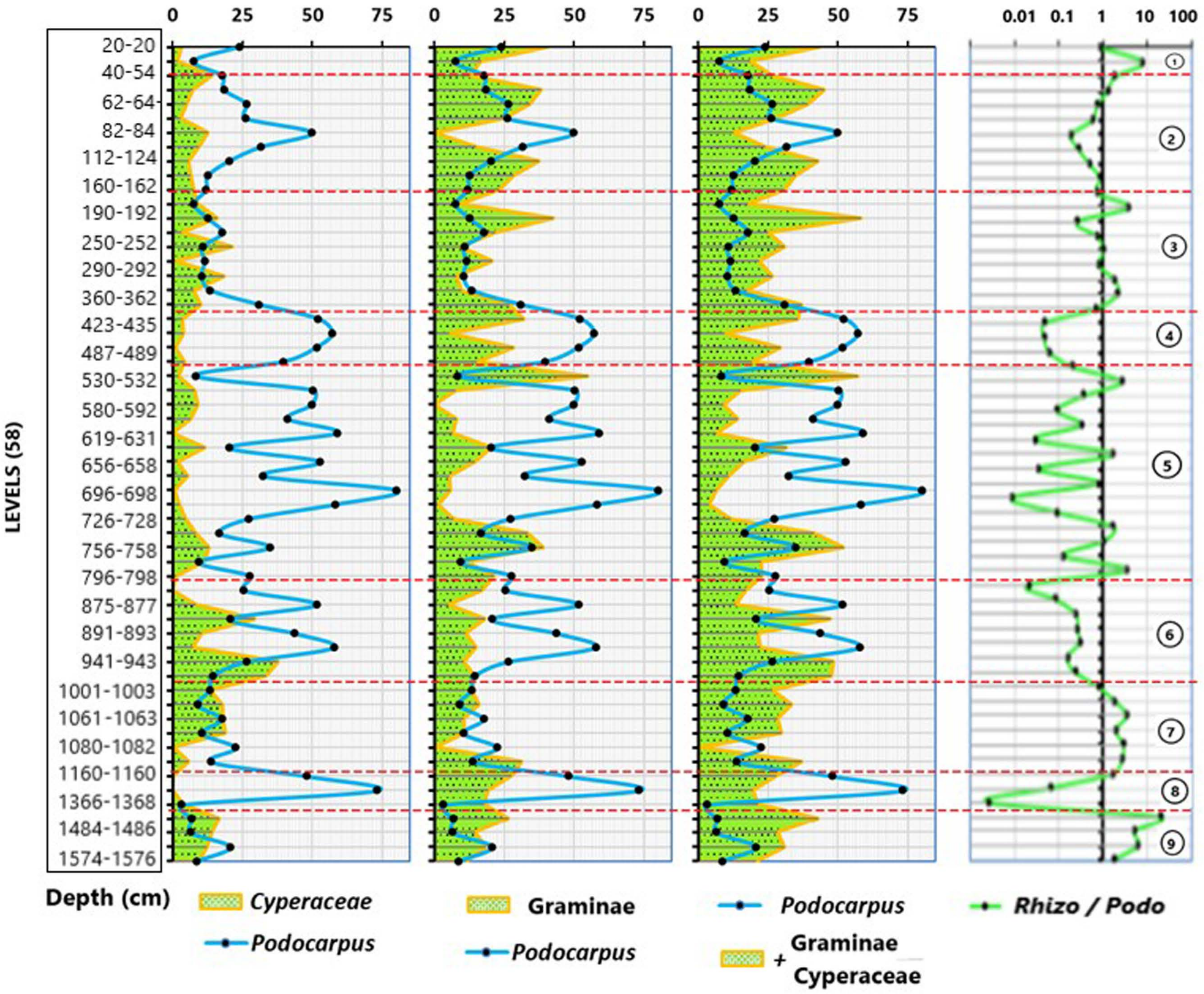

Figure 4. Pollen diagram (2): main taxa.

with the exception of temperate taxa.

This representation makes it possible to identify the different vegetation types present during successive climatic phases, as defined by the alternation of bioindicator taxa. Analysis of the transition zones corresponding to a value of 1 in the *Rhizophora*/*Podocarpus* ratio further allows the identification of the boundaries of the nine marine isotope stages as well as those of interstadials over the last 300,000 years.

3.6. Correspondence between the *Rhizophora*/*Podocarpus* Pollen Ratio and Established Climatic Models

Figure 5 illustrates the correlation between the pollen spectrum (Rhizophora/Podocarpus ratio), the δ^{18}O isotopic curve of the benthic foraminifer Melonis barleeanum, Milankovitch orbital cycles, and data from the Vostok ice core. This analysis highlights convergent trends among these indicators. Variations in the pollen ratio coincide with the main oscillations in isotopic and orbital records,

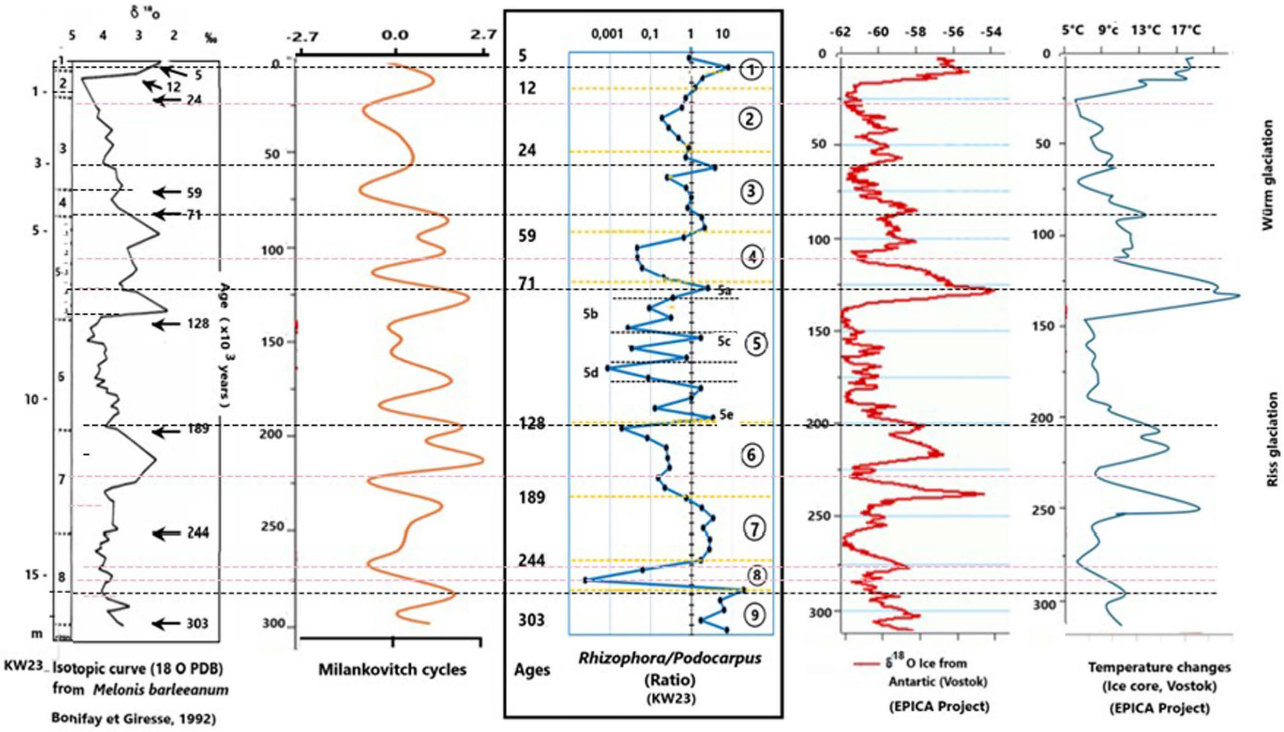

Figure 5. Comparison of the Rhizophora/Podocarpus ratio curve with standard climatic curves.

demonstrating a strong coherence between the Rhizophora/Podocarpus ratio and the oxygen-18 isotopic curve, particularly at stages 1, 2, 3, 4, 5a, 5b, 5e, the beginning of stage 7, as well as stages 8 and 9, over the past 300,000 years.

4. Discussion

4.1. Taxonomic Diversity and Representativeness of the Pollen Signal

Pollen assemblages derived from the complete analysis of core KW23 exhibit a high level of taxonomic diversity, comparable to that observed in earlier preliminary studies conducted on the upper part of the core [6] [37]. This diversity reflects the multiplicity of vegetation formations within the vast Congo Basin and confirms the ability of deep-sea marine archives from the Gulf of Guinea to integrate a continental pollen signal that is representative at the regional scale. Apart from spores, pollen from *Podocarpus*, *Rhizophora*, and *Gramineae* constitute the dominant taxa, highlighting the combined importance of montane, littoral, and open vegetation formations in the composition of the marine pollen signal.

The strong agreement observed between pollen profiles recorded at different levels of the core and the present-day and past distribution of continental flora underscores the major role of terrigenous inputs from the Congo River and its tributaries in transferring pollen to the marine domain. By draining a basin covering more than 3.7 million km^2, the Congo River acts as a powerful integrator of signals originating from diverse vegetation units, thereby limiting the influence of localized sources and enhancing the regional representativeness of the pollen assemblages recorded at site KW23.

Gramineae (Poaceae) constitute the main pollen contribution from herbaceous vegetation and indicate the presence of open environments such as savannas and grasslands within the Congo Basin. Their mean proportions remain relatively stable through time, except during certain phases marked by climatic cooling and a strong abundance of *Podocarpus*, which induces a relative dilution effect.

This relative stability can be explained by the extensive spatial coverage of savannas, which account for nearly one third of the surface area of the Congo Basin, and by their continuous contribution to the pollen flux exported to the ocean. Consequently, in deep-sea marine archives, *Gramineae* maxima do not systematically oppose forest phases, in contrast to what is frequently observed in small continental drainage basins.

This contrast is particularly clear when marine records are compared with those derived from small lacustrine sequences, such as Lake Barombi Mbo in Cameroon, where variations in *Gramineae* appear more strongly contrasted and directly opposed to phases of expansion of dense humid forest [38]. In such lacustrine contexts, forest expansion is often marked by the dominance of pioneer taxa (*Alchornea*, *Elaeis*) and forest taxa such as *Pycnanthus*, *Uapaca*, and *Aucoumea klaineana*, as well as by various families characteristic of Guineo-Congolian forests (Caesalpiniaceae, Sapotaceae, Sterculiaceae, Meliaceae, Sapindaceae) [39].

These observations fit within the broader debate on the Quaternary history of the African tropical rainforest. Many authors have suggested that during arid periods, the forest persisted in the form of forest refugia, while peripheral areas were invaded by savanna formations of the Sudanian–Zambezian type [40]. The results obtained from core KW23 suggest that, at the regional scale integrated by the Congo Basin, pollen signals record both the persistence of forest formations and the long-term importance of open environments, without a systematic opposition between the two. This pattern reflects a complex landscape mosaic modulated by Quaternary climatic fluctuations.

4.2. Dominance of *Rhizophora*

High proportions of *Rhizophora* pollen have been observed in recent dredging samples [8] and during marine isotope stage 1 of the Late Holocene in marine cores C61 [9] and CF [10] from the Cameroonian continental shelf. Comparable abundances have also been reported in several marine sequences from the Gulf of Guinea, notably off Gabon (GIK16867) [7], Congo (GeoB1008) [6] [14], and Angola (GeoB1016) [15], indicating a regionally consistent distribution of this taxon during recent warm and humid phases.

Rhizophora pollen is mainly recorded in coastal and marine sediments, either in offshore settings or in estuarine environments such as the Niger Delta [41] [42] and the estuaries of the Congolese coast, particularly around Pointe-Noire [43]. It is rarely found in continental archives, as pollen grains are predominantly exported to the marine domain by fluvial networks, a pattern confirmed by surface studies conducted in the Sanaga River basin [44].

Along core KW23, *Rhizophora*-rich levels reflect periods of shoreline stabilization and mangrove expansion under warm and humid conditions, characterized by mean temperatures exceeding 22˚C [33]. The concomitant absence of *Podocarpus* during these phases contrasts with conditions prevailing at the end of the mid-Holocene, which are marked by higher proportions of this taxon and are interpreted as cooler climatic conditions favoring a downslope expansion of montane vegetation [10].

The progressive decline of *Podocarpus* during the Late Holocene is a well-documented phenomenon in Central Africa, notably on the Batéké Plateau [45], in the Pointe-Noire region and at Sinnda [46], as well as in Cameroon at Lake Barombi Mbo [39] [47], Lake Bambili [48]-[50], Lake Njupi [51], Lake Mbalang [52], Lake Mboandong [53], and Lake Ossa [54].

4.3. Dominance of *Podocarpus*

In absolute terms, the taxon *Podocarpus* dominates large portions of core KW23. Throughout the sequence, its abundance peaks consistently oppose those of *Rhizophora*, which are strongly developed during warm and humid phases, suggesting that *Podocarpus* is associated with cooler climatic conditions. This taxon is indeed characteristic of cool and humid montane environments, generally located above 1,000 m a.s.l., where frequent fog and persistent cloud cover provide substantial moisture inputs in the form of occult precipitation, typical of cloud forests [55].

Podocarpus represents a major component of Afromontane forests, notably in the Kivu-Ruwenzori massifs, along the Cameroon Mountain chain that marks the southern margin of the Congo Basin, and on the southern flank of the Chaillu Massif near the Atlantic coast [56]. Its presence has also been documented in low-altitude continental archives, such as the Bois de Bilanko site, located at approximately 600 m a.s.l. and about 40 km north of Brazzaville. Pollen analyses at this site show that prior to the onset of the Holocene, montane forest vegetation dominated by *Podocarpus* (exceeding 50%), associated with *Olea hochstetteri* and *Ilex mitis*, was widely established across the Batéké Plateaus [34].

The convergence of these continental and marine data indicates that during cold periods of the Late Quaternary, an Afromontane vegetation dominated by *Podocarpus* expanded downslope over large sectors of the western Congo Basin and adjacent regions, producing a clearly identifiable pollen signal in deep-sea marine archives such as core KW23.

4.4. Bioindicators and Climatic Zones

The alternation and successive variations in the abundances of *Podocarpus* and *Rhizophora* along core KW23 reflect major climatic changes over the last 300,000 years. The *Rhizophora/Podocarpus* pollen ratio curve highlights climatic transition zones that closely correspond to the boundaries of marine isotope stages, as defined from the benthic foraminifer *Melonis barleeanum*, as well as to standard Milankovitch orbital forcing curves [57] and isotopic and temperature records derived from the Vostok ice core [58] [59].

Changes in the *Rhizophora/Podocarpus* ratio make it possible to distinguish nine climatic zones corresponding to the first nine marine isotope stages. Warm climatic zones, characterized by *Rhizophora* dominance and successive grouped data points with ratio values greater than 1, coincide with odd-numbered isotope stages (MIS 1, 3, 5, 7, and 9). In contrast, cold climatic zones, dominated by *Podocarpus* and marked by ratio values lower than 1, correspond to even-numbered isotope stages (MIS 2, 4, 6, and 8). Marine isotope stage 5 is distinguished by several internal fluctuations, consistent with the existence of classically recognized interstadials (5a to 5e; or 5.0 to 5.5), and represents a major interglacial period situated between the Riss and Würm glaciations.

Comparable patterns of alternation between *Podocarpus* and *Rhizophora* have been identified in numerous marine cores from the Gulf of Guinea and the tropical Atlantic off Africa, notably offshore Liberia [60], Côte d'Ivoire [5] [13], Ghana [61], Niger [62], Cameroon [9], Gabon [7], Congo [14], and Angola [15]. This regional convergence confirms the relevance of the *Rhizophora*/*Podocarpus* ratio as an indicator of major Quaternary climatic oscillations in Central Africa.

5. Conclusions

This study aimed to: 1) reconstruct paleoenvironmental and climatic variations in Central Africa over the last 300,000 years based on a marine pollen record, 2) assess the relevance of the *Rhizophora/Podocarpus* pollen ratio as a climatic proxy, and 3) compare regional vegetation signals with the main global climatic forcings.

The palynological analysis of marine core KW23, based on 58 samples and more than 32,000 counted grains, reveals a strong dominance of spores (46.5%) and pollen (53.5%), indicating an abundant and well-preserved continental signal. Among the main pollen taxa, *Podocarpus* accounts for 24.60%, *Rhizophora* for 21.05%, *Gramineae* for 14.54%, *Cyperaceae* for 12.05%, temperate taxa for 6.26%, while other forest taxa together represent 17.35%. This distribution confirms the regional representativeness of the pollen signal, which is largely dominated by fluvial inputs from the Congo Basin.

The contrasted evolution of the two major bioindicators shows that cold climatic phases are characterized by high proportions of *Podocarpus*, an Afromontane taxon, whereas warm and humid phases are marked by a strong increase in *Rhizophora*, indicating the expansion of littoral mangroves. The *Rhizophora*/*Podocarpus* pollen ratio thus makes it possible to identify nine climatic zones corresponding to marine isotope stages MIS 1 to MIS 9, in excellent agreement with the foraminifera benthic isotopic ($\delta^{18}O$) record, Milankovitch orbital cycles, and data derived from Antarctic ice cores.

These results demonstrate that vegetation formations of the Congo Basin have responded sensitively, repeatedly, and in a quantitatively measurable way to past climatic variations. The strong relative contributions of mangroves, Afromontane forests, and open vegetation formations highlight the vulnerability of Central African tropical ecosystems to changes in temperature, humidity, and sea level. In this sense, the present study provides an essential paleoenvironmental reference framework for assessing the potential impacts of ongoing and future climate change on one of the world's major reservoirs of biodiversity and carbon.

Acknowledgements

For their material and scientific contributions that made it possible to write this article, sincere thanks are given to:

1) Jean Maley, Honorary Research Director of the IRD, Associate Researcher at the University of Montpellier II (France);

2) Pierre Giresse, Professor at the University of Perpignan (France).

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

References

[1] Ericson, D.B. and Wollin, G. (1968) Pleistocene Climates and Chronology in Deep-Sea Sediments. *Science*, **162**, 1227-1234. https://doi.org/10.1126/science.162.3859.1227

[2] Shackleton, N.J. and Opdyke, N.D. (1976) Oxygen-Isotope and Paleomagnetic Stratigraphy of Pacific Core V28-239 Late Pliocene to Latest Pleistocene. *Geological Society of America Memoirs*, **162**, 449-464. https://doi.org/10.1130/mem145-p449

[3] lmbrie, J., Hays, J.D., Martinson, D.G., Mclntyre, A., Mix, A.C., Morley, J.J., Pisias, N.G., Prell, W.L. and Shackleton, N.J. (1984) The Orbital Theory of Pleistocene Climate: Support from a Revised Chronology of the Marine 61aO Record. In: Berger, A.L., Imbrie, J., *et al.*, Eds., *Milankovitch and Climate*, Reidel, 269-305.

[4] Dupont, L.M. and Agwu, C.O.C. (1991) Environmental Control of Pollen Grain Distribution Patterns in the Gulf of Guinea and Offshore NW-Africa. *Geologische Rundschau*, **80**, 567-589. https://doi.org/10.1007/bf01803687

[5] Lezine, A. and Cazet, J. (2005) High-Resolution Pollen Record from Core KW31, Gulf of Guinea, Documents the History of the Lowland Forests of West Equatorial Africa since 40,000 Yr Ago. *Quaternary Research*, **64**, 432-443. https://doi.org/10.1016/j.yqres.2005.08.007

[6] Bengo, M.D. and Maley, J. (1991) Analyses des flux polliniques sur la marge sud du Golfe de Guinée depuis 135 000 ans. *Comptes Rendus de l'Académie des Sciences de Paris*, *Série II*, **313**, 843-849.

[7] Dupont, L.M., Marret, F. and Winn, K. (1998) Land-sea Correlation by Means of Terrestrial and Marine Palynomorphs from the Equatorial East Atlantic: Phasing of SE Trade Winds and the Oceanic Productivity. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, **142**, 51-84. https://doi.org/10.1016/s0031-0182(97)00146-6

[8] Bengo, M.D., Gomat, H., Giresse, P., Maley, J. and Nganga, D.M. (2025) Implications of Marine Hydrodynamism in the Dispersal and Modern Distribution of Pollen on the Cameroonian Continental Shelf. *Open Journal of Geology*, **15**, 716-734. https://doi.org/10.4236/ojg.2025.1510035

[9] Bengo, M.D., Gomat, H., Ifo, S.A., Maley, J. and Giresse, P. (2025) Late Quaternary Paleoenvironmental Dynamics on the Cameroonian Continental Shelf (Gulf of Guinea): Palynological and Sedimentary Insights. *Journal of Geoscience and Environment Protection*, **13**, 92-115. https://doi.org/10.4236/gep.2025.1312006

[10] Bengo, M.D., Gomat, H., Bita, A.M., Ifo, S.A., Maley, J. and Giresse, P. (2026) High-resolution Study of the Late Holocene from Pollen of a Marine Core in the Gulf of Guinea (Cameroon): Paleoenvironmental and Ecological Dynamics in Central Africa during the Last 2,500 Years. *Open Journal of Forestry*, **16**, 83-105. https://doi.org/10.4236/ojf.2026.161006

[11] Bonifay, D. (1987) Interaction des accumulations terrig6nes et oc6aniques dans le Quaternaire moyen et sup6rieur des marges profondes du Gabon et de la ride m6dio-guin6enne. Ph.D. Thesis, University of Perpignan, 185 p.

[12] Bonifay, D. and Giresse, P. (1992) Middle to Late Quaternary Sediment Flux and Post-Depositional Processes between the Continental Slope off Gabon and the Mid-Guinean Margin. *Marine Geology*, **106**, 107-129. https://doi.org/10.1016/0025-3227(92)90057-o

[13] Fredoux, A. (1994) Paléoenvironnements enregistres dans une carotte marine du golfe de Guinée depuis 225 000 ans: Analyse pollinique. In: Maire, R., Pomel, S. and Salomon, J.N., Eds., *Enregistreurs et indicateurs de l'évolution de l'environnement en zone tropicale*, Presses Universitaires de Bordeaux, 85-102. https://doi.org/10.4000/books.pub.9929

[14] Jahns, S. (1996) Vegetation History and Climate Changes in West Equatorial Africa during the Late Pleistocene and Holocene, Based on a Marine Pollen Diagram from the Congo Fan. *Vegetation History and Archaeobotany*, **5**, 207-213. https://doi.org/10.1007/bf00217498

[15] Ning, S. and Dupont, L.M. (1997) Vegetation and Climatic History of Southwest Africa: A Marine Palynological Record of the Last 300,000 Years. *Vegetation History and Archaeobotany*, **6**, 117-131. https://doi.org/10.1007/bf01261959

[16] Le Pichon, X. and Hayes, D.E. (1971) Marginal Offsets, Fracture Zones, and the Early Opening of the South Atlantic. *Journal of Geophysical Research*, **76**, 6283-6293. https://doi.org/10.1029/jb076i026p06283

[17] Larson, R.L. and Ladd, J.W. (1973) Evidence for the Opening of the South Atlantic in the Early Cretaceous. *Nature*, **246**, 209-212. https://doi.org/10.1038/246209a0

[18] Giresse, P. and Tchikaya, C. (1975) Contribution à la carte géologique de la plate-forme sous-marine congolaise (Mission N.O. Nizery de janvier 1974). *Annales de l Université de Brazzaville*, **11**, 23-34.

[19] Giresse, P. (1980) Carte sédimentologique du plateau continental du Congo. ORSTOM, Notice Explicative No. 85, Editions ORSTOM.

[20] Malounguila-Nganga, D. (1983) Les environnements sédimentaires des plateformes du nord-Congo et du sud-Gabon au quaternaire supérieur d'après les données de vibro-carottages. Ph.D. Thesis, Université de Toulouse, 169 p.

[21] Kinga-Mouzeo (1986) Transport particulaire actuel du fleuve Congo et de quelques affluents; Enregistrements quaternaires dans l'éventail détritique profond (sédimentologie, minéralogie et géochimie). Ph.D. Thesis, University of Perpignan, 251 p.

[22] Moguedet, G. (1988) Les relations entre le fleuve Congo et la sédimentation récente sur la marge continentale entre l'embouchure et le Sud du Gabon. Etude hydrologique, sédimentologique et g6ochimique. Doctoral Thesis, University of Angers, 185 p.

[23] O!ivry, J.C., Bricquet, J.P., Thiebaux, J.P. and Sigha, N. (1988) Transport de matiere sur les grands fleuves des régions intertropicales: Les premiers resultats des mesures de flux particulaires sur le bassin du fleuve Congo. *Proceeding of the Porto-Alegre Symposium*, Porto Alegre, 11-15 December 1988, 509-521.

[24] Nzila, J. D., Kimpouni, V., Watha-Ndoudy, N., Nanitelamio, M.M., Salisou, Y.M. and Nguila-Ntsoko, D.P. (2018) Soils Typology and Floristic Diversity of the Forest of the “Cité Scientifique” of Brazzaville, Congo. *Open Journal of Ecology*, **8**, 286-304.

[25] Wauthy, B. (1983) Introduction à la Climatologie du Golfe de Guinée. *Océanographie Tropicale*, **18**, 103-108.

[26] Piton, B. and Kartavtseff, A. (1986) Utilisation de bouées dérivantes à positionnement par satellite pour une meilleure connaissance de l’hydrologie de surface du Ggolfe de Guinee. ORSTOM, 34, 41.

[27] Leroux, M. (1983) Le climat de l’Afrique tropicale. Vols. 1-2. Champion.

[28] Piton, B. (1987) Les anomalies océanographiques et climatiques de 1983 et 1984 dans le Golfe de Guinée. *Veille Climatique Satellitaire*, **16**, 18-31.

[29] Suchel, J.B. (1988) Les climats du Cameroun. Master’s Thesis, Université de Saint-Étienne.

[30] Aubreville, A. (1948) Etude sur les forêts de l’Afrique équatoriale française et du Cameroun. *Secteur Technique de l’Afrique Tropicale Bulletin Scientifique*, No. 2, 132.

[31] Letouzey, R. (1968) Étude phytogéographique du Cameroun. Lechevalier.

[32] Boyé, M., Baltzer, F., Caratini, C., Hampartzoumian, A., Olivry, J.C., Plaziat, J.C. and Villiers, J.F. (1975) Mangrove of the Wouri Estuary, Cameroon. In: Walsh, G.E., Snedaker, S.C. and Teas, H.J., Eds., *Proceedings of the International Symposium on Biology and Management of Mangroves*, Institute of Food and Agricultural Sciences, University of Florida, 431-454.

[33] Din, D. (1991) Contribution à l’étude botanique et écologique des mangroves de l’estuaire du Cameroun. Ph.D. Thesis, University of Yaoundé.

[34] Elenga, H. and Vincens, A. (1987) Paléoenvironnements quaternaires d’après l’étude du sondage du Bois de Bilanko. Diplôme d’Études Approfondies (DEA), Université Aix-Marseille, 37 p.

[35] Maley, J. (1991) The African Rain Forest Vegetation and Palaeoenvironments during Late Quaternary. *Climatic Change*, **19**, 79-98. https://doi.org/10.1007/bf00142216

[36] Thunell, R.C. (1976) Optimum Indices of Calcium Carbonate Dissolution, in Deep-Sea Sediments. *Geology*, **4**, 525-528. https://doi.org/10.1130/0091-7613(1976)4<525:oioccd>2.0.co;2

[37] Bengo, M.D. (1990) Analyses des flux polliniques sur la marge sud du Golfe de Guinée depuis 135.000 ans. Diplôme d’Études Supérieures (DES), Université Montpellier 2, 62 p.

[38] Maley, J. and Brenac, P. (1998) Vegetation Dynamics, Palaeoenvironments and Climatic Changes in the Forests of Western Cameroon during the Last 28,000 Years B.P. *Review of Palaeobotany and Palynology*, **99**, 157-187. https://doi.org/10.1016/s0034-6667(97)00047-x

[39] Kimpouni, V., Loumeto, J. and Mizingou, J. (2015) Woody Flora and Dynamic of *Aucoumea klaineana* Forest in the Congolese Littoral. *International Journal of Biological and Chemical Sciences*, **8**, 1393-1410. https://doi.org/10.4314/ijbcs.v8i4.4

[40] Aubréville, A. (1962) Flore du Gabon, Volume 3. Muséum national d’Histoire na-

turelle.

[41] Sowunmi, M.A. (1991) Late Quaternary Environments in Equatorial Africa: Palynological Evidence. *Palaeoecology of Africa*, **22**, 213-238.

[42] Sowunmi, M.A. (1987) Palynological Studies in the Niger Delta. In: Alagoa, E.J., Anozie, F.N. and Nzewunwa, N., Eds., *The Early History of the Niger Delta*, University of Port Harcourt, 29-64.

[43] Malounguila-Nganga, D., Giresse, P., Boussafir, M. and Miyouna, T. (2017) Late Holocene Swampy Forest of Loango Bay (Congo). Sedimentary Environments and Organic Matter Deposition. *Journal of African Earth Sciences*, **134**, 419-434. https://doi.org/10.1016/j.jafrearsci.2017.05.022

[44] Bengo, M.D., Elenga, H., Maley, J. and Giresse, P. (2020) Evidence of Pollen Transport by the Sanaga River on the Cameroon Shelf. *Comptes Rendus. Géoscience*, **352**, 59-72. https://doi.org/10.5802/crgeos.1

[45] Elenga, H. and Vincens, A. (1990) Paléoenvironnements quaternaires récents des plateaux Bateke (Congo): Étude palynologique des dépôts de la dépression du bois de Bilanko. In: Lanfranchi, R. and Schwartz, D., Eds., *Paysages quaternaires de l'Afrique centrale atlantique*, ORSTOM, 271-282.

[46] Vincens, A., Buchet, G., Elenga, H., Fournier, M., Martin, L., Namur, C., Schwartz, D., Servant, M. and Wirrmann, D. (1994) Changement majeur de la végétation du lac Sinnda (vallée du Niari, sud-Congo) consécutif à l'assèchement climatique holocène supérieur: Apport de la palynologie. *Comptes Rendus de l'Académie des Sciences de Paris*, **318**, 1521-1526.

[47] Brenac, P. (1988) Évolution de la végétation et du climat de l'Ouest-Cameroun entre 25 000 et 11 000 ans BP. *Travaux de la Section Scientifique et Technique de l'Institut Français de Pondichéry*, **25**, 91-103.

[48] Assi-Kaudjhis, C. (2012) Dynamique des écosystèmes et biodiversité des montagnes du Cameroun au cours des derniers 20 000 ans: Analyse palynologique d'une série sédimentaire du Lac Bambili. Ph.D. Thesis, Université de Liège and Université de Versailles Saint-Quentin-en-Yvelines.

[49] Assi-Kaudjhis, C., Lézine, A.M. and Roche, E. (2008) Dynamique de la végétation d'altitude en Afrique centrale atlantique depuis 17 000 ans BP: Analyses préliminaires de la carotte de Bambili (Nord-Ouest du Cameroun). *Geo-Eco-Trop*, **32**, 131-143.

[50] Assi-Kaudjhis, C., Zéli Digbehi, B., Roche, E. and Lézine, A.M. (2010) Synthèse sur l'évolution des paléoenvironnements de l'Afrique occidentale atlantique depuis la fin de la dernière période glaciaire: Influences climatiques et anthropiques. *Geo-Eco-Trop*, **34**, 1-28.

[51] Zogning, A., Giresse, P., Maley, J. and Gadel, F. (1997) The Late Holocene Palaeoenvironment in the Lake Njupi Area, West Cameroon: Implications Regarding the History of Lake Nyos. *Journal of African Earth Sciences*, **24**, 285-300. https://doi.org/10.1016/s0899-5362(97)00044-4

[52] Vincens, A., Buchet, G. and Servant, M. (2010) Vegetation Response to the "African Humid Period" Termination in Central Cameroon (7° N)—New Pollen Insight from Lake Mbalang. *Climate of the Past*, **6**, 281-294. https://doi.org/10.5194/cp-6-281-2010

[53] Richards, K. (2021) A Holocene Pollen Record from Mboandong, a Crater Lake in Lowland Cameroon. In: Runge, J., Gosling, W., Lézine, A.M. and Scott, L., Eds., *Quaternary Vegetation Dynamics—The African Pollen Database*, CRC Press, 207-224. https://doi.org/10.1201/9781003162766-13

[54] Reynaud-Farrera, I., Maley, J. and Wirrmann, D. (1996) Végétation et climat dans les

forêts du Sud-Ouest camerounais depuis 4770 ans BP: Analyse pollinique des sédiments du lac Ossa. *Comptes Rendus de l'Académie des Sciences de Paris*, *Série IIa*, **322**, 749-755.

[55] Kerfoot, O. (1968) Mist Precipitation on Vegetation. *Oxford Forestry Abstracts*, **29**, 8-20.

[56] Maley, J. (1990) L'histoire récente de la forêt dense humide africaine: Essai sur le dynamisme de quelques formations forestières. In: Lanfranchi, R. and Schartz, D., Eds., *Paysages quaternaires de l'Afrique Centrale Atlantique*, ORSTOM, 367-382.

[57] Levrard, B. (2005) Cycles de Milankovitch et variations climatiques: Dernières Nouvelles. Planet Terre. https://planet-terre.ens-lyon.fr/ressource/milankovitch-2005.xml

[58] Petit, J.R., Jouzel, J., Raynaud, D., Barkov, N.I., Barnola, J., Basile, I., *et al.* (1999) Climate and Atmospheric History of the Past 420,000 Years from the Vostok Ice Core, Antarctica. *Nature*, **399**, 429-436. https://doi.org/10.1038/20859

[59] Vimeux, F., Cuffey, K.M. and Jouzel, J. (2002) New Insights into Southern Hemisphere Temperature Changes from Vostok Ice Cores Using Deuterium Excess Correction. *Earth and Planetary Science Letters*, **203**, 829-843. https://doi.org/10.1016/s0012-821x(02)00950-0

[60] Jahns, S., Hüls, M. and Sarnthein, M. (1998) Vegetation and Climate History of West Equatorial Africa Based on a Marine Pollen Record off Liberia (site GIK 16776) Covering the Last 400,000 Years. *Review of Palaeobotany and Palynology*, **102**, 277-288. https://doi.org/10.1016/s0034-6667(98)80010-9

[61] Lézine, A. and Vergnaud-Grazzini, C. (1993) Evidence of Forest Extension in West Africa since 22,000 BP: A Pollen Record from the Eastern Tropical Atlantic. *Quaternary Science Reviews*, **12**, 203-210. https://doi.org/10.1016/0277-3791(93)90054-p

[62] Dupont, L.M. and Weinelt, M. (1996) Vegetation History of the Savanna Corridor between the Guinean and the Congolian Rain Forest during the Last 150,000 Years. *Vegetation History and Archaeobotany*, **5**, 273-292. https://doi.org/10.1007/bf00195296