T I T O R G

IN: **Essays on the Ecology of the Guinea–Congo Rain Forest**

A U G

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The African rain forest – main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary

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Synopsis

This chapter sets out to give a historical overview of the African rain forest from its origins, towards the end of the Cretaceous period. The areas around the Gulf of Guinea, in particular from Ivory Coast to Nigeria and especially Cameroon, Gabon and Congo, appear to have been already occupied at this time by wet tropical forest formations mainly composed of Angiosperms which were then becoming established. In the course of the Tertiary period the combined effect of the equator being situated further north than now and the development of the Antarctic ice cap favoured the development of wet tropical conditions over a large part of North Africa which in turn led to the extension of tropical forest to various sites on the shores of the Tethys Sea. There were probably at this time common taxa and similar vegetation patterns stretching from the Gulf of Guinea to the Tethys Sea.

Towards the end of the Tertiary, the equator reached its present position and the northern hemisphere ice caps appeared, and these phenomena resulted in the disappearance of the forest formations spread across the north of Africa, and the concentration of these formations near the equatorial zone around the Gulf of Guinea and in the Congo–Zaïre basin. From 800 000 years ago onwards the marked glacial variations at middle and high latitudes in both hemispheres, with a periodicity of about 100 000 years determined by the orbital variations of the earth around the sun, lowered temperatures in equatorial areas and brought arid climates at times of maximum glacial extension. The most arid periods resulted in the fragmentation of the forest cover, and the forest biotopes and their biodiversity were preserved in a series of refugia. The lowering of temperatures also resulted in the extension of montane flora to low altitudes, with migration of montane flora and fauna between main mountain ranges. These compounded phenomena of isolation and migration, probably involving genic exchange, must have resulted in numerous speciation phenomena. Subsequently, such montane flora or fauna became isolated on mountain areas during periods of maximum warming, in the last instance in the course of the Holocene, when a vast forest cover became re-established from Guinea westwards, and to the East as far as the Lake Victoria area. The phases of maximum fragmentation, which appear to have been connected with only the coldest periods – in the last instance during the second part of isotopic stages 6 (from c. 160 to 130 000 years) and 2 (from c. 24 to 12 000 years BP) – relate to less than 10% of the last 800 000 years, and the phases of maximum forest extension would likewise appear to be less than 10% of the period. The remaining 80–90% of the time relates to 'intermediate situations' which varied from period to period, and these intermediate extension situations seem to have been the norm over the larger part of the Quaternary, rather than the present situation which is closer to a situation of maximum extension.

Introduction

A study of the history of the African rain forest, which at present extends around the Gulf of Guinea and is composed entirely of Angiosperms in the tree strata, must begin at the time when Angiosperms first appeared or at least first began to expand, i.e. the Cretaceous period. At the beginning of this period the areas which are at present covered by this forest were in the centre of the huge super-continent of Gondwana, prior to separation and subsequent drift of the African and South American plates. The establishment of the concept of continental drift in the 1960s via the development of plate tectonics has revolutionised African palaeobiogeography (Axelrod & Raven 1978).

The drift of the African plate

The drift of the African and South American plates since the Upper Cretaceous is now fairly well understood, and in particular it is known that the movement of the African plate consisted in a shift to the north and an apparent rotation of the north southwards, the rotation axis being situated a little off the present coast of Senegal (Guiraud & Maurin 1991, fig. 5). Given the position of this rotation axis, it was the eastern parts of Africa that underwent the most displacement, with considerable alteration to their palaeolatitudes. Thus, near the end of the Cretaceous, about 70 million years ago, the equator extended along the south of the present day Sahara, then rising eastwards towards the present southern border of Egypt (Fig. 1). According to reconstructions by Parrish et al. (1982), high rainfall prevailed as far as the north of Egypt and to Arabia which was then joined to Africa. This high rainfall can probably be attributed to the fact that the whole area was at the time surrounded by the warm waters of the Tethys Sea, which opened onto a vast ocean to the east (Parrish et al. 1982).
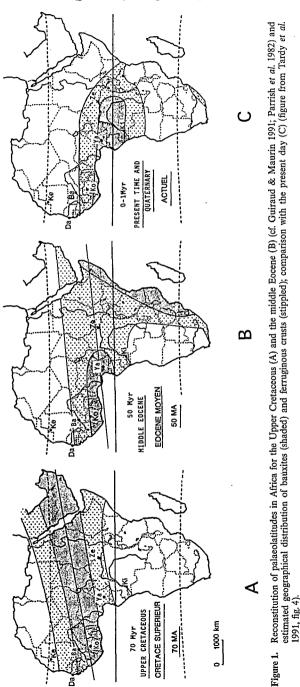
The displacement of the palaeolatitudes subsequently continued, and, for instance, in the middle Eocene, about 50 million years ago, the equator was quite close to its present position, generally about the present day 5°N (Fig. 1).

Climatic changes during the Tertiary

The distribution of ancient vegetation cover over Africa and its fluctuations in the course of time provide palaeoclimatic data, but there are also variables relating to sediment formation that can provide important complementary information.

A large sandy complex, connected with the 'Kalahari Formation', was deposited at the end of the Cretaceous in the central areas of South Africa reaching as far as the Congo–Zaïre basin (Bateke sands). This Formation lasted until about the end of the Neogene period (Cahen 1954; Lepersonne 1961; Le Maréchal 1966; De Ploey et al. 1968; Wright 1978). These authors concluded that this Formation was laid down, especially during the Neogene, in seasonally contrasted semi-arid and arid climates (cf. Maley 1980).

The study of clay sediments off the African coast, in DSDP (Deep Sea Drilling Project) sites situated from north to south of the eastern Atlantic and for periods from the Eocene to the Plio-Pleistocene, provides interesting data on the evolution of tropical palaeoclimates on the continent because most of these clays are of detritic origin (Robert 1980; Robert & Chamley 1987). While smectite dominates almost completely until the Eocene, kaolinite appears everywhere in small amounts around the start of the Oligocene. This type of clay then occurs increasingly up to the beginning of the Miocene. In the lower Miocene, kaolinite gives way to smectite, and then in the middle Miocene kaolinite again increases considerably, before declining towards the end of the Miocene and in the course of the Pliocene, especially off West Africa. In this sector, the fluctuations of kaolinite in the course of the upper Miocene are associated with the arrival of wind-borne sands, showing that aridity was becoming established over the north of Africa (cf. Ruddiman et al. 1989). Because kaolinite is particularly abundant in equatorial regions with hot wet climates, it is possible to associate the fluctuations of this mineral with the progressive development of wet tropical conditions from the start of the Oligocene (Robert 1980; Robert & Chamley 1987). Moreover, Robert & Chamley (1987) have also

Figure 1. Reconstitution of palaeolatitudes in Africa for the Upper Cretaceous (A) and the middle Eocene (B) (cf. Guiraud & Maurin 1991; Parrish et al. 1982) and estimated geographical distribution of bauxites (shaded) and ferruginous crusts (stippled); comparison with the present day (C) (figure from Tardy et al. 1991, fig. 4).

clearly demonstrated that fluctuations in kaolinite deposits evolved in phase with the development of glacial conditions in the Antarctic from the start of the Oligocene onward.

Melguen (1978) has also shown, through the study of siliceous micro-fossils from marine sediments in the south Atlantic (DSDP sites stretching from the Cape to the north of Angola), that the Benguela current originated in the upper Eocene and that the upwellings of cold water connected with its activity were significant from the upper Miocene onwards (Siesser 1978). The early existence of this current is linked to the trade winds activity which began in the upper Eocene. This phenomenon was associated to the overall pattern of atmospheric circulation over the southern hemisphere, where the strengthening of the St Helena anticyclone and of the south-erly winds, particularly the trade winds, was related to the increase in the Pole–Equator thermal gradient. This gradient is mainly dependant upon the variation in temperatures of the polar troposphere, as the variations in the equatorial troposphere are, in comparison, much smaller. With regard to this gradient, it should also be recalled that there is a considerable time lapse in the course of the Tertiary between the appearance of glacial conditions in the Antarctic and their appearance in the Arctic: the first ice to appear at sea level in the Antarctic was around the Eocene–Oligocene boundary, between 38 and 36 million years ago (Barron *et al.* 1988; De Robin 1988; Miller *et al.* 1991), while the phenomenon only occurred in the Arctic 3 to 4 million years ago (Kennet 1977; Mercer 1983; De Robin 1988). During the Oligocene and the Miocene there were periods when the Antarctic ice-cap expanded greatly (Barron *et al.* 1988; Zachos *et al.* 1992).

The palaeoclimatic consequences of this time-lapse are considerable. Indeed, the displacement of the meteorological equator; materialised at the convergence of the northern and southern trade winds, is mainly controlled by the Pole–Equator thermal gradient in both hemispheres, the main consequence of which is that the Intertropical Convergence Zone (ITCZ) is displaced northwards by atmospheric circulation in the southern hemisphere in winter and southwards by atmospheric circulation in the northern hemisphere in winter (Kraus 1977; Flohn 1978; Leroux 1993). In the present day, it is primarily the strengthening in winter of the St Helena Anticyclone and the southern hemisphere trade winds associated with it that draw the monsoons into the lower atmospheric levels north of the equator (Citeau *et al.* 1994). At the same time, the penetration of the monsoon further north in the northern hemisphere is reinforced by its being drawn in by the thermic depressions that develop over the continental areas of Africa, then in summer. These phenomena are mainly governed by the energy balance between the two hemispheres and the activity of the subtropical anticyclones correlated with them. In the present day the Antarctic is colder than the Arctic by about 11 °C yearly average (from 700 to 300 mb), the maximum difference of 25 °C occurring in the southern winter (July), which explains why the meteorological equator is always further north than the geographical equator, with the biggest advance in July (Lamb 1972; Flohn 1978, 1984). However, the time lapse in the Tertiary between the appearance of glacial conditions in the Antarctic and the Arctic caused a considerable energy deficit between the northern and southern hemispheres. This deficit was considerably greater than it is today. All of this makes it possible to conclude that the monsoons must have become established in Africa at the time of the Oligocene (cf. Maley 1980). During the summer, the land-mass of central and northern Africa must also have created, in the lower

atmosphere, a depression system facilitating the attraction of the monsoon towards the north of the continent. Moreover, it is only since the end of the Miocene that the uplifting of Tibet and the Himalaya has been sufficient to create a strong Tropical Easterly Jet-stream in the higher atmosphere (Ruddiman *et al.* 1989). This easterly jet-stream, which reaches maximum speed over India, slows down above the African monsoon, the particular consequence of which is a dynamic subsidence on the northern edge which seriously limits rainfall over the Sahel and southern Sahara (Flohn 1971). In the absence of this jet, there was presumably only a regional easterly jet in the lower atmosphere, comparable to the present-day African Easterly Jet. In addition, before the development of desert conditions over northern Africa, the thermic contrast with the Atlantic ocean to the south (Guinea Gulf) must have been less pronounced; hence it can be deduced that this jet was slower than the present African Easterly Jet (cf. syntheses on present-day conditions in Maley 1981; Fontaine 1991, etc.). In conclusion, it would appear that from the Oligocene onwards the monsoon rains extended much further north than they do today, and counter-balanced or delayed the shift southwards of wet tropical climates caused by the rotation northwards of the African plate.

Palaeobotanical data pertaining to the history of African forest formation in the course of the Upper Cretaceous and the Tertiary

The review conducted by Axelrod & Raven in 1978 was mainly based on various studies of plant fossils (wood, fruit, leaf impressions). Seventeen years later, it is time to update this work by giving a summary of significant new researches (as well as some older work which escaped these two authors), most of which is based on palynology.

The persistence as far as the Miocene of wet tropical climates over what is now the northern Sahara has been confirmed by studies in Libya on fossil wood and imprints, and in Egypt on pollen.

Libyan Tertiary palaeoflora

In Libya, first of all, many samples of fossil wood have been collected. These are associated with the Tertiary epicontinental sea deposits which spread out over the continental shelf after the lower Eocene when the transgression was at its peak, reaching the Tibesti foothills (Louvet & Magnier 1971; Louvet 1973; Boureau *et al.* 1983; Dupéron-Laudouneix & Dupéron 1994).

For the taxa determined, present-day distribution is based on botanical work by Letouzey (1968, 1985) in Cameroon and Hall & Swaine (1981) in Ghana.

Lower Eocene (from the Ouaou en Namous deposit – 24°45′N   18°E):

- *Combretoxylon (Anogeissuxylon) bussoni*, assigned to *Anogeissus leiocarpus* (Combretaceae), a species occurring today from the northern edge of the rain forest as far as the Sudanian savanna.
- *Detarioxylon libycum*, assigned to *Detarium microcarpum* (Caesalpiniaceae) a species typical of the Sudano–Guinean savanna.
- *Pterocarpoxylon tibestiense*, assigned to *Pterocarpus erinaceus* (Papilionaceae), a species found in the Sudano–Guinean savanna.

- *Sterculioxylon freulonii*, assigned to *Sterculia oblonga* (Sterculiaceae) a rain forest species.

Upper Eocene (from the Graret el Gifa deposit – 30°08′N 16°48′E):

- *Sonneratioxylon aubrevillei* assigned to the *Sonneratia* occurring in the mangroves in the wet tropical areas (India, Madagascar, Indonesia) (Louvet 1970).

Oligocene (from Djebel Coquin and surrounding area, around 25°50′N   20′E)

- *Combretoxylon* (*Anogeissuxylon*) *bussoni* (see above) and leaf impressions assigned to the genus *Nauclea* (Rubiaceae), *Detarium* (Caesalpiniaceae), *Milletia*, *Erythrina*, *Pterocarpus erinaceus* (Papilionaceae) at present occurring in wooded savanna or semi-deciduous rain forest.

Further north, towards Gehannen (29°15′N   18°48′E) a fossilised wood named *Entandrophragmoxylon magnieri* has been assigned to *Entandophragma candollei* (Meliaceae), a species typical of semi-deciduous rain forest.

Lower Miocene
The sites explored are located in the same area, from 28°20′N to 29°15′N and 18°45′E to 20′E, and they produced the following:

- *Xymaloxylon zeltenense*, assigned to the genus *Xymalos* (Monimiaceae), at present occurring in the montane forests near Bamenda (West Cameroon) and in East Africa.
- *Palmoxylon aschersoni*, assigned to *Borassus aethiopicum* (Palmae), typical of Sudano–Guinean and Sudanian savanna.
- *Combretoxylon* (*Anogeissuxylon*) *bussoni* (see above).
- *Bombacoxylon oweni*, assigned to *Bombacaceae* (*Bombax?*) occurring in forest and savanna.
- *Caesalpinioxylon craense*, assigned to Caesalpiniaceae occurring in forest and savanna.
- *Pterocarpoxylon syrtense*, assigned to *Pterocarpus erinaceus* (Papilionaceae) (see above).
- *Pahudioxylon gehannemense*, assigned to *Afzelia africana* (Caesalpiniaceae), typical of Sudano–Guinean and Sudanian savanna.

If all of these fossil woods and impressions from the Eocene to the Lower Miocene were to be resited, for instance, in present-day Cameroon vegetation patterns, they would be found in an area between the northern part of the rain forest and the north of the Sudanian zone, covering only a strip about 6° wide. However, in Tertiary Libya, the forest vegetation was probably fairly near to sea coast areas and the savanna vegetation further inland.

Tertiary palaeoflora of northern Egypt
In the neighbouring region of Egypt, fossilised woods have also been described, associated either with rain forests, as for example *Nipa burtonii*, or with savanna, with specimens similar to those already described for Libya (Boureau et al. 1983; Dupéron-Laudouneix & Dupéron 1994). Further to this, petroleum drillings in the extreme north, and particularly Siqueifa 1 (31°10′N 27°15′E) and Almaz 1 (30°55′N 28°15′E) yielded sporopollinic assemblages spanning from the lower

Eocene to the middle Miocene (El Sabrouty 1984). A number of the pollen grains identified belonged to the Leguminosae and in particular to the Mimosoideae. The following genera and species were identified and situated in present-day context (Guinet et al. 1987).

Parkieae tribe:
- *Pentaclethra*, type *P. macrophylla*. Today *P. macrophylla* is a large tree endemic to the African rain forest, common in wet or swamp forest formations.

Mimoseae tribe:
- *Adenanthera* type, close to the genera *Adenanthera* and *Pseudoprosopis*. These two genera concern trees restricted to rain forests. *Pseudoprosopis* is exclusively African, while *Adenanthera* occurs in tropical Asia.
- *Calpocalyx brevibracteatus* type and *Calpocalyx ngouniensis* type. *Calpocalyx* are trees, and more rarely climbers, only occurring in African rain forests.
- *Xylia torreana* type. This is a species belonging to semi-deciduous rain forests which stretch from East Africa to South Africa.

Acacieae tribe:
- *Acacia* type *Acacia aculeiferum* (sub-genus). This pan-tropical sub-genus today comprises some 250 species occurring in varied habitats from savanna to rain forest. In the latter, the species are mostly climbers in the *Acacia pennata* group.

Ingeae tribe:
- *Albizia* type, close to *Albizia coriaria* widespread in tropical Africa (forest and savanna) and *Albizia ferruginea*, a species only occurring in the African rain forest.

Guinet et al. (1987), following this detailed study, also noted that as Mimosoideae pollination is not by wind but by insects or other animals, it was consequently over short distances only. As these pollen grains, with the exception of *Pentaclethra*, are polyades, they can be split as a result of mechanical action, for example if river-borne; hence, since the polyades observed were most often whole, the hypothesis of this sort of transport can be dismissed. Thus this study shows that the assemblage described here was indeed local, and also that from the Eocene to the middle Miocene there was a notable extension to the north-west of Africa of an element that at present occurs almost exclusively in African rain forests. It will be seen below that a certain number of pollen taxa observed in the north of Egypt have been found in Oligocene and Miocene deposits in south Cameroon. The study of pollen from dated Miocene deposits taken from cores from the deep-sea Nile delta confirms this trend, the middle Miocene containing numerous rain forest taxa while the upper Miocene is characterised by the dominance of taxa from open arid habitats (Poumot & Suc 1984).

In conclusion it can be thought that there was a mosaic-type vegetation cover over north-east Africa (Libya and Egypt), with patches and galleries of forest surrounded by savanna (cf. Boureau et al. 1983). Further to this, in central Sudan (Gezira), Awad & Brier (1993) and Awad (1994) have brought to light pollen assemblages dating from the Oligocene and the Miocene, in which the main taxa are botanically close to rain forest formations. These different data link to an equator further north in the Tertiary than it is now (Fig. 1) and also confirm that wet tropical climates (Guinean to Sudanian) then extended much further from the

equator than is at present the case (for instance in Cameroon as far as 10°N and in West Africa as far as 12° to 14°N).

The origin of Angiosperms and Cretaceous and Tertiary palaeoflora in south Cameroon and Gabon
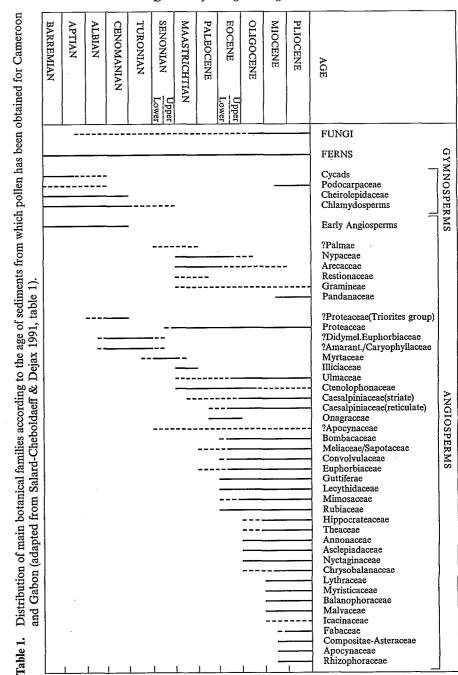
As has been remarked earlier with the work of Guinet *et al.* (1987), it is through efforts to classify fossil pollen and to establish their affinities with present-day taxa that it has been possible to make relatively accurate floristic and climatic interpretations. In the past, pollen samples from Cretaceous and Tertiary sediments were almost exclusively classified as morphotypes only, their significance being merely stratigraphic (as frequently used by petroleum companies). But over the last 20 years or so, the collation of considerable reference collections of modern pollen grains (as for example more than 40 000 slides from all over the world in the Montpellier Palynological Laboratory) as well as related research on pollen grains of modern plants, has meant that numerous fossil pollen forms have been assigned or compared to present-day taxa, as was shown by Guinet *et al.* (1987).

Palynological research on Cretaceous and Tertiary deposits in the wake of oil prospecting by various companies has also been carried out in the south of Nigeria and Cameroon, and in Gabon and Congo, in areas where the rain forest today shows greatest wealth and diversity. These studies also illustrate the remarkable efforts at identification made by a number of researchers. Foremost among these are Germeraad and his colleagues (1968), followed by Salard-Cheboldaeff (1977, 1981) and his colleagues (Boltenhagen *et al.* 1985; Salard-Cheboldaeff & Dejax 1991; Salard-Cheboldaeff & Boltenhagen 1992), (referred to below respectively as follows: G 68; SC 77, 81; B 85; SC&D 91; SC&B 92) as well as Doyle and colleagues (Doyle *et al.* 1977, 1978, 1982, 1990a, 1990b, 1991, 1993) (referred to below as D 77, 78, 82, 90a, 90b, 91, 93), whose studies have a particular bearing on the origin of Angiosperms, since the first pollen assigned to them was observed in the Barremian. Table 1, which collates the scattered data from around the Gulf of Guinea, gives an overview of the results.

The **Barremian** and **lower Aptian** belong, in this region, to the 'Pre-saliferous Series' (B 85), and the deposits occurred at a time when the African and South American continents were joined forming a super-continent named Gondwana and when, consequently, there was a continental-type climate. However a rift was already active, initiating the separation of the two future African and South American continents (Guiraud & Maurin 1991). There are tectonic, sedimentological and climatic analogies between this palaeo-rift and the present day Rift of East Africa (Le Fournier 1980). During this period the equator was far to the north and the climate was probably relatively dry (semi-arid sub-tropical zone). The tree flora was mainly composed of various Gymnosperms (Cheirolepidaceae with *Classopollis*, Araucariaceae with *Araucariacites*, Chlamydospermae with *Ephedrites* and *Cycadales*), adapted to hot, dry or even arid conditions (B 85; SC&D 91; SC&B 92; cf. Aubréville 1973b). However, bisaccate pollen types belonging to the Podocarpaceae (genera *Podocarpites* and *Vitreisporites*) (B 85) have been observed in small quantities. Doyle *et al.* (D 82) have suggested that the low frequencies recorded for these bisaccate pollen types could be due to their originating in distant montane habitats with a fairly cool climate. The regional existence of Podocarpaceae is confirmed by a study of Dupéron-Laudouneix & Pons (1985) on fossil woods

Table 1. Distribution of main botanical families according to the age of sediments from which pollen has been obtained for Cameroon and Gabon (adapted from Salard-Cheboldaeff & Dejax 1991, table 1).

AGE		
BARREMIAN		
APTIAN		
ALBIAN		
CENOMANIAN		
TURONIAN		
SENONIAN (Lower / Upper)		
MAASTRICHTIAN		
PALEOCENE		
EOCENE (Lower / Upper)		
OLIGOCENE		
MIOCENE		
PLIOCENE		

GYMNOSPERMS:
FUNGI
FERNS
Cycads
Podocarpaceae
Cheirolepidaceae
Chlamydosperms

ANGIOSPERMS:
Early Angiosperms
?Palmae
Nypaceae
Arecaceae
Restionaceae
Gramineae
Pandanaceae
?Proteaceae(Triorites group)
Proteaceae
?Didymel.Euphorbiaceae
?Amarant./Caryophyllaceae
Myrtaceae
Illiciaceae
Ulmaceae
Ctenolophonaceae
Caesalpiniaceae(striate)
Caesalpiniaceae(reticulate)
Onagraceae
?Apocynaceae
Bombacaceae
Meliaceae/Sapotaceae
Convolvulaceae
Euphorbiaceae
Guttiferae
Lecythidaceae
Mimosaceae
Rubiaceae
Hippocrateaceae
Theaceae
Annonaceae
Asclepiadaceae
Nyctaginaceae
Chrysobalanaceae
Lythraceae
Myristicaceae
Balanophoraceae
Malvaceae
Icacinaceae
Fabaceae
Compositae-Asteraceae
Apocynaceae
Rhizophoraceae

collected in the northern part of the Gondwana continent, particularly near the centre of Cameroon. These woods dated from the middle Jurassic to the middle Cretaceous, especially from the Aptian–Albian, were linked to this family.

The major phenomenon in this period, still mainly dominated by Gymnosperms, is the appearance of the first Angiosperm pollen grains. By studying these pollen grains, Doyle and colleagues (D 77, 82, 91, 93) have succeeded in reconstituting the first stages of their emergence on the northern part of the Gondwana continent.

In the **Barremian**, Doyle and colleagues first noted the appearance and then the proliferation of a single-furrow pollen grain (monosulcate phase). This pollen type was linked to the pollen grain of some Magnoliidae with an herbaceous tendency, such as the Chloranthaceae which occur particularly today in wet undergrowths in tropical rain forests of South East Asia (Blanc 1989), and also to pollen grain of some rhizomatous Nymphaeales colonising the shores of rivers or ponds (D 82, 91, 93). This adaptation to wet environments is interpreted by Doyle *et al.* (D 93) 'as evidence that Angiosperms spent an initial phase in aquatic habitats where they diversified slowly and only later diversified rapidly as a result of reinvading the land'.

Near the **end of the Barremian** and in the **early Aptian** the first pollen grains with three furrows (tricolpate phase) appear. This is the basic pollen type of the most evolved Dicotyledons. At the same time other pollen forms appear which could also derive from monosulcate forms, such as *Walkeripollis* (pollen in tetrad) and *Afropollis* (solitary pollen) which each exhibit a reticulate exine relatively comparable in having tall muri and short columellae. Pollen grains of *Walkeripollis* were observed rarely in Gabon, when *Afropollis* was much more numerous – up to 5% in Gabon and between 10 and 15% in Ghana, Ivory Coast and Sénégal, the last three countries being then closest to the equator (D 82). This was also the case in the south of Israel where *Walkeripollis* was found in Aptian–Albian levels (Walker *et al.* 1983). These two pollen forms were assigned to Winteraceae which are primitive Magnoliidae mainly characterised by vessel-less wood (D 90a, 90b). The fact that the pollen grains of these primitive Winteraceae exhibit an exine with a well marked ornamentation could be explained by insect pollinisation. The rarity of the *Walkeripollis* pollen grains would support this explanation, but, on the other hand the relative abundance of the *Afropollis* pollen grains could be best explained by wind pollinisation (D 90a, D 90b). The present-day Winteraceae live essentially in two biotopes: in the austral temperate forests (South America, Madagascar, Australia and neighbouring islands, but not in Africa); and in mountainous areas of tropical regions where the climate is cooler and relatively wet (D 90a, 90b). A distribution linked to these same climatic conditions is also found among some present-day Podocarpaceae, particularly the African *Podocarpus* (cf. Troll 1960; White 1981) (see p. 47). On functional bases, Carlquist (1975, in D 90b) estimated that wet and cool environments in tropical mountains or in austral temperate forests are more favourable to vessel-less plants like the Winteraceae, than the lowland tropical regions where seasonal climatic contrasts are more important.

In comparing these pollen data with others from North America, Europe and Asia (regions which then formed another continental block named Laurasia), Doyle and colleagues (D 82, D 91, D 93) have concluded that the first stages of the evolution of the Angiosperms occurred in tropical environments of the northern part of Gondwana. During these first stages, the primitive Angiosperms could have been pioneer plants adapted to disturbed places such as the edges of water courses

or gaps cut in the Gymnosperm formations. They could be regarded as a sort of secondary vegetation in terms of modern vegetation patterns (D 78; Aubréville 1973a). However the diversity in form and structure of these first pollen grains has led researchers to admit that the phenomenon which occurred in the Barremian was the first *expansion* of Angiosperms, but that their real beginning being situated much earlier, maybe during the Trias (Le Thomas 1981; Muller 1984; D 82, 91, 93).

In the course of the **upper Aptian**, the African and South American plates were beginning to break apart, which initiated the formation of numerous lagoons (Guiraud & Maurin 1991). The hot, dry climate led to significant salt deposits (Salifereous Series). The occurrence of the early Angiosperm pollen grains, particularly *Afropollis*, declines for this period, possibly for climatic reasons or pedological reasons (saline soils), but other types persist and develop (D 77, 82). Gymnosperm pollen remains abundant, including in particular 70–80% *Classopollis* (Cheirolepidaceae) (SC&B 92).

In the course of the **Albian**, the expansion of Angiosperms becomes apparent, as underlined by the diversification of their pollen grains: some can be allied to present-day Didymelaceae/Euphorbiaceae (SC&D 91). However the Gymnosperms are still dominant (Cheirolepidaceae, Chlamydospermae, Cycads, Ginkgoales, and Araucariaceae) with various ferns; the Podocarpaceae seem to disappear around the end of this period (B 85; SC&D 91) (see p. 51). Due to the influence of marine transgression between the two plates, the climate at this stage became progressively wetter (SC&D 91).

The **Cenomanian** (at the beginning of the Upper Cretaceous), at least during the early part, is characterised on the one hand by the disappearance of *Afropollis* and on the other by the extension of more evolved Angiosperms with the appearance of new pollen types which were assigned to the Proteaceae and Caryophyllaceae/ Amaranthaceae. However the climate was again one of great seasonal contrast, as can be deduced from the lithology of deposits ('Red Series') and from the persistance of numerous Gymnosperms (SC&D 91). Concerning the disappearance of *Afropollis*, one must notice that a pollen association including Winteraceae and other pollen types characterising the two first phases of the development of Angiosperms (Chloranthaceae, Palmae, Podocarpaceae, etc.) was found in lower Miocene levels near the Cape in South Africa (Coetzee & Muller 1984). In the next levels of the middle Miocene the most archaic taxa disappeared (Chloranthaceae and Winteraceae) and during the upper Miocene the Palmae disappeared in their turn (Coetzee 1978). One can hypothesise that during the Barremian and the Albian the climate of Gabon and surrounding countries must have been rather similar to that of the lower Miocene in the Cape region. The general outline of the floristic history of the Cape during the Miocene seems to have exhibited in short what happens in our region from the middle Cretaceous to the first part of the Tertiary.

In the course of the **Turonian**, the **Senonian** and the **Campanian** the Gymnosperms can be seen to be on the way out, and pollen from *Classopollis* (Cheirolepidaceae) and the Proteaceae (common in the Cape flora) disappears, which could indicate increased humidity as a result of marine influence. The Angiosperms continue to diversify, as is shown by the considerable increase in the relative percentages of their pollen. In association with a warm, wet, climate, **the archetype of the rain forest, dominated by Angiosperms, appears to have emerged at this stage** (SC&D 91; D 78), with various pollen types belonging to dicotyledons, but above all a considerable

development of Palmae pollen, later characteristic of a vast province stretching from Africa to South America (Herngreen & Chlonova 1981). Among these palms can be noted in particular forms close to the present-day *Nypa*, now only occurring in South East Asia (cf. Moore 1973). Several of these forms disappear by the beginning of the Oligocene, including *Nypa* (G 68). Another stage in the disappearance of the palms is situated in the upper Miocene (Morley & Richards 1993). While palms declined considerably in Africa in the course of the Tertiary, they have persisted in large numbers up to the present day in the South American tropical forests, where they constitute one of the characteristic features (Kahn 1993).

Thus it can be seen that from the beginning of the Aptian, about 120 million years ago, the period when the Angiosperms appeared, it took about 35 million years for this group of plants to become dominant in tropical vegetation.

In the **Maestrichtian** a few gymnosperm pollen types can still be observed (Chlamydosperms and Cycads). Angiosperms continue to diversify with new Palmae and Proteaceae, in the same warm, humid conditions (SC&D 91) (cf. Horrell 1991). At this time rain forests were widely spread over Africa, as witnessed by the palynological data from the Gulf of Guinea to present central Niger (Boudouresque *et al.* 1982), and towards the south and centre of Sudan (Awad 1994).

The **Maestrichtian–Palaeocene transition** is characterised by a complete upheaval of pollen assemblages accompanied by total disappearance of Gymnosperms (B 85). This can no doubt be associated with the extinctions and speciations that occurred at global level at the Cretaceous–Tertiary boundary (Upchurch & Wolfe 1987). Several hypotheses are discussed below (p. 49) to explain the decline over time of the Gymnosperms from the Barremian/Aptian onwards, and their progressive replacement by Angiosperms which dominate completely from the beginning of the Tertiary onwards, with the possible exception of a few marginal montane sites.

The Kwa-Kwa core, north of the Sanaga estuary (Cameroon), studied in detail by SC (77, 81) has provided a lot of information on the floristic evolution of the equatorial type forest. However in the **Eocene** certain pollen grains with unknown botanical affinities occur, but disappear at the next stage, and palms are still abundant, while they are not so in the present-day African forest. Gramineae disappear in the middle Eocene, probably indicating that the whole region was then covered in dense rain forests and swamps. The equator was by then close to its present position (Fig. 1).

It is only in the **upper Eocene**, about 45 million years ago, that the floristic composition of the south Cameroon vegetation really begins to resemble its present state. It is indeed at this time that many genera still living today appear (SC 81). Among the Mimosaceae *Pentaclethra*, *Calpocalyx* and *Acacia* can be mentioned. As has been seen earlier these genera were observed in sediments of similar age in the north of Egypt. Caesalpiniaceae, with striated pollen, also appear, belonging in almost all cases to tree types typical of evergreen forests. Among the Euphorbiaceae, the genera *Amanoa* and *Alchornea* appear, as do *Symphonia globulifera* in the Guttiferae, *Petersianthus macrocarpus* in the Lecythidaceae, *Bombax buonopozense* in the Bombaceae, *Mitragyna inermis* in the Rubiaceae and *Ctenolophon* in the Ctenolophonaceae. The Combretaceae/Melastomataceae group also appears at this time with *Combretum* and *Terminalia*. Striated pollen of the Anacardiaceae type is also observed.

In the **Oligocene**, river deposits increased in the Kwa-Kwa area, no doubt brought

by the palaeo-Sanaga and palaeo-Wouri. A considerable development of Pteridophytes is noted, and palms regress. Among the Angiosperms there is massive appearance of new forms, as for example in the Mimosaceae (Guinet & Salard-Cheboldaeff 1975) with the genera *Sindora*, *Fillaeopsis*, *Amblygonocarpus*, *Tetrapleura*, *Pseudoprosopis*, *Calpocalyx*, *Xylia*, *Adenanthera* and even *Leucaena* which has disappeared from present-day spontaneous flora. In the Caesalpiniaceae, reticulated pollen types appear that could be allied to *Afzelia* and *Brachystegia*; in the Euphorbiaceae, *Klaineanthus* is observed along with various *Merremia* in the Convolvulaceae and *Pentadesma* in the Guttiferae. The Rubiaceae diversify with *Randia*, *Macrosphyra* and *Mitragyna*. New families appear, such as the Chrysobalanaceae with *Parinari* and *Hirtella*, the Goodeniaceae with *Scaevola*, the Asclepiadaceae with *Tacazzea*, the Annonaceae with *Annona*, the Meliaceae with *Lovoa* and *Trichilia*, the Hippocrateaceae with *Hippocratea*, *Campylostemon*, etc. (SC 81).

In the **Miocene** all the Angiosperm families found earlier remain. Some develop further, as for example the Papillionaceae, the Hippocrateaceae, the Rubiaceae with the genera *Gardenia*, *Oligodon* and *Morelia*, the Bombacaceae with *Rhodognaphalon brevicuspe*, the Sapotaceae with *Mimusops* or *Manilkara*, the Meliaceae with *Melia*, the Lythraceae with *Crenea* or *Rotala*, the Myristicaceae with *Pycnanthus angolensis*, the Icacinaceae with *Iodes africana*, etc. (SC 81). In the upper Miocene the genus *Rhizophora* appears for the first time in this area, indicating the development of mangroves (B 85).

Conclusions

All of this palaeobotanical research has provided information on the nature of the various tropical vegetation patterns that developed through central and northern Africa from the Cretaceous to the end of the Tertiary, and has in particular brought to light several stages in the development of the rain forest.

Although the dataset is not numerous, the fact that for certain families, such as the Mimosoidaceae, a whole set of common genera is observed from the north of Egypt to south Cameroon and from the middle Eocene to the middle Miocene, would suggest that the areas of distribution were, at least in some periods, uninterrupted, and thus that, in the wettest periods at least, the rain forest stretched between the two regions. For East Africa, studies on the Neogene fauna indicate that rain forest environments were widespread at the end of the Oligocene and in the lower Miocene (Denys *et al.* 1985). Various palaeobotanical data then make it possible to conclude that it is from the middle Miocene that the vegetation cover became more open, with mosaic type patterns of forest and savanna (Boureau *et al.* 1983; Bonnefille 1984; Denys *et al.* 1985; Van Zinderen Bakker & Mercer 1986; Gros 1990; Hamilton 1991; Harris 1993).

The climatic imbalance between the two hemispheres that led to the development of wet tropical climate linked with the monsoon in the course of the Oligocene resulted in Africa in a marked development of the forest northwards, but not to the south, where the sands of the Kalahari Formation were being deposited in relatively arid conditions as far north as the area which is now Congo. However on the southern tip of Africa the Cape area, over a large part of the Tertiary and up to the lower Miocene, accomodated subtropical forest vegetation rich in palms (Coetzee

& Muller 1984); part of this vegetation of Gondwanian origin is still found today in the Cape and African montane flora.

The comparison of wet tropical flora on a global scale shows a marked impoverishment of Africa, a disparity that is particularly noticeable in relation to South America. Families that are particularly abundant in wet habitats and forest undergrowth such as the Lauraceae, the Palmae the Araceae, the Piperaceae, the Gesneriaceae, the Melastomataceae and the Urticaceae are represented by numerous genera and species in South America as well as in Southeast Asia, but only by a few genera and species in Africa (Aubréville 1955, 1975; Richards 1973; Blanc 1989, 1993). This lack of variety in the African flora is thought to have climatic causes and to be the result of arid phases that affected the tropical areas of Africa more severely than the other continents, from the beginning of the break-up of Africa and South America, in the Cretaceous. Studies of pollen make it possible to trace the main stages of this impoverishment of tropical Africa. However, the families enumerated above are, generally speaking, poorly represented in pollen studies (low pollen production, early damage, etc.). Nevertheless, the Palmae escape such difficulties since they produce large quantities of fairly resistant pollen, and can thus be used to trace the various stages of the impoverishment process observed (cf. Moore 1973).

The occurrence of Gramineae pollen, which constitutes a characteristic marker for open environments, provides complementary information. Such pollen has been found in south Cameroon and Gabon as early as the Palaeocene (SC 81). Further to this, in the Maestrichtian, pollen has been observed belonging to the Restionaceae, a group of herbaceous plants close to Gramineae, of Gondwanian origin (B 85). Thus it can be thought that in these regions xeric flora coexisted with wetter forest flora until the Palaeocene (SC 81). In north-east Africa (Egypt: Kedves 1971) it is from the lower Eocene onwards that grass pollen becomes relatively frequent, with a marked increase towards the Eocene–Oligocene boundary, which would indicate phases of savanna extension.

In conclusion, and on the basis of the trends observed for Monocotyledons (Gramineae and Palmae), **the main stages of impoverishment of hygrophilous African flora can be thought to be situated at the Cretaceous–Tertiary boundary, at the end of the Eocene and at the end of the Miocene**, to which should also be added those which occurred in the Plio-Pleistocene (see biogeographical section below). These main stages in fact correlate with the main phases of climatic deterioration on a global level which must have also affected the tropical zones of South America and South-East Asia. It can thus be thought that the arid phases were much more severe in Africa than they were in the other two vast continents.

Major variations in climate and in the rain forest from the end of the Neogene

The data available from the upper Miocene in the north of Africa is more sparse, but generally points to the appearance of elements of flora and fauna of Asian and European origin, adapted to seasonally contrasted and sometimes markedly arid climates (Maley 1980; Boureau et al. 1983). The very marked increase in wind-borne dust from 4.5 to 4 million years ago (Ruddiman et al. 1989), and data such as the occurrence in northern Chad of fossil wood from species adapted to arid conditions (*Tamarix* and *Retama* type *raetam*) in deposits dated between 5 and

4 million years, indicate that the Sahara appeared as early as the lower Pliocene (Maley 1980). On the other hand, to the south of the Chad basin, wet conditions favoured the development of a thick lacustrine Formation (Chad Formation) (Burke 1976; Servant-Vildary 1973) and the formation of a thick ferruginous crust (Maley 1980) in a Sudano–Guinean vegetation environment (cf. the palynological study, and leaf impressions found in the Anloua site on the Adamoua plateau: Salard-Cheboldaeff et al. 1992). It seems to be at this time that a climatic zone pattern similar to that existing today became established. In comparison with earlier periods, the rain forest contracted, its area being possibly close to that estimated for the periods of highest rainfall and temperature in the Quaternary (see p. 51).

Pollen data from 10.5 million years ago (upper Miocene) to 2 million years ago (middle Pliocene) have been published for the Niger delta in Nigeria (Poumot 1989), showing the variations in forest composition, and, in certain periods, the development of herbaceous vegetation (Fig. 2). Indeed, the pollen spectra from the upper Miocene contain between 30 and 40% Gramineae pollen, which is a good indication of more open habitat and the relative importance of savanna (cf. Bonnefille & Vincens 1977; Maley 1981; Brenac 1988). Since pollen deposited in tropical delta zones like the Niger delta came with river-borne sediment from varying distances (Muller 1959; Sowunmi 1981), and since similar percentages of Gramineae pollen were obtained in Holocene deposits in the same delta (Sowunmi 1981), it could be concluded that in the upper Miocene fairly large savanna areas already existed north of the forest area around the Gulf of Guinea. This interpretation is confirmed by a recent study by Morley & Richards (1993) which presents the parallel variations in Gramineae pollen and cuticles found in upper Cenozoic deposits in the Niger delta. They have also shown a marked increase in Gramineae pollen in the upper Miocene, with two peaks around 50%, and grass cuticles from bush fires.
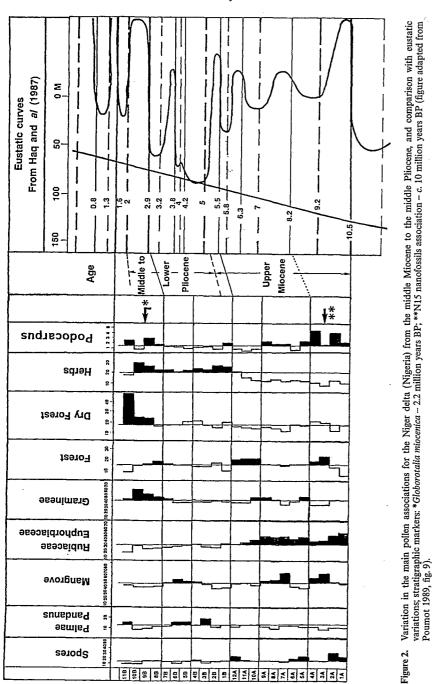
This considerable phase of extension of the savannas in tropical Africa towards the end of the Miocene correlates well with a more general phenomenon situated between 5 and 7 million years ago, detected in India and North America by Cerling et al. (1993), through the study of the isotopic composition (δC^{13}) of fossil carbonates, which shows an extension of plants characterised by C4 type photosynthesis which affects all the herbaceous plants of tropical savanna: in low altitude tropical areas, there is a very clear discrimination between herbaceous plants from open habitats (C4 type) and trees (C3 type) (Mariotti 1991). Similarly Cerling (1992) also detected this phenomenon in eastern Africa, towards the end of the Miocene (c. 8–9 million years ago).

The extension of montane vegetation associated with cooling at the end of the Neogene and in the Quaternary

Extension phases at the end of the Neogen

Pollen analyses for the end of the Neogene in the Niger delta (Poumot 1989) show a new taxon, *Podocarpus*, very rare or absent previously, characterised by notable variations in frequency of occurrence of its pollen grains (Fig. 2). *Podocarpus* is an arborescent Gymnosperm now occurring in montane forests on various mountains on the volcanic ridge in western Cameroon, at altitudes from 1600–1800 m to 2200–2700 m (Letouzey 1968). Podocarpaceae were noted in Upper Cretaceous deposits, but after the disappearance of Gymnosperms towards the end of the Cretaceous, it can be supposed that representatives from this family survived in

Figure 2. Variation in the main pollen associations for the Niger delta (Nigeria) from the middle Miocene to the middle Pliocene, and comparison with eustatic variations; stratigraphic markers: *Globorotalia miocenica* – 2.2 million years BP; **N15 nanofossils association – c. 10 million years BP (figure adapted from Poumot 1989, fig. 9).

marginal habitats in mountain areas, or that new migrations took place towards the end of the Tertiary or in the course of the Quaternary from east African mountains (cf. White 1981; Maley 1989, 1991). In the core studied, the two peaks for *Podocarpus* pollen correspond with two phases of montane vegetation extension, a regional consequence of the drop in temperature. It is interesting to note that these two *Podocarpus* phases occur at the same time as the two most marked marine regressions in this time interval (Haq *et al.* 1987) – between 10.5 and 9.2 million years ago (upper Miocene) and between 2.9 and 2 million years ago (middle Pliocene). These marine regressions are associated with marked extension of the Antarctic ice cap, in particular for the first, the second being accompanied by the first major development of the northern hemisphere ice cap, which culminated around 2.5 million years ago (Mercer 1983; Barker *et al.* 1988). The eustatic oscillations at the end of the Miocene, between 8 and 5 million years ago, produced lesser extensions of *Podocarpus*. Thus the changes in vegetation at the end of the Neogene can be interpreted in a global context of temperature variation, since these changes were synchronous with the main eustatic variations (Fig. 2) (Poumot 1989) in response to polar ice variations in the high latitudes in both hemispheres (Broecker & Denton 1989).
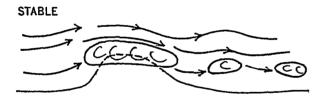
The development phase of *Podocarpus* which occurred in the course of the middle Pliocene is very important because it shows up in very marked peaks in several other cores in the Niger delta (Knaap 1971; Maley 1980). This *Podocarpus* peak coincides with a considerable increase in Gramineae pollen, reaching 60% (Fig. 2) which reflects a marked increase in savanna and open environments in the Niger basin. These correlations confirm that tropical lowland aridification is linked to global cooling. Linked also with these *Podocarpus* and Gramineae peaks, the lithology in the deposits changes drastically from a rather clayey Formation (Agbada Formation) to a markedly sandy Formation (Benin Formation) (Knaap 1971), the latter being linked to a more seasonally contrasted and more erosive climate over a large part of the Niger basin. The pollen assemblages characteristic of forest environments recede, giving way to those typical of drier savanna habitats, reflecting a decrease in the area covered by rain forest. In East Africa, (south-west Ethiopia) a transition also occurred between 2.5 and 2.2 million years ago towards more arid vegetation types in lowlands and to cooler, drier types in highlands (Bonnefille 1980, 1983).

Climatic and ecological conditions relating to the development of montane formations characterised by tropical conifers: cloud forests

From a climatic point of view, the link between the marked cooling at high latitudes and the drop in temperatures near the equator is to be found in the increase in the Pole–Equator thermal gradient and the general acceleration in atmospheric circulation that resulted from this. Indeed, an increase in the P/E thermal gradient reinforces the subtropical anticyclones, the main effect of which is to accentuate the trade winds, which in turn leads to penetration of masses of cooler air into lower latitudes (Leroux 1993). In addition to this direct cooling effect, the strengthening of the trade winds causes increased upwelling at sea which can considerably lower sea-surface temperatures (Flohn 1982, 1987). Thus, for example, at the time of the last glacial maximum, the temperature of surface waters in the Gulf of Guinea dropped by 4° to 9 °C (Prell *et al.* 1976; Mix *et al.* 1986). A fall in sea-surface temperatures has a twofold climatic effect on neighbouring land masses, resulting

in cooling and aridification (Maley 1987, 1989; Maley & Elenga 1993). Indeed, when the sea-surface temperature drops below that of the monsoon air flow, the result is a stabilisation of this flow and a sharp decrease in the amount of water vapour (Mahé & Citeau 1993). Since all of this is also associated with an increase in anticyclonic conditions at high altitudes, only stratiform clouds can form. These slowly-evolving cloud formations are very persistent, but give little rainfall. On the neighbouring land mass the result is almost complete disappearance of rainfall, and also a cooling of the lower atmospheric layers as a result of the persistence of this cloud cover which intercepts solar radiation (Aspliden & Adefolalu 1976). In the African equatorial zone today the coolest part of the year is that dominated by stratiform cloud (Maley 1987, 1989).

Stratiform cloud often hangs on the tops of hills or on mountain slopes, thus becoming mist near the ground (Fig. 3). It thus favours the development of typical cloud forest conditions, in which tropical Gymnosperms such as *Podocarpus* and *Juniperus* (Kerfoot 1968; Moll 1972), and also Angiosperms such as *Olea, Ilex, Erica*, etc., typical of various African montane formations, develop (White 1983; Hall 1984). The trees and shrubs in formations of this sort have very dense foliage composed of numerous small, rigid, sclerified leaves, often elongated and pointed, which enable them, through slight differences in electric potential, to condense atmospheric moisture in the form of the fine droplets that make up mist and low cloud (Troll 1956). Isolated trees demonstrate this phenomenon clearly, since it is from their canopy that falling drops engender luxuriant development of herbaceous undergrowth (Troll 1956) (cf. also 'fountain' trees used as water captors, Gioda *et al.* 1992). Kerfoot (1968) has shown that certain east African montane forests
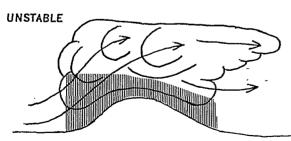

STABLE

UNSTABLE

Figure 3. The effect of upward air motion caused by relief in stable and unstable air. In stable air (top) stratiform clouds form, but there is virtually no direct precipitation. Mist is however abundant and is associated with indirect precipitation by way of condensation on the vegetation, or fog-stripping, both typical cloud forest conditions. In unstable air (below) thick cumuliform clouds form giving heavy and abundant rainfall (figure adapted from Tyson 1969, fig. 19).

can, in this way, increase annual precipitation by more than 25%. In some cases, mist precipitation can even exceed actual rainfall in exceptional situations, as on Table Mountain above Cape Town, South Africa, where in one year mist precipitation reached 3294 mm and rain only 1940 mm. The quantities of moisture precipitated in this way can therefore be considerable (cf. Bruijnzeel & Proctor 1993), even in arid regions such as the Sahara, in the form of 'mist oases' (Kasas 1956).

In the course of the Quaternary, certain periods appear to have particularly favoured the development of conditions of this sort, as for instance the late Holocene in mountain areas of the African equatorial zone. Indeed the climate, which in the middle Holocene was warm and humid (*c.* 6500–4000 years ago), became considerably drier at the beginning of the late Holocene, from 3800/3700 years BP, characterised by a general drop in lake levels, accompanied in mountains by a considerable extension of *Podocarpus* forest (Perrot 1982; Hamilton 1982, etc.), also occurring in Cameroon (Maley 1995) and in Nigeria (Sowunmi 1981). The drop in lake levels resulting from lower rainfall coincides with the extension of *Podocarpus* and very probably reflects the development of cloud forests. It should however be noted that not all the phases of cooling are systematically accompanied by phenomena of this sort (Maley & Elenga 1993). Indeed, they are the result of the extension of anticyclonic conditions that give rise to stratiform cloud formation rather than other cloud formations with a vertical cumuliform build-up which produce most rain (cf. Maley 1982) (Fig. 3). This climatic model can also be applied to the phases of *Podocarpus* development described above towards the end of the Neogene and in the course of the Quaternary, in isotopic stages 5d, 5b, 4, etc. (Maley & Elenga 1993) (see pp. 56 & 60). These stratiform cloudy conditions could likewise explain the development and fluctuations of some Mediterranean tree taxa such as *Cedrus altantica* (H. Le Houérou, personal communication) or of species of more temperate regions, such as *Fagus sylvatica* (cf. Thiébaut 1982). Indeed, these two species were also in a marked extension phase in the late Holocene, cedar from about 4000 years BP in the middle Atlas in Morocco (Lamb *et al.* 1989) and beech from about 4500 years BP in the French Massif Central (De Beaulieu *et al.* 1988).

Seasonal persistence of stratiform cloud formation, bringing cool and moist conditions, probably also favoured certain lowland forest formations, such as the rain forest enclaves in northern Angola ('Dembos') isolated some distance south of the main forest block (White 1979, 1983), or certain evergreen Caesalpiniaceae forests most likely to be found on hill tops (see instances in south Cameroon: Letouzey 1985; Achoundong 1985) or in Gabon and Congo with *Monopetalanthus* formations (cf. Maley *et al.* 1990) or again in certain isolated forests north of the main forest block, like the Niayes in Senegal (Trochain 1939) which are the northern equivalent of the north Angola forests. The persistence of such stratiform cloud can also explain the survival today, in a number of relict sites at altitudes between 500 and 900 m, of associations of several typically montane taxa such as *Podocarpus, Olea, Ocotea*, etc. – modern witnesses to past extension phases – alongside lowland forest taxa (White 1981; Letouzey 1985; Thomas 1986; Maley *et al.* 1990; Maley & Elenga 1993, etc.).

Ecological pressures responsible for the decline of tropical Gymnosperms, and, conversely, the rise of Angiosperms in the course of the Cretaceous

To explain the decline and then virtual disappearance of tropical Gymnosperms towards the end of the Cretaceous, a phenomenon associated with the rise and

finally the domination of Angiosperms, authors such as Midgley & Bond (1989) and Bond (1989) mainly cite the competition between these two groups, mostly on the basis of the very great regeneration speed of Angiosperms as compared with Gymnosperms. However, a full explanation of the decline of tropical Gymnosperms and the rise of Angiosperms cannot neglect the influence of climatic and ecological variations.

Indeed, as has been shown above, the marked ecological preference of Gymnosperms like *Podocarpus* and *Juniperus* for cloudy conditions that are characteristic of certain tropical and subtropical montane forests, could lead to a new hypothesis to explain the decline, and then the nearly complete disappearance from tropical Africa, of Gymnosperms towards the end of the Cretaceous (see also Aubréville 1964; Dupéron-Laudouneix & Dupéron 1994). Indeed, the fact that the hot arid areas of the vast Gondwana continent were mainly colonised by Gymnosperms until the beginning of the Cretaceous could be explained by their ability to compensate for the low rainfall by absorbing atmospheric moisture from dew, mist, or, more generally, from low stratiform cloud (Fig. 3). The very specific mechanism of pollinisation in the Podocarpaceae could be explained by this atmospheric humidity; indeed a water drop surrounding the micropyle considerably increases the efficiency of pollen scavenging (Tomlinson *et al.* 1991). Because pollinisation takes place during the dry season, mist is probably responsible for the deposition of water droplets on the micropyle. However, from the upper Aptian, the opening-up of the Atlantic and the consequent reorganisation of atmospheric circulation (see pp. 38–42), resulted in an increase in rainfall, and in particular thundery rainstorms, in place of stratiform cloud formation. These climatic upheavals appear to have been very favourable to the Angiosperms, but not so to the Gymnosperms. In fact the Gymnosperms disappear almost completely during the Turonian from the then tropical regions, whilst the mid and high latitudes of the northern Hemisphere saw only a slight diminution in this vegetal group during the Upper Cretaceous (Lidgard & Crane 1990). These data show clearly that, with rare exceptions, the Gymnosperms cannot have survived the tropical climate which developed in lowland during the end of the Cretaceous.

In conclusion, largely for ecological reasons, Gymnosperms, owing to their capacity to collect the atmospheric humidity, are adapted to the heat and aridity of continental climates, unlike to the Angiosperms which developed later under the influence of hot, wet tropical-type climates, with mainly thundery rain which progressively increased, in particular in the course of the Tertiary, becoming monsoon-type rainfall.

So one can hypothesise that climatic and ecological changes could have played an important role during the Cretaceous in controlling the evolutionary processes which have acted upon the Angiosperms. Indeed the pollen studies of Doyle and colleagues (D 82, 91, 93) indicate two principal phases, the first characterised by pollen grains of monosulcate type assigned to Magnoliales with herbaceous tendencies, the second by pollen grains of tricolpate type, linked also to other pollen forms, some of which were assigned to Winteraceae with *Walkeripollis* and particularly *Afropollis* which was then relatively numerous. One has also pointed out above (p. 40) that the present-day biotopes of Winteraceae are similar to those of Podocarpaceae, as for instance to the genus *Podocarpus* in Africa. These biotopes are either the temperate austral forest (for instance, the Knysna forest to the east

of the Cape), or some mountainous areas of the tropical zone where the cloud condensation at altitude recreates wet and cool conditions similar to those of the lowland temperate forests (see also Troll 1960; Van Zinderen Bakker 1973).

The fact that the pollen grains of *Podocarpus* and *Afropollis* disappeared almost at the same time at the end of the Albian or in the early Cenomanian suggests the involvement of similar climatic and ecological controls. One can hypothesise that the disappearance of *Afropollis* from north-Gondwanian regions was caused by the development of more tropical climatic conditions, characterised particularly by a large increase in thundery rain. The following stage of the evolution of Angiosperms beginning in the Turonian was marked for the first time by the domination of these plants over the Gymnosperms. This phenomenon is linked to the establishment of the tropical rain forest. However in Africa this forest was of a rather archaic type, characterised by numerous palm trees which were progressively excluded from the African rain forests during the Tertiary, but have persisted until the present day in the Amazonian rain forests. The diverse hypotheses submitted in this paragraph should be questioned and tested in the light of new data.

Major temperature variations in the course of the Quaternary and repercussions on the African rain forest

It has been seen above that the main variations in vegetation noted in the Niger delta for the end of the Neogene can be interpreted within the context of global temperature variations, in particular variations of the Arctic and Antarctic ice caps.

Figure 4 presents a diagram of the main stages and the periodicity of the northern hemisphere ice caps which are known to control the main fluctuations of the Antarctic ice cap by way of eustatic variations (cf. Broecker & Denton 1989). This diagram shows a progressive increase in the amplitude of glacial variation, with two main stages, the first towards 2.5 million years ago, and the second about 800 000 years ago. The study of marine cores has shown that from 800 000 years ago climatic variability increased, with, in particular, phases of more marked cooling following a dominant periodicity of 100 000 years (Stuart & Prell 1984). The first glacial advance around 2.5 million years ago had the effect of reducing the area of the rain forest in favour of savannas (Poumot 1989; Morley & Richards 1993) and it is therefore probable that the other glacial advances in the Quaternary had similar effects. Indirect information on the history of the rain forest and its fluctuations could be provided by biogeographical data (Maley 1987).

Biogeography and the history of the African rain forest

Since the climatic conditions prevailing in the equatorial zone covered by rain forest are relatively homogeneous both for temperature and rainfall distribution over the year (White 1983), it would seem reasonable to expect the distribution of species also to be homogeneous, or at least that it should be affected only by marked geographical features like mountain ranges, rivers, etc. However, the study for example of the Dahomey Gap, in which Sudan-type savanna vegetation extends as far as the sea, cutting through the forest block over some 200 km in Togo and Benin, shows that this gap plays only a minor role in the distribution of typical forest plant species (Léonard 1965; Brenan 1978; White 1979) or animal species: small mammals (Robbins 1978; Grubb 1982), birds (Moreau 1963, 1966; Crowe &
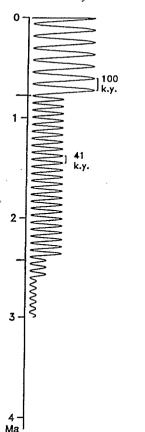
Figure 4. Schematic representation of the major cycle variations in the northern hemisphere ice cap, with indications of the main periodicities. The two main stages are the establishment of glacial conditions towards 2.5 million years ago, and the increased amplitude in the cycles towards 800 000 years ago (from Ruddiman *et al.* 1989, fig. 8B).

Crowe 1982), batrachians (Amiet 1987), insects (Carcasson 1964; Lachaise *et al.* 1988). Indeed, this gap constitutes a barrier to the distribution of very few typically forest species. However, examination of the same type of data for Cross River, in east Nigeria, shows that this river constitutes a major break in the Guinea–Congo forest block. Thus Brenan (1978, fig. 2.) has defined the Guinean Domain to the west of Cross River, and the Congolian Domain to the east. There would therefore seem to be no immediate connection between the size of a geographical break and its biogeographical impact. Indeed, the geographical hiatus formed by Cross River is insignificant compared with the biogeographical phenomenon observed, and conversely for the Dahomey Gap. For this reason most of the authors who have examined these questions (see the various authors quoted in this paragraph), consider that the geographical break of Cross River, and other smaller breaks observed in

other locations, (cf. White 1979; Mayr & O'Hara 1986; Maley 1987, 1991) are probably the result of early fragmentation of the forest block as a result of climatic changes.

Since climatic distribution is, to a large extent, conditioned by geographical factors, which were stable over the time lapses considered, the recurrence in the past of climatic changes with only slight variation, probably affected the same regions in comparable manner on each occasion. This implies that the main breaks in continuity of the forest block must have recurred many times in a relatively constant manner, in geographical terms, since the end of the Pliocene. Examination of data available for the last climatic cycle could provide a model for the main fluctuations that affected the African rain forest in the course of this period, given the cyclic nature of the main world-wide climatic events (Fig. 4) which are known, from various sedimentary and micropalaeontological data obtained in the Gulf of Guinea (Prell *et al.* 1976; Jansen *et al.* 1984, 1986; Ruddiman *et al.* 1989; Bonifay & Giresse 1992) to have affected the African equatorial zone regularly and in a very marked manner.

The fragmentation of the rain forest and the question of refugia

As was remarked by Mayr & O'Hara (1986), the fact that present-day biogeographical gaps do not cover large tracts (where sampling resolution is sufficient), but are limited to restricted zones like the Cross River, would tend to refute the explanation for such gaps put forward by Endler (1982). He suggested that these gaps are solely the result of parapatric speciation (in partially overlapping zones) and that the isolation necessary for the emergence of new species should be associated with the diversity and number of ecological niches existing in the rain forest habitat (cf. Fedorov 1966; Richards 1969; etc.). However it would seem that these two explanations – speciation phenomena occurring in habitats isolated only ecologically (niches), and speciation occurring in geographically isolated habitats (vicariance), in particular as a result of climatic variations – are not incompatible, and are in fact probably complementary (cf. Haffer 1982, 1993; Gentry 1989).

Certain climatic variations, and in particular a trend towards aridity, could, as a first stage, lead to the formation of small areas constituting refugia for forest biotopes. A second stage can then be envisaged in which extreme aridity could cause complete disappearance of the forest. However, this extreme situation appears never to have occurred for two main reasons: firstly the African rain forest has a rich and varied flora and fauna, which is incompatible with complete disappearance of the biotope, in particular during the Quaternary; secondly, since forest taxa from the Eocene, the Oligocene and the Miocene can be seen to be related to present-day taxa, (see p. 37), this implies that such taxa also persisted through the climatic vicissitudes of the Quaternary.

Biogeographers who have studied the distribution of flora and fauna in the African forest (see the authors quoted on pages 51 and 52) have reached the conclusion that certain sectors were much richer in species and endemic taxa than others. The richest area is that which comprises the Biafran forest formation (near the Bight of Biafra, i.e. the inside curve of the Gulf of Guinea) from the Cross River to the Sanaga (west Cameroon *sensu lato*) on the one hand, and, on the other, further south, from the south-west Cameroon evergreen forests to those in west Gabon (Letouzey 1968, 1985; Aubréville 1968; Brenan 1978; Breteler 1990). Another slightly less rich sector is situated to the far west of the forest block, encompassing the south-east part of

the Guinea uplands (Guinea and Liberia) and stretching to the south-east of Liberia and to the extreme west of Ivory Coast in the Grabo area (Guillaumet 1967; Van Rompaey 1993, 1994). The forest-covered south-west of Ghana and the adjacent area in Ivory Coast are also noteworthy for the presence of various endemic species (Hall & Swaine 1981; Swaine & Hall 1986; Hawthorne, personal communication). Finally, the central part of the Congo–Zaïre depression, from biogeographical data obtained both on various mammal groups, particularly simian primates (Colyn 1987, 1991; Colyn *et al.* 1991) and on vascular plants (Ndjele 1988), has been shown to be relatively rich in endemic taxa.
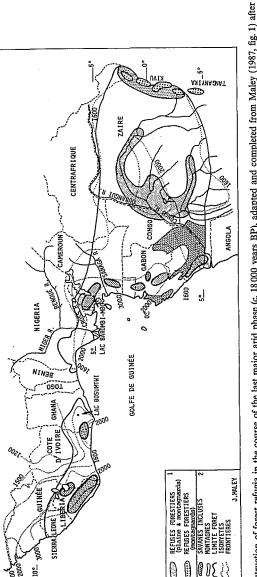
All these biogeographers have concluded that this specific wealth and the large numbers of endemic taxa could be explained by the fact that these sectors are located on former refugia. Aubréville published the first sketch maps of such refugia (1949, p. 66; 1962, p. 62). Detailed botanical studies by P. W. Richards (1963) in west Cameroon led to the conclusion that the area could have been a refuge. More recent botanical studies lead to similar conclusions (Fig. 5). For instance the study of the *Begonia* occurring in the Guineo–Congolian forest Domain suggests that the areas at present occupied by various endemic species could correspond to former refugia (Sosef 1991, 1994), or the study of the Caesalpinioideae from Gabon (Rietkerk *et al.* 1995). Reference should also be made to sketch-maps established for the African rain forest as a whole by Moreau (1969), Hamilton (1976), and Mayr & O'Hara (1986), and for the Zaïre depression by Colyn (1987, 1991). Further to this, the subdivision of the Pygmies of central Africa into three main groups can be taken into consideration: one group to the west (south Cameroon and Gabon – the Kola-Gyeli), one central group (Congo–Zaïre basin – the Twa) and one eastern group (Ituri, NE Zaïre – the Mbuti and the Baakaa, the latter migrating westwards towards north Congo and south-east Cameroon, possibly following climatic deterioration between 3000 and 2000 years BP; Maley 1992). This distribution has been thought by the ethnologist Bahuchet (1993, his fig. 4.6) to be associated with the Cameroon and Gabon refugia and the central refuge in the Congo–Zaïre basin (Fig. 5) where these ancient populations could have survived through the last arid period of maximum fragmentation between about 20 000 and 15 000 years BP (for the central refuge it could be possible that the Ituri Pygmies might have occupied the north-east branch and the Twa the south and central part).

Recent research by Colyn (1987, 1991) has also shown montane forest refugia on the western slopes of the Nile–Congo watershed and also on the part running down to Lake Tanganyika (Fig. 5). This hypothesis would appear to be supported by pollen analyses carried out in Uganda at Lake Mobutu Sese Seko (Sowunmi 1991) and in Burundi (Bonnefille & Riollet 1988). These forest refugia probably existed in cloud forest conditions. However, particularly in view of the present-day very rich fauna in the eastern Zaïre (T & J. Hart, personal communication) and analyses of the palaeo-fauna (see the Matupi cave data: Van Neer 1990) a lowland forest refuge is also possible.

These data, combined with information on palaeo-environments, have led to the establishment of a new diagramatic map of possible refuges in the forest areas of Africa (Fig. 5).

Pollen data available for the last 140 000 years

Toward the middle of this period there is a long, relatively cold period which began about 75 000 years ago and came to an end about 10 000 years ago with the start

Figure 5. Reconstruction of forest refugia in the course of the last major arid phase (*c.* 18 000 years BP), adapted and completed from Maley (1987, fig. 1) after Van Rompaey (1993, 1994) for Liberia and Ivory Coast, Sosef (1994) for Gabon and Congo, and Colyn (1987, 1991) for the Congo–Zaïre basin. In the key: 1, 18 000 years BP; 2, present day.

Remarks: the Liberia refuge could have been linked to that around Mount Nimba. Van Rompaey (1994) and Robbrecht (1994) consider that the secondary refuge in south-west Ghana and south-east Ivory Coast was probably linked to the main Liberia refuge. For Mount Cameroon, Cheek *et al.* (1994) have shown that this area was rich in endemic species, which would suggest the existence of a secondary refuge that should be linked to the major refuge in west Cameroon/Oban. In Gabon Sosef (1994) considers another smaller refuge west of the Chaillu Massif (Doudou Mountains).

of the Holocene (isotopic stages 4, 3 and 2). Prior to this, there was a relatively warm, or interglacial period (stage 5), dated from about 75 000 to 128 000 years ago, which was interrupted by two main cooling phases (stages 5b and 5d) and which began by a markedly warm period (stage 5e) named the Eemian in Europe. This period lasted about 10 000 years, like the Holocene, running from about 128 000 to 118 000 years ago (see the chronology by Martinson *et al.* 1987). The period between 128 000 and 140 000 years ago constitutes the end of another cold period (end of stage 6). The succession of these different periods was mainly studied from marine sediments and based on the fluctuations of the oxygen $^{16}O/^{18}O$ isotopic ratio obtained from Foraminifera carbonates found in these sediments. These 'isotopic stages' are global phenomena, largely determined by the volume of polar ice (north and south), and dated by way of correlation on a world-wide scale (Martinson *et al.* 1987).

Marine sediments from the Gulf of Guinea

Three marine cores extracted from the Gulf of Guinea have produced fairly detailed pollen analyses for the period under consideration, one from off west Guinea (Hooghiemstra & Agwu 1988), the second from off Ivory Coast (Frédoux & Tastet 1988, 1993) and the third from off Gabon on the northern side of the deep-sea Congo–Zaïre delta fan (Bengo & Maley 1991), which reflect the main fluctuations in vegetation over the watershed. The results obtained from the three cores are coherent. For the third, the main remarks are as follows (Fig. 6):
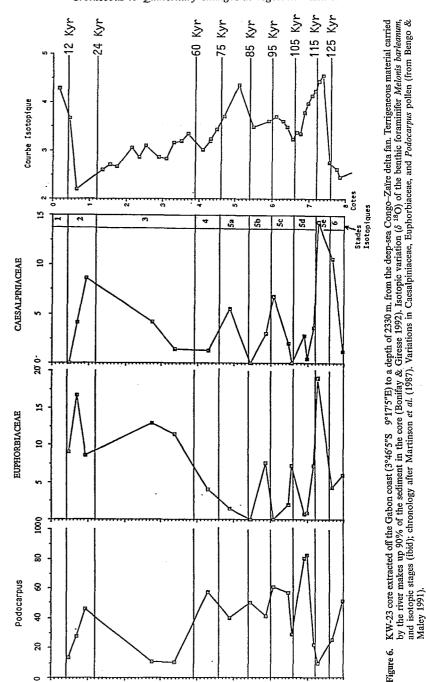
- The end of stage 6 shows very reduced forest cover.
- In stage 5e, the warmest (Eemian), maximum development of rain forest is observed (peaks for Caesalpiniaceae and Euphorbiaceae pollen, these being two important families in rain forests) probably comparable to the maximum extension phase in the early and middle Holocene.
- Stage 5d, a cooling phase, shows a particular extension of montane tree *Podocarpus* in association with marked reduction of lowland forest taxa.
- Stages 5c and 5a are both periods cooler than 5a, and they show lesser development of forest taxa (a moderate peak for the Ceasalpiniaceae)
- Stage 5b is an intermediate cooler period showing a less marked development for *Podocarpus*.
- Stage 4 (*c.* 75 000 to 60 000 years ago) is a period of cooling comparable to stage 5d, characterised by the extension of *Podocarpus* and regression of most forest species.
- Stage 3 (*c.* 60 000 to 24 000 years ago) is the least well known. All that can be said is that pollen from forest taxa fluctuates, with percentages well below those in the Eemian and the Holocene.

Low-altitude lake sediments

The history of the African rain forest is much better known for the last 28 000 years from pollen studies carried out on sediments in Lake Bosumtwi in Ghana and Lake Barombi Mbo in west Cameroon. The sediments studied in Lake Bosumtwi go back to about 28 000 years BP (Maley & Livingstone 1983; Maley 1987, 1989, 1991) and for Lake Barombi Mbo to a similar date (Maley & Brenac 1987; Brenac 1988; Maley 1989, 1991; Giresse *et al.* 1994; in preparation). Thus fairly precise information
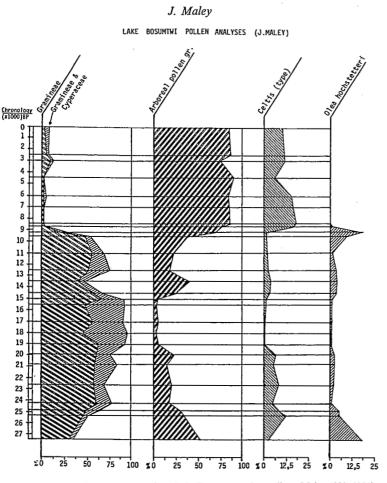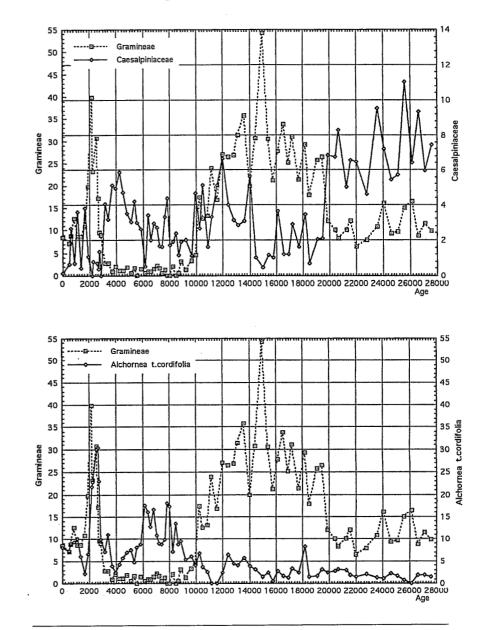
Figure 6. KW-23 core extracted off the Gabon coast (3°46′5′′S 9°17′5′′E) to a depth of 2330 m. from the deep-sea Congo–Zaïre delta fan. Terrigeneous material carried by the river makes up 90% of the sediment in the core (Bonifay & Giresse 1992). Isotopic variation (δ ^{18}O) of the benthic foraminifer *Melonis barleanum*, and isotopic stages (ibid); chronology after Martinson *et al.* (1987). Variations in Caesalpiniaceae, Euphorbiaceae, and *Podocarpus* pollen (from Bengo & Maley 1991).

LAKE BOSUMTWI POLLEN ANALYSES (J.MALEY)

Figure 7. Main results of pollen analyses from Lake Bosumtwi, Ghana, (from Maley 1989, 1991).

Figure 8. The evolution of relative percentages of the pollens of three characteristic taxons from Quaternary sediments of Lake Barombi Mbo (West Cameroon) (according to Brenac & Maley, in preparation). Interpolated ages from 12 radiocarbon dates. For information concerning this site and the geological and stratigraphical data, see Brenac (1988); Maley (1989, 1991, 1992); Giresse *et al.* (1991, 1994).

Gramineae. This taxon makes up almost all of the non-aquatic herbaceous pollen and is characteristic of open environments of savanna type. Its extension was greatest between 20 000 and 10 000 years BP during dry periods. However, since tree pollens continued to dominate between 20 and 15 000 years at a mean of 50%, it shows that forest environments have persisted in this region, establishing a 'refuge' (see the text).

Alchornea cordifolia type. In or at the edge of the forest, this taxon is a pioneer tree characteristic of the 'secondary' colonising forests: they develop abundantly in all types of openings, where they actively participate in the reconstitution of the forest, like for example during the late Holocene climatic pejoration phase (c. 3000–2000 years BP).

Caesalpiniaceae (total of the pollens of the Caesalpiniaceae). This family, with mainly trees, occurs mainly in 'primary' forest environments of sempervirent type. The Caesalpiniaceae produce little pollen, thus even 1 or 2% are significant of a certain local occurance (cf. Brenac, 1988). Their high percentages before 20 000 years BP must be noted, indicating their

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domination of the forest environment. Later, although they decreased greatly, they persisted in the sector between 20 and 15 000 years BP. After that, they are relatively abundant from 14 000 years on until c. 3000 years BP when they regressed greatly during the phase of climatic pejoration which culminated between 2500 and 2000 years BP. For the last 2000 years their occurrance has been very variable.

are available for the end of stage 3, for stage 2 which includes the last glacial maximum, and for stage 1 which mainly covers the Holocene.

In brief, from the publications quoted above, in Ghana in the region of Lake Bosumtwi where the surrounding hills reach an altitude of 500 to 600 m, the following phenomena have been brought to light (Fig. 7):

- Between 28 000 and 24 000 years BP (end of stage 3) there was forest with montane elements (*Olea capensis*, syn. *O. hochstetteri*), in a relatively cool and wet climate.
- Between 24 000 and 19–20 000 years BP the forest progressively recedes.
- Between 19 000 and 15 000 years BP, under the influence of a very arid climate, the forest disappears (tree pollen is at this time less than 5%), giving way to very open habitat which can be compared, not to low-altitude savanna, but to medium-altitude prairie with scattered groups of trees composed of montane taxa and a few forest taxa whose distribution area also extends into lowland areas (cf. Schnell 1977; Letouzey 1968, 1985).
- Following this, after 15 000 years BP, the climate improves and favours forest recolonisation in the area with an initial advance around 12 500–13 500 years BP. A return to drier conditions can be noted between 12 000 and 10 000 years BP, this phase possibly corresponding in part to the 'Younger Dryas' event in higher latitudes.
- Between 9500 and 8500 years BP; at the same time as the montane element disappears, the forest becomes completely re-established and has remained until the present.

In west Cameroon, for Lake Barombi Mbo, situated at an altitude of about 300 m with surrounding hills reaching between 400 and 600 m, observations and main interpretations are as follows (Fig. 8):

- Between 24/29 000 years (the sedimentation was disturbed at the base of the core, cf. Giresse *et al.* 1991) and 20 000 years BP there was forest with abundant Caesalpiniaceae which also included montane elements (mainly *Olea capensis* syn. *O. hochstetteri*). The development of this montane element could be explained by a cloud forest type habitat on the hills above the lake (Brenac 1988; Maley 1987, 1989, 1991). It can be recalled here that in Congo, on the Batéké plateaux, in a site at about 600 m, Elenga (1992) has brought to light a forest phase before the Holocene dominated by an afro-montane vegetation, with about 60% of the pollen spectra composed of *Podocarpus* (dominant at 50%), *Ilex mitis* and *Olea capensis*. The development of this montane formation has been explained by the considerable cloud cover (Elenga *et al.* 1991; Maley & Elenga 1993).
- Around Barombi Mbo a sudden dry phase began about 20 000 years BP, causing the forest to recede and give way to more open vegetation. This situation lasted until about 14 000 years BP, but as the tree pollen types oscillate around 50% it is thought that the climate was not as dry as in Ghana where tree pollen fell below 5%, and that significant patches of forest survived in the area. This interpretation is confirmed by isotopic studies carried out on detritic organic matter from the watershed that were preserved in the sediments from this period:

$\delta^{13}C$ measurements provide values generally situated near the lower limit for typical forest values (Giresse *et al.* 1994).
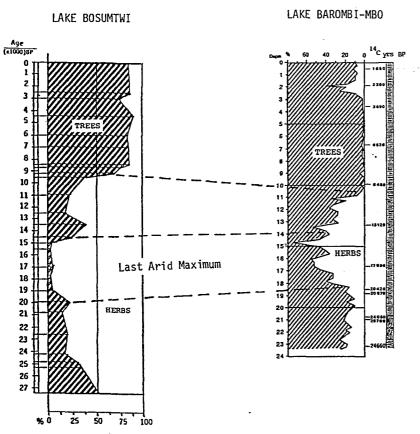
- Between 14 000 and 9500 years BP a forest recolonisation phase is observed with a negative oscillation before 10 000 years BP that could, as for Lake Bosumtwi, relate to the 'Younger Dryas' event.
- From this date and until 3000 years BP the forest reached its maximum extension (herbaceous pollen, mostly Gramineae, oscillating between 0 and 2%).
- From 3000 years BP a large increase in occurrence of Gramineae pollen is observed, with maxima values near 40% between 2500 and 2000 years BP, indicating a sudden phase in which habitats opened out and the forest regressed, accompanied by severe erosion (Maley 1992). These phenomena, for which synchronous evidence has been found in other parts of wet tropical Africa (Uganda, central and eastern Zaïre, northern Ethiopia, south Chad basin, etc.), and also as far as the Sahel (Maley 1981; Lézine 1989), on account of their generalised nature, must be the result of a considerable climatic variation (Maley 1992). The open environment and the regression of the forest that occurred in the First Iron Age probably facilitated penetration of the forest block by Bantu iron workers (Schwartz 1992). It should also be noted that this sudden opening up of the rain forest constitutes the beginning of a fragmentation that occurred in an interglacial period, i.e. in a globally warm phase. In the Amazon forest a comparable destruction phase occurred in the eastern part during the middle Holocene, between about 8000 and 4000 years BP, as has been shown by pollen analyses of the Carajas lake sediments and also by the presence of large quantities of charcoal fragments (Absy *et al.* 1991; Servant *et al.* 1993; Martin *et al.* 1993). From a chronological point of view, this regression of the Amazon forest is out of phase with equatorial Africa. It can therefore be concluded that tropical forests can become fragmented in the course of either warm or cold global phases, that is to say, under different climatic conditions.
- After 2000 years BP the forest expanded again over part of the ground lost, but not to the extent reached in the early and middle Holocene. *Elaeis guineensis* (oil palm) pollen increases rapidly during this new forest extension, but this pollen grain appears, first at low percentages, at exactly the same time as the first forest extension in the early Holocene. In fact this palm tree belongs to the African forest vegetation: its pollen first appeared in Miocene deposits of the Niger delta (Zeven 1964). The oil palm was first a pioneer tree living naturally near the periphery of the rain forest (Letouzey 1978, 1985; Maley, to be published). Its first extension between 3000 and 2500 years BP mirrors that of *Alchornea* type *cordifolia*, another important pioneer tree (Fig. 8). Pollen analyses of other sites in or around the rain forest block also indicate a significant increase in oil palm pollen near the beginning of the late Holocene (Maley, to be published). It is possible that, during the post-2000 year BP forest extension, the oil palm could have been favoured by Man and so progressively domesticated.
- Roughly the last 500 years are missing from the core studied.

The comparison between the two sites is important (Fig. 9). Firstly, similarities are as follows:

- Before *c.* 20 000 years BP the montane type forest phase terminates, more or less progressively.

Figure 9.   Comparison of synthetic pollen spectra from Lakes Bosumtwi (Ghana) and Barombi Mbo (west Cameroon). Graphs for tree pollen versus to herbaceous pollen (AP/NAP).

- Between 19/20 000 and 14/15 000 years BP maximum forest regression occurs, except for a series of forest refugia, such as in West Cameroon, in which the biodiversity was preserved.
- Between 14/15 000 and about 9500 years BP there was a forest recolonisation phase, with a setback that could be related to the 'Younger Dryas' event.
- From *c.* 9500 years BP to the present day there was first a phase of maximum forest extension, and then from about 3800 or 3000 years BP, according to sector, a forest regression and then, after 2000 years BP, a new forest extension reaching the present outline of the forest block.

The first most marked difference between the two sites is the disappearance of the forest in the Bosumtwi region in the course of the last glacial maximum, and, conversely, its survival in west Cameroon. These data confirm conclusions reached by biogeographers as to the existence of a large forest refuge in the latter region (Fig. 5), which would explain the Cross River gap, if it is assumed that the forest

had disappeared to the west. The second notable difference is the persistence of the forest around the Bosumtwi in the course of the late Holocene, as no abrupt regression of the forest between *c.* 3000 and 2000 years BP is observed, as it is in the Barombi Mbo area. On the other hand, in the Bosumtwi region, Talbot *et al.* (1984) have shown a marked drop in lake levels from 3700/3800 to 3000 years BP with no corresponding regression of the forest around the lake. However one could estimate that at distance from Bosumtwi there was probably at this time a reopening of the Dahomey gap (cf. discussion on climatic evolution in Maley 1991). Indeed, the high lake levels in the early Holocene and especially in the middle Holocene relate to a much wetter climate than in the late Holocene (after 3700 years BP) or than in the present day (Maley 1989, 1991). Thus it seems likely that forest recolonisation at the beginning of the Holocene completely over-ran the Dahomey Gap and that forest cover stretched to the north well beyond its present-day limits, particularly in the course of the middle Holocene which was the wettest period. In connection with this, it can be noted that fossil stumps of trees typical of rain forest have been found along the Congo coast (in the southern part of the forest block), in an area at present covered by savanna; they date from the middle Holocene, confirming a forest extension phase beyond present boundaries (Schwartz *et al.* 1990).

Conclusions

Two observations can provide a model for the extreme fluctuations of the forest block: on the one hand, the last period of maximum fragmentation was associated with the last large glacial extension (isotopic stage 2, between 20 000 and 15 000 years BP), and, on the other, the most marked forest extension phase correlates with the thermal optimum in the middle Holocene. This model can be transposed to earlier periods in the Quaternary, or at least to the last 800 000 years (upper Pleistocene). The 'intermediate' periods of cooling (comparable to the period from about 28 000 to 20 000 years BP) or warming (as that from about 15 000 to 9500 years BP) also seem to relate respectively to phases of forest decrease or increase.

Thus, as is shown in Figure 4, over the last 800 000 years the phases of forest extension of the Holocene type (the total area at present covered by forest is markedly smaller than the maximum extension in the middle Holocene – see p. 61) probably account for about 10% of the time span. The phases of maximum fragmentation, comparable to the situation that has been reconstructed for the cool, dry period between 20 000 and 15 000 years BP, with forest types preserved in a series of refugia (Fig. 5) probably also covered about 10% of the time span.

However, recent pollen studies by Dupont & Agwu (1992) on a marine core taken offshore from west Guinea (19°5'W 9°34'N) dating back to about 800 000 years BP, suggest that the main fluctuations in forest vegetation only began in the course of stage 7, i.e. about 250 000 years ago. Nevertheless, given that the core was taken about 500 km from the mainland, it is difficult to distinguish, in the pollen variations observed, between those due to variations in the vegetation and those due to variations in the modes of pollen transport involved. Winds and marine currents, of varying origins, could indeed differ from present-day patterns used for reference (Hooghiemstra & Agwu 1986, 1988; Dupont & Agwu 1991; Calleja *et al.* 1993). Further to this, it should be noted that for all the upper Cenozoic deposits examined by Morley & Richards (1993) in the Niger delta, it is towards the base of the Pleistocene that they observed the highest percentages of Gramineae pollen, indicat-

ing pronounced aridity and already probably considerable fragmentation of the forest in the area. Moreover, from results obtained from the deep-sea delta fan of the Congo–Zaïre river, Jansen *et al.* (1986) suggest that the period from *c.* 800 000 to 300 000 years BP was more arid in the watershed of this river, which is today covered for a large part by rain forest, and relatively wetter from around 250 000 years ago to the present day. Thus there may have been differences in timing of some climatic phases between the north tropical zone and the equatorial zone (Jansen *et al.* 1986). The study of further marine cores and in particular of long cores obtained inland from lakes in the forest zone, such as Lake Bosumtwi and Lake Barombi Mbo which are located in craters about 1 million years old, should provide more accurate data on the history of the African rain forest during the middle and upper Pleistocene. Before 800 000 years BP, and going back to the beginning of the major glaciations in the northern hemisphere, around 2.5 million years ago, the amplitude of climatic variation was not so great (Fig. 4), which would suggest lesser fluctuations in the African forest block.

Finally, on the basis of data available, it would appear that the most common state, accounting for 80–90% of the time span in the upper Pleistocene, would be that of the 'intermediate periods', with relatively fragmented forest masses, but with rather larger surface areas than those of the refugia postulated for the arid phases of isotopic stages 6 and 2. Stone lines, which are made up of a concentration of fairly coarse gravel and form the base of most forest soils today, could be indicators of the extent of vast sectors where the forest disappeared in an earlier period. Indeed, these stone lines have been interpreted by many authors as erosion pavements formed in semi-arid climatic conditions and associated with very open vegetation (cf. Vogt 1966; Lanfranchi & Schwartz 1991; Thomas & Thorp 1995). For example, in northern Congo (the Sangha region) stone lines have been observed overlaid by *in situ* prehistoric workshops dated from the Sangoan, which enabled Lanfranchi & Schwartz (1991) to situate a semi-arid phase between about 70 000 and 40 000 years ago, thus illustrating what has been termed here an 'intermediate' period.

The forest flora in the 'intermediate periods' defined above probably also comprised varying proportions of montane taxa, as has been noted for the Bosumtwi and Barombi Mbo regions, and also the Batéké Plateaus (see p. 58 and 60). As a result of the fall in temperatures, montane flora moved down to lower altitudes, where it came into contact with lowland forest flora, under the influence of various local climatic and topographical factors. The climatic conditions created by the cloud cover or mist would have facilitated phenomena of this sort. It is probably in the course of these long 'intermediate periods' that the migrations of montane taxa took place (Maley 1987, 1989, 1991; Bengo & Maley 1991), thus explaining, for example, why mountains in Cameroon and East Africa have numerous species in common, or very closely related, both for the flora – 53% of montane forest species and 49% of montane grassland species are in common between Mount Cameroon and East Africa (Hall 1973) – and for the fauna (Eisentraut 1963, 1970). The periods during which montane vegetation was in contact with lowland vegetation was probably very favourable to genetic exchange and speciation (cf. Gentry 1989).

Acknowledgements

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