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Palaeobotanical studies from tropical Africa: relevance to the evolution of forest, woodland and savannah biomes

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Fossil plants provide data on climate, community composition and structure, all of which are relevant to the definition and recognition of biomes. Macrofossils reflect local vegetation, whereas pollen assemblages sample a larger area. The earliest solid evidence for angiosperm tropical rainforest in Africa is based primarily on Late Eocene to Late Oligocene (*ca*. 39–26 Myr ago) pollen assemblages from Cameroon, which are rich in forest families. Plant macrofossil assemblages from elsewhere in interior Africa for this time interval are rare, but new work at Chilga in the northwestern Ethiopian Highlands documents forest communities at 28 Myr ago. Initial results indicate botanical affinities with lowland West African forest. The earliest known woodland community in tropical Africa is dated at 46 Myr ago in northern Tanzania, as documented by leaves and fruits from lake deposits. The community around the lake was dominated by caesalpinioid legumes, but included *Acacia*, for which this, to my knowledge, is the earliest record. This community is structurally similar to modern miombo, although it is different at the generic level. The grass-dominated savannah biome began to expand in the Middle Miocene (16 Myr ago), and became widespread in the Late Miocene (*ca*. 8 Myr ago), as documented by pollen and carbon isotopes from both West and East Africa.

Keywords: Africa; forest; woodland; savannah; biome evolution; palaeobotany

1. INTRODUCTION

Modern tropical forest, woodland and savannah biomes bring to mind angiosperm-dominated communities of varied diversity, richness and physiognomy, limited in distribution primarily by rainfall and seasonality. Each region of the world is characterized by biomes with unique composition, although structurally and physiognomically regional biomes may be similar. Therefore, the task of identifying Africa's past biomes based on the fossil record should be straightforward if the criteria used to define them are the same as those used to define biomes today. In this paper, physiognomic, structural and taxonomic criteria are used to identify the origin and evolution of forest, woodland and savannah biomes in Africa primarily based on plant fossils. The taxonomic criteria used here are focused at the family (and sometimes genus) level because the composition of communities changes dynamically at the species level over relatively short time-scales.

(a) *Modern tropical African forest, woodland and savannah biomes*

The biomes in question are most easily distinguished physiognomically (table 1): tropical forests are composed of tall trees (higher than 20 m) with overlapping crowns, woodlands have smaller trees and crowns that may touch but overlap little if at all, and savannahs have the most open structure, dominated by grasses with a minor to substantial (up to 40%) woody component (i.e. wooded grasslands; White 1983; Richards 1996). Within each biome are communities that vary at a smaller scale, reflecting soil conditions or physical features affecting local climate. Among forest communities are rainforests, which receive 2000 mm yr^{-1} or higher rainfall, have no or minor dry periods, are evergreen and are the tallest in stature (Richards 1996). Drier variants receiving smaller amounts of annual rainfall and with dry seasons of up to five months are termed, in order of increasing water-deficits: semi-evergreen forest (lowland moist or tropical wet forests of Richards (1996)), dry forest and deciduous forest (White 1983; Richards 1996). Montane forests exist in environments characterized by a much greater range in diurnal temperature and lower mean temperature than lowland forests. This affects species composition, and stature (they are somewhat smaller), but otherwise montane forests are physiognomically similar to lowland forests, depending on availability of water. Woodlands can be relatively dense or open, depending on annual rainfall and dry season intensity, but have a grass understorey. The woody component of savannah environments generally varies along a moisture gradient, but is strongly influenced by fires, which suppress the development of woody vegetation, and by grazing, which promotes grass productivity (Frank *et al.* 1998).

African forest communities are most often dominated by a variety of caesalpinioid legume species and, in order of decreasing species numbers, representatives of the families

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Table 1. Characteristics of forest, woodland, and savannah biomes.

biome	dominant families	physiognomy	leaf size	rainfall
forest	Leguminosae (caesalpinioid), Apocynaceae, Euphorbiaceae, Ruabiaceae, Annonaceae, Sterculiaceae, Sapindaceae, Olacaceae, Ebenaceae	trees greater than 20 m, overlapping crowns	mesophyll and microphyll most common	1000 mm yr^{-1} or higher, minor dry season
woodland	Leguminosae, Burseraceae, Combretaceae, Gramineae (Poaceae)	trees less than 20 m, little crown overlap	microphyll and smaller common	1000 mm yr^{-1} or less, pronounced dry season
savannah	Gramineae, Leguminosae	open, woody component less than 40%	notophyll and smaller common	less than 1000 mm yr^{-1}, pronounced dry season

Apocynaceae, Euphorbiaceae, Rubiaceae, Annonaceae, Sterculiaceae, Sapindaceae, Olacaceae and Ebenaceae, among others (Gentry 1988; Richards 1996). Leguminosae (Fabaceae) play a critical role in woodland communities as well, as do Burseraceae, Combretaceae and Gramineae (Poaceae). Savannah communities are dominated by grasses, as they are everywhere, but the woody component is again strongly influenced by the presence of legume species.

2. THE TROPICAL AFRICAN PLANT FOSSIL RECORD

Recognizing the combined physiognomic, compositional and climatic criteria for African forest, woodland and savannah communities is challenging when considered from the perspective of the fossil record. The quality of preservation and the accuracy with which fossils represent the source community varies among assemblages, and the record is spatially and temporally inconsistent. In addition, fossil assemblages can sample anywhere along the continua of physiognomic, compositional and climatic criteria that link each biome. Nevertheless, Palaeogene and younger plant fossils often represent forest, woodland and savannah communities faithfully; older records can be more difficult to interpret palaeoecologically and are not as well sampled. Evidence of biome physiognomy can be directly observed in some autochthonous assemblages such as *in situ* silicified forests or at untransported ash-fall localities (e.g. Jacobs & Winkler 1992), but otherwise data are limited. Biome taxonomic composition is determined from both autochthonous assemblages and, circumstantially, from dispersed leaves, seeds, wood and fruits. Estimates of palaeoclimate, especially mean annual and seasonal rainfall, suggest what sorts of biome might reasonably be supported. In the following sections, the fossil record is reviewed for evidence of forest, woodland and savannah biomes for the criteria in table 1. Forest and woodland biomes are discussed together as they grade into one another and their characteristics overlap.

(a) *Forest and woodland*

Modern tropical forests and woodlands are angiosperm-dominated. Thus, this review of the fossil record begins when angiosperms first became common in tropical Africa. Extensive palynological research, driven by oil exploration, documents a significant diversification of angiosperms and associated reduction in gymnosperm taxa beginning *ca.* 95 Myr ago during the Cenomanian stage of the Upper Cretaceous (Jardiné & Magloire 1965; Kaska 1989; Schrank 1991; Morley 2000, p. 85). Salard-Cheboldaeff & DeJax (1991) suggest that some pollen, such as *Triorites* spp. and periporate forms, may be related to extant Proteaceae and Caryophyllaceae/Amaranthaceae (families difficult to distinguish based on pollen morphology), although others such as *Cretacaeiporites* sp. may belong in a variety of families (see, for example, Morley 2000, p. 289). Angiosperm macrofossils with *in situ* pollen would help to clarify the botanical affinities of the pollen taxa, but such fossils are unknown from the African Cretaceous. Angiosperm woods, the most common fossils of younger Cretaceous sediments, are absent from Cenomanian and older deposits (Dupéron-Laudoueneix 1991). Other macrofossils of Cretaceous age are very rare; thus, understanding the structure and physiognomy of early angiosperm-dominated communities is challenging. However, the absence of Cenomanian angiosperm wood is consistent with a tree component comprising primarily or only gymnosperms (for which wood fossils are present). Evidence for a hot and dry climate in the Cenomanian includes the common occurrence of pollen from xerophilous conifers (Cheirolepidiaceae), with sedimentological and lithologic indicators (Salard-Cheboldaeff & DeJax 1991). There is no evidence of tropical forest at this time, and no indication that angiosperm-dominated woodland would have been present. Grasses, which are an essential component of woodland and savannah biomes today, cannot be unequivocally demonstrated in the Cretaceous (Linder & Ferguson 1985; Jacobs *et al.* 1999), and legumes, which dominate taxonomically in modern forests and woodlands, are also equivocal in Late Cretaceous deposits (Herendeen *et al.* 1992; Wheeler & Baas 1992).

West African palynological records from the past 28 Myr of the Cretaceous (Turonian, Coniacian, Santonian, Campanian and Maastrichtian stages) are characterized by the disappearance of Cheirolepidiaceae in the Turonian, reduction of *Ephedrapites* spp. in the Santonian–Coniacian, and a concomitant increase in angiosperm richness, including taxa with no known botanical affinities within the angiosperms (Jardiné & Magloire 1965; Salard-Cheboldaeff & DeJax 1991; Morley 2000). By the Maastrichtian, palm pollen taxa were diverse, thus giving rise to the Upper Cretaceous northern Gondwanan 'palm province' of Herngreen & Chlonova (1981) (Herngreen *et al.* 1996). In addition to palms (Palmae (Arecaceae)), the Upper Cretaceous West African records share Illiciaceae, Linaceae (*Ctenolophon*), Proteaceae, Restionaceae, and the more specialized palms *Proxapertites* spp. and *Spinizonocolpites* spp. The last two genera are interpreted as indicating mangrove vegetation because of their relationship to the living mangrove palm genus *Nypa* (Salard-Cheboldaeff 1981; Salard-Cheboldaeff & DeJax 1991). These are the earliest angiosperms thought to be specifically associated with a brackish shoreline setting, and the first plants known to occur in this ecological role since the conifer family Cheirolepidiaceae, which disappeared at least 20 Myr earlier.

Cretaceous macrofossils are quite rare, but Chesters (1955) documented two new species of the seed genus *Anonaspermum* from Nigeria, which are Maastrichtian based on associated marine fauna. Distinct ruminated internal casts of the seeds are good evidence of their relationship to living Annonaceae. Isolated seeds from other localities in Nigeria, thought to be Maastrichtian in age, are identified as *Icacinicarya* sp. (Icacinaceae) and a possible relative of Passifloraceae (Chesters 1955). Fruits and seeds from Senegal, firmly dated at the Campanian–Maastrichtian boundary based on associated marine fossils, are similar to the living Palmae, Meliaceae, Leguminosae (Caeasalpinioideae), Rubiaceae and Annonaceae (Monteillet & Lappartient 1981). However, the identifications are problematic because of an absence of internal structure and significant differences from living relatives (Monteillet & Lappartient 1981).

In North Africa, pollen records from Tunisia document considerable influence from the Laurasian (Northern Hemisphere) *Normapolles* Pollen Province in the Maastrichtian, and an abundance of palm pollen taxa in common with West Africa (Méon 1990). The northern influence remains after the Cretaceous–Palaeogene boundary, when pollen from such families as Juglandaceae is found with other Laurasian taxa. The record of Late Cretaceous angiosperm wood from northern and equatorial Africa documents extant families such as Euphorbiaceae and Rutaceae in Tunisia and Cameroon, respectively (Koeniguer 1967; Duperon-Laudoueneix 1991).

Pollen sequences in cores from Egypt and Sudan are transitional in composition between the palm province of tropical Africa and the more northern latitudes, including species of the Laurasian genus *Aquillapollenites* and others typical of the *Normapolles* Pollen Province (Kaska 1989; Schrank 1991; Mahmoud 2003). The inland setting of these cores explains the absence of the mangrove palm, *Nypa*. However, a Maastrichtian pollen core from Somalia, close to the palaeoshoreline, contains nypoid pollen, *Ctenolophon*, Proteaceae, Illiciaceae and taxonomic unknowns such as *Buttinia*, also known from Sudan and tropical West Africa (Schrank 1994).

Kamal El-Din (2003) reports Campanian wood from Egypt's Farafra Oasis, including the genera *Celastrinoxylon* and *Ficoxylon*. *Celastrinoxylon* is also known from Ethiopia in deposits cited as 'Cretaceous–Eocene' (Beauchamp & Lemoigne 1973). *Ficoxylon* is known from localities in Egypt, Ethiopia, Mali and Tunisia, ranging in age up to the Miocene. *Celastrinoxylon celastroides* specimens from the Farafra Oasis have distinct growth rings, vessel tangential diameters of less than 100 μm, and *ca*. 25–50 vessels mm^{-2}, features that compare favourably with taxa from temperate climates today. *Ficoxylon cretaceum* lack growth rings, have vessels with larger (95–165 μm) diameters and occur at a low density. These characters are found commonly among taxa from tropical aseasonal climates (Kamal El-Din 2003).

Other macrofossil records from northeastern Africa include mesophyll-sized leaf fossils reported by Seward (1935) from the Nubian Sandstone of Egypt, including *Dipterocarpophyllum* spp. (possibly, but not necessarily, related to the living Dipterocarpaceae), *Dicotylophyllum* spp. (unknown affinity), and *Nelumbium* sp. (Nelumbonaceae). Schrank (1992) reports the Egyptian *Dipterocarpophyllum* specimens as Campanian–Maastrictian, and Axelrod & Raven (1978) and Morley (2000) consider Seward's locality to be Palaeocene. Regardless of the exact age, the palaeoecological interpretation of the leaf fossils is tropical and wet (Axelrod & Raven 1978; Morley 2000). A leaf flora from Sudan dated Turonian – early Senonian based on correlation with the North American Potomac Group includes relatives of Aristolochiaceae, Annonaceae, Magnoliaceae, Lauraceae and Ulmaceae. The assemblage is interpreted as representing a seasonally dry climate based on leaf size and sedimentological data (Schrank & Ruffle 2003). Assuming the dates and palaeoenvironmental interpretations for the Egyptian Campanian–Maastrichtian and Sudanese Turonian–Senonian palaeofloras are correct, they are consistent with an increasingly humid climatic trend through the Late Cretaceous.

Although several pollen taxa from the latest Cretaceous are not well understood in terms of the ecological requirements of the parent plants, Morely (2000) suggests that multi-stratal forests may have been present based on the occurrence of large seeds and fruits from Senegal reported by Monteillet & Lappartient (1981), and the presence of some families, such as Meliaceae, Moraceae and Ctenolophonaceae (Linaceae), which are found in wet forests today. Upchurch *et al.* (2004), and Axelrod & Raven (1978) conclude that rainforest was established by the end of the Cretaceous in the northern part of the continent. This hypothesis is consistent with a moist ever-wet climate in the equatorial zone by *ca*. 70 Myr ago owing, at least in part, to the widening Atlantic Ocean (Morley 2000; Scotese *et al.* 1988).

I agree with Morley (2000) that rainforests structurally analogous and compositionally (at the family level) similar to today were not present in equatorial Africa during the Mesozoic (see also Dupéron-Laudoueneix 1991). Clearly, palms, including several whose taxonomic relationships are unknown, played a significant role in the latest Cretaceous plant communities of tropical Africa (Salard-Cheboldaeff 1978, 1981). Other constituents of communities of that age include families now either restricted in range, such as Ctenolophonaceae (Linaceae) and

Illiciaceae, or found elsewhere today (e.g. Proteaceae). Other taxa, such as *Buttinia*, have unknown affinities or their age is uncertain. Without better macrofossil data it is not possible to use physiognomy or community structure as palaeoecological criteria in evaluating the presence of tropical forests in the Cretaceous, and our limited knowledge of the composition of these communities suggests they were not comparable to forests of today.

Palaeocene vegetation is poorly understood. The Mesozoic–Cenozoic boundary marks the disappearance of some palm and *Proteacidites* pollen species, along with several other pollen taxa in West, North and northeastern Africa (Salard-Cheboldaeff 1979; Kaska 1989; Méon 1990; Salard-Cheboldaeff & DeJax 1991; Schrank 1994; Morley 2000). Palaeocene silicified wood from Niger has affinities with Meliaceae and Euphorbiaceae; other described woods have unknown affinities (Koeniguer 1971). These, and wood fossils of Late Cretaceous age, are interpreted by Koeniguer (1971) as quite different in species composition and abundances from samples of Eocene and younger age. But, Salard-Cheboldaeff (1981) remarks that with the exception of some relatives of *Nypa* known since the Maastrichtian, Palaeocene pollen assemblages are new and different compared with Cretaceous samples, and include unique dicots of unknown affinity. The Palaeocene may have been as enigmatic as the latest Cretaceous in terms of community composition, essentially in agreement with Koeniguer (1971). Palms remain important, despite the extinction of some taxa at the Cretaceous–Palaeocene boundary. The Leguminosae is firmly documented for the first time in the Palaeocene by Crawley (1988), who described caesalpinioid wood from Mali having characteristically vestured pits. Other Palaeocene macrofossils include fructifications from Bir Abu Munqar in southwestern Egypt identified as Palmae, Olacaceae, Icacinaceae and Flacourtiaceae (Gregor & Hagn 1982). Chandler (1954) reported fruits of Euphorbiaceae, Nipaceae (Palmae) and Annonaceae from Palaeocene deposits in Egypt.

Palaeocene macrofossils are frustratingly scarce, and many pollen taxa are without known relatives primarily because of a lack of information (Salard-Cheboldaeff 1981). Nevertheless, families characteristic of lowland forest today are known to have been present in the Palaeocene, including Leguminosae, Annonaceae, Euphorbiaceae and Icacinaceae. Thus, important constituents of modern forests were in place. In the same way, the documentation of Leguminosae wood and Gramineae pollen indicates that families important in woodlands and savannah today were playing a role in Palaeocene communities (Adegoke *et al.* 1978; Salard-Cheboldaeff 1979). However, grass pollen quantities reported from Nigerian core samples never exceed 4% (Adegoke *et al.* 1978), whereas grass-dominated environments today produce grass pollen percentages of 20% to more than 60% in surface sediments (Bonnefille & Vincens 1977; Leopold *et al.* 1992). Thus, the paucity of grass pollen is a reliable indicator of the absence of grass dominance in West Africa, the only place where pollen counts are available. If woodland communities were present, information to identify them is lacking, as are climate reconstructions, which could offer insight into what kinds of vegetation could have been supported.

West African pollen records continue to document grass pollen in the Early to Middle Eocene, which is noted by Salard-Cheboldaeff (1981) as occurring in a 'relatively important quantity', together with palm pollen and angiosperm taxa having unknown botanical affinities. Germeraad *et al.* (1968) established an Early to Middle Eocene pantropical *Monoporites annulatus* Zone on the basis of African and South American grass pollen. Indeterminate monoporate pollen are noted by Boltenhagen (1965) as characteristic of Late Palaeocene and Eocene core samples from Gabon, and grass pollen is common (together with Cycadaceae) in Eocene pollen samples from Egypt (Kedves 1971). In a review of fossil wood from North and Equatorial Africa, Boureau *et al.* (1983) indicate that there is evidence of rainforest along the northern and southern coasts of West Africa, consistent with the presence of genera such as *Entandrophragmoxylon*, related to the modern forest genus *Entandrophragma* (Meliaceae), but the interior of the continent is interpreted to have been a 'savannah' or woodland on the basis of occurrence of *Combretoxylon*, thought to be a relative of the modern savannah genus *Combretum* (Combretaceae). Thus, there are hints that open vegetation may have been developing during the first half of the Eocene in tropical Africa, and perhaps South America, but quantitative pollen data are unavailable. Morley (2000) suggests that because this time interval coincides with the Eocene thermal maximum, a time of warm temperatures at mid- and high-latitudes, tropical communities may have been reflecting temperatures warmer than today. If parts of the continental interior were experiencing aridity, as a result of increased temperatures or decreased rainfall, it would be the first time since the arid phases of the middle Cretaceous some 40 Myr earlier that angiosperms in tropical Africa were faced with increasing rather than decreasing annual water deficits.

The climatic implications of tropical Early to Middle Eocene plant communities is of global significance. Early to Middle Eocene thermophilous plant and vertebrate assemblages at high arctic latitudes, together with contemporaneous marine isotopes and palaeobotanical records from middle latitudes, are consistent with this being the warmest interval of the Cenozoic (e.g. McKenna 1980; Wolfe & Schorn 1989; Sloan & Barron 1992; Sloan & Morrill 1998; McIver & Basinger 1999; Sloan 2001). But, comparatively little is known about Eocene climatic parameters at tropical latitudes, particularly in terrestrial settings. Marine isotope records document sea surface temperatures cooler than modern day (Zachos *et al.* 1994). Global modelling experiments are unable to produce a climate system that results in cool tropical sea surface temperatures and warm middle to high latitudes with equable continental interiors (Barron 1987; Sloan *et al.* 1995). Models that use high atmospheric CO_2 concentrations to drive elevated high-latitude temperatures indicate the tropics would have been several degrees warmer than today as well. This contradicts the marine isotope record, but is consistent with Morley's hypothesis of terrestrial tropical temperatures warmer than modern day (Morley 2000; Sloan & Rea 1995). The thermal budget and dynamics of the hydrological cycle during the Early to Middle Eocene are poorly understood. Upper atmosphere water vapour is a strong greenhouse gas, and temperature and rainfall do not operate independently in ocean–atmosphere climate dynamics (Valdes 2000) or with respect to plant adaptations. Therefore, the global distribution of water vapour, which is an important component of the Earth's climate system, needs to be better understood for the Early to Middle Eocene, especially latitudinal temperature gradients and combined moisture–temperature effects on the evolution of tropical biomes.

Documentation of a Middle Eocene environment comes from the Mahenge palaeontological site, palaeolatitude 12° S, in north–central Tanzania. The leaves and fruits of a woodland community, structurally similar to modern miombo, are preserved in lacustrine deposits associated with a crater-lake (Mannard 1962; Herendeen & Jacobs 2000; Harrison *et al.* 2001; Jacobs & Herendeen 2004). Volcanic rock underlying lake sediments is dated at 45.83 ± 0.17 Myr ago (^{206}Pb/^{238}Ur), the time of the eruption and formation of the crater. This radioisotopic date provides a maximum age, assuming sedimentation to have begun soon after crater formation. In addition to plant fossils, the lake sediments preserve fishes, a frog with stomach contents, and a bat, one of only a few mammal fossils known from the Eocene of Africa (Báez 2000; Murray 2000, 2001; Harrison *et al.* 2001; Murray & Budney 2002; Gunnell *et al.* 2003). Leaf impressions are all microphyll or smaller, and include at least 19 and possibly 21 species (Jacobs & Herendeen 2004). Among these are at least seven Leguminosae species, four of which are caesalpinioid. Three mimosoid species include the earliest unequivocal record of the genus *Acacia* (Herendeen & Jacobs 2000). Indeterminate graminoid impressions are abundant at Mahenge. These could represent either aquatic grasses or groundcover or both. Rainfall reconstructions estimated by using regression models derived from samples of modern low-latitude leaf and rainfall data (Jacobs 2002) are approximately equivalent to modern (*ca.* 660 mm yr^{-1}), but the dry season may have been less severe than it is today (Jacobs & Herendeen 2004). Thus, Early to Middle Eocene moisture gradients in tropical Africa were likely to have been more pronounced than continent-scale reconstructions, which show widespread lowland rainforest across the tropical region (e.g. Axelrod & Raven 1978; Willis & McElwain 2002).

By the Late Eocene and into the Oligocene, the diversity of pollen in coastal West Africa increases dramatically (Salard-Cheboldaeff 1981). Palms, a greater component of the vegetation than they are today, saw several last occurrences at the Eocene–Oligocene boundary (Salard-Cheboldaeff 1979; Morley 2000). By the Middle Oligocene, grass pollen disappears from the West African record (Salard-Cheboldaeff 1979), indicating a shift to more forested and presumably more mesic conditions. Wood fossils document the contraction of wet forest in North Africa as the continent moved northwards, shifting the equatorial zone towards the south. There was an increase in North Africa of taxa such as *Combretoxylon* and *Detarioxylon* species, which are related to trees found in savannahs today (Boureau *et al.* 1983).

In the northeast, fruits, seeds, leaves and wood from the Early Oligocene Jebel Qatrani Formation in the Fayum, Egypt, document a seasonally dry forest along the coast, where a mangrove environment is indicated by the leaves of *Acrostichum* (a marsh or mangrove fern) and wood of *Gynotrochoxylon* (Tiffney 1991). The forest localities are associated directly with fluvial deposits, indicating a riparian environment. Their extent away from the water is unknown. However, Bown *et al.* (1982) suggests that savannah woodlands are implied by the presence of the genus *Triplochiton*. Wing *et al.* (1982) described fruit of the Asian genus *Epipremnum* and mention the occurrence of the wood taxon *Quercoxylon* (Krausel 1939) as indicating affinity to the northern and eastern margins of the Tethys Seaway.

Late Oligocene macrofloras from Chilga, in the state of Amhara on the northwestern Ethiopian Plateau, document *in situ* forests of silicified trees with maximum diameters in excess of 1.5 m, assemblages of large fruits and seeds, and mesophyllous leaves; all consistent with forest communities. A basalt underlying the fossiliferous units is dated at 32.4 ± 0.11 Myr ago and a tuff interbedded with the fossiliferous sediments is dated at 27.38 ± 0.11 Myr ago (Kappelman *et al.* 2003). A compression assemblage found below the tuff documents the presence of palm leaves, rachises and flowers. Palms are common in Palaeogene pollen assemblages but are absent from modern dry-land forests (Moore 1973; Morley 2000). A pollen sequence from Chilga was originally reported as Late Miocene (Yemane *et al.* 1985), but is now known to be Oligocene and contemporaneous with the plant macrofossils (Kappelman *et al.* 2003). The pollen sequence documents genera found today in wet forests of equatorial and West Africa such as *Oligocodon*, *Holoptelea* and *Rauvolfia* (Yemane *et al.* 1987). However, presence of the woodland genera *Combretum*, *Brachystegia* and *Isoberlinia* in some samples is indicative of variation in environment during the time represented by the sediments (Yemane *et al.* 1987).

To summarize the evidence for African forest and woodland origins, there is pollen evidence for tropical forest vegetation in the Palaeocene (*ca.* 64 Myr ago) based on the presence of plant families associated with modern forest environments. However, whether representatives of these families were tall in stature and to what extent palm species contributed to plant cover is unknown. The Middle Eocene (46 Myr ago) Mahenge site in Tanzania documents the first legume dominated woodland community from interior tropical Africa (Herendeen & Jacobs 2000; Harrison *et al.* 2001; Jacobs & Herendeen 2004). Early to Middle Eocene wood from various localities in equatorial and North Africa documents woodland communities (e.g. *Combretoxylon*; Boureau *et al.* 1983). Thus, interior tropical Africa had a climate that created water-stress for plants, whereas at middle and high latitudes global climate was uniquely warm and wet. During the Late Eocene and into the Oligocene (*ca.* 37–25 Myr ago), pollen records show diverse lowland forest taxa in West Africa. Macrofossils and pollen from Ethiopia document widespread forest communities. West African pollen records and macrofossils from Ethiopia demonstrate that palms were an important component in Palaeogene forest communities, although significant species turnover took place between the Late Eocene and Late Oligocene (Morley 2000).

(b) *Savannah*

In this section, I review the floral, faunal and isotope records as they pertain to the origin of the savannah biome in tropical Africa. A more detailed global review can be found in Jacobs *et al.* (1999). The plant fossil record of this biome depends heavily on the fossil record of grasses, which are represented primarily by pollen. Grass pollen morphology is uniform to the extent that identification at lower than the family level is not possible (although cultivars are recognizable as significantly larger). Thus, grass pollen quantity, rather than composition, is used as a Cenozoic palaeoenvironmental indicator. Fortunately, most of the family consists of wind-pollinated taxa, which produce copious amounts of easily dispersed pollen that contribute to the fossil record. Leaves and shoots are found, but rarely distinguished from other similar monocots. Identifiable floral structures make their way into the fossil record under special circumstances (e.g. Elias 1932; Thomasson & Voorhies 1979).

The vertebrate fossil record also provides significant information about savannah development, and was the primary source of evidence before pollen analysis became common in the middle of the last century. Adaptations of the teeth and limbs of grassland mammals make grazing behaviour identifiable from fossils. Grazers share high-crowned (tall-crowned) teeth to accommodate substantial wear from a diet of siliceous grasses, and the cursorial animals (runners) have long slender limbs.

More recently, stable carbon isotopes have been used to document the spread of C_4 photosynthesis, a physiological adaptation shared among tropical savannah grasses. Naturally occurring isotopes of carbon, ^{13}C and ^{12}C, which are assimilated by plants through fixation of atmospheric CO_2, are fractionated differently in C_3 and C_4 plants: C_4 plants assimilate more ^{13}C relative to ^{12}C than do C_3 plants. This differential can be detected in ancient soil carbonates, which reflect the vegetation growing during soil formation, and in fossil tooth enamel apatite, which reflects the diet of the animal. Although C_4 photosynthetic physiology occurs among a wide variety of dicots, the savannah and woodland grasses are by far the most abundant plants on the landscape having this physiology. Therefore, the relative amounts of ^{13}C and ^{12}C in fossil tooth enamel apatite or palaeosol carbonates, compared with a standard, can be used to indicate the presence of C_4, most likely grass, vegetation in the diet or on the landscape.

Savannah development in western Africa is clearly documented by grass pollen and charred grass cuticle in a drill core from the Niger Delta spanning the interval from the Early Miocene to the Holocene (Morley & Richards 1993). Charred grass cuticle washed or blown into delta sediments is taken to be an indicator of seasonal grassland fires. The Niger Delta core documents 2% grass pollen and no charred cuticle in the Early Miocene. By 16 Myr ago (Middle Miocene) grass pollen increases to 10% and charred cuticle is present at 2%. There is a substantial increase in both grass pollen and charred grass cuticle after 8.2 Myr ago. Grass pollen fluctuates between a few per cent to over 50% in the Late Miocene, when charred cuticles reach maxima of 25% and 30%. This record is interpreted as indicating an equable wet climate during the early Miocene when little or no savannah vegetation would have been present in West Africa, followed by an expansion of grass cover at *ca*. 16 Myr ago, and development of extensive savannah across most of the Niger Delta by the Late Miocene (Morley & Richards 1993).

The Neogene pollen and plant macrofossil records for eastern Africa are less continuous, more local and more complex than the core from the Niger Delta. Fortunately, they are supplemented by good faunal and isotope records. Leaf and wood floras from the Ethiopian Plateau, considered to be Early Miocene based on stratigraphic position, have affinities with modern Central and West African dry forest taxa (Lemoigne *et al.* 1974; Lemoigne 1978). Wood anatomical evidence points to seasonally dry environments. Pollen analyses of Pliocene and younger deposits consistently record grass pollen percentages of at least 50%, indicating widespread grass cover (e.g. Bonnefille 1995).

In Uganda, early Miocene flowers, fruit and leaves from Bukwa are related to living forest trees such as *Bersama abyssinica* and *Cola cordifolia* (Hamilton 1968; Walker 1968, 1969; Brock & Macdonald 1969). An autochthonous leaf bed from a single horizon at the same locality is composed primarily of unidentified grasses. Rhizomes identified as *Juncellus laevigatus* demonstrate the presence of an alkaline lake indicating that the grasses are likely to have been near-shore aquatics (Hamilton 1968). Other records from Uganda include a small collection of leaves associated with Early Miocene volcanics from Mount Elgon. Chaney's (1933) analysis of the relatively small size of the leaves from this collection when compared with those he studied of Eocene age (from other continents) led him to conclude that the Ugandan specimens came from a savannah or savannah woodland environment. However, grasses were not recorded.

Faunal data are available from the Middle Miocene (14.7 Myr ago) Ugandan site of Maboko, which support a woodland palaeoenvironment based on the abundance of browsing animals, the limited number of forest species, abundant monkeys and derived rodents (see Andrews *et al.* 1981; Evans *et al.* 1981; Winkler 1997, 1998; Jacobs *et al.* 1999).

Kenya has a wealth of Miocene plants, vertebrates and isotope studies, all relevant to the question of savannah origins. Early Miocene (17.8 Myr ago) sites on Rusinga and Mfwangano Islands in Lake Victoria produced abundant fruit and seed casts. Taxa with affinities to West and Central African forest plants, such as *Entandrophragma*, were interpreted by Chesters (1957) as indicating gallery forest. The palaeoflora was reinterpreted as indicating lowland wet forest (Andrews & Van Couvering 1975) as did faunal composition (Andrews & Van Couvering 1975; Andrews & Nesbit Evans 1979; Evans *et al.* 1981). Several other Early Miocene localities in western Kenya produce mammalian fossils consistent with forest vegetation (Jacobs *et al.* 1999). They include diverse primates, scaly-tailed flying squirrels, other rodents, tenrecs and elephant shrews (Jacobs *et al.* 1987).

The Middle Miocene Fort Ternan locality in western Kenya, dated at 13.9–14.0 Myr ago (Shipman *et al.* 1981), has been studied intensively because it preserves a diverse fauna including hominoids and grass macrofossils. Thus, it became an important site for documenting the ecological association between hominoids and vegetation. Grass leaves preserved *in situ* in volcanic sediments were interpreted as indicating a wooded grassland environment comparable to the modern Serengeti (Retallack *et al.* 1990; Dugas & Retallack 1993). However, palaeosol carbon

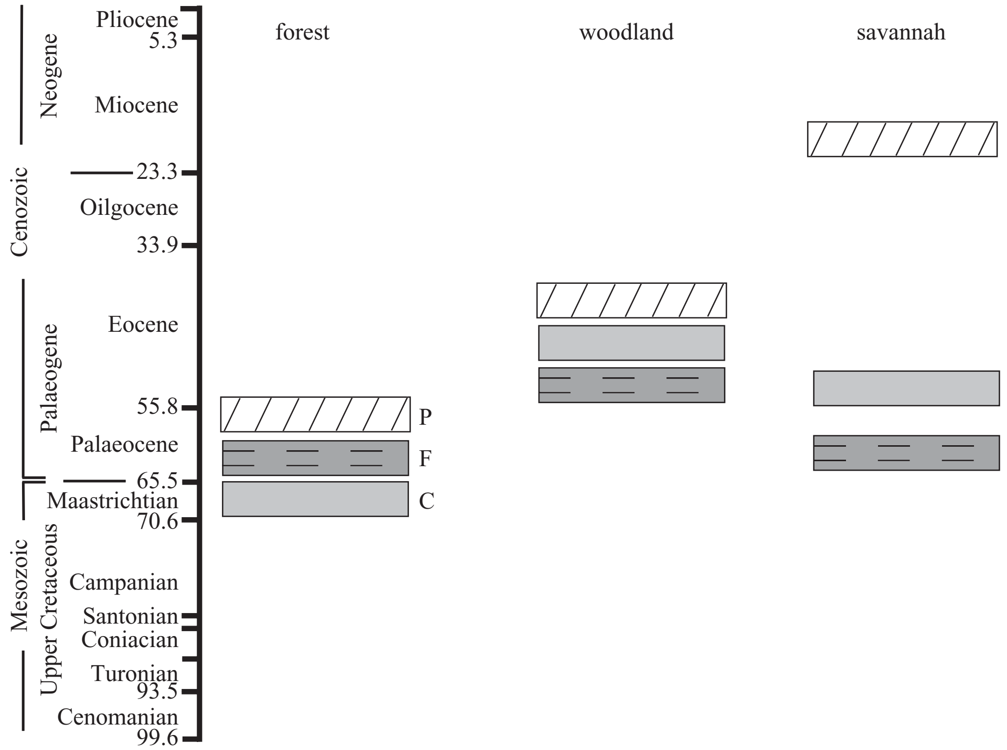

Figure 1. The earliest occurrences of climate (C), key families (F) and physiognomy (P) associated with forest, woodland and savannah biomes are shown. Warm and wet climate is documented for the Maastrichtian, but key forest families such as Leguminosae, Annonaceae, Euphorbiaceae and Icacinaceae are not known in the fossil record until the Palaeocene. The physiognomy characteristic of forests is represented by silicified wood of forest trees in families such as Meliaceae and Euphorbiaceae in the Palaeocene of Mali. The key woodland families are represented by Early Eocene silicified wood from North Africa, also indicative of the appropriate physiognomy, and Middle Eocene leaves and fruit from northern Tanzania, where annual rainfall is reconstructed at less than 800 mm yr^{-1}. The key savannah family, Gramineae (Poaceae), is present in the Palaeocene, and the climate is appropriate for open communities in the Early Eocene, but physiognomic evidence for savannah environments (charred grass cuticle) is not present until the Middle Miocene.

isotope studies, tooth enamel apatite studies, faunal analyses based on morphological characters and tooth microwear patterns all indicate that Fort Ternan was a mixed environment with some open areas. Herbivores subsisted on a C_3 diet (Shipman 1986; Cerling & Quade 1991; Kappelman 1991; Cerling *et al.* 1997*a*). A single pollen assemblage from Fort Ternan contains 54% grass pollen, aquatics and montane taxa, indicating an open woodland, with montane species in nearby highlands (Bonnefille 1984).

The Tugen Hills of Kenya, a mountain range in the Rift Valley basin, produced numerous vertebrate fossils, including hominoids and fossil plants (Hill *et al.* 1985, 1992; Jacobs & Kabuye 1987, 1989; Winkler 1992; Hill *et al.* 2002). Localities range in age from the Middle Miocene to Pliocene (Hill 1985). Plant macrofossils, vertebrate fossils and carbon isotopic studies on palaeosols and fossil tooth enamel apatite are all in agreement that environments in the Tugen Hills sequence were varied temporally and spatially (Jacobs & Kabuye 1987; Kingston *et al.* 1994; Morgan *et al.* 1994; Jacobs *et al.* 1999; Jacobs 2002). An autochthonous assemblage of leaves, twigs and fruits documents lowland forest at 12.6 Myr ago. Lacustrine deposits dated stratigraphically at 9–10 Myr ago preserve a microphyllous leaf flora indicating a seasonally dry woodland or a more open environment. Silicified trees and leaves from sites dated at 6.8 Myr ago indicate the presence of woodland or dry forest (Jacobs & Kabuye 1987, 1989; Jacobs 2002; Kingston *et al.* 2002).

Grazing horses immigrate into the Tugen Hills between 9.5 and 8.5 Myr ago, indicating grasses composed a significant part of plant communities. However, vertebrate fossils from this time interval do not all represent grazers and indicate vegetation was mixed (Jacobs *et al.* 1999).

Tugen Hills palaeosol isotope records and carbon isotopes from fossil tooth enamel apatite consistently indicate the presence of a C_4 component on the landscape and in the mammalian diet as early as 15 Myr ago (Kingston *et al.* 1994; Morgan *et al.* 1994). Palaeosol carbonates document mixed C_3–C_4 vegetation throughout the sequence, but herbivore tooth enamel apatite indicates a shift towards an exclusive C_4 diet between 8.5 and 6.5 Myr ago (Morgan *et al.* 1994). Cerling *et al.* (1997*b*) documented herbivore tooth enamel carbon isotopes from a variety of Miocene sites in Kenya, which showed that horses and elephants began consuming primarily C_4 grasses between *ca.* 8 and 7 Myr ago.

In summary, carbon isotope, plant and vertebrate fossil evidence pertaining to evolution of the savannah biome in Africa, are in agreement. The West African pollen and grass cuticle records shows that grasses were present in Africa in the Palaeocene (64 Myr ago), diversified and spread to some degree during the Early to Middle Eocene (55–46 Myr ago), began an initial Neogene expansion in the Middle Miocene (16 Myr ago), and finally occupied large areas by the Late Miocene (8 Myr ago). In eastern Africa, numerous records are consistent with the presence of a variety of community types in the topographically complex Rift Valley. Plant and vertebrate fossils from the Tugen Hills indicate a range of settings from forest to open woodland or savannah in the interval between 12.6 and 6.8 Myr ago, in agreement with palaeosol isotope data. Faunal and isotope data together indicate a significant change towards exclusive C_4 diets after *ca.* 8.5 Myr ago, although the woody component of the landscape remained significant.

3. CONCLUSIONS

Figure 1 summarizes key events and developments relevant to the origin and evolution of forest, woodland and savannah biomes in tropical Africa. These are summarized below.

(i) Angiosperms become common in fossil assemblages beginning *ca.* 95 Myr ago, but there is no evidence of angiosperm trees from fossil wood, and the dominant families of forests, woodlands and savannahs today were absent.

(ii) By the latest Cretaceous, angiosperm wood was present, but there is no unequivocal evidence for legumes or grasses, which are important elements of forest, woodland and savannah biomes today. Plant communities were dominated by palms, but community structure is unclear as most taxonomic data are based on pollen assemblages.

(iii) The first unequivocal records of grass (pollen) and legumes (wood) occur in the Palaeocene epoch (65.5–55.8 Myr ago). Forest families such as Leguminosae, Annonaceae, Euphorbiaceae and Icacinaceae were present, but several pollen taxa have unknown botanical affinities and evidence of community structure is lacking.

(iv) The Early to Middle Eocene marks a time when angiosperm families continue to diversify in West Africa, but the interior of the continent was relatively dry. A woodland community dominated by legumes is documented for the first time at 46 Myr ago (Middle Eocene).

(v) The diversity of lowland forest pollen species reaches a peak in West Africa during the Late Eocene (40–34 Myr ago) and into the Oligocene (34–23 Myr ago). Plant macrofossils document forest communities in northwestern Ethiopia, and gallery or dry forest is present in the Fayum, Egypt.

(vi) Evidence from plant and vertebrate fossils together with stable carbon isotopes from fossil tooth enamel apatite and palaeosol carbonates consistently document the development of savannah in tropical Africa. Grass pollen from the Niger Delta clearly demonstrates the presence of grass during the Early Miocene (17–23 Myr ago), increased grass abundance by 16 Myr ago, and widespread savannah by 8 Myr ago (Late Miocene). In East Africa, environments were heterogeneous in the Rift Valley throughout the Miocene, as shown by varied mammals, plant communities and palaeosol carbon isotopes. However, tooth enamel apatite records show that some grazers had a purely C_4 diet by 8.5 Myr ago.

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