

Paleontological Investigations at the Eocene Locality of Mahenge in North- Central Tanzania, East Africa

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1. Introduction

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Since the early 1930s, a number of geologists prospecting for diamonds in the

region of Singida in north-central Tanzania have reported the occurrence of superbly preserved fossils in lake beds overlying kimberlite pipes (Teale, 1931, 1932; Eades and Reeve, 1938; Williams, 1939; Greenwood, 1960; Mannard, 1962; Greenwood and Patterson, 1967). The sediments containing the fossils consist of shales and mudstones deposited in small crater lakes. These fossil localities have never been the subject of detailed paleontological investigation. As a consequence, in 1966 the senior author initiated excavations at the middle Eocene locality of Mahenge, the most productive fossil-bearing locality in the region (Greenwood, 1960; Mannard, 1962). The results of this expedition confirm the exceptional productivity and scientific importance of this site, and serve to highlight the paleontological potential of the region in general. A sizeable collection of fossil fishes, frogs, insects and plant remains was recovered. The fossils are remarkably well-preserved and, in the case of vertebrates, are generally represented by entire and articulated skeletons, occasionally preserving details of their soft anatomy (Greenwood, 1960; this report).

Because paleontological sites with strictly continental sediments of Paleogene age are almost entirely unknown in sub-Saharan Africa, Mahenge offers a unique opportunity to document the diversity, biogeography and evolutionary history of the flora and fauna of Africa during this time period. The fact that all of the vertebrates so far recovered from Mahenge are found nowhere else, serves to emphasize just how little we know about Eocene African faunas. Detailed systematic studies of the fauna and flora are still underway, but we present here a preliminary synthesis of our findings to date.

2. History of Paleontological Research

Exploration of the region began in 1930 with the report that C. J. T. Boshoff, a South African prospector, had discovered diamonds at Kionboi on the Tramba Plateau. There was a major influx of prospectors and geologists during the early 1930s, but interest waned with the discovery that all of the kimberlite occurrences were either barren or unprofitable. Nevertheless, at least one European prospector, known only by his Kiswahili name of *Bwana chimba panya* (Mr. digging rat), remained active during the late 1930s and 1940s, until he succumbed from malaria. During this period, Reeve (with the Geological Survey of Tanganyika) apparently discovered a kimberlite occurrence in the vicinity

Table 1. List of localities in the Singida Region that have yielded fossil remains

Localities	Fossils Recovered	References
Blangeti	Silicified wood	Mannard, 1962: 240
Kinginya	Silicified wood	Mannard, 1962: 167-169
Magoba	Silicified wood	Mannard, 1962: 117, Figure 36a
Magwe ya Ghana	Silicified wood	Mannard, 1962: 48
Mahenge	Fishes, frogs, insects, fruits, leaves, & seeds	Mannard, 1962: 244; Greenwood, 1960; Greenwood and Patterson, 1967; this report
Maluga Kulamba	Silicified wood	Mannard, 1962: 205
Minusi?	Fishes	Greenwood and Patterson, 1967
Munyu (Mtawira)	Plant stem and leaf impressions & fragments of large bone	Teale, 1932; Mannard, 1962: 140, Figure 48a
Pyamahumbe	Fishes, leaves, plant stems & seeds	This report
Songeli (=Sungili)	Stems, leaves, seeds, & root casts	Teale, 1932; Mannard, 1962: 200; this report

of Mahenge (Williams, 1939), although no such occurrence is described by Eades and Reeve (1938) or identified on their geological map. From 1953 to 1959, Williamson Diamond Limited, based at the productive kimberlite pipe at Mwadu in Shinyanga Region, sponsored a major program of prospecting in the Singida Region. A systematic survey was conducted from 1957-1959 by George Mannard, a Canadian geologist (known locally as *dagandi* in Kinyiramba—the one who searches from place to place, Mannard, 1962). The occurrence of fossil-bearing lake beds in the area was first noted by Du Toit (Teale, 1931, 1932), who recovered leaf impressions, stems, seeds and pieces of a large bone at Songeli and Mtawira. Mannard (1962) subsequently reported the occurrence of fossil leaves and silicified wood at six additional localities (see Table 1 for a complete list of paleontological sites in the region), and recovered a small collection of fossil fishes from Mahenge. The latter material was sent to Humphrey Greenwood for study (at the Natural History Museum, London), who later received additional fish specimens from the site of Minusi. Greenwood (1960) and Greenwood and Patterson (1967) referred these fish to *Palaeodenticeps tanganyikae*, a new genus and species of clupeo-morph belonging to the Denticipitidae; *Singida jacksonoides*, a new genus and species of osteoglossomorph belonging to its own extinct family, the

Singidiidae; and a genus of cichlid with affinities to *Haplochromis*, a taxon widespread in East Africa today.

In 1994, TH and CPM made a brief excursion to the sites of Sungili, Mtwara and Mahenge, and recovered fossil wood, leaves, root casts, and fishes. This prompted a full-scale expedition to Mahenge during the summer of 1996, in which over five hundred specimens were collected.

3. Research Area and Geological Context

The locality at Mahenge ($4^{\circ}47'38''\text{S}$; $34^{\circ}15'28''\text{E}$) is situated 63 km west of the town of Singida in north-central Tanzania (Figures 1 and 2). The site is reached by taking the Singida-Usumbu road westwards as far as Sepuka, and then diverting along a small track to Mwaru. This latter village is usually identified on maps as Mahenge, and is the source of the name given to the fossil locality by Mannard (1962). However, the regional and district administrative officers in Singida, as well as the local inhabitants, refer to the present-day village as Mwaru. The locality is situated 0.4 km south of the village, and is reached by car via a forest trail that is used sporadically by trucks for transporting charcoal. The Singida kimberlite field, with more than fifty kimberlite pipes and dykes, is located on a broad peneplain, just to the south of the Iramba Plateau

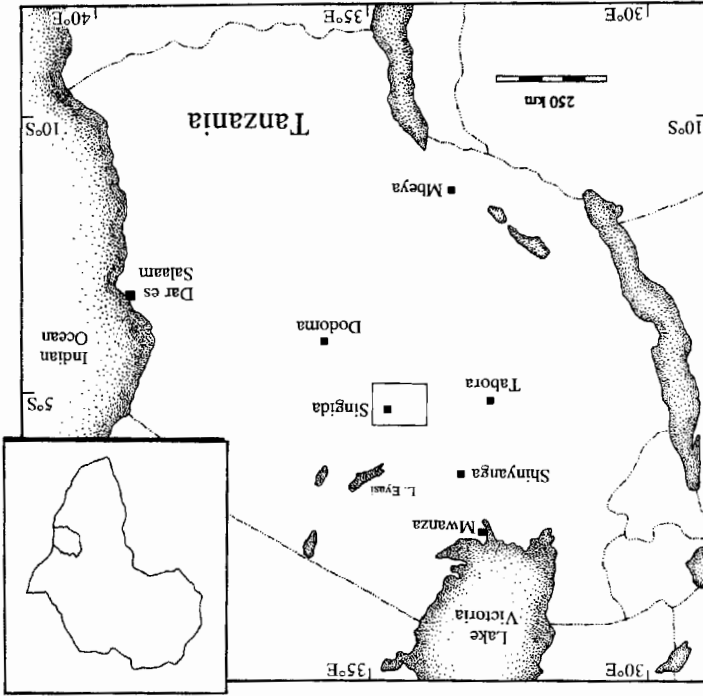


FIGURE 1. Map showing the location of the research area in north-central Tanzania. See Figure 2 for detail of inset.

area and this creates logistical problems for aerial reconnaissance and surface exploration.

The region is sparsely populated. The low and unreliable rainfall is an important factor; 800 mm is generally considered the minimum to support domestic livestock and intensive cultivation. In addition, tsetse flies (*Glossina* spp.), important vectors of bovine trypanosomiasis or nagana, have prevented people and their cattle from penetrating the densely wooded and bush-covered areas to the south (Harrison *et al.*, 1997). The Wanyiramba and Wanyituru, the predominant tribal groups in the area, are small-scale agriculturalists and cattle herders that generally live in cleared areas close to the margins of the woodland. As a consequence, few people, except itinerant woodcutters and charcoal burners, are encountered in the remotest regions of the research area.

The basement rocks in the region are part of the Dodoman system, formerly referred to as the Lower Basement Complex (Stockley, 1935, 1943; Grantham and Temperley, 1939; Teale and Cates, 1946; Quennell *et al.*, 1956). These rocks consist of a complex of pelitic schists, granitic gneisses and migmatites, ranging in composition from potassic granite to diorite. Dykes and veins of dolerite are common, and those of pegmatites, apfites, dolerite and quartz occur locally (Teale, 1932; Eades and Reeve, 1938; Mannard, 1962). An intrusive pegmatite dyke within the Dodoman has yielded a provisional Sr-Rb date of 3.25 ± 0.325 Ga (Quennell *et al.*, 1956).

The Nyanzian system, formerly known as the Upper Basement Complex, is inferred to be younger and superpositional to the Dodoman, but the nature of the contact between the two systems is unknown because of the lack of pertinent outcrops. The Nyanzian system consists primarily of a series of volcanic rocks, schists, and banded ironstones (Grace and Stockley, 1931; Eades, 1936; Eades and Reeve, 1938; Williams and Eades, 1939; Grantham *et al.*, 1945; Stockley, 1947; Quennell *et al.*, 1956; Borg, 1992; Walraven *et al.*, 1994). The most distinctive component of the Nyanzian is the Banded Ironstone Formation (BIF), with a U-Pb age of 2.7 Ga (Stockley, 1934; Borg, 1992; Walraven *et al.*, 1994), although outcrops in the Singida region are few (Eades, 1936; Eades and Reeve, 1938). Micas from a pegmatite segregation in the Nyanzian granite at Mwadui in Shinyanga Region have yielded K-Ar dates of 2.518 ± 42 Ma and 2.526 ± 42 Ma (Edwards and Howkins, 1966).

The Nyanzian was subject to several episodes of batholithic intrusion of granitoid rocks, with a widespread event of migmatization occurring at ~2.4–2.6 Ga (Old and Rex, 1971; Dodson *et al.*, 1975; Cahen *et al.*, 1984). The resulting granitoid shield forms a significant component of the Tanzanian craton (Kuntz, 1909; Eades, 1936; Wade, 1937; Stockley, 1948; Quennell *et al.*, 1956; Old and Rex, 1971; Dodson *et al.*, 1975; Cahen *et al.*, 1984; Walraven *et al.*, 1994). The Iramba Plateau and Singida peninsular straddle the divide between the Nyanzian and Dodoman belts respectively (Mannard, 1962).

During the Cretaceous and early Tertiary, the basement rocks were disrupted by the intrusion of a complex of kimberlite pipes (Williams, 1939; Mannard, 1962). The kimberlite occurrences lie on a broad NNW-SSE zone originating at the southern shore of Lake Victoria (Dawson, 1970; Mitchell, 1986).

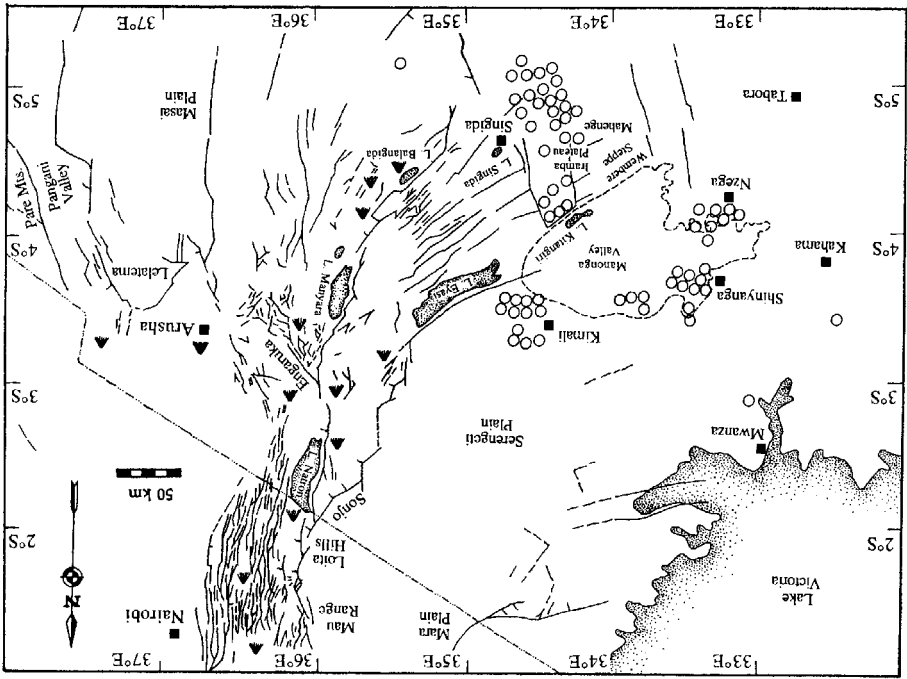


FIGURE 3. Map showing the distribution of kimberlite occurrences (open circles) in northern Tanzania in relation to the fault patterns, major volcanic centers, and the Manonga Valley (King, 1970; Harrison and Mbago, 1997).

This kimberlite province has been subdivided geographically into a number of separate fields (Edwards and Howkins, 1966; Mitchell, 1986; Figure 3). The largest of these is the Singida field, where more than fifty kimberlite bodies have so far been identified (Mannard, 1962). The Singida field appears to be part of a much larger kimberlite complex that also includes the Nzege, Shinyanga, Tramba and Kimali fields to the east and north (Edwards and Howkins, 1966; Mitchell, 1986). The present-day geographical separation of these fields may have been exaggerated, in part, by subsequent geological events. As can be seen in Figure 3, the kimberlite fields are located around the margins of the Manonga Valley and Wembere depression (Harrison & Mbago, 1997; Verniers, 1997). The thick series of late Miocene and Pliocene terrestrial and lacustrine sediments deposited in these basins may have obscured kimberlite outcrops in the central part of the province. However, individual fields are defined as geographically and genetically closely related groups of kimberlites of similar age, usually located within a 50 km diameter (Mitchell, 1986). The wide distribution (the main occurrences are spread over an area exceeding 200 km in diameter), different ages (at least for occurrences in the Singida, Shinyanga and Nzege fields—see dating below), and geochemistry of the kimberlites in the different clusters support the recognition of separate fields.

This sequence of geological events, comprising different episodes of kimberlite intrusion during the late Mesozoic and early Tertiary, warping of the basement complex to produce the Manonga Basin in the late Miocene and early Pliocene, and subsequent convergence of the Eyasi and Wembere grabens at the center of the Manonga Basin to form a triple junction, are not coincidental. It points to a long-term susceptibility to tectonic instability in this region of the craton, and indicates that the intrusion of the kimberlites is directly related to epeirogenic movements along fractures or lines of weakness in the basement at great depth, possibly coinciding with the contact zone between the Dodoman and Nyanzian belts (Williams, 1939; Dawson, 1970; Mitchell, 1986). Increased activity of the African superplume at ≈ 45 Ma could well be implicated in the intrusion of these kimberlites (Kerr, 1999; Haggerty, 1999).

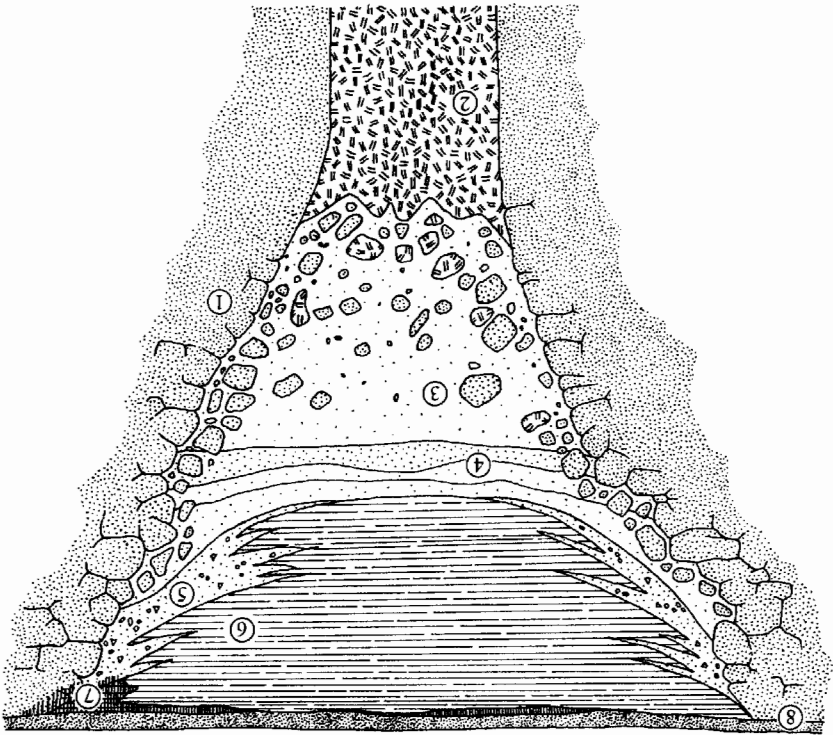
Preliminary geological research at Mahenge suggests that the structure of the kimberlite pipe and the nature of the associated sediments conform closely to those described for similar occurrences in other parts of Africa (e.g., Edwards and Howkins, 1966; Hawthorne, 1975; Smith, 1986; Kayner *et al.*, 1991). Based on these data, and on studies of modern crater lakes, it is possible to reconstruct the general events that contributed to the formation of the crater and sedimentary sequence at Mahenge (Figure 4).

As kimberlites intruded through the basement rock and pierced the crustal layer the rising magma came into contact with permeating surface water to produce a violently explosive phreatomagmatic eruption (Lorenz, 1973; Scarth, 1994). As the conduit penetrated to the surface it shattered the surrounding country rock. Subsequent explosions further weakened the walls of the conduit, and these collapsed inwards to form a trumpet-shaped diatreme. Eventually, the throat of the diatreme became choked with coarse breccia composed of large blocks of shattered granite and lava, with massive, poorly-stratified pyroclastic kimberlite filling the interstices (Edwards and Howkins, 1966; Hawthorne, 1975). Close to the surface, the pyroclastic kimberlite is leached and oxidized to form a soft, friable, cream-colored "yellow ground" (Mammar, 1962). The edge of the crater is defined by a breccia collar, composed of fractured blocks of granite, that are exposed in the Luwala River, a small stream that crosses the center of the pipe from northeast to southwest. Based on test pits and from the location of the breccia collar, it is possible to reconstruct the crater as being roughly circular in outline, with a maximum diameter of 550 m (Figure 5).

The initial explosive events would have been short-lived, probably lasting no more than a few days, because of the lack of availability of water (Scarth, 1994). At the surface, the diatreme formed a crater bounded by steep-sided walls of exposed country rock. Minor eruptions later produce fine-grained pyroclastic kimberlites deposited as a series of well-stratified tuffs, up to 1 m in thickness, in and around the crater (Mammar, 1962; Hawthorne, 1975). These accumulated to form a low tuff cone, probably less than 10 m in height, around the rim of the crater. The primary tuffs typically contain pyrope (i.e., red magnesium garnet or "Cape ruby"), magnesian ilmenite, dark green diopside, olivine (generally altered to serpentine) and zircon (Teale, 1932; Hawthorne, 1975). The presence of this assemblage of minerals can be used as an aid to locating subsurface kimberlites.

After cessation of volcanic activity, the crater filled with water from local run-off to produce a shallow crater lake or maar (Lorenz, 1973). The crater lake at Mahenge occupies a roughly circular area with a maximum diameter of 370 m (Mannard, 1962; Harrison, unpublished data; Figure 5). The inner slope of the tuff cone would have been relatively steep, probably resulting in a restricted shoreline (Edwards and Howkins, 1966; Smith, 1986). Material eroding from the tuff cone was washed into the lake by means of slumping and heavy seasonal rains, and these formed a series of sedimentary tuffaceous beds (Mannard, 1962; Smith, 1986; see Figure 4). In the center of the lake, the sediments produced well-stratified microlaminated mudstones and shales that grade laterally into coarser siltstones and sandstones located closer to the

FIGURE 4. Schematic section (not to scale) through an idealized kimberlite pipe to illustrate the main geological features (after Mannard, 1962; Hawthorne, 1975; Smith, 1986). (1) shattered basement rock; (2) intrusive kimberlite—mostly “yellow ground” consisting of leached and oxidized primary kimberlite; rarely less oxidized “blue ground” and hardbank; (3) pyroclastic kimberlite and breccia—massive to crudely stratified pyroclastic kimberlite with shattered and permeated blocks of basement kimberlite tuffs—alternating beds of coarse- to fine-grained tuffs; (5) sedimentary tuffaceous beds at the edge of the lake—silt, sands and poorly-sorted bouldery conglomerates with much granitic detritus; (6) sedimentary tuffaceous beds at the center of the lake—well-stratified microlaminated mudstones and shales containing well-preserved fossils; (7) silicified sedimentary beds and crater wall—alteration of sedimentary beds by chalcidonic silica and silicification of granite due to hydrothermal activity; (8) mbuga clay and loam—superficial layer comprising dark gray mbuga clay and sandy loams.



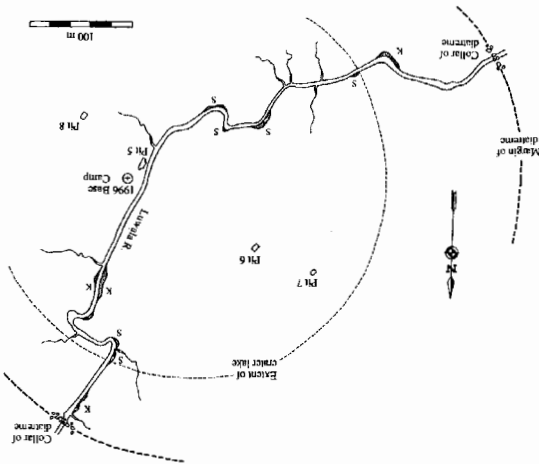


FIGURE 5. Map of Mahenge showing the location of the major outcrops of lake sediments (S) and kimberlites (K) in the Luwala River. Also shown are some of Mannard's pits and the position of the eroded collar of the diatreme. These natural exposures and test pits allow estimation of the shape and diameter of the diatreme and crater lake.

margin of the lake. These beds dip slightly (5° – 20°) towards the center of the pipe, probably as a consequence of slumping (Williams, 1939; Harrison, unpublished data). The mudstones are calcareous, pale yellow-gray to buff-colored, and contain numerous well-preserved fossils.

The sedimentary tuffaceous beds and granites are siltified in places, probably as a result of intermittent hydrothermal activity. A thin crust of chalcedonic silica occurs around the margin of the crater, and a remnant of siltified shaly beds has been located along its southwestern edge (Williams, 1939; Mannard, 1962). A surface debris of brightly colored, angular chert chips and banded jaspers derived from the eroding surface of this layer is commonly associated with kimberlite diatremes in the Singida area (Bades and Reeve, 1938). The lake sediments are covered by a superficial layer, up to 2 m thick, of dark gray to black mbuga clays and gray sandy loam (Figure 4). The general area is relatively flat, and there are no surface clues from the composition of the soil, the type of vegetation, or differences in topography to indicate the presence of an underlying kimberlite pipe (Mannard, 1962; Edwards and Howkins, 1966). The lake sediments were exposed primarily as a result of test pits dug by Mannard in the late 1950s. However, several outcrops of kimberlite and lake sediments containing fossils are exposed along the course of the Luwala River (Figure 5).

4. Stratigraphy

Excavations at Mahenge in 1996 have permitted the reconstruction of a detailed stratigraphic section of the fossiliferous sediments (Figure 6). The bottom of

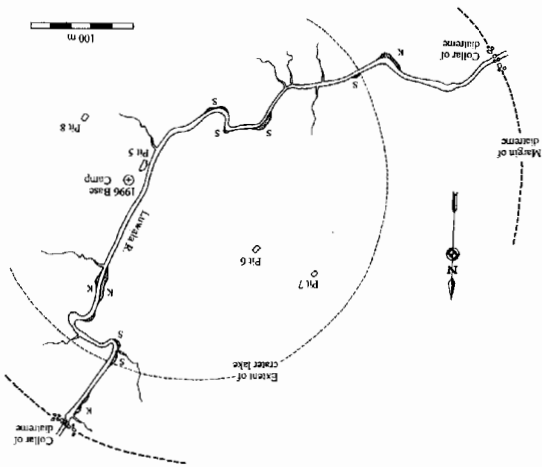


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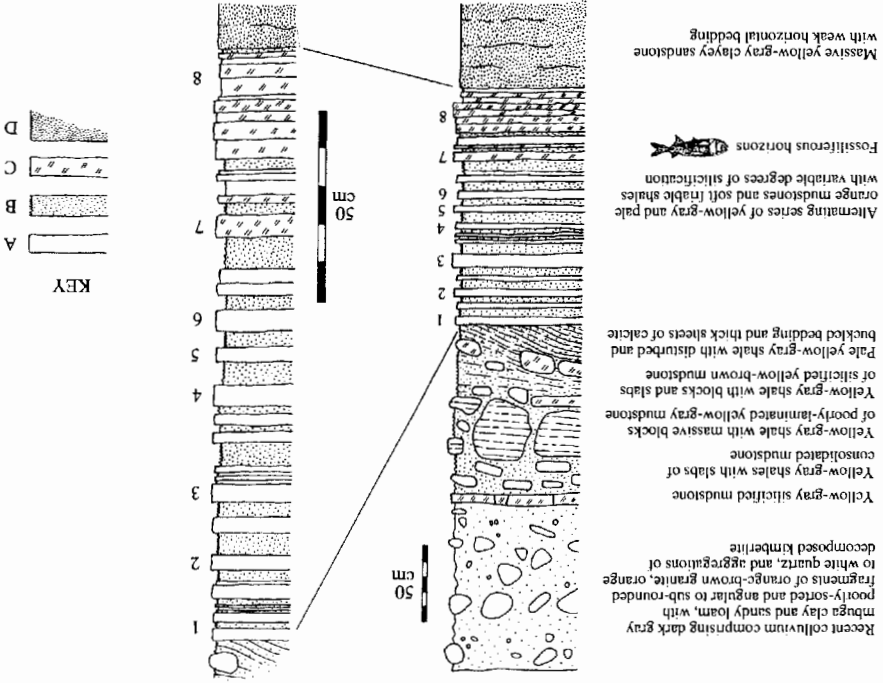
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the section consists of a massive yellow-gray (5Y 8/1) clayey sandstone (of which only 0.6 m has been exposed). The sediments are relatively soft and friable, and exhibit only weak indications of horizontal bedding. No fossils have yet been recovered from this horizon. This bed apparently represents the result of a major influx of pyroclastic sediments towards the end of the eruptive phase that were deposited either as an ash-fall directly into the crater or as reworked sediments derived from the inner slopes of the tuff cone (Figure 6).

Overlying the sandstone is a series of fine-grained, well-stratified mudstones with an overall thickness of 1.59 m (Figure 6). These are predominantly yellow-gray in color (5Y 8/1 and 5Y 7/2), but occasionally pale orange (10YR 8/2). The sediments consist of an alternating series of well-consolidated, compact calcareous mudstones, with or without distinct laminations, and soft friable shales. The sequence can be subdivided into 16 cycles, each comprising a couplet of one or more consolidated mudstones and a friable shale (Figure 6). Each cycle has an average thickness of 10 cm (range = 4–17 cm). The cycles in the lower part of the sequence are slightly thicker on average (10.5 cm) than

FIGURE 6. Stratigraphic section at Pit 5c at Mahenge. The numbers refer to marker horizons comprising compact and easily identifiable mudstones in the fossil-bearing beds. Fossils are found throughout the sequence from Level 1 through Level 8. Key to right-hand column: (A) compact mudstone with microlaminations strongly to weakly developed; (B) friable shales; (C) partially silt-clayed mudstones; (D) clayey sandstones.



those from the upper part (9.4 cm), and the proportion of consolidated mudstones is also somewhat higher (70% of the section thickness compared to 53%). The mudstones have an average thickness of 3.5 cm, but can form prominent pavement-like layers up to 6 cm thick. Microscopic examination shows that these layers have fine subparallel laminations, with an average thickness of 2.9 mm, often separated by calcite (or more rarely carbonaceous) films. The precipitation of calcium carbonate presumably occurred initially at the sediment-water interface during the annual turnover of the water column (see below). If our estimate of sedimentation rate and compaction factors is reasonable, each lamination represents an average cycle of between 15 and 40 years. It is interesting to note that a similar phenomenon has been reported for modern-day African crater lakes, such as Barombi Mbo in Cameroon, where a 15 year periodicity in sedimentation is related to major flooding of large rivers (Giresse *et al.*, 1994).

In addition to calcite films between microlamination, there are often relatively thick sheets of calcite formed at the interbedding planes of the main sedimentary units. Smith (1986) has interpreted similar calcite layers at Stompor, South Africa (late Cretaceous) as the result of periodic droughts that caused temporary shrinkage of the crater lake and precipitation of calcite on the lake floor. However, in the Mahenge sequence calcite is not restricted to the bedding planes, but often penetrates deeply into joints and cracks in the rock, implying that its precipitation occurred after consolidation and lithification of the sediments.

The thickest and most easily definable of the mudstones have been designated as marker beds (Figure 6). These were numbered Levels 1 through 8 from the top of the sequence down. The sediments between each marker bed were identified as sub-levels. Thus, Level 1 was separated from Level 2 by Sub-level 1. Fossils were recovered from all levels and sublevels, except for Sub-levels 4 and 6. However, fossils were not evenly distributed throughout the sequence; the most numerous and best-preserved specimens were recovered from the lowermost levels. For example, the percentage of fossil fishes obtained from different levels are: Level 1 to Sub-level 4, 18.5% (n = 43); Level 5 to Sub-level 6, 24.6% (n = 27); and Level 7 to Level 8, 56.9% (n = 215). However, since these represent units of uneven thickness, a more telling index of frequency is the number of fish specimens recovered per cm thickness of sediment: Level 1 to Sub-level 4 = 0.6; Level 5 to Sub-level 6 = 0.8; and Level 7 to Level 8 = 4.2. In addition, all of the insects and frogs, and most of the leaves (56%), were recovered from Level 7 through Level 8.

The mudstones show varying degrees of silicification, but this is most evident in the lower one-third of the sequence. This presumably relates to hydrothermal activity after the close of the main eruptive event. Silicification

¹This estimate is based on a crater lake of 370 m diameter, with a diameter-depth ratio of 5–10 (giving an estimated depth of 37–74 m), a sediment accumulation rate of 0.7–2.0 mm per year, and a sediment compaction factor of 10 (Bradley, 1929; Smith, 1986; Scarth, 1994; Maley *et al.*, 1990, 1991; Giresse *et al.*, 1991; Cornen *et al.*, 1992).

makes the mudstones extremely hard and more difficult to fracture along bedding planes, resulting in a greater tendency for fractures to be conchoidal. Above the fossiliferous beds is a layer, more than 1 m thick, consisting of slumped blocks and slabs of consolidated mudstones in a matrix of friable yellowish-gray shale (Figure 6). This layer presumably results from a single episode of slumping, produced by heavy seasonal flooding or local tectonic activity. The lowermost section (up to 30 cm thick) consists of pale yellow-gray shale. Bedding is distinct, but buckled and disturbed, and thick sheets of calcite occur throughout. Overlaying this is a poorly-laminated and distorted series of yellowish-gray shales (up to 90 cm thick) with inclusions that grades upwards as follows: (1) small blocks and slabs of silicified yellow-brown mudstone without distinct laminations; (2) massive slump blocks, some more than 60 cm in diameter, of poorly-laminated yellow-gray mudstone; and (3) slabs of consolidated mudstones, up to 5 cm thick, contained in a matrix richly impregnated with calcite (Figure 6). The partial preservation of the original bedding structure implies that the transport distance of slumped material was relatively limited. Capping this layer is a well-consolidated, heavily silicified and poorly-laminated yellow-gray mudstone, 8 cm thick (Figure 6).

The uppermost layer consists of a recently formed colluvium (1.1 m thick) of dark gray mudgy clay and sandy loams containing numerous detrital fragments of orange-brown weathered granite, quartz, and aggregations of decomposed kimbberlite (Figure 6). The larger clasts are poorly sorted, angular to sub-rounded pebbles and cobbles, some exceeding 20 cm in diameter.

5. Lake Paleocology

Excellent comparative information is available on present-day crater lakes in tropical Africa (e.g., Trewavas *et al.*, 1972; Green, 1972; Green *et al.*, 1973; Melack, 1978; Beadle, 1981; Maley *et al.*, 1990, 1991; Giresse *et al.*, 1991, 1994; Cornen *et al.*, 1992), and this has proved especially helpful in reconstructing the paleoecology and taphonomic relationships at Mahenge. The remarkably complete preservation of the fossils, and the absence of any evidence of damage by benthic scavengers or bioturbation, is suggestive of thermal-chemical stratification of the water column. This indicates that the crater lake at Mahenge was relatively deep—greater than 18 m (Kling, 1988). The cooler, anoxic hypolimnion would have been hostile to most organisms (Beadle, 1981; Smith, 1986). Therefore, dead animals that settled to the bottom of the lake would have been rarely disturbed by scavengers.

The presence of varves in the sediments at Mahenge indicates that there were seasonal fluctuations in temperature that resulted in a periodic turnover of the water column (Bradley, 1948). Tropical lakes are generally relatively stable in terms of stratification, but they do experience seasonal oscillations in the depth of the thermocline, and even complete turnover in which mixing of the hypolimnion and epilimnion occurs (Beadle, 1981; Kling, 1987; Giresse *et al.*, 1991, 1994). Heavy cloud cover, lower ambient temperatures, increased

influx of cooler water from run-off, and changing wind patterns during the rainy season all contribute to reducing the temperature of the epilimnion, and resulting in circulation of water from the hypolimnion (Talling, 1969; Livingstone and Melack, 1984; Kling, 1987). Turnover during cooler weather may result in an algal bloom or the circulation of toxic gases, such as carbon dioxide, methane or hydrogen sulphide, which can lead to catastrophic mass deaths of fish and other animals (Kling, 1987; Kling *et al.*, 1987; Livingstone and Melack, 1984; Eider and Smith, 1988). However, the density and distribution of the fish remains at Mahenge indicate an attritional death assemblage rather than one due to mass mortality. In sum, the lithological evidence suggests that the sediments at Mahenge were deposited in a relatively deep and stratified crater lake that experienced periodic turnover of its water column as a result of marked seasonal variation in climatic conditions.

6. Age of the Fossil Beds

There has been a good deal of speculation in the past about the age of the kimberlite occurrences in the Singida region. Teale (1932) suggested that sandstone fragments found as xenoliths in the Kiomboi pipe in the Iramba field are lithologically reminiscent of Upper Karoo sediments; placing the eruptive phase later than the early Jurassic. Du Toit, who accompanied Teale on a reconnaissance to Singida in 1931, considered the kimberlites to be younger than the early Cretaceous, possibly of Tertiary age (Teale, 1932; Eades and Reeve, 1938; Williams, 1939). Eades and Reeve (1938) suggested that the lake beds may have been deposited during the main phase of regional peneplanation, which they speculated to have occurred in the Miocene.

Based on his preliminary assessment of the systematics of the fossil fishes from Mahenge, particularly the cichlids, Greenwood (1960) suggested that the sediments were probably middle to late Tertiary in age. However, the reevaluation of additional fossils led Greenwood and Patterson (1967) to re-evaluate the relationships of the fish fauna, and to favor a Paleogene (probably Oligocene) age. Estimated ages of kimberlites in neighboring fields provide circumstantial evidence to support a late Cretaceous-early Tertiary eruptive phase for the Singida kimberlite field. The diamoniferous kimberlite pipe at Mwadu in Shinyanga Region (the largest such occurrence in Africa, with a surface area of 1.5 km²), located about 150 km to the northwest of Mahenge, is overlain by a thick series of lake sediments, up to 380 m in depth (Edwards and Howkins, 1966). These have yielded fossil vertebrates and plant remains, as yet undescribed, as well as a microfossil assemblage that indicates an age of late Cretaceous or younger (Edwards and Howkins, 1966). A kimberlite near Nzege, 120 km to the west of Mahenge, has yielded U-Pb dates of 52.2 and 53.2 Ma, and fission track dates of 54.3 ± 14 Ma and 51.1 ± 3.8 Ma (Davis, 1977; Naeser and McCallum, 1977; Haggerty *et al.*, 1983). This places the intrusive event for the Nzege field in the early Eocene (= Ypresian).

During the 1996 expedition a single 508 mg hyacinth-colored zircon crystal was recovered from the stream bed at Mahenge. RM and KRL analyzed two

Table 2. Summary of U-Pb isotopic analyses of Mahenge zircon

Split #	ppm U	Th/U	(1)	(2)	Age, Ma (3)	Age, Ma (3)	207Pb/206Pb
1	16.1	0.31	278.5	45.96 ± 0.31	79 ± 80	45.79 ± 0.20	45.83 ± 0.17 Ma
2	15.7	0.29	170.7	45.79 ± 0.20	78 ± 110		
Weighted mean							

(1) Calculated from radiogenic $^{208}\text{Pb}/^{206}\text{Pb}$ assuming $\text{Th}/\text{Pb} - \text{U}/\text{Pb}$ concordance.

(2) Measured.

(3) Calculated assuming a common Pb with $^{206}\text{Pb}/^{204}\text{Pb} = 18.6 \pm 0.4$, $^{207}\text{Pb}/^{204}\text{Pb} = 15.60 \pm 0.35$, and corrected by $+0.10$ Ma for estimated deficiency of initial ^{230}Th . Errors are 2-sigma.

milligram-sized splits of fragments from the crushed crystal, which yielded essentially identical and internally-concordant $^{206}\text{Pb}/^{238}\text{U}$ ages of 45.83 ± 0.17 Ma (Table 2). Because of the young age, low uranium-content (~ 16 ppm U) and internal concordance of the zircon, the date can be regarded as accurate. This indicates that intrusion of kimberlites in the Singida field occurred during the middle Eocene (= Lutetian), slightly later than those of the Nzege field, and probably also later than those of the Shinyanga field (e.g., Mwadui). It also confirms that the kimberlite occurrences in Tanzania are younger than those from southern Africa (which are mainly late Jurassic to Cretaceous in age, ranging from ~ 65 – 150 Ma) (Dawson, 1970; Hawthorne, 1975; Haggerty *et al.*, 1983; Mitchell, 1986).

An important point here is that the radiometric age determination provides a date for the intrusive event (i.e., the formation of the crater and eruption of the kimberlite), rather than the age of the fossiliferous sediments that subsequently filled the crater lake. However, studies of similar crater lakes in Europe and Africa show that sediments begin to accumulate relatively soon after initial formation of the crater (Lorenz, 1973; Smith, 1986; Rayner and McKay, 1986; Rayner, 1987; Gresse *et al.*, 1991; Cornen *et al.*, 1992). Although sedimentation rates and degree of compaction may vary, conservative estimates derived from data on modern maars indicate that the crater at Mahenge would have been filled in 0.2–1.0 myrs (see above). For example, McKay and Rayner (1986) estimate that the much larger crater at Orapa in Botswana (late Cretaceous), with at least 80 m of sediment, would have been completely filled in less than 0.5 myrs. We can confidently assume, therefore, that the fossils date to ~ 45 – 46 Ma. Equally important, if our estimates of sedimentation rates are correct, is that the deposits which yielded all of the fossils represents a very narrow time window of only 8000–22,700 years.

7. Renewed Fieldwork at Mahenge

Fossil vertebrates were originally discovered at Mahenge by George Mannard in the late 1950s as part of his intensive survey of the diamond-bearing potential of the Singida kimberlites (Mannard, 1962). During his investigations at Mahenge, Mannard excavated more than twenty test pits that penetrated the surface soil into the underlying kimberlite and basement rocks. The depth of Mannard's test pits in the region do not exceed 10 m in depth (Mannard, 1962), but it would appear that those at Mahenge were less than 5 m, and the majority of pits at the edge of the pipe were less than 2 m in depth. Mannard (1962: 243) provided a sketch map of the location of his pits and kimberlite outcrops, but he provided no further documentation or key to the individual pits.

In 1994 TH and CPM were able to relocate many of Mannard's pits, which remained unflled except for some incidental back-filling of the excavated sediments. Individual pits and pit complexes were given reference numbers; those located within the boundary of the pipe (i.e., those that exposed lake sediments or kimberlite) were assigned an Arabic numeral, while those located outside the pipe (i.e., those that penetrated the granitic basement only) were assigned a Roman numeral. Pit complexes, consisting of several pits in close association, were given the same number, but were differentiated by a letter suffix. Mannard's sketch map is reproduced in Figure 7, with the addition of the pit reference numbers introduced in 1994.

The main pit complexes of Mannard (Pits 5 and 6) are located near the center of the crater, in close proximity to the Luwala River (Figures 5 and 7). The pit complex on the eastern bank of the Luwala, designated Pit 5, consists of three separate pits. Pit 5c is the deepest of these pits (~4 m deep). On the western side of the Luwala is a complex of pits that have been identified as Pit 6. Both of these pit complexes have yielded the remains of fossil vertebrates and plants. A few fossils were recovered from Mannard's spoil heaps at Pit 6 in 1994, but no further work was conducted in 1996.

The main focus of the 1996 season was on pit 5c. The recovery of more than forty fossil fish from Mannard's spoil heaps in 1994 suggested that this would be the most productive site to begin operations. Excavations involved clearing Mannard's original pit (which measured 6.0 m × 3.4 m) and enlarging it to form a small quarry (10.0 m × 5.7 m). This allowed compilation of a stratigraphic section and a more detailed assessment of the sedimentology (see above). In addition, the course of the Luwala River and the horizontal extent of the crater lake and diatreme were mapped (Figure 5).

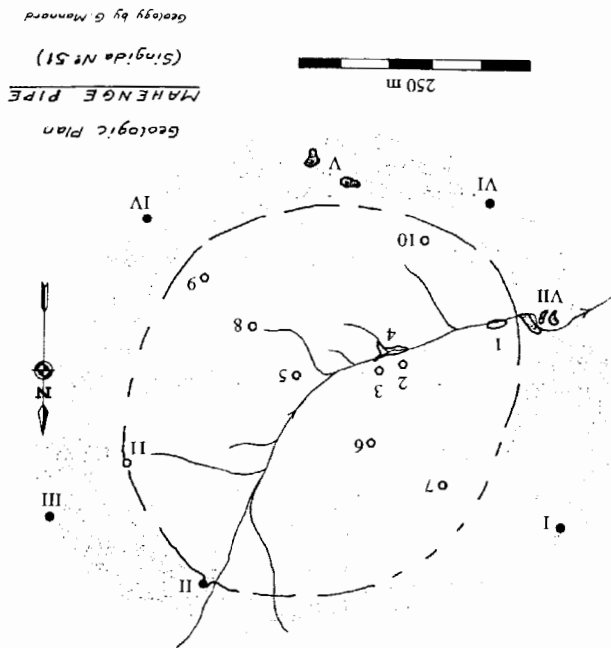
Excavation of the quarry involved removal of the horizontal shales and mudstones one layer at a time. Although masonry saws were occasionally used to cut large slabs, in most cases the weight of the overlying sediments had caused the layers to crack into small irregular slabs that could easily be removed from the quarry by hand. After removal, fossils were recovered by splitting slabs along natural cleavage planes using fine masonry chisels. In general, only relatively complete specimens were retained and catalogued. All of the specimens discovered in 1994 and 1996 are housed in the National

Of the 54 kimberlite pipes in the Singida field only ten have lacustrine sediments derived from a former crater lake (Mannard, 1962). The mean surface area of kimberlite pipes in the region is approximately 34,000 m², but most of the occurrences (78%) are smaller than this, with over half having an area less than 15,000 m². The smallest pipes with crater lake sediments are Magoba, Munyu, and Kinginya; medium-sized pipes with surface areas of between 16,000 m² and 20,000 m². However, crater lake deposits are most commonly associated with large kimberlite bodies, and some significance can probably be attached to the fact that 6 of the 7 pipes (83%) with a surface area of over 100,000 m² are positively associated with lake sediments. These include Pyamahumbe (105,000 m²), Mahenge (238,000 m²) and Songeli (256,000 m²)—all of which have sediments known to contain fossils (see Figure 2, Table 1). There are good reasons for this association. Large kimberlite pipes are more likely to produce a depression of sufficient volume to accommodate a crater lake deep enough to allow the accumulation of fine-grained sediments and a

8. Other Localities in the Singida Area

Museums of Tanzania, Dar es Salaam, while earlier collections are housed in the Natural History Museum, London.

FIGURE 7. Sketch map adapted from Mannard (1962) to show the location of Mannard's test pits and their current pit designation numbers. See text for further details.



stratified water column that is conducive to the preservation of relatively complete organisms. The data suggest that kimberlite pipes smaller than 15,000 m² are unlikely to be associated with crater lakes, while those between 15,000 m² and 100,000 m² may support small lakes that are generally too shallow for the preservation of fossils (the exception here is Munyu, which has well-preserved leaves in lake sediments overlying a pipe with an estimated area of just over 20,000 m²). One can assume, therefore, that relatively few of the kimberlite pipes in the Singida region have the potential to yield fossils similar to those at Mahenge. Apart from the localities listed in Table 1 which have already yielded fossils, two further kimberlite occurrences with lacustrine sediments overlying relatively large pipes—Tabola (130,000 m²) and Kolongo (140,000 m²)—would probably merit further investigation.

In 1994 and 1996 team members made brief excursions from Mahenge to other kimberlite occurrences in the Singida area to explore their potential for further paleontological investigations. Visits were made to Songeli (= Sungili or Sunguli), Munyu (= southern "Mitwira"), Karusi ya Kasunga, Lusilukulu, Tabola (= Ntola), and Pyamahumbé (see Figure 2).

Songeli is of interest for several reasons. It is the largest diatreme in the Singida Region (with a maximum diameter of at least 760 m), and is the second largest in Tanzania after Mwadu. Kimberlites were first discovered in the area in 1931 (Teale, 1931, 1932; Eades and Reeve, 1938; Williams, 1939; Mannard, 1962). Teale (1931) reported the discovery of well-stratified lake beds overlying the pipe containing fossil stems, leaf impressions and seeds. In 1994 the Songeli stream was surveyed as far as its confluence with the Msungwe River and we mapped extensive outcrops of kimberlite in the gullies. No fossils were recovered, although we recorded fossilized wood and root casts *in situ* in the yellow ground and pyroclastic kimberlite. In addition, the river gravels and sands contain a coarse litter of brightly colored chert fragments derived from the silicified cap of the diatreme, as well as numerous Middle Stone Age hand-axes and flakes made from the same material.

Several kimberlite occurrences have been recorded in the vicinity of Mitwira (Teale, 1932). These have been identified as Mitwira, Kolongo, Munyu and Munyu North pipes by Mannard (1962). Du Toit recovered impressions of plant remains and pieces of a large bone from Munyu (Teale, 1932), while Eades collected some well-preserved fossil leaves in a shale 6 m below the surface (Mannard, 1962). The Mitwira area is heavily vegetated and quite remote, being difficult to reach by car. Swarms of tsetse flies make prospecting burdensome. The former pits and spoil heaps of previous prospectors are now much overgrown, and little useful information can be gleaned from the exposures without opening further test pits.

At Karusi ya Kasunga, Lusilukulu, and Tabola, about 15 km to the north-east of Mahenge, numerous shallow pits were investigated, many of which were overgrown and partially filled. Local informants told us that some of the pits were dug prior to World War II—presumably the work of the South African prospector, Pienaar, who was known to have surveyed the area in the early

1930s. Outcrops of kimberlite were recorded, but there was no evidence of lake sediments.

The pipe at Pyamahumbe, with a maximum diameter of 360 m, is located on a flat, sparsely forested terrain. A small river transects the pipe and exposes limited outcrops of kimberlite and lacustrine sediments. The uppermost layer of sediments consists of a thin cherty bed, up to 30 cm thick, that exhibits strong warping and folding. This bed represents a series of heavily silicified mudstones, with individual layers up to 5 cm thick, that retain much of their original laminar structure. They are mostly gray-green with bright orange streaks and mottling. Large white crystalline and red-orange inclusions are possibly of organic origin. The beds are difficult to split mechanically because of their chemical alteration, but they do contain fossils—mostly stem and leaf fragments, seeds and/or fruits, and isolated fish scales and bones. Better material might be recovered with more extensive sampling. The cherty mudstone grades down into a friable light gray shale that rests unconformably on kimberlite. The lake sediments are covered by a 1.0–1.5 m thick layer of dark gray mbuga clay.

In addition, mention should be made of two localities, not visited by our expedition, that are potentially of some paleontological interest. Local informant who worked with Mannard in the late 1950s reported that large fossil bones were recovered from a site near the village of Masorsa. However, Mannard (1962) makes no mention of these discoveries, and since he was aware of the obvious significance of the fossil fish from Mahenge, it seems unlikely that he would not have documented such an occurrence. We are inclined, therefore, to discount the validity of this claim. The other locality, potentially much more important, is the site of Minusi. Greenwood and Patterson (1967) made reference to a specimen of *Singida jacksonoides* and two specimens of cichlids collected at this site by Mr. Phillip J. King. The fossils are preserved in buff colored mudstones comparable to those at Mahenge. Unfortunately, the provenience and details of the discovery are unknown, except that the specimens were found by accident during construction of a house (Patterson, personal communication). Minusi cannot be found on maps and the name is unfamiliar to local inhabitants. It is possible that the name represents a corruption of Minyughe or Minyughe—a river and village located about 30 km to the southeast of Mahenge. However, none of the pipes in the vicinity of Minyughe are associated with lake sediments, except for Magoba, which has previously only yielded silicified wood (Mannard, 1962; Table 1).

9. The Mahenge Fauna and Flora

A detailed analysis of the fauna and flora from Mahenge is still underway, but we present here a preliminary account of our initial findings. Our study is based on more than six hundred specimens recovered from Mahenge in 1994 and 1996 (Table 3). The collection consists predominantly of fossil fishes

Table 3. Number of specimens recovered from sites in the Singida Region in 1994 and 1996

	Frogs	Fishes	Invertebrates	Plants	Other ¹	Total
Mahenge 1996	4	466	3	74	17	564
Mahenge 1994	0	47	2	11	0	60
Pyamahumbe 1996	0	1	0	6	2	9
Total	4	514	5	91	19	633

¹ Includes coprolites and indeterminate specimens

(81.2%), while frogs (0.6%), insects and gastropods (0.8%), plants (14.4%) and indeterminate specimens (3.0%) make up the remainder.

9.1. Fishes

Only two species of fish have previously been described from Mahenge: *Palaeodenticeps tanganyikae* and *Singida jacksonoides* (Greenwood, 1960; Greenwood and Patterson, 1967). In addition, Greenwood (1960) and Greenwood and Patterson (1967) also noted the occurrence of haplochromine cichlids, although preservation of the material was not adequate to assign them to a particular species. The ichthyofauna can now be expanded to include two further taxa—a catfish (Siluriformes) and a second species of osteoglossomorph.

Additional excellent examples of *Singida jacksonoides* have now been recovered. This species represents the most common fish at the site, and is found throughout the fossiliferous sequence. Specimens have a standard length (SL) from 20 mm to about 180 mm, with the majority being under 70 mm SL. Some specimens preserve impressions of scales.

Singida jacksonoides is the sole representative of an extinct family, the Singididae (Greenwood and Patterson, 1967). It is the only fossil osteoglossoid fish known from Africa, and its closest extant relatives (i.e., species belonging to the Osteoglossidae, Pantodontidae and Heterotrididae) form relic taxa in the Nile and Zairean basins. *Singida* is unique among osteoglossomorphs in lacking teeth, but otherwise its cranium is similar to that of other osteoglossoids, especially to the extant Australasian *Scleropages* and the South Ameri-

can *Osteoglossum* (Greenwood and Patterson, 1967). In a recent phylogenetic analysis, Li and Wilson (1996) concluded that *Singida* represents the sister-taxon to the extant *Scleropages* + *Osteoglossum* within the family Osteoglossidae. However, *Singida* is more primitive than all known osteoglossids, including the Paleogene phareodontines, in retaining a hidodontoid-like caudal skeleton that retains two unoneurals (Greenwood and Patterson, 1967). It is possible, therefore, that it represents a stem osteoglossoid, a clade that had already diverged from other osteoglossomorphs by the early Cretaceous (Lundberg, 1993; Li and Wilson, 1996).

The distribution of extant osteoglossoids in southern tropical freshwater regions suggests that the initial diversification of the modern families occurred on Gondwana prior to the separation of South America and Africa in the late Cretaceous (Nelson, 1969; Taverne, 1979; Lundberg, 1993; but see Cracraft, 1974; Briggs, 1987 for alternative views). This biogeographical scenario is given additional support from the fossil record. The occurrence of the earliest representatives of the Heterotididae in the Cretaceous (i.e., *Chandlerichthys* from the early Cretaceous of North America, *Laellichthys* from the late early Cretaceous of Brazil and *Paradercetus* from the late Cretaceous of West Africa; Da Silva Santos, 1985; Grande, 1986; Lundberg, 1993), and the wide geographical distribution of the extinct members of the Osteoglossidae in the early Tertiary, including the Phareodontinae, both point to a South American-African distribution of these families prior to the break up of western Gondwana (Lundberg, 1993). Regardless of whether *Singida* proves to be a stem osteoglossoid or the sister taxon to extant osteoglossids, the biogeographical evidence implies that *Singida* is part of a distinct lineage that originated before the close of the Mesozoic.

In addition to *Singida jacksonoides*, the recent collections from Mahenge have yielded what appears to be a second, previously undescribed, species of osteoglossomorph. This taxon occurs throughout the deposits. The specimens are all fairly large, about 150 mm SL. Scales are associated with most specimens. The new species is distinguishable from *Singida jacksonoides* by the presence of teeth. One of us (AMM) is currently working on a detailed description for publication.

Palaeodenticeps tanganikae is the only known fossil representative of the Denticipitidae, a family based on a single extant species, *Denticeps clupeoides*, confined today to the rivers of western Nigeria and Benin (Clausen, 1959; Greenwood, 1960, 1965; Gras, 1961). Apparently, *Denticeps* is a relic taxon. The retention of largely plesiomorphic traits in *Denticeps* and *Palaeodenticeps* suggests that the Denticipitidae is the primitive sister group of all other clupeomorphs (Greenwood, 1960, 1968; Lecointre and Nelson, 1996). *Palaeodenticeps* is relatively rare at Mahenge, where it represents less than 2% of fish specimens. Interestingly, Greenwood (1960) examined eight specimens of *Palaeodenticeps tanganikae* collected by Mannard at Mahenge, while the much larger fossil collection obtained in 1996 included only two individuals. *Palaeodenticeps tanganikae* are small fish (about 25–28 mm SL), but

since they are not much smaller than some of the *Singida jacksonoides* and cichlid specimens, it seems unlikely that their rarity is caused by sampling or taphonomic biases, and probably reflects an ecological distinction.

Cichlids are common and are found in all levels. All appear to be "haplochromines" with ctenoid scales. Preliminary comparisons suggest that there may be some diversity among the taxa represented, possibly with different communities being sampled at different horizons. Greenwood (1960) suggested that all of the specimens that he examined could be included in a single genus, with closest affinities to extant *Haplochromis*. The relatively small size, stout unicuspid teeth, and deep dentaries of the fossil cichlids suggest that they were feeding on phytoplankton, organic debris, and small aquatic insect larvae. The mid-Eocene age of the Mahenge cichlids makes them the earliest known members of the family, at least from Africa, and they should eventually provide important clues to understanding the evolutionary history and zoogeographic origins of the group (Van Couvering, 1982; Stiasny, 1991; Lundberg, 1993).

Three specimens of a catfish were recovered. These are all from the lowest levels, Sub-level 7 and Level 8. The absence of catfish above the bottommost levels may indicate a change in the faunal community structure over time. It is conceivable that these catfish, whose modern-day counterparts are air-breathers tolerant of deoxygenated and swampy conditions, were better able to exploit the lake when it was first formed (i.e., when the water column was at its deepest and sedimentation rates were relatively rapid). However, these horizons also correspond to the levels in which the greatest number of fossils are preserved, so the restricted stratigraphic distribution of the catfish could simply reflect a problem of sampling. The catfish and the osteoglossoids would have been the major predators of other fish and invertebrates in the lake.

Preservation of the fish specimens varies. Most of the *Singida jacksonoides* specimens, as noted by Greenwood and Patterson (1967), are preserved as natural molds, with some "cheesy" bone still adhering. The other osteoglossomorph, although found in the same layers as *S. jacksonoides*, has well-preserved, hard bones, often associated with scales. The cichlids vary in preservation, some being natural molds and others having bones and scales preserved, but the bone is quite fragile. The catfish specimens are all well-preserved, including the ornamentation of the cranial bones, but the matrix is extremely hard and difficult to remove. Greenwood (1960) reported isolated vertebrae, ribs and fin rays from Mahenge. In 1996 only a single isolated bone, a fragment of a preopercle, and portions of several vertebral columns belonging to unidentified taxa were recovered—almost all of the remaining specimens were entire. In addition, coprolites of fish are extremely common throughout the sequence.

The greatest diversity of the fish fauna is in the lowest levels of Mahenge. At least five different species have been identified, although it is likely that multiple species of cichlids are represented at each level. The general correlation between lake size and number of species of fish in modern-day tropical lakes (Barbour and Brown, 1974) indicates that the crater lake at Mahenge would have supported fewer than ten species. However, data on modern

African lake communities suggest that a slightly higher diversity might be possible. For example, the modern-day crater lake at Barombi Mbo, although considerably larger than the lake at Mahenge (being 2.5 km across), might provide a reasonably good model. The fauna comprises 17 species of fish, including eleven species of cichlids, a cyprinid, three species of cyprinodontids (found primarily in the inflow stream) and two species of clariid catfish (Trewavas *et al.*, 1972). Most species are relatively small (less than 160 mm SL), while the catfish, the main predators, are somewhat larger (up to 300 mm SL). As noted by Greenwood (1960) and Greenwood and Patterson (1967) the closest living relatives of *Singida* and *Palaeodenticeps* are riverine species, rather than lacustrine, implying that the fossil species had different ecological and behavioral characteristics. It is conceivable, however, that *Palaeodenticeps*, being a relatively rare species at Mahenge, may have lived in the feeder streams or adjacent parts of the lake. In addition, studies of modern African fish faunas indicate that small crater lakes are readily colonized at times of heavy seasonal flooding, particularly by cichlids, and that rapid changes in behavior of the immigrants are a common theme (Trewavas *et al.*, 1972; Kingdon, 1989).

9.2. Anurans

Partially articulated skeletons of four individuals were recovered in the recent collections from Mahenge. They appear to belong to a single species of pipid frog, representing different developmental stages. They are relatively small in size, with a maximum head and body length of about 40 mm. Several of the individuals appear to preserve stomach contents in the abdominal region, including coarse sand grains, presumably derived from the margin of the crater lake (probably ingested accidentally along with its prey shortly before the time of death). SEM analysis of one of the specimens (by W. J. Sanders, University of Michigan) found no trace of any organic materials in the detritus. Similar materials have been recovered from the stomachs of extant African lake fishes that prey on near shore insect larvae (Trewavas *et al.*, 1972). The species from Mahenge shares several derived character-states with Pipinae, a clade represented today in northeastern South America by *Pipa* and in sub-Saharan Africa by the Hymenochirini (i.e., *Pseudhymenochirus* and *Hymenochirus*). Preliminary examination of this material shows the presence of the following plesiomorphies: wedge-shaped skull in lateral profile, wide parasphenoid in the floor of the braincase, coracoids broadly expanded at their sternal ends, squamosal lacking a well-developed zygomatic ramus, vomer appears to be absent, the first two presacral vertebrae are fused, the sacrum is formed by at least three vertebrae, and the sacral diapophyses are greatly expanded. A close relationship with the Hymenochirini is suggested by the blunt anterior margin of the parasphenoid, the deep eustachian canals crossing the otic capsules in an anterolateral-posteromedial direction, and the ventrally curved postzygapophyses. However, the species from Mahenge

appears to be more plesiomorphic than the extant hymenochirins in the presence of pterygoids bearing an anterior arm. Although some instances of hyperossification are evident, such as the fusion of the nasals and frontoparietal, extension of the frontoparietal over the otic capsules, and ossification of the planum antorbitale, there are no indications of the bizarre specializations seen in the new hymenochirin genus from the late Cretaceous of Niger (Bâez and Rage, 1998; Bâez *et al.*, in press).

This record confirms that pipid frogs, confined to Africa and South America at present, are components of the freshwater faunas of Western Gondwana. The combination of fossil occurrences (Haughton, 1931; Nevo, 1968; Estes, 1975, 1977; Duellman, 1993; Bâez, 1996) and current hypotheses of pipid phylogenetic relationships (Cannatella and Trueb, 1988a, b; Bâez and Trueb, 1997) suggest that pipids were well-diversified prior to the complete separation of Africa and South America in the middle Cretaceous. Although the biology of extant African pipines (*sensu* Cannatella and Trueb, 1988a, b) is poorly known, they are fully aquatic and restricted to equatorial lowland forests, ranging from Nigeria and Cameroon to eastern Zaïre. The occurrence of a pipine at Mahenge demonstrates that this clade had a more eastern distribution in the past.

9.3. Invertebrates

Only a few insects were recovered from Mahenge, including a beautifully preserved ant (Formicidae, Hymenoptera) and a partially preserved winged insect of indeterminate taxonomic status.

Mollusks are extremely rare. A single poorly-preserved and unidentifiable shell of a small gastropod was recovered from Mannard's spoil heap at Pit #5 in 1994. There are two possible explanations for this isolated occurrence. First, in a thermally stratified lake the hypolimnion is generally acidic and calcium carbonate shells tend to dissolve completely (Wutke, 1992). Second, in modern African crater lakes, such as that at Barombi Mbo in Cameroon (Giresse *et al.*, 1991), gastropods are restricted to the feeder streams, and do not occur in the lake itself. If this is typical, rare finds of mollusks are likely to be aquatic gastropods derived from the in-flow streams or possibly shells of terrestrial gastropods washed into the lake from the same source as the terrestrial plant material.

9.4. Plants

Paleobotanical studies were conducted on an initial collection of 70 specimens from Mahenge, which consists almost entirely of leaf compressions/impressions, but also includes a few stem fragments. Although the collection is small, it adds a significant new dimension to our currently limited knowledge of African Paleogene environments. Mahenge plant fossils

represent the first Eocene vegetative remains from equatorial Africa. They complement what little is known from West African palynological core samples (Van Hoeken-Klinkenberg, 1966; Salarid-Cheboldaëff, 1979, 1981; Salarid-Cheboldaëff and DeJax, 1991), fossil wood from mainly poorly-dated deposits of West and North Africa (Boureau *et al.*, 1983; Dupéron-Laudouenèix and Dupéron, 1995), and isolated fruit or seed specimens from Egypt and West Africa (Chandler, 1954; Chesters, 1955). Preliminary study of the Mahenge paleoflora also provides some valuable data that contribute to an improved understanding of the evolutionary history of East African floras.

A minimum of 20 species is represented among the leaf specimens. Five of these are in the Leguminosae family and have been classified as *Acacia* sp. nov. (subfamily Mimosoideae), cf. *Aphanocalyx* (subfamily Caesalpinoideae), cf. *Gynometra* (subfamily Caesalpinoideae), and two species of unknown affinity (Herendeen and Jacobs, submitted). The presence of *Acacia* at Mahenge marks the first unequivocal occurrence of this genus in Africa.

A complex of character patterns among extant species of *Aphanocalyx* and its relative, *Monopetalanthus*, create problems for systematic placement within this group. Further documentation (from additional Mahenge fossils) of character distribution in relatively primitive members of these groups may aid in understanding the phylogenetic relationships of extant relatives. The legume family is diverse in Africa today, but has a limited fossil record, especially in the Paleogene. Caesalpinoideae and mimosoid legumes are recorded among Eocene pollen and wood specimens (Salarid-Cheboldaëff, 1979; Gros, 1992; Dupéron-Laudouenèix and Dupéron, 1995), and a probable Caesalpinoideae leaf is known from the Oligocene Jebel Qatrani Formation, Egypt (Bown *et al.*, 1982). However, the Mahenge site confirms that legumes were well-established and diverse in equatorial Africa at this time.

A qualitative study of leaf physiognomy among the 20 species provides a general indication of the paleoenvironmental setting. Of the 18 dicot leaf taxa for which measurements could be made, all are smaller than mesophyll (<20.25 to 45.00 cm²) size. In modern equatorial Africa, the proportion of species with mesophyll leaves in a plant community is positively correlated with both mean annual rainfall and wet months rainfall (months having more than 50 mm on average; Hall and Swaine, 1976; Jacobs, 1999). The predominance of small-leaved species at Mahenge is an indication that rainfall was less than that which would support forest vegetation today (generally >1100 mm/yr).

All but one of 18 dicot taxa have entire (smooth) margins. Today, across a broad latitudinal temperature gradient, the proportion of species with an entire margin is directly correlated with mean annual temperature (Bailey and Simnett, 1915; Wolfe, 1995). This indicates that the Mahenge flora represents a hot or warm environment with markedly seasonal or relatively low (<1000 mm/yr) mean annual precipitation. This interpretation is compatible with the presence of *Acacia*, a large genus confined today to warm or hot regions where rainfall supports woodland or wooded grassland environments. More precise climate reconstruction, and perhaps a better understanding of the

relatively open structure of this plant community, might be possible with an enlarged collection of specimens.

Taphonomic studies of stream-fed lacustrine depositional systems have shown that leaves are derived from both allochthonous upstream vegetation and local plant communities (Spicer, 1981; Ferguson, 1985; Greenwood, 1991). However, just over one-third (6 of 16) of the species for which leaf shape could be determined have leaves that are linear, narrowly oblong, or narrowly elliptic. Plants which grow in or immediately adjacent to fast-flowing streams often have narrow (stenophyllous) leaves (Richards, 1996). It is possible, therefore, that the narrow leaves derive from (possibly distant) streamside vegetation, although there is currently no sedimentological or geomorphological evidence of in-flowing streams at Mahenge. Nevertheless, the small size of the vast majority of the collection, including taxa without narrow leaves, supports the hypothesis that the surrounding vegetation was not forest, but a more open plant community indicative of a drier climate.

Much of the Paleogene palynological work is biostratigraphic, associated with oil exploration in coastal West and North Africa (e.g., Boltenhagen, 1965). However, Salard-Chebolidaeff and Dejax (1991) summarize the paleoenvironmental significance of West African Late Cretaceous and Tertiary palynological records. They document an overall increase in diversity of angiosperm taxa, especially since the middle Eocene, and attribute this to angiosperm diversification, the northward movement of Africa between the terminal Cretaceous and middle Eocene, and the increasing availability of moisture along coastal West Africa after the later Cretaceous split with South America. The marked increase in angiosperm richness after the middle Eocene is taken to represent the origin of wet lowland forest. On the basis of fossil wood, Bourreau *et al.* (1983) reconstruct a tropical forest along the western and northern coasts of the continent during the middle Eocene, with a savanna environment in-between. However, as these reconstructions are based on fossil wood, there are not data to address the existence of grasses that would be associated with a savanna environment today. Axelrod and Raven (1978) suggested lowland rain-forest had been established by the Paleocene, and extended northward from about 15°S, but this was before some of the West African pollen records had been published. The Mahenge paleoflora indicates the absence of wet forest at paleolatitude 15°S, at least in the vicinity of the site.

A global review of the origin of grass-dominated ecosystems indicates that grasses may have diversified during the middle Eocene in tropical Africa and South America (Jacobs *et al.*, 1999). Palynological assemblages consistently record the presence of *Monoportites annulatus*, a form genus that represents the grass family (Salard-Chebolidaeff, 1979; Germeraad *et al.*, 1968). However, paleobotanical evidence of the savanna biome is not common until at least the middle Miocene. The botanical affinities of Eocene tropical grasses and their ecological role(s) are unknown. The Mahenge leaf assemblage includes at least one probable grass blade fragment. Additional monocot fossils may shed light on the question of the role of grasses in Eocene tropical plant communities.

10. Discussion and Conclusions

When fully studied and described, the fossils from Mahenge will yield important information on the evolution, paleoecology and biogeography of the fauna and flora of East Africa during the early Tertiary. The site is of especially significance because it samples a geographical province and time period for which we have almost no fossil record. The following discussion briefly highlights the scientific importance of the site and identifies potential avenues of future research.

10.1. A Unique Temporal and Geographical Window

Paleogene sites with continental sediments are extremely rare in sub-Saharan Africa, so the evolutionary history and biogeography of the fauna and flora of the region during this time period is almost entirely undocumented. The fossils from Mahenge help to fill a major gap. Preliminary study of the fossil fishes and frogs provides a good indication of just how exotic this fauna is—all of the species are unique, being found nowhere else except for localities in the Singida region.

Only a limited exchange of terrestrial faunas was possible between Arabia and Eurasia throughout much of the Paleogene. At this time a shallow epicontinental sea joined the Atlantic to the Indian Ocean, and separated Africa from Eurasia. The isolation of Africa is reflected in high levels of endemism at early Tertiary sites in North Africa (Sigé *et al.*, 1990; Godinot and Mahaboubi, 1992, 1994; Cheebran *et al.*, 1993), and the development of several distinctive African mammalian clades (i.e., Proboscidea, Hyracoidea, Tenrecidae, Macroscelidae, Chrysochloridae, and Tubulidentata) (Springer *et al.*, 1997, 1999; Liu and Miyamoto, 1999). However, Storch and Scharaschmidt (1992) have suggested that limited faunal interchange did occur between Africa and Eurasia during the early Eocene. The first appearance of certain mammals in central Europe may signal the arrival of taxa from Africa, possibly including the earliest artiodactyls, perissodactyls, and primates. Other vertebrate groups that arrive in Europe at this time include the Ceratophyinae, ziphodont mesosuchians and Phorusrhacidae, all of which are known to have South American distributions, and imply a broader connection with faunas of western Gondwana (Storch and Scharaschmidt, 1992).

Unfortunately, we know nothing of the diversity or distinctiveness of early Tertiary faunas in East Africa. In fact, the only sites with terrestrial mammals of Eocene age in sub-Saharan Africa are M'Bodione Daderé in Senegal (middle to late Eocene) and Malembe in Angola (late Eocene), both with small faunas sampling predominantly marine, near-shore facies, similar to those in North Africa (Sudre, 1979; Pickford, 1986). Although no mammals have been discovered at Mahenge, it is possible that with better sampling of the sediments such fossils will eventually be discovered (see Rose and Silcox, 1999). The recovery of fossil mammals from a terrestrial continental setting in East Africa

would contribute significant new insights into the evolutionary history and biogeography of mammalian faunas in Africa.

10.2. Zoogeography

As mentioned above, the zoogeographic relationships of the Mahenge fauna clearly point to a strong association with western Gondwana. For example, of the fossil groups represented at Mahenge, the Osteoglossidae, Cichlidae and Pipidae all have living species found today (although not exclusively) in both Africa and South America. The fossil record suggests that these taxa were widely distributed in western Gondwana prior to the final separation of Africa and South America in the late early Cretaceous (~95–100 Ma) (Pitman *et al.*, 1993). The distribution is best explained by a continental drift-based vicariance model (Lundberg, 1993). The Dentcipitidae only has a relic-tual distribution in West Africa today, but its occurrence at Mahenge implies that the group may have been more widely distributed across tropical Africa during the early Tertiary. A more detailed assessment of the phylogenetic relationships of the Mahenge fish and frogs (and possibly the insects) will contribute to a better appreciation of the origins, zoogeographic distribution, and diversity of Gondwanan faunas.

On a more local level, an analysis of the ichthyofauna and amphibians, in conjunction with study of the regional geology and geomorphology, may provide helpful clues to reconstructing the early development of East African hydrological systems prior to the formation of the Rift Valley. Past connections with the Zaire Basin and West African river systems are indicated by the taxonomic relationships of the Mahenge fish (Greenwood and Patterson, 1967).

10.3. Paleocology

The plant macrofossils contribute to an improved understanding of the systematics, evolutionary history and paleobiology of the East Africa flora, and also provide intriguing new data on the vegetation and paleoecology. A preliminary analysis of leaf physiognomy indicates that the vegetation at Mahenge was a predominantly dry, seasonal woodland, rather than humid tropical rainforest.

Given what we know about early Eocene climate and vegetation patterns on a worldwide scale, the paleoecological inference drawn from the Mahenge fossil plants is somewhat surprising. Several independent lines of evidence have demonstrated that the early Eocene was a period of global warming (e.g., Frakes and Kemp, 1973; Savin, 1977; Shackleton, 1986; Miller *et al.*, 1987; McGowan, 1990; Zachos *et al.*, 1993; Sloan and Rea, 1995), which had a significant impact on the taxonomic and ecological composition of floras at high latitudes (Frakes and Kemp, 1973; Wolfe, 1980; Hubbard and Boulter, 1983; Uppchurch and Wolfe, 1987; Schaarschmidt, 1992). However, the effect, if any,

of elevated global temperatures on the floras of equatorial Africa (Mahenge was probably located about 10°S of its present location during the Eocene) is unknown.

Placed temporally midway between the Latest Paleocene Thermal Maximum (LPTM) at ~58 and the Early Oligocene Glacial Maximum at ~35–36 Ma (Shackleton, 1986; Zachos *et al.*, 1993), one would anticipate that the climate at Mahenge would have been somewhat warmer than modern-day temperatures. However, oxygen isotopic data indicate a reduced latitudinal sea surface temperature gradient relative to the present, so temperatures may not have been very different in equatorial Africa from present-day conditions (Stoan and Rea, 1995). Oxygen isotope studies show that during the early Paleogene deep sea temperatures at high latitudes warmed from 8–12°C, while tropical ocean temperatures remained constant or were somewhat cooler than the present-day (Shackleton and Boersma, 1981; Zachos *et al.*, 1993). This is referred to as the “cool tropic paradox” (D’Hondt and Arthur, 1996).

It has been claimed that during the early Eocene eastern Africa would have supported humid subtropical to tropical rainforest (Axelrod and Raven, 1978; Parrish *et al.*, 1982; Parrish, 1987). However, Coetzee (1993) indicates that microfossil evidence shows that the present-day Congo basin was savanna woodland at that time, with subtropical woodlands extending into East Africa, while Salard-Cheboldaëff (1981) and Salard-Cheboldaëff and Dejax (1991) have shown the co-existence of dry and humid forests in West Africa. When integrated with data from Mahenge and from published reports of plant macrofossils from other Eocene sites in Africa (Adamson, 1931; Rennie, 1931; Van Hoeken-Klinkenberg, 1966; Koeniguer, 1971; Axelrod and Raven, 1978; Gros, 1992; Dupéron-Laudoueneix and Dupéron, 1995), the evidence indicates that equatorial Africa was dominated by a combination of dry seasonal woodlands and more humid forests. While high latitude regions experienced elevated temperatures and the establishment of subtropical and tropical floras, equatorial Africa had dry woodlands associated with cooler temperatures and markedly seasonal precipitation.

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