



Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: V. Palynological evidence for deforestation and increased erosion

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Abstract

Pollen spectra from seven short cores taken from deltaic sites in the central and northern parts of Lake Tanganyika provide information about vegetation changes around the lake during the last 5000 years. Pollen analysis was undertaken to understand the history and timing of catchment deforestation and its causal linkage to excess sedimentation and ecosystem change in Lake Tanganyika. The spectra are dominated by grass pollen at all levels in every core. Grass pollen percentage values range between 40 and 80%. Low values of arboreal pollen taxa (1–20%) were documented from most cores except core LT-98-2M. Core LT-98-2M represents the longest duration vegetation record of this study (close to 5000 years BP), and records the onset of increasingly arid conditions in the Late Holocene, especially after ~500 A.D., with the probable replacement of forest by open grassland in the Mahale Mountains region. The pollen/spore content for other cores showed a consistent trend of a decrease in grass pollen and an increase in pteridophyte and forest indicator pollen taxa during the last few centuries, contemporaneous with other indications of increased watershed disturbance from forest clearing (especially isotopes and lake faunal change). The timing or strength of this trend is not tied to specific levels of watershed disturbance. However, increasing fern spore abundance does occur progressively later towards the south, where modern human population densities are lower. Although increasing fern spore abundance is consistent with a land-clearing hypothesis, the rising arboreal pollen percentages are seemingly counterintuitive. One possible explanation is that increasing arboreal pollen proportions reflects the recycling of abundant pollen of this type from rapidly eroding soils. Another likely explanation for this finding is that land clearing involved the replacement of miombo woodland, with its mixture of trees producing little pollen and understory grasses producing large amounts of pollen, by the present day cassava, banana, and legume agricultural systems, all of which are poor pollen producers. This shift in catchment vegetation would increase the relative contribution of Afromontane pollen transported long distances from the surrounding highland regions. This hypothesis is consistent with both the lack of correlation of palynological history with specific watershed deforestation attributes, as well as the broader historical record of human habitation in the Lake Tanganyika region. This study also highlights the need for both modern pollen transect data from the region and comparative cores from low elevation swamps or ponds (wetlands) in the region with smaller catchment areas.

Introduction

Documenting the pattern of land-use change within a watershed and the possible effects of these changes on nearby terrestrial and aquatic ecosystems requires an historical record of the timing of changes in vegetation for the region of interest. This study presents the results of palynological investigations of cores taken from the deltas of a series of watersheds along the east coast of Lake Tanganyika. The work was conducted as part of the Lake Tanganyika Biodiversity Project's special study on impacts of increased sedimentation rates from anthropogenic activities around the lake. We have taken a paleolimnological approach towards reconstructing past environmental conditions and changing terrestrial and aquatic communities over the past few thousand years for Tanganyikan watersheds selected to represent a spectrum of sizes and degrees of modern forest cover and human activity. The analysis of fossil pollen forms an extremely important part of many paleolimnological studies concerned with land-use change, because it allows connections to be drawn between watershed processes (in terms of vegetation structure and the presence of plant species indicative of human activity) and lake paleoecology.

Study areas and regional vegetation

Details and maps of deltaic characteristics, coring localities, and sampling strategies for the entire project are given in the companion paper by Cohen et al. (2005a). Briefly, we have analyzed seven cores collected with a Hedrick–Marrs multicorer from six deltas along the Tanzanian and Burundian coastlines of the lake. These are discussed in south to north order, because regional geographic trends are apparent in this study. The Lubulungu River (represented by cores LT-98-2M, collected in 110 m water depth (WD), 49 cm core length; and LT-98-12M, 126 m WD, 40 cm) drains a small, low disturbance watershed on the west side of Mahale Mountains National Park. The Kabesi River (LT-98-18M, 75 m WD, 42 cm) drains an intermediate-sized, intermediate disturbance watershed on the northern side of the Mahale Mountains, outside of the national park boundary. The Nyasanga/Kahama River (LT-98-58M, 76 m WD, 39 cm) drains a very small, low

disturbance watershed within Gombe Stream National Park along the northern Tanzanian coastline. The Mwamgongo River (LT-98-37M, 95 m WD, 45 cm) drains a very small but highly disturbed watershed immediately north of Gombe Stream National Park, in northernmost Tanzania. The Nyamuseni River (LT-98-98M, 60 m WD, 37 cm), drains a very highly disturbed, small watershed along the northern Burundi coastline. The Karonge/Kirasa River (LT-98-82M, 96 m WD, 46 cm) drains a very highly disturbed, medium-sized watershed, also along the northern Burundi coast.

The watersheds involved in this study receive between 900 and 1600 mm/year of rainfall, with higher values occurring in the more southerly Tanzanian sites near the Mahale Mountains. Precipitation is highly seasonal, following the migration pattern of the Intertropical Convergence Zone, with rainfall concentrated between October and April. During the dry season (May–September), fire activity is common.

Lake Tanganyika lies within the vegetation zone known as Zambezian miombo woodland, dominated by the trees *Brachystegia*, *Julbernardia*, and *Isobertia*. Miombo vegetation covers western Tanzania, Zambia, South Democratic Republic of Congo and Angola. Within the lake catchment, miombo woodland dominates between 773 m (modern lake level) and 1900 m altitude. Above 1900 m altitude, miombo woodlands are replaced by humid evergreen Afromontane Forest with some bamboo bushland and montane grassland (Vincens 1991; Bygott 1992).

Methods

Details of the physical stratigraphy and geochronology (AMS ^{14}C and ^{210}Pb) of the seven cores discussed here are provided in companion papers (McKee et al. 2005; Palacios-Fest et al. 2005). Pollen samples were taken every 3 cm from each core. A total of 109 samples were analyzed. For each sample 1 cm³ of sediment was processed. Pollen was extracted using standard methods employed by the University of Arizona Palynology Laboratory. Volumetric sediment samples were added to water and detergent, washed, and screened using a 180- μm mesh sieve. An exotic spike, *Lycopodium clavatum* (ca. 1 tablet), was

added to each sample as a tracer, and the samples were progressively acidified with 10% HCl and 36% HCl for carbonate removal and 48% HF for removal of silicates. The samples were then subject to acetolysis (acetic acid, acetic anhydride, and sulfuric acid treatment), decanted, and boiled in a KOH bath prior to staining (safranin "O"). Samples were then transferred to shell vials for storage prior to mounting and counting. Counts averaged 300 grains, and pollen data are presented as percentages based on these counts. Counting was done at 400 \times using an Olympus microscope and "Kounter" software.

Pollen identification was based on the ~35,000 slide pollen reference collection at Duke University. Unpublished keys in Dr. Livingstone's laboratory were used as guides to the reference collection. Most pollen was identified to genus. To date there have been no detailed surface sediment pollen collections from the watershed study areas. Therefore, pollen distribution patterns and habitat inferences were based on the *Flora of Tropical East Africa* (Polhill 1982, 1987), *Flora Zambesiaca* (Pope 1960, 1961, 1963, 1966, 1970, 1971, 1978, 1983, 1985, 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1995) and *Flora of Tropical West Africa* (Hepper 1963, 1968), in that order of preference. Additional habitat information was obtained from comparison of our results with floristic surveys of

Gombe Stream National Park (Clutton-Brock and Gillett 1979). The pollen diagram was plotted using Tilia and Tilia Graph software[®], with subsequent graphical modifications in CorelDraw[®].

Results

Pollen preservation in the study cores was generally quite good. As is typical of regional African pollen floras, grasses dominated the spectra, even from currently forested or woodland regions. Grass pollen percentages range between 40 and 80%. Despite the deltaic setting of the coring sites, aquatic and emergent marsh taxa are generally rare, reflecting the very limited development of marshland or littoral vegetation typical of the steep coastline present at all study areas. Low percentages of arboreal pollen taxa (from <1 to ~20%) were recorded in most cores. The presence of native *Lycopodium* unfortunately made it impossible to calculate pollen fluxes in this study.

Core LT-98-2M (Figure 1) provides the longest duration vegetation record of our study, covering the interval from about 2660 B.C.–1540 A.D. The core top was completely recovered and there is no sediment dating after the mid 16th century A.D. The core record is dominated by grass pollen (Poaceae-Gramineae). However, it gives clear

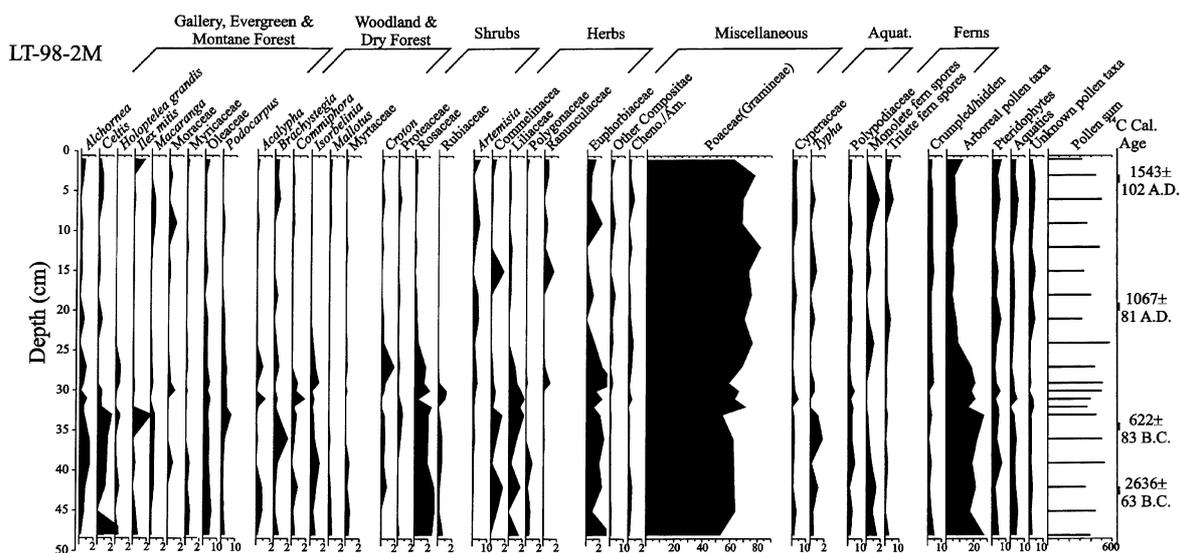


Figure 1. Palynological profiles for Core LT-98-2M, central Lubulungu delta, 110 m water depth (currently undisturbed site). Total core length 49 cm. See Cohen et al. (2005a, Figure 2) for location and bathymetric map. Analyst: Emma Msaky.

indication of a significant decline in forest and woodland taxa (*Celtis*, *Oleaceae*, *Podocarpus*, *Rosaceae*, *Polypodiaceae*), replaced almost entirely by grasses above 25 cm. This record of Late Holocene drying is consistent with prior studies from the region (e.g. Vincens 1993; Verschuren 2004; Verschuren et al. 2000; Alin and Cohen 2003). This change appears to have occurred in stages. An initial decline in arboreal pollen at around 600–500 B.C. (33–34 cm) is coincident with the first rapid changes in lake sedimentological and paleontological indicators discussed in companion papers to this one (Palacios-Fest et al. 2005a, b). From this time until ~500 A.D. (22–21 cm), there is a decline in the abundance of high-elevation conifers (*Podocarpus*). After about 500 A.D., arboreal pollen abundance stabilized at the low levels maintained throughout the remainder of the Late Holocene record, and simultaneously both charcoal flux and sedimentation rates began to rise (Palacios-Fest et al. 2005). A minor increase in arboreal pollen near the top of the core may reflect a partial reversal in the apparent Late Holocene decline of forest cover, or may be part of the long term pattern of arboreal pollen increase observed in other cores over the last few centuries (discussed below).

All remaining cores covered intervals extending up to the present. Cores LT-98-12M, LT-98-18M, LT-98-58M, LT-98-37M, and LT-98-82M all cover periods of at least the last two centuries, and show similar patterns to each other. Therefore, they are best discussed as a group (Figures 2 through 5 and 7). All show unexpected, recent declines in grass pollen abundance upcore. Except at the southernmost site, LT-98-12M (Lubulungu River delta, undisturbed site) this is coupled with substantial increases in pteridophyte spores. The timing of this transition varies geographically, starting in the early 19th century (or before) in the Burundi and northernmost Tanzanian sites and in the southernmost (and currently undisturbed) site, but not until the latest 19th to mid-20th century at the central sites. However, it is not correlated with the specific disturbance levels of individual watersheds, suggesting instead a response to a broader geographic phenomenon. For most of the cores this transition also involved an upcore increase in the euphorbs (especially low elevation taxa such as *Acalypha*, *Alchornea*, and *Mallotus*), the proportion of arboreal indicator taxa, increasing herbaceous plant pollen from groups such as the Compositae and Commelinaceae, and increases in charcoal and mass sediment accumulation rates

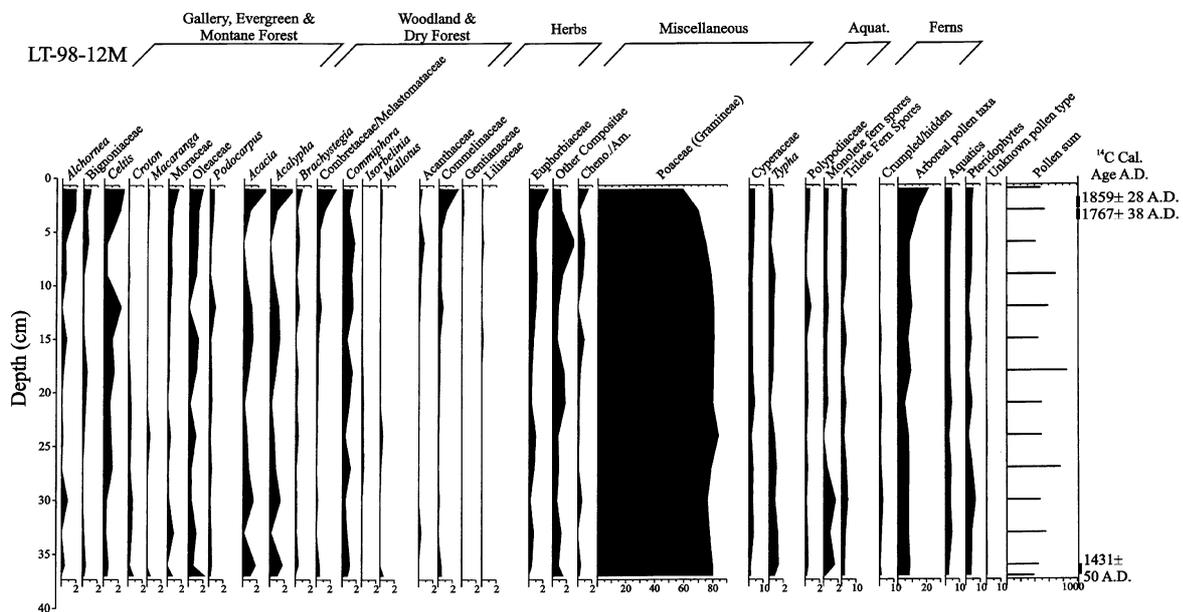


Figure 2. Palynological profiles for Core LT-98-12M, central Lubulungu delta, 126 m water depth (currently undisturbed site). Total core length 40 cm. See Cohen et al. (2005a, Figure 2) for location and bathymetric map. Analyst: Emma Msaky.

(Palacios-Fest et al. 2005). For example, in LT-98-12M (Figure 2) between the base and top of the core, pollen percentages for evergreen taxa (dominantly low-elevation species, e.g. *Acalypha*, *Macaranga*, *Mallotus*, *Celtis*, and Moraceae) increase from less than 1% to about 3%, and total arboreal taxa increase from about 5 to 20%. The most marked change occurs starting in the late 18th century (~6 cm below the core top). A few woodland taxa, such as *Brachystegia*, *Isobertinia* and *Commiphora*, are also represented, although at low values (0–1%). Pteridophyte spores are uncommon throughout the core.

In core LT-98-18M (Figure 3, Kabesi River delta, moderately disturbed site) the grass pollen shows a slow period of decline starting in the late 19th or early 20th century (though within the range of 19th century variability), followed by a precipitous decline starting in the early 1960s. The 1960s change coincides with a major sedimentation rate increase, discussed elsewhere (McKee et al. 2005). Upper elevation woodland and montane forest taxa pollen such as *Podocarpus* and Oleaceae increased substantially since the 1960s. Euphorbiaceae pollen and pteridophyte spores also increase markedly over the same interval.

In core LT-98-58M (Figure 4, Nyasanga/Kahama River delta, undisturbed site), the decline in grass pollen occurred in the early to mid-20th century accompanied by a corresponding dramatic rise in pteridophyte spores. In the upper portion of LT-98-58M (post 1950s) *Acacia*, *Brachystegia*, *Podocarpus* and Polypodiaceae increase markedly. However, somewhat further north, at LT-98-37M (Figure 5, Mwamgongo River delta, high disturbance site), the decline in grass pollen was much more protracted, again accompanied by increasing pteridophyte spores. Arboreal pollen increases along with pteridophytes in LT-98-37M until the mid-20th century, when it begins to decline.

Core LT-98-98M (Figure 6, Nyamuseni River delta, very highly disturbed site in northern Burundi), a high sedimentation rate core that covers the shortest time interval of any core studied, shows no consistent trend of grass pollen replacement by arboreal taxa. It does, however, show a general fern spore increase during the late 20th century. This increase may be synchronous with other core tops, although the vastly different resolutions of LT-98-98M (and its very short duration) versus all other cores makes it difficult to determine this with any certainty. The much longer record from the nearby LT-98-82M

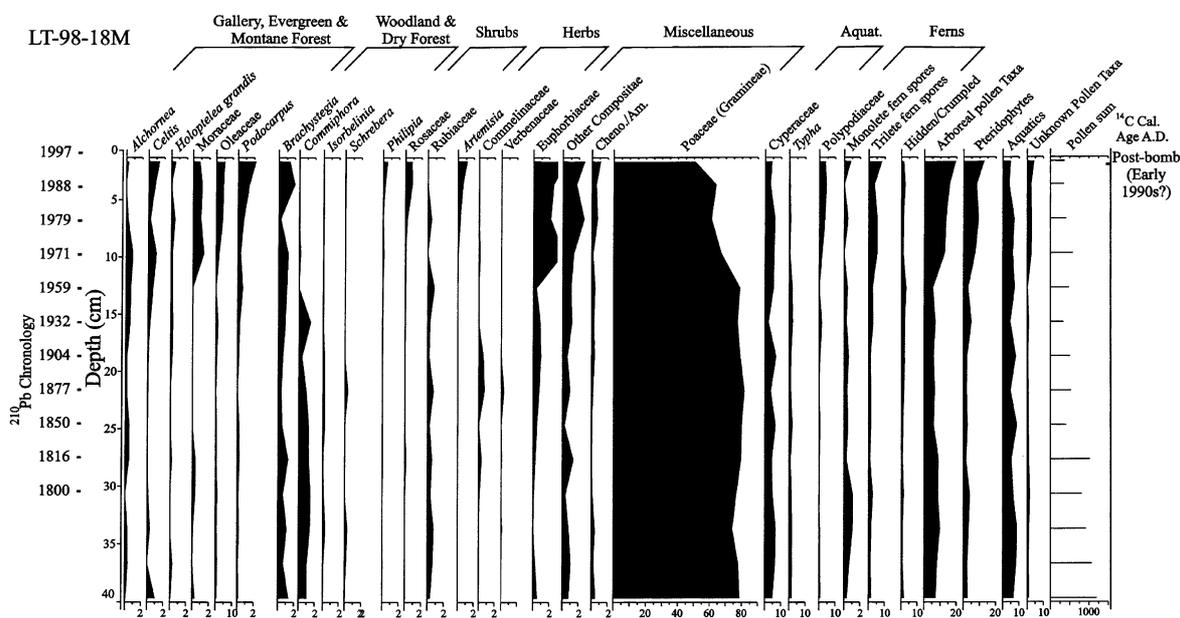


Figure 3. Palynological profiles for Core LT-98-18M, Kabesi River delta, 75 m water depth (currently moderately disturbed site). Total core length 42 cm. See Cohen et al. (2005a, Figure 3) for location and bathymetric map. Analyst: Emma Msaky.

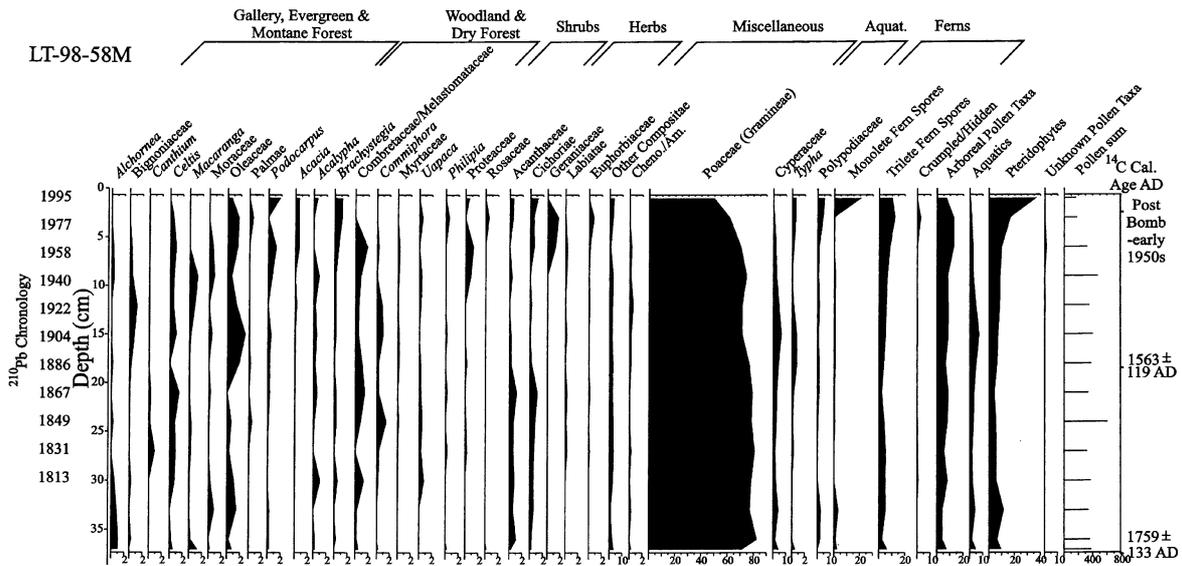


Figure 4. Palynological profiles for Core LT-98-58M, Nyasanga/Kahama Rivers delta, 76 m water depth (currently undisturbed site in Gombe Stream National Park). Total core length 39 cm. See Cohen et al. (2005a, Figure 4) for location and bathymetric map. Analyst: Emma Msaky.

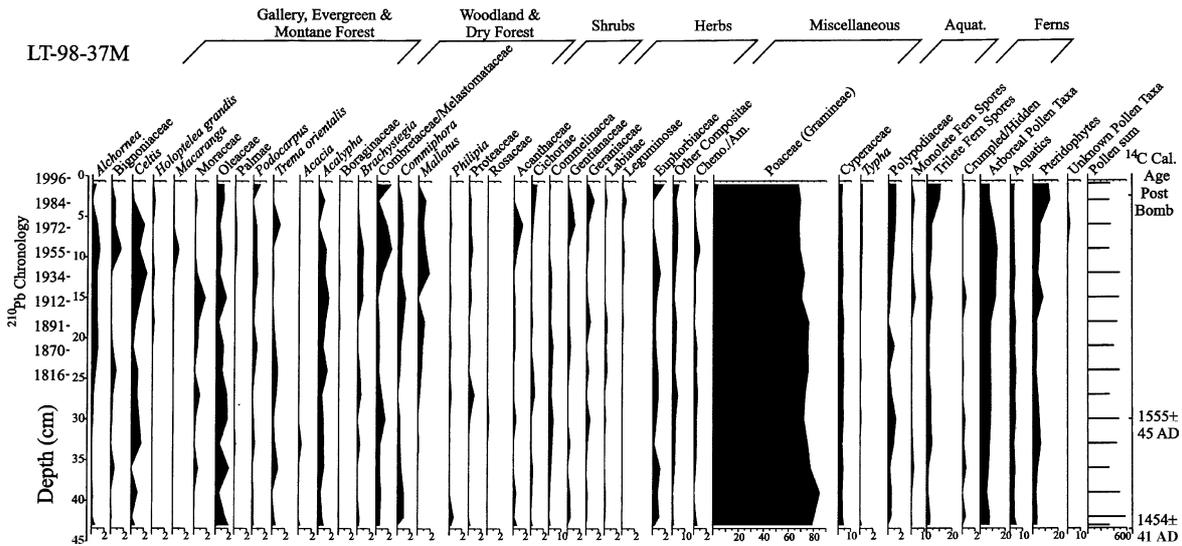


Figure 5. Palynological profiles for Core LT-98-37M, Mwamgongo River delta, 76 m water depth (currently highly disturbed site). Total core length 45 cm. See Cohen et al. (2005a, Figure 4) for location and bathymetric map. Analyst: Emma Msaky.

(Figure 7, Karonge/Kirasa River delta, very highly disturbed site) shows a long-term decline in grass pollen and increases in arboreal pollen and ferns throughout the core length, starting at least as early as the mid 18th century. Particularly notable are increases in low-elevation euphorbs (especially *Mallotus*) and *Celtis*. Myrtaceae

percentages increase dramatically after the 1930s, consistent with the widespread planting of *Eucalyptus* in Burundi starting in the 1930s (P. Ndabaneze and K. West, pers. comm., 1999). However, native Myrtaceae were clearly present prior to the first *Eucalyptus* introductions, and the two types could not be distinguished in this

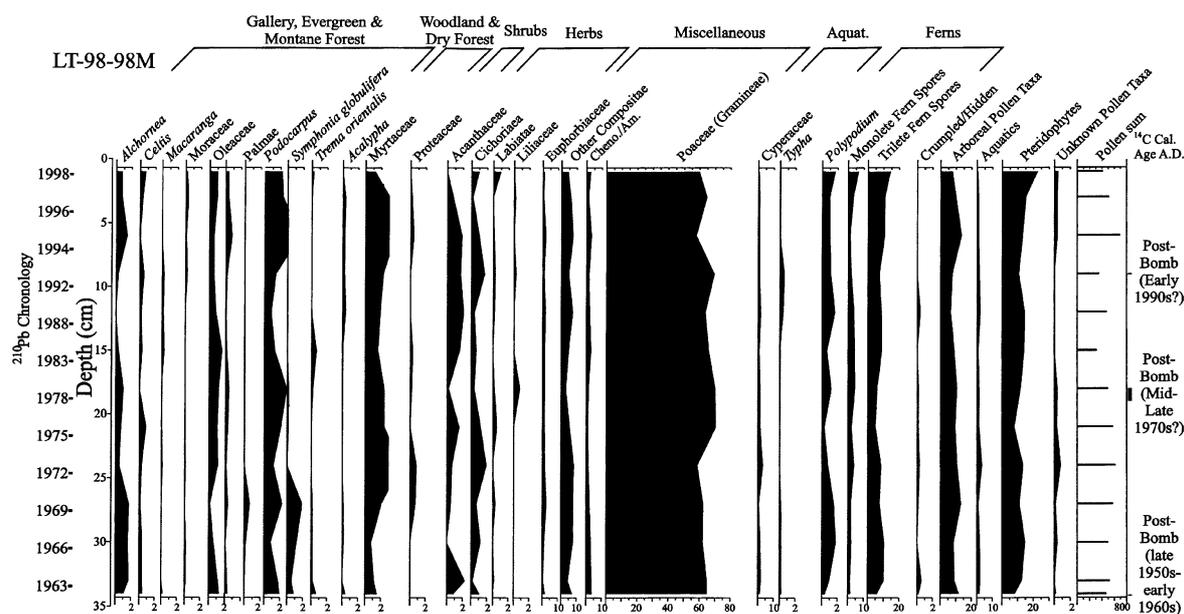


Figure 6. Palynological profiles for Core LT-98-98M, Nyamusenyi River delta, 60 m water depth (currently very highly disturbed site). Total core length 37 cm. See Cohen et al. (2005a, Figure 5) for location and bathymetric map. Analyst: Emma Msaky.

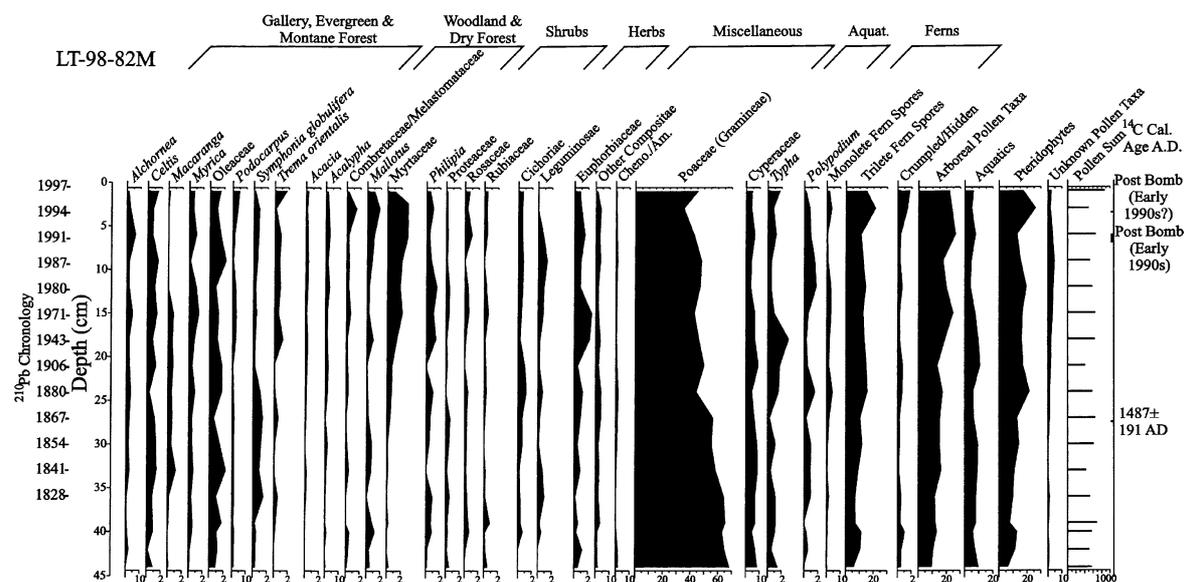


Figure 7. Palynological profiles for Core LT-98-82M, Karonge/Kirasa River delta, 96 m water depth (currently very highly disturbed site). Total core length 46 cm. See Cohen et al. (2005a, Figure 5) for location and bathymetric map. Analyst: Emma Msaky.

study. Myrtaceae is also abundant in LT-98-98M but absent or extremely rare in other cores, consistent with the much more widespread planting of *Eucalyptus* in Burundi than in Tanzania.

The presence of *Acacia* pollen, even at relatively low abundance, is noteworthy in the LT-98-82M core. Acacias are uncommon plants in the modern Karonge/Kirasa watersheds, but occur abundantly

in the Ruzizi River basin, about 30–40 km to the northwest. The occurrence of *Acacia* pollen throughout the middle and upper parts of this core suggests relatively long distance transport of pollen into the core area, possibly by wind, but also perhaps as a result of coastal transport of suspended sediment. The fact that no well-defined northern margin of an offshore delta exists for the Karonge/Kirasa (shallowing continues all the way to the Ruzizi) is consistent with the second explanation, although clearly both processes could be involved. These data also show the scale of spatial averaging of arboreal pollen “rain” that our core sites can be expected to record.

Discussion

Given the partial to near-total absence of forest and woodland cover from the disturbed habitats of the Kabesi, Mwamgongo, Nyamuseni, and Karonge/Kirasa watersheds, the most remarkable finding of this study is the consistent pattern of rising proportions of arboreal, fern and herbaceous pollen/spores relative to grass pollen recorded in many of our cores. This pattern is evident in every core that covers the 19th–20th century interval, including the record from cores at currently undisturbed sites (LT-98-12M at the Lubulungu River watershed in Mahale Mountains National Park and LT-98-58M at the Nyasanga/Kahama River watershed in Gombe Stream National Park, although at the former site, fern increases are very small), and thus appears to reflect a Lake Tanganyika regional phenomenon. For ferns, the timing of this transition is strongly correlated with geography, with the earliest change (18th century) occurring in the northern sites, and progressively later increases towards the south. For arboreal pollen the pattern is more complex, starting in the 18th century in the Mahale Mountains, northernmost Tanzania and Burundi, and in the late 19th-early 20th century in central Tanzania.

At least three explanations can be suggested for the overall pattern of increasing arboreal and fern pollen and decreasing grass pollen observed in multiple cores and over a wide area. The first possibility is that these data record a real trend towards increased forest, fernland or herbaceous cover, at the expense of grasslands, over the past

few centuries. For pollen of herbaceous plants and spores of ferns, this is possible, as both are common indicators of land clearance and disturbance (Kio 1982). However, for the arboreal pollen increase, this explanation seems implausible. First, there is no historical record of such forest expansion, and what little data exist would argue the opposite. Several of our core records span the transition from regionally drier “Little Ice Age” climates to the wetter climatic conditions of the later 19th–20th century, which, in principle, could have driven such a change in vegetation. However, of these, only LT-98-12M shows a long-term trend of increasing arboreal pollen percentages whose timing is consistent with such a climatic forcing mechanism. The increasing percentages of arboreal pollen challenge us to examine the relative proportions of pollen types at the core tops, which for all cores except LT-98-2M record late 20th century conditions, the only time period for which we can examine the proportions of vegetation types directly. Comparisons made in this way show that the most deforested watersheds (Karonge/Kirasa and Nyamuseni) show little difference in terms of proportions of arboreal vs. grass pollen from the least (Nyasanga/Kahama and Lubulungu). All late 20th-century core tops have arboreal pollen percentages in the 10–20% range. Thus, we reject the hypothesis that forest cover has expanded throughout the Lake Tanganyika catchment, beginning in the 18th–19th century in the northern regions and later in the south, and continuing to the present as being too simplistic to adequately explain the data. Whereas forest expansion starting in the early 19th century may explain some of the data from older core records, it does not adequately explain the more recent and abrupt increases in arboreal pollen and fern spores seen in most of our 20th-century records.

A second possibility is that increases in soil erosion rates may have led to the liberation of abundant arboreal pollen previously held in the soil (D. Kinyanjui, pers. comm., 2002). This is certainly possible, although it raises the additional question of why this has occurred simultaneously with the fern and herbaceous spores/pollen increase. A third possibility is that upcore increases in forest pollen actually reflect differential pollen production and are consistent with progressive land use conversion to more intensive, subsistence agriculture. At first glance,

this interpretation may seem surprising and counterintuitive. Particularly where slash-and-burn or rotating types of agriculture are pursued, agriculture might be expected to increase the aerial extent and pollen production of fallow-year elephant grass, and other grasses such as *Andropogon*, *Eragrostis*, etc. However, a consideration of both the nature of the agricultural crops involved and the nature of agricultural practices in these heavily settled areas suggests an alternative scenario. First, almost all of the agricultural species involved in the region's forest/woodland-to-agriculture conversion (cassava, bananas, mangoes, agricultural legumes, tea, coffee, and sisal) either produce very small quantities of pollen, or produce pollen that is not readily dispersed. Unfortunately, the same is true of the common *miombo* woodland trees (e.g., *Brachystegia*, *Julbernardia* and *Isoberlinia*) that grow at low to mid-elevations where human settlement is densest. Second, agricultural lands are used extremely intensively over long time intervals, often to the point of soil nutrient depletion, because of the scarcity of available and suitable land. Continual weeding of subsistence plots and continuous grazing of grasses by livestock (especially goats) prior to flowering may have significantly limited the growth of non-agricultural species, and this process may have been progressive over time. The remaining pollen flux into the lake would then have increasingly been derived from progressively more distant (and higher montane) sources, away from lowland clearance. These upland areas are dominated by trees and fernlands. We favor this hypothesis (perhaps augmented by hypothesis #2 concerning pollen released from soil erosion) because it is consistent with nitrogen isotopic and sedimentary organic matter records from both northern Tanzanian and northern Burundian parts of the lake indicating that soil and eroded material characteristics were changing synchronously with our observed pollen floral changes (O'Reilly et al. 2005). At two of our sites with continuous 19th-/20th-century records (Kabesi and Gombe) charcoal flux also rises synchronously with the palynological changes, although this is not evident from Mwamgongo or Karonge/Kirasa (Palacios-Fest et al. 2005). Also, the geographic pattern of earlier local disturbance indications, in the form of earlier increases in fern spore abundance further north is consistent with what information exists

concerning regional history of human population density and disturbance in the Lake Tanganyika catchment, that Burundi and northernmost Tanzania were probably densely settled in the mid-19th century, whereas population density in west-central Tanzania at that time was probably much lower (Cohen et al. 2005b). A more definitive test of our hypothesized explanation for the relationship between pollen accumulation and watershed clearance would require knowing the absolute flux of the pollen "rain" into the core sites, since the model predicts that overall pollen accumulation rates should be declining to account for a relative increase in the proportion of long-distance arboreal pollen and fern spores. Unfortunately, such a test is rendered impossible with our existing samples because of the presence of native *Lycopodium* in the samples, eliminating the utility of the *Lycopodium* spikes added to the samples.

Another important factor in interpreting the Lake Tanganyika pollen profiles is the likely mode of transport for different pollen types, as this will undoubtedly play a role in where pollen of different species will ultimately be deposited. Pollen of Poaceae (Gramineae) and montane forest taxa such as *Podocarpus* and *Olea* are mainly wind-transported. The pollen of evergreen forest taxa such as *Macaranga* and *Myrica*, woodland taxa such as *Brachystegia* and *Acacia*, and aquatic taxa such as *Typha* and *Cyperaceae* is primarily transported by water (DeBusk 1998). *Podocarpus* pollen, present throughout the Gombe cores, can also be water transported (Peglar et al. 2001), but the nearest regions of sufficient elevation to support this species are probably in southern Burundi, where major streams drain northward away from Lake Tanganyika. Keeping in mind the variation in transport vectors and variable habitats of taxa, no single pollen source area can be defined for the pollen diagram. The composition of a pollen diagram at any point in the lake is thus a complex function of catchment vegetation and the position of the site relative to river discharges and wind currents (DeBusk 1997). Interpretation of this study's pollen diagrams is both complex and difficult because the Lake Tanganyika catchment from which pollen enters the lake is both large and extends over a 2000 m altitudinal range. A more spatially resolved record from small permanent surface water bodies present in the Lake

Tanganyika catchment may assist in interpreting the lake palynological records. The potential taphonomic complexity of the Tanganyikan pollen records highlights the need for modern pollen distributional transect studies in the lake's catchment area.

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References

- Alin S.R. and Cohen A.S. 2003. Lake-level history of Lake Tanganyika, East Africa, for the past 2500 years based on ostracode-inferred water depth reconstruction. *Palaeogeogr. Palaeoclim. Palaeoecol.* 199: 31–49.
- Bygott D. 1992. Gombe Stream National Park. Tanzania National Parks and African Wildlife Foundation, 71 pp.
- Clutton-Brock T.H. and Gillett J.B. 1979. A survey of forest composition in the Gombe National Park, Tanzania. *Afr. J. Ecol.* 17: 131–158.
- Cohen A.S., Palacios-Fest M.R., McGill J., Swarzenski P., Verschuren D., Sinyinza R., Songori T., Kakagozo B., Syampila M. and O'Reilly C. 2005a. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: I. An introduction to the project. *J. Paleolimnol.* 34: 1–18.
- Cohen A.S., Palacios-Fest M.R., Msaky E.S., Alin S.R., McKee B., O'Reilly C.M., Dettman D.L., Nkotagu H.H. and Lezzar K.E. 2005b. Paleolimnological Investigations of Anthropogenic Environmental Change in Lake Tanganyika: IX. Summary of paleorecords of environmental change and catchment deforestation at Lake Tanganyika and impacts on the Lake Tanganyika ecosystem. *J. Paleolimnol.* 34: 125–145.
- DeBusk G.H. 1997. The distribution of pollen in the surface sediments of Lake Malawi, Africa, and the transport of pollen in large lakes. *Rev. Paleobot. Palynol.* 97: 123–153.
- DeBusk G.H. 1998. A 37,000 year pollen record from Lake Malawi and implications for the biogeography of afro-montane forest. *J. Biogeogr.* 25: 479–500.
- Hepper F.N. (ed.) 1963. *Flora of West Tropical Africa*, 2nd ed., vol. II. Crown Agents for Overseas Governments and Administration (Nigeria, Ghana, Sierra Leone, and Gambia), London.
- Hepper F.N. (ed.) 1968. *Flora of West Tropical Africa*, 2nd ed., vol. III, Part 1. Crown Agents for Overseas Governments and Administration (Nigeria, Ghana, Sierra Leone and Gambia), London.
- Kio P.R.O. 1982. Forest conservation strategies for tropical Africa, Chapter 7. In: MacDonald L. (ed.), *Agro-forestry in the African Humid Tropics*. United Nations University, Tokyo, Japan. ISBN 92-808-0364-6, 171 p. Viewed online at <http://www.unu.edu/unupress/unupbooks/80364e/80364E00.htm> Oct., 2004.
- McKee B., Cohen A.S., Dettman D.L., Palacios-Fest M.R., Alin S.R. and Ntungumburanye G. 2005. Paleolimnological investigations of anthropogenic change in Lake Tanganyika: II. Geochronologies and mass sedimentation rates based on ^{14}C and ^{210}Pb data. *J. Paleolimnol.* 34: 19–29.
- O'Reilly C.M., Dettman D.L. and Cohen A.S. 2005. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: VI. Geochemical indicators from lacustrine organic matter. *J. Paleolimnol.* 34: 85–91.
- Palacios-Fest M.R., Alin S.R., Cohen A.S., Tanner B. and Heuser H. 2005a. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: IV. Lacustrine paleoecology. *J. Paleolimnol.* 34: 51–71.
- Palacios-Fest M.R., Cohen A.S., Lezzar K.E., Nahimana L. and Tanner B.M. 2005b. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: III. Physical stratigraphy and charcoal analysis. *J. Paleolimnol.* 34: 31–49.
- Peglar S.M., Birks H.H. and Birks H.J.B. 2001. Terrestrial pollen record of recent land-use changes around nine North African lakes in the CASSARINI Project. *Aquat. Ecol.* 35: 431–448.
- Polhill R.M. (ed.) 1982. *Flora of Tropical East Africa. Gramineae (part 3)*. A.A. Balkema, Rotterdam, 155 pp.
- Polhill R.M. (ed.) 1987. *Flora of Tropical East Africa: Euphorbiaceae, (part 1)*. A.A. Balkema, Rotterdam, 407 pp.
- Pope G.V. (ed.) 1960. *Flora Zambesiaca. Introduction, Cycadaceae, Podocarpaceae, Cupressaceae, Ranunculaceae – Polygonaceae*. Vol. 1, Part 1. Royal Bot. Gardens, Kew, London, 336 pp.
- Pope G.V. (ed.) 1961. *Flora Zambesiaca. Caryophyllaceae – Sterculiaceae*. Vol. 1, Part 2. Royal Bot. Gardens, Kew, London, 245 pp.
- Pope G.V. (ed.) 1963. *Flora Zambesiaca. Tiliaceae – Icacinaceae*. Vol. 2, Part 1. Royal Bot. Gardens, Kew, London, 351 pp.
- Pope G.V. (ed.) 1966. *Flora Zambesiaca. Aquifoliaceae – Connaraceae*. Vol. 2, Part 2. Royal Bot. Gardens, Kew, London, 300 pp.

- Pope G.V. (ed.) 1970. Flora Zambesiaca, Leguminosae, subfamily Mimosoideae, Vol. 3, Part 1. Royal Bot. Gardens, Kew, London, 153 pp.
- Pope G.V. (ed.) 1971. Flora Zambesiaca, Gramineae (Bambuseae - Pappophoreae), Vol. 10, Part 1. Royal Bot. Gardens, Kew, London, 152.
- Pope G.V. (ed.) 1978. Flora Zambesiaca, Rosaceae - Cornaceae (excl. Escalloniaceae and Crassulaceae), Vol. 4. Royal Bot. Gardens, Kew, London, pp. 658 pp.
- Pope G.V. (ed.) 1983. Flora Zambesiaca, Escalloniaceae, Crassulaceae, Valerianaceae, Dipsacaceae and Goodeniaceae – Salvadoraceae, Vol. 7, Part 1. Royal Bot. Gardens, Kew, London, 394 pp.
- Pope G.V. (ed.) 1985. Flora Zambesiaca. Apocynaceae Vol. 7, Part 2. Royal Bot. Gardens, Kew, London, 108 pp.
- Pope G.V. (ed.) 1987. Flora Zambesiaca, Convolvulaceae – Cuscutaceae, Vol. 8, Part 1. Royal Bot. Gardens, Kew, London, 142 pp.
- Pope G.V. (ed.) 1988. Flora Zambesiaca, Rubiaceae, subfamily Rubioideae Vol. 4, Part 1. Royal Bot. Gardens, Kew, London, 250 pp.
- Pope G.V. (ed.) 1989. Flora Zambesiaca, Gramineae (Paniceae, Isachneae and Arundinelleae), Vol. 10, Part 3. Royal Bot. Gardens, Kew, London, 231 pp.
- Pope G.V. (ed.) 1990. Flora Zambesiaca, Canellaceae – Boraginaceae, Vol. 7, Part 4. Royal Bot. Gardens, Kew, London, 114 pp.
- Pope G.V. (ed.) 1991. Flora Zambesiaca, Ulmaceae – Ceratophyllaceae (excluding Myricaceae), Vol. 9, Part 6. Royal Bot. Gardens, Kew, London, 135 pp.
- Pope G.V. (ed.) 1992. Flora Zambesiaca, Compositae, Tribes Mutisieae, Cardueae, Vernoniae, Lactuceae, Arctotideae Vol 6 Part 1. Royal Bot. Gardens, Kew, London, 264 pp.
- Pope G.V. (ed.) 1993. Flora Zambesiaca Iridaceae, Vol. 12, Part 4. Royal Bot. Gardens, Kew, 106 pp.
- Pope G.V. (ed.) 1995. Flora Zambesiaca, Orchidaceae, Vol. 11, Part 1. Royal Bot. Gardens, Kew, London, 328 pp.
- Verschuren D. 2004. Decadal and century-scale climate variability in tropical Africa during the past 2000 years. In: Battarbee R.W., Gasse F. and Stickley C. (eds), Past Climate Variability through Europe and Africa. Developments in Paleoenvironmental Research. Vol. 6. Springer, Dordrecht.
- Verschuren D., Laird K.R. and Cumming B.F. 2000. Rainfall and drought in equatorial east Africa during the past 1100 years. *Nature* 403: 410–414.
- Vincens A. 1991. Late quaternary vegetational history of the south-Tanganyika basin. Climatic implications in south-central Africa. *Palaeogeogr. Palaeoclim. Palaeoecol.* 86: 207–226.
- Vincens A. 1993. Nouvelle sequence pollinique du lac Tanganyika. 30,000 ans d'histoire botanique et climatique du bassin Nord. *Rev. Paleobot. Palynol.* 78: 381–394.