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THE PALEOECOLOGY AND PALEOGEOGRAPHIC CONTEXT OF LEMUDONG'O LOCALITY 1, A LATE MIOCENE TERRESTRIAL FOSSIL SITE IN SOUTHERN KENYA

STANLEY H. AMBROSE[1], CHRISTOPHER J. BELL[2], RAYMOND L. BERNOR[3], JEAN-RENAUD BOISSERIE[4,5], CHRISTYANN M. DARWENT[6], DAVID DEGUSTA[7], ALAN DEINO[8], NURIA GARCIA[5,9,10], YOHANNES HAILE-SELASSIE[11], JASON J. HEAD[12], F. CLARK HOWELL[5], MWANZIA DAVID KYULE[13], FREDRICK KYALO MANTHI[14], ELIUD M. MATHU[15], CHRISTOPHER M. NYAMAI[15], HARUO SAEGUSA[16], THOMAS A. STIDHAM[17], MARTIN A. J. WILLIAMS[18], AND LESLEA J. HLUSKO[19]*

[1]Department of Anthropology
University of Illinois, 109 Davenport Hall, 607 S. Mathews Ave.,
Urbana, Illinois 61801-3636
[2]Department of Geological Sciences
Jackson School of Geosciences; The University of Texas at Austin,
Austin, Texas 78712-0254
[3]College of Medicine, Department of Anatomy,
Laboratory of Evolutionary Biology, Howard University,
520 W St. N.W., Washington, District of Columbia 20059
[4]CNRS, Muséum National d'Histoire Naturelle,
UMR5143, 75005 Paris, France
[5]Human Evolution Research Center, Museum of Vertebrate Zoology,
University of California, Berkeley, California 94720-3160
[6]Department of Anthropology
University of California, Davis, California, 95616-8522
[7]Department of Anthropological Sciences
Stanford University, Building 360, 450 Serra Mall,
Stanford, California 94305-2117
[8]Berkeley Geochronology Center, 2455 Ridge Road,
Berkeley, California 94709
[9]Departamento de Paleontología
Universidad Complutense de Madrid, F.C. Geológicas,
Ciudad Universitaria s/n, 28040 Madrid, Spain
[10]Centro (UCM-ISCIII) de Evolución y Comportamiento Humanos,
C/ Sinesio Delgado 4, Pabellón 12, 28029 Madrid, Spain
[11]The Cleveland Museum of Natural History, 1 Wade Oval Drive,
Cleveland, Ohio 44106-1767
[12]Department of Paleobiology, National Museum of Natural History,
Smithsonian Institution, P.O. Box 37012,
Washington, District of Columbia 20012-7012
[13]Archaeology Program, Department of History
University of Nairobi, P.O. Box 30197 GPO 00100, Nairobi, Kenya
[14]Department of Palaeontology, National Museums of Kenya
P.O. Box 40658, Nairobi, Kenya
[15]Department of Geology, University of Nairobi
P.O. Box 30197-0100, Nairobi, Kenya
[16]Museum of Nature and Human Activities, Yayoigaoka-6, Sanda, Hyogo, 669-1546 Japan

*Corresponding author: Leslea J. Hlusko, hlusko@berkeley.edu

[17]Department of Biology, Texas A&M University,
3258 TAMU, College Station, Texas 77843-3258
[18]Department of Geographical & Environmental Studies
Adelaide University, SA 5005, Australia
[19]Department of Integrative Biology
University of California, 3060 Valley Life Sciences Building,
Berkeley, California 94720-3140

ABSTRACT

The Lemudong'o Formation in the Narok District of Kenya comprises a 135-m-thick series of predominantly lacustrine and lake basin margin sedimentary rocks with interstratified primary and reworked tuffs. The formation, deposited ~6 Ma, records deposition within the second of three sequential lake basins created by tectonic and volcanic activity on the western margin of the southern Rift Valley of Kenya. These sedimentary paleobasins are exposed in the vicinity of the confluence of three rivers cutting steep cliffs into rugged, vegetated terrain. Over 1200 fossils of terrestrial vertebrates have been recovered from the site of Lemudong'o Locality 1 (LEM 1), which was formed at the edge of a shallow lake fed by slow-moving streams. Much like smaller Rift Valley lake basins in Kenya today, the Lemudong'o lake margin probably supported a mosaic of habitats ranging from closed riparian woodland to grassland and swamps.

There are two fossiliferous horizons at LEM 1, clayey sands and gravels and overlying mudstones. Although the mudstones yielded the majority of the fossil material, there are significant faunal differences between the two horizons. The mudstone assemblage consists of taxa whose modern representatives primarily prefer relatively closed environments such as riparian forests, as well as many species that prefer open woodland to wooded grasslands. The sandstone assemblage samples fauna from a wider range of habitats. This contrast in taxonomic composition suggests that the mudstone and sandstone horizons sample a lakeshore environment that was varying through time. The apparent shift in habitat preferences of the fauna is consistent with the geological and geomorphological evidence for a mosaic of closed to open habitats that characterize rapidly variable rift-valley lake basins in mesic climatic regimes.

One of the salient characteristics of these assemblages is the complete absence of fish, and the paucity of large mammals and reptiles, such as hippos, crocodiles, and larger bovid species that would be expected at the edge of lake basins fed by large rivers. Modern central rift-valley lake basins that are fed by small streams vary widely in size and salinity in response to climate change, and occasionally dry out completely. They do not contain fish and crocodiles, and only one has a substantial hippo population. These modern rift-valley lakes may therefore provide an analog to the depositional environment of Lemudong'o.

The LEM 1 fossil assemblage is also unusual because it is dominated by small mammalian taxa, including numerous rodents, small colobine monkeys, hyracoids, and a diversity of viverrid and other carnivores. Given the lack of evidence for fluvial transport in the main fossil horizon, the biased size composition, and the significant carnivore damage on the bones, we interpret this site to represent an accumulation of carcasses by several avian and small mammalian carnivores. This paleoecological and paleogeographic reconstruction is discussed relative to penecontemporaneous fossil sites in Africa.

Introduction

Lemudong'o Locality 1 (LEM 1) exposes 6 million-year-old sedimentary rocks, volcaniclastic rocks, and primary tuffs deposited within the second of three late Neogene paleolake basins reconstructed by Wright (1967) in the Ewaso Ngiro and Siyabei River valleys (Ambrose, Nyamai et al., 2007; Deino and Ambrose, 2007). Paleoanthropological research has been conducted in this region since 1994 (Ambrose, Kyule, and Hlusko, 2007). Here we provide a reconstruction of the paleoecological and depositional environments in the area of LEM 1 within the Lemudong'o paleolake basin, combining preliminary geological

research with more in-depth paleontological studies that are published in detail in this issue of *Kirtlandia* (Bernor, 2007; Boisserie, 2007; Darwent, 2007; Head and Bell, 2007; Hlusko, 2007a and 2007b; Hlusko and Haile-Selassie, 2007; Hlusko et al., 2007; Howell and Garcia, 2007; Manthi, 2007; Pickford and Hlusko, 2007; Saegusa and Hlusko, 2007; Stidham, 2007).

Paleolandscape of the Lemudong'o Formation

The three main types of rift-valley sedimentary basins include large, deep, fresh-water basins (such as Lakes Tanganyika and Malawi), closed basins supplied by very large river systems (such

as Lake Turkana) and smaller closed basins (Frostick and Reid, 1990; Tiercelin, 1990). The Lemudong'o basin may have been of the third general rift-basin type, a small half-graben on the western margin of the nascent eastern (Gregory) Rift Valley, which is exemplified by the Baringo and Bogoria basins in the north-central Rift Valley of Kenya. Although a fault named the Naitiami Fault (Wright, 1967; Crossley, 1979) that may have formed such a half-graben is recognized south of this paleobasin, the hypothesized fault scarps that should have bounded this basin have not yet been identified. The Lemudong'o paleobasin lies above the western margin of the Rift Valley, so it may have more closely resembled rift-margin plateau basins such as the modern Amboseli basin or the Olduvai Gorge paleobasin (Hay, 1976).

Although Baringo and Bogoria may provide useful modern analogs for the geology and geomorphology of Lemudong'o, they are located within a comparatively hot and arid segment of the northern/central Kenya Rift Valley. The Naivasha and Nakuru/Elementeita basins in the central Rift Valley of Kenya, where rainfall is higher, may provide more appropriate ecological analogs for the Lemudong'o paleobasin.

Volcanic eruptions and tectonic activity along rift-valley margins often block drainages, forming small lakes with limited catchment areas. Such closed-basin lake levels will fluctuate rapidly in response to variations in rainfall, evaporation, seepage, stream flow, and groundwater recharge. Water loss will primarily result from evaporation, and as such, water quality can change quickly from fresh to saline and/or alkaline in response to short and long term variation in rainfall. Fossil preservation is favored by such rapid sedimentation in closed lake basins (Hay, 1976; Frostick and Reid, 1990; Tiercelin, 1990; Pickford, 1994).

Within the lake-margin zone, where sedimentation is rapid and subaerial exposure of sediments is intermittent, soil horizons will be weakly developed, and easily eradicated by large-mammal trampling and other agents of bioturbation. Such fine-grained sediments are usually classified as claystones and mudstones, similar to those seen in the Lemudong'o Formation, and represent shallow lakes, swamps, or frequently inundated floodplains. Paleosol carbonates are rare in such wet environments, but fossils of terrestrial species may be common. Again, this is similar to what we find at LEM 1 and more widely within the Lemudong'o Formation (Ambrose, Nyamai et al., 2007).

Because such rift-valley lakes can vary rapidly from fresh to highly alkaline, and occasionally dry out completely, fish populations are not able to establish and populations of crocodiles and hippopotamuses are limited. Therefore, the absence of these animals does not always indicate that water was not present, or rather, a lake could well have existed in the area that did not support such aquatic faunal elements.

Transgressive and regressive shorelines are marked by horizons of well-sorted sands and fine gravels. Where ephemeral or seasonal streams flow into a lake, deltaic fans of coarse-grained sands and gravels would be juxtaposed with fine-grained lake silts and clays. Depending on elevation and distance from the permanently inundated basin center, and the frequency of inundation, lake-margin microhabitats may span the continuum from bare sediment and open grass to woodland and dense groundwater-fed riparian forest. Gallery forest and woodlands may also occur where slow-moving streams meander across relatively flat lake-margin zones.

The fauna preserved at LEM 1 suggests that these late Miocene sediments captured such a relatively closed environment. The sedimentology suggests that this environment was associated with an ephemeral rift-valley lake system.
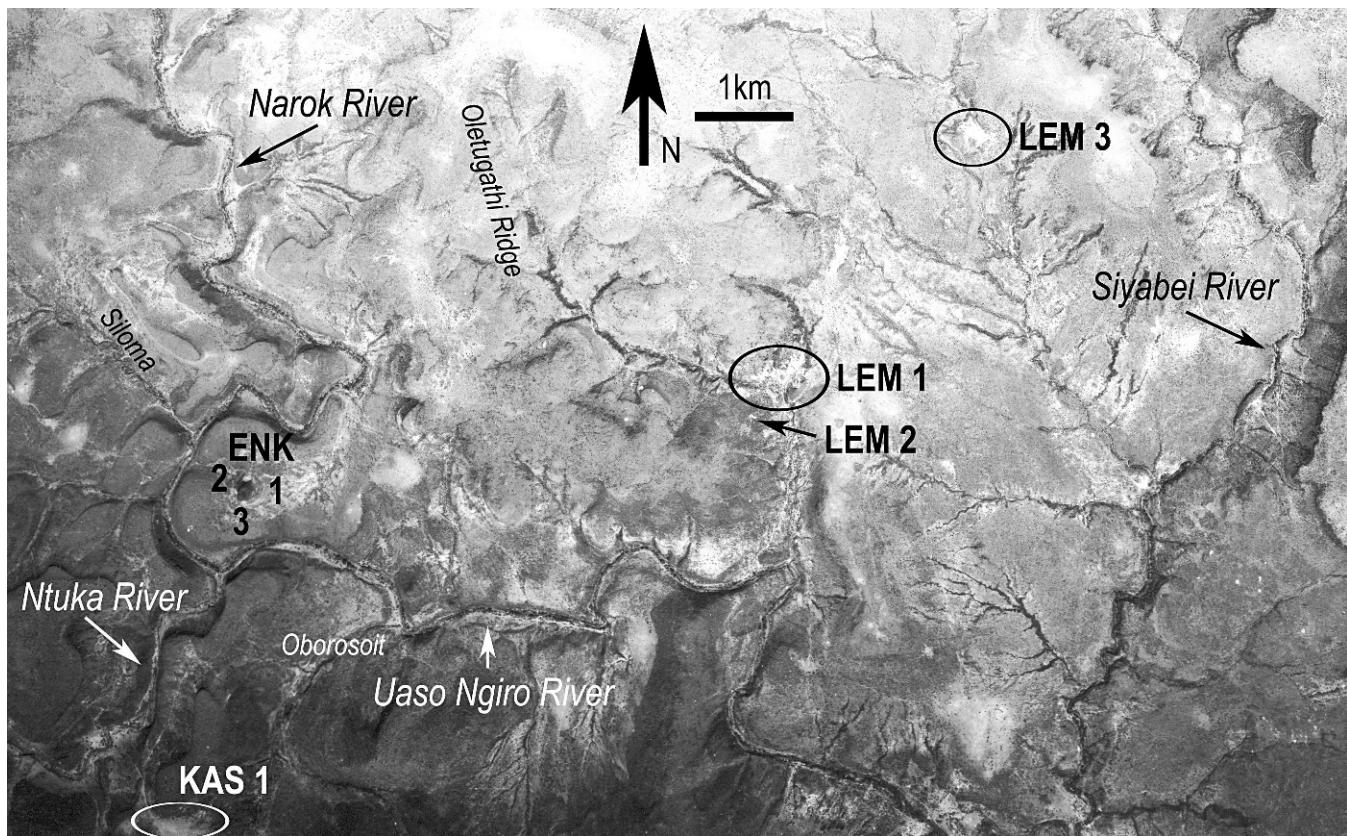
Structural Geology and Sedimentary Environments of the Lemudong'o Formation

Based on the distribution of waterlain sedimentary rocks and volcaniclastic strata, Wright (1967, p. 31) reconstructed the minimum extent of the Lemudong'o paleolake basin, which he called the "first Uaso Ngiro lake," as >16 km from north to south and >8 km from east to west (Figure 1). The south shore of the lake was partly bounded by a prominent hill of erosion-resistant Archaean metamorphic rocks called Ol Doinyo Oborosoit ("hill of white rocks" in the Masai language). The western margin of the lake was bounded by lava flows and sedimentary rocks. The eastern and northern margins are poorly exposed and not well-defined. The Oletugathi Ridge lies east of the Ewaso Ngiro River and parallels the north/south-trending Enkorika Fault. Eroded basalts underlying the Lemudong'o Formation may have formed a line of low hills within the paleobasin during the earliest phases of basin sedimentation.

Horizontal bedding suggests syn- or post-depositional uplift and tilting of the Lemudong'o Formation was insignificant in most of the localities in the center and west side of the paleobasin. However, the elevation of the top of the Lemudong'o Formation is 60–70m lower in the Lemudong'o area. The normal N-S trending Enkorika Fault, a major post-depositional structure, defines the east side of the Lemudong'o Gorge (Wright, 1967), and a smaller E-W trending fault at the north end of LEM 1 may have dropped strata belonging to the youngest paleolake episode (Wright's Siyiapei Lake) to the level of the Lemudong'o Formation. We suspect this block is down-faulted because the east side of the paleobasin lies closest to the modern Rift Valley, and faulting has shifted toward the modern rift axis over time (Birt et al., 1997).

The Lemudong'o Formation is formally named and described elsewhere (Ambrose, Nyamai et al., 2007). The formation is exposed at several localities dispersed over an area of more than 1250 km^2, shown in part in Figure 1. The formation records three main phases of sedimentation in the paleobasin. Phase 1 is represented by a sedimentary sequence dominated by siltstones, mudstones, and sandstones. Phase 2 consists of paleosols in the basin center, and fluvial and alluvial sedimentary rocks on the eastern margin of the basin. Phase 3 comprises mostly waterlain tuffs and siltstones, with a gray ignimbrite welded tuff capping the formation. Thus, the sequence represents a cycle of wetter, drier, and then wetter depositional environments. Vertebrate fossils are most abundant in the upper half of sedimentary phase 1, which is therefore the focus of our discussion.

The Lemudong'o paleolake formed on a deeply eroded and undulating land surface of Neoproterozoic gneiss (Oldoinyo Oborosoit) and early Miocene lavas and ignimbrites, as observed by elevation changes at the basal contact of the late Miocene section. In particular, we note the 65 m of relief observed in the top of the basal gray welded ignimbrite at Enamankeon Locality 2 (ENK 2), and the Oletugathi Ridge, where Lemudong'o Formation exposures lie unconformably on eroded lavas. Although the paleotopography of the Lemudong'o sedimentary basin floor may have been carved in part by streams and rivers, fluvial deposits have not been observed at the base of most of the sedimentary sequences studied. Speculatively, sedimentary depositional rates may have been rapid in the topographic lows

Figure 1. Aerial photograph showing the geography of the correlated late Miocene localities that expose sediments of the Lemudong'o Formation in the Narok District of Kenya. KAS 1 = Kasiolei Locality 1; LEM = Lemudong'o Localities; ENK = Enamankeon Localities. Scale is approximate. Figure is modified from Ambrose, Nyamai et al. (2007).

filled during this period, so despite the substantial thickness of the section (up to 65 m), the phase 1 sedimentation episode may have been brief. This complex paleotopography may have supported a diverse range of semi-aquatic and terrestrial floral microhabitats.

As sedimentation progressed, previously isolated small sedimentary loci such as those at ENK 2 and Kasiolei (KAS 1) may have coalesced into larger basins, forming the more continuously traceable beds of claystones, mudstones, and volcaniclastic units of the later stages of phase 1 accumulation, and the paleosols, alluvium, laminated siltstones, and tuffs of phases 2 and 3 in the upper 70 m of the Lemudong'o Formation.
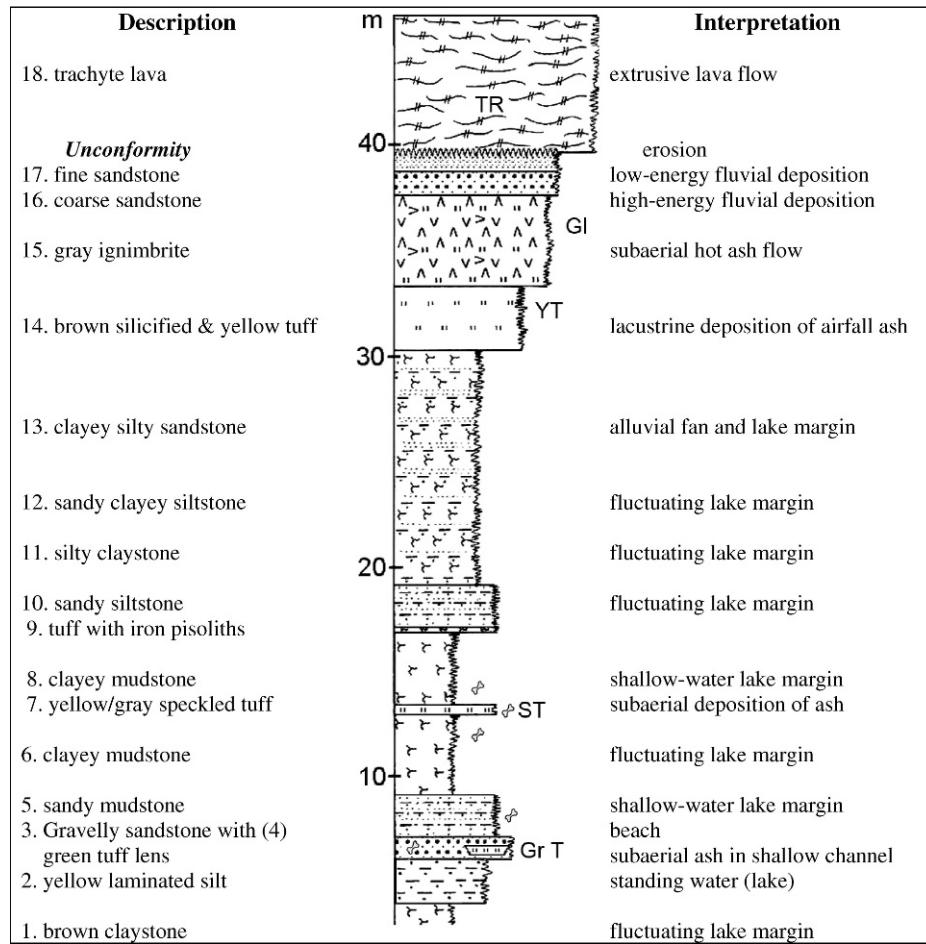
Depositional Environments of LEM 1

The main fossil horizons at LEM 1 are relatively high in the sequence of phase 1 mudstone deposits (Figure 2). They are comprised predominantly of mudstones and claystones, with thin, discontinuous beds of poorly sorted coarse sandstones. Sediments above the fossil-bearing levels grade into phases 2 and 3 of the wider paleobasin sedimentary sequence.

At LEM 1, deposition begins with mudstones and claystones, representing a lake-margin environment (Figure 2, unit 1). Only the top meter of this bed is exposed in LEM 1. However, at Lemudong'o Locality 2 (LEM 2) it is over 20-m thick, and contains three tuffs dated to 6.09 to 6.12 Ma (Ambrose et al.,

2003; Deino and Ambrose, 2007). Yellow laminated lacustrine silts (unit 2), representing deep-water deposits of a larger lake, overlie the basal mudstones. Clayey sands and imbricated, fine, well-sorted sandy gravels, fining upward to mudstones, overlay these lacustrine silts (units 3 and 5). These coarse sediments are fossiliferous sands and comprise the lower of the two fossil-bearing horizons at LEM 1. These sands may reflect a regressive beach shoreline or a small stream delta. The imbricated gravels could also reflect fluvial deposition, but stream-channel features such as cross-bedding and channel margins are lacking. A lens of green, fine-grained tuff within the coarse lower clayey sands (unit 4) may be a channel fill, but the tuff may have filled a small depression in the lake margin.

The overlying fine-grained clayey mudstones (unit 6) contain the majority of the fossils described from LEM 1 (Table 1), and the speckled tuff (unit 7), dated to 6.08 Ma (Deino and Ambrose, 2007). Sediments above the speckled tuff (units 10–13) gradually change from clays and silts to poorly sorted sands, reflecting predominantly alluvial/colluvial deposition, perhaps from a nearby fault scarp or upland. These coarse-grained sediments mark the onset of phase 2 basin-wide sedimentation. The yellow tuff and gray ignimbrite (units 14 and 15), cap the LEM 1 and 2 sequences, marking the last major expansion and termination of phase 3 basin-wide sedimentation of the Lemudong'o Formation lake. Trachyte lava (unit 18) lies

Figure 2. Stratigraphic column for Lemudong'o Locality 1 South (GvJh15) paleontological site, Narok area, southwest Kenya. Locality is at 1°18′1″ S, 35°58′44″ E, at an elevation of 1648 m. Abbreviations: TR, trachyte lava; GI, gray ignimbrite; YT, yellow tuff; ST, speckled tuff; GrT, green tuff.

unconformably (units 16–17) above the gray ignimbrite, which defines the upper boundary of the Lemudong'o Formation in the Lemudong'o Gorge.

Lateral facies variations in depositional subenvironments are pronounced within LEM 1. For example over a horizontal distance of approximately 100 m, the yellow lacustrine silts vary in thickness from two to six meters from east to west. This lacustrine silt bed is prominent and well defined at LEM 1, and it dips 3° east, toward the present Rift Valley, but thins at LEM 2 and thickens again in the lower Lemudong'o Gorge. These laminated silts are exposed only within the Lemudong'o Gorge localities. The beach/delta sands (Figure 2, units 3 and 5) and gravels at LEM 1 vary in thickness from 0.1 to ~2 m along the N/S axis of the gorge, disappearing completely near the northern limits of the outcrop, and thickening rapidly toward the south end of the main collection area. These coarse deposits contain fossils of predominantly large mammals, with more aquatic species, including crocodiles and hippos.

Sediments above and lateral to this beach (Figure 2, units 6–8) grade from clayey and sandy siltstones to claystones (collectively mudstones), reflecting low energy deposition in a swampy, fluctuating lake margin zone. Modern exposed surfaces of the dark gray,

green and dark gray-brown claystones form deep cracks when dry, and are mantled by spheroidally weathered rounded peds, typically 1–3 cm in diameter informally referred to as "popcorn clays" (Richard Hay, personal communication, 1995). Dark, drab colors indicate deposition in predominantly wet or frequently inundated anoxic lake-margin environments, and bentonitic ("waxy") clays often indicate alkalinity (Hay, 1976). These silts and clays contain exclusively terrestrial-vertebrate fossils and seeds of the forest tree *Celtis zenkeri* (Ambrose et al., 2003).

Sediments above the speckled tuff coarsen upward from waxy, silty and sandy claystones to poorly sorted silts, sands and fine sandy gravels (units 10–13), most likely reflecting a distal alluvial/colluvial fan depositional environment. These coarse deposits lack fossils. At Enamankeon West (Figure 1 ENK Locality 2) this position in the stratigraphic section contains an ~11-m-thick series of paleosols with vertebrate fossils. This may have been a period of greater aridity, lower vegetation density and higher rates of erosion.

The alluvial sediments at LEM 1 are overlain by poorly exposed claystones and mudstones (uppermost unit 13), reflecting a return to a fluctuating lake-margin environment before lacustrine deposition of the yellow tuff (unit 14). At Enamankeon a thick bed of lacustrine silts beneath the yellow tuff reflects

Table 1. Faunal List, Lemudong'o Locality 1 mudstones (NISP = 600).

Aves
  Galliformes
    Phasianidae
  Falconiformes
    Acciptridae
  Strigiformes
    Strigidae (cf.)
Mammalia
  Insectivora
  Primates
    Cercopithecidae
      Colobinae
        Paracolobus enkorikae
        large species
        small species
  Rodentia
    Hystricidae
      Atherurus sp.
      Hystrix sp.
      Xenohystrix sp.
    Muridae
      Gerbillinae
        Tatera sp.
      Murinae
        Acomys sp.
        Aethomys sp.
        Arvicanthis sp.
        Lemniscomys sp.
        Mastomys sp.
        Saidomys sp.
    Sciuridae
      Sciurinae
        Paraxerus sp.
        Xerus sp.
    Thryonomyidae
      Thryonomys sp.
  Hyracoidea
    Procaviidae
      Dendrohyrax validus (cf.)
  Lagomorpha
    Leporidae
  Carnivora
    Canidae
      Eucyon aff. *intrepidus*
    Felidae
      Leptailurus sp.
    Mustelidae
      Plesiogulo botori
    Procyonidae
      Simocyon sp.
    Herpestidae
      Helogale sp.
      Herpestes sp.
      Ichneumia aff. *albicauda*
    Viverridae
      Genetta sp. 'Y'
Perissodactyla
  Rhinocerotidae
Artiodactyla
  [1]Suidae
  [2]Hippopotamidae
  Bovidae
    Aepycerotini
      Aepyceros aff. *A. premelampus*
    Boselaphini
    Neotragini
      Madoqua sp.
    cf. Tragelaphini
Reptilia
  Crocodylia
  Serpentes
    Colubroidea
    Pythoninae

[1] represented by an associated set of deciduous teeth

[2] represented by one fragmentary specimen

a larger lake, and probably wetter climate during paleobasin sedimentation phase 3. No significant fossils have been observed in phase 3 sediments.
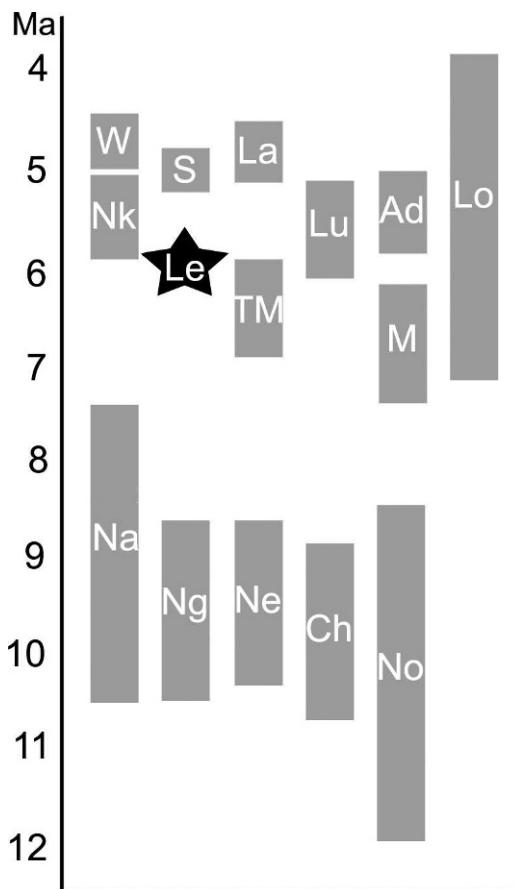
The geological and geomorphological evidence presented above suggests that the main fossil locality of LEM 1 occupies a position on the eastern margin of the Lemudong'o Formation paleobasin. The habitat preferences of the modern counterparts of the tree and vertebrate fossil species suggests that predominantly forest habitats characterized the paleolake margin zone during the main period of fossil accumulation at Lemudong'o. The fossils probably accumulated in riparian gallery forests near the fluctuating margin of the paleolake. The vertebrate fossil evidence is discussed in the following section.

Vertebrate Paleontological Approaches to Paleoenvironmental Reconstruction

Andrews (1996), Bobe and Eck (2001), and Reed (2002) have provided useful reviews of the objectives, methods and limitations of paleoenvironmental reconstruction based primarily on mammalian fossil communities and their modern analogs. Paleoecological reconstructions based on vertebrate faunal assemblages are inherently less accurate and imprecise because of the mobility and wide range of habitat preferences of many species. The ecology and habitat preferences of modern species are usually assumed to be the same as those of fossil representatives of the same species, genera or families. However, their adaptations may have evolved and changed during the Neogene (Solounias and Dawson-Saunders, 1988; Andrews, 1996; Sponheimer et al., 1999). This becomes an important consideration when the fossil assemblages are older and species are less closely related to their extant relatives. Members of extinct lineages, such as sabre-toothed felids and megaherbivores, may have influenced community structure in ways that we can never fully appreciate from studies of modern ecosystems. Moreover, niche shifts in extant lineages may have occurred in response to extinctions of lineages with no modern counterparts, and in response to competition with immigrant species. Therefore modern species cannot be assumed uncritically to be living fossils that can be used as exact analogs for members of ancient faunal communities unless their ecological attributes can be independently demonstrated to be similar by functional morphology, dental microwear and/or stable isotope analyses (Solounias and Dawson-Saunders, 1988; Sponheimer et al., 1999).

Taxon-free methods of environmental reconstruction based on ecomorphological attributes, including body size, locomotor anatomy, substrate preference, and dietary adaptation (Andrews et al., 1979; Kappelman, 1988; Legendre, 1991; Andrews, 1996; Reed, 2002; DeGusta and Vrba, 2003; Haile-Selassie et al., 2004b; DeGusta and Vrba, 2005) may overcome some of the limitations of taxon-based referential models. Multidisciplinary approaches using analog species, ecomorphology, macro- and micropaleontology, geology, geomorphology, and soil and fossil stable isotope geochemistry (Cerling et al., 1997; Williams et al., 1998; Retallack, 2001; Cerling et al., 2003) are therefore the preferred approach for paleoenvironmental reconstructions as they provide crosschecks to individual methods.

Correlation with global climatic records (DeMenocal and Bloemendal, 1995) provides an additional source of evidence for reconstructing environments. However, correlation requires precise and accurate geochronology, and the role of local geological influences must also be considered, especially in tectonically active rift-valley settings (Hill, 1987). Here we summarize the results of
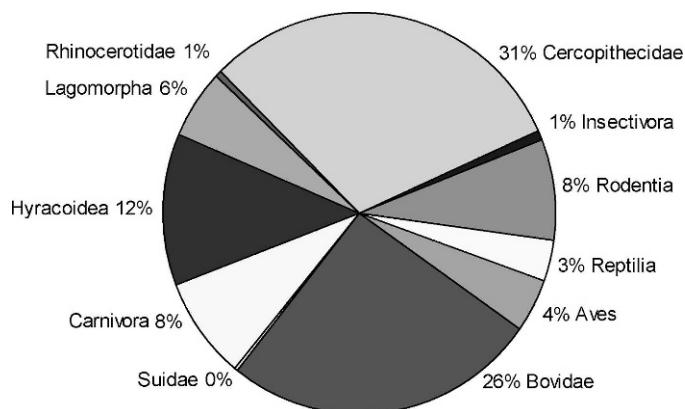
Figure 3. Temporal distribution of African late Miocene and early Pliocene paleontological sites, after Haile-Selassie et al. (2004a). Key: Ad = Adu-Asa; Ch = Chorora; La = Langebaanweg; Le = Lemudong'o; Lo = Lothagam; Lu = Lukeino; M = Mpesida; Na = Nakali; Ne = Namurungule; Ng = Ngeringerowa; Nk = Nkondo; No = Ngorora; S = Sahabi; TM = Toros-Menalla; W = Wembere-Manonga.

Figure 4. Pie chart of taxonomic representation in the mudstones of LEM 1, based on NISP = 600.

multiple independent studies for reconstructing the local environment of the LEM 1 fauna, using both taxon-based and taxon-free methods.

LEM 1 Vertebrate Fauna

Only terrestrial vertebrate fossils and a few crocodile and hippopotamus teeth were found at LEM 1. Although the assemblage consists primarily of highly fragmentary specimens, given the rarity of mammal-dominated fossil sites of this age, these fossils provide important insights to the evolution of terrestrial animals in the late Miocene of Africa. Figure 3 shows the temporal position of the Lemudong'o Formation relative to other late Miocene to early Pliocene African fossil sites.

The Lemudong'o and other Narok fossils are described in detail elsewhere (Bernor, 2007; Boisserie, 2007; Darwent, 2007; Head and Bell, 2007; Hlusko, 2007a and 2007b; Hlusko and Haile-Selassie, 2007; Hlusko et al., 2007; Howell and Garcia, 2007; Manthi, 2007; Pickford and Hlusko, 2007; Saegusa and Hlusko, 2007; Stidham, 2007). Table 1 lists taxa represented in the mudstone horizon, identified by collection location and/or

distinctive preservation (number of identifiable specimens, NISP = 600). Taxonomic proportions are shown in Figure 4. Table 2 lists the fauna from the underlying sandstone (NISP = 21), and Table 3 presents a composite list, including specimens whose provenience to horizon is not certain, as well as those specimens included in Tables 1 and 2 (NISP = 1245). These fossil assemblages derive from strata that lie between tuffs with indistinguishable radiometric ages of 6.084 ± 0.018 and 6.087 ± 0.013 Ma (Deino and Ambrose, 2007), and so were deposited in a short interval of geologic time.
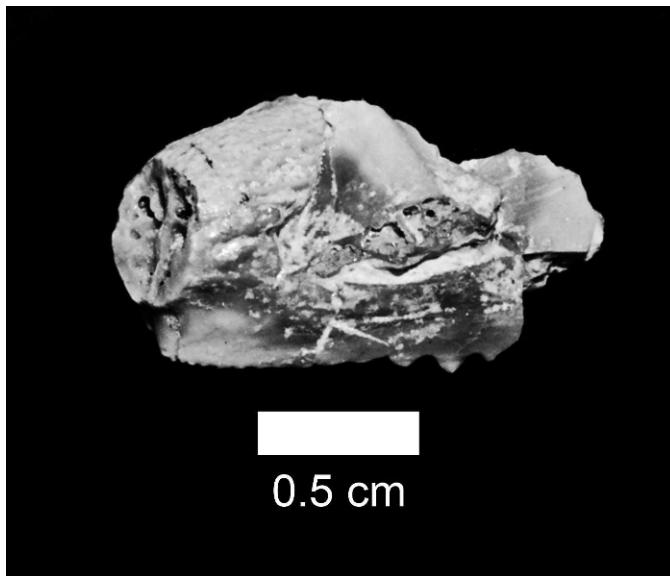
Reptilia
A few crocodylid teeth have been recovered from the sandstone horizon, however the most common reptiles found at LEM 1 are Serpentes. Unfortunately, only serpent vertebral elements were recovered limiting the alpha taxonomy of the material. However, these specimens indicate that Pythoninae and a colubroid snake were present (Head and Bell, 2006). In 2004 we found a partial skull of a Chamaeleonidae (Figure 5).

Aves
LEM 1 has yielded skeletal remains of an eagle, an owl, and possibly a pheasant (Stidham, 2007). The eagle is large, possibly similar to a fish eagle. The owl is approximately the size of *Asio flammeus* and *Strix woodfordi*. Additionally, two specimens are morphologically quite similar to modern pheasants, although this is a tentative designation given the fragmentary nature of the specimens. The avifauna of LEM 1 is predominately terrestrial and similar to Eurasian taxa, as has been noted for other contemporaneous and penecontemporaneous sites (Stidham, 2007). The lack of aquatic birds is relatively unusual, although this may be a result of the small sample size or a lack of fish for them to feed on in the aquatic environment, rather than from the absence of a local water source. The presence of an eagle and an owl most likely suggests proximity to appropriate roosting sites and indicates that carnivorous birds were present in the area, perhaps accounting for some of the bone accumulation.

Insectivora
Five edentulous or fragmentary insectivore mandibles have not yet been described.

Figure 5. Partial skull of a Chamaeleonidae from Lemudong'o Locality 1 (KNM-NK 45775).

Table 2. Faunal List, Lemudong'o Locality 1 sandstone (NISP = 21).

Aves
Indeterminate
Mammalia
Primates
Cercopithecidae
Colobinae
Rodentia
Hyracoidea
Carnivora
Felidae
Lokotunjailurus emageritus
Hyaenidae
Hyaenictis aff. *hendeyi*
Mustelidae
Plesiogulo botori
Proboscidea
Gomphotheriidae
Anancus kenyensis
Perissodactyla
Equidae
Eurygnathohippus cf. *E. feibeli*
Artiodactyla
Bovidae
Aepycerotini
Tragelaphini
Tragelaphus
Hippopotamidae
Hippopotaminae
Suidae
Nyanzachoerus syrticus
Reptilia
Crocodylia
Indeterminate

Primates

To date, only cercopithecoid primates have been found at LEM 1. Cercopithecoids comprise a large proportion of the total assemblage (~31% of the mudstone assemblage), sampling at least three taxa. This assemblage is unusual compared to other late Miocene/early Pliocene African sites, except for, perhaps, the Kapsomin site at Lukeino, Kenya (Pickford and Senut, 2001), in that all specimens identifiable to subfamily belong to Colobinae (Hlusko, 2007b). The best represented is a new species *Paracolobus enkorikae* that is much smaller than other known species of *Paracolobus*, approximately 7–8 kg in estimated body weight (based on dental metrics from Hlusko, 2007b, and regressions from Delson et al., 2000). There are a few teeth from a larger colobine (approximately the size of a small *Parapapio*) and several jaws of a much smaller colobine (similar in size to *Prohylobates tandyi*). Associated postcranial elements of *Paracolobus enkorikae* suggest that this colobine was dedicated to an arboreal habitus. Although other contemporaneous sites have yielded colobines (Pickford and Senut, 2001; Vignaud et al., 2002; Leakey and Harris, 2003), they lack the species diversity seen at LEM 1. Slightly younger assemblages in the Middle Awash and Lothagam (Leakey and Harris, 2003; Haile-Selassie et al., 2004b) include a wider range of taxa within the Cercopithecinae.

Rodentia

Ninety-three rodent specimens were recovered from LEM 1. These represent two families of hystricomorphs: Hystricidae (*Atherurus*, *Hystrix*, and *Xenohystrix*) and Thryonomyidae (*Thryonomys*); two families of sciuromorphs: Muridae (Gerbillinae: *Tatera*; and Murinae: *Acomys*, *Aethomys*, *Arvicanthis*, *Lemniscomys*, *Mastomys*, and *Saidomys*), and Sciuridae (*Paraxerus* and *Xerus*) (Hlusko, 2007a; Manthi, 2007). The hystricids, or porcupines, are quite diverse, sampling all three genera known to live or have lived in Africa (Hlusko, 2007a). This is similar to the diversity of hystricids found at the western margin Adu-Asa Formation localities in Ethiopia (Haile-Selassie et al., 2004b), although LEM 1 predates the western margin sediments by at least 200,000 years. The small rodent fauna is quite diverse although the taxa derive primarily from more mesic habitats (Manthi, 2007).

Lagomorpha

No lagomorph specimens have yet been recovered from the sandstones. Based on known provenience and preservation, all of the lagomorph specimens appear to derive from the mudstones at LEM 1. One maxillary fragment was recovered, which has been tentatively assigned to the genus *Alilepus* within the Leporidae. All of the remaining specimens, primarily postcranial, are also attributed to Leporidae, making this one of the earliest occurrences of leporids in Africa (Darwent, 2007).

Carnivora

The carnivore assemblage is fragmentary but quite diverse (Howell and Garcia, 2007). Seven families are represented: Canidae, Felidae, Herpestidae, Hyaenidae, Mustelidae, Procyonidae, and Viverridae. The specimens from the mudstones are primarily small (Table 1) and include at least two species of *Genetta* within the Viverridae and three genera of Herpestidae. The larger carnivores are typically found in the sandstones, including a mustelid, *Plesiogulo botori*, the type specimen of which comes from LEM 1 (Haile-Selassie et al., 2004a).

Proboscidea

Only one elephantoid specimen has been recovered from LEM 1, a mandibular fragment of *Anancus kenyensis* from the

Table 3. Faunal List, Lemudong'o Locality 1 composite (NISP = 1245).

Aves
  Galliformes
    Phasianidae
      Phasianus (cf.)
  Falconiformes
    Acciptridae
  Strigiformes
    Strigidae (cf.)
Mammalia
  Insectivora
  Primates
    Cercopithecidae
      Colobinae
        Paracolobus enkorikae
        large species
        small species
  Rodentia
    Hystricidae
      Atherurus sp.
      Hystrix sp.
      Xenohystrix sp.
    Muridae
      Gerbillinae
        Tatera sp.
      Murinae
        Acomys sp.
        Aethomys sp.
        Arvicanthis sp.
        Lemniscomys sp.
        Mastomys sp.
        Saidomys sp.
    Sciuridae
      Sciurinae
        Paraxerus sp.
        Xerus sp.
    Thryonomyidae
      Thryonomys sp.
  Hyracoidea
    Procaviidae
      Dendrohyrax validus (cf.)
  Lagomorpha
    Leporidae
      Alilepus sp.
  Carnivora
    Canidae
      Eucyon aff. *intrepidus*
    Mustelidae
      Plesiogulo botori
    Procyonidae
      Simocyon sp.
    Herpestidae
      Helogale sp.
      Herpestes sp.
      Ichneumia aff. *albicauda*
    Viverridae
      Genetta sp. 'X'
      Genetta sp. 'Y'
    Hyaenidae
      Hyaenictis aff. *hendeyi*
    Felidae
      Lokotunjailurus emageritus
      Leptailurus sp.
      Metailurus major
  Proboscidea
    Gomphotheriidae
      Anancus kenyensis
  Perissodactyla
    Equidae
      Eurygnathohippus cf. *E. feibeli*
    Rhinocerotidae

Table 3. continued

  Artiodactyla
    Suidae
      Nyanzachoerus syrticus
    Hippopotamidae
      Hippopotaminae
    Bovidae
      Aepycerotini
        Aepyceros aff. *A. premelampus*
        cf. *Aepyceros*
      Boselaphini
      Neotragini
        Madoqua sp.
      Tragelaphini
        Tragelaphus sp.
Reptilia
  Chelonia
  Crocodylia
  Serpentes
    Colubroidea
    Pythoninae

sandstone. An unusual mandibular molar that may represent a new elephantid taxon has been recovered from nearby LEM 2 (Saegusa and Hlusko, 2007).

Hyracoidea

A large proportion of the mudstone assemblage is attributable to the Hyracoidea. Specimens identifiable below the superfamily level are small and most similar to the genus *Dendrohyrax*, the extant arboreal tree hyrax (Pickford and Hlusko, 2007).

Perissodactyla

Very few perissodactyl specimens are present in the LEM 1 assemblage. Four very weathered and rolled equid cheek teeth assigned to *Eurygnathohippus* cf. *E. feibeli* were recovered from the sandstone horizon (Bernor, 2007). There are also three isolated rhinocerotid teeth (two upper molars and a premolar), a talus, a metapodial that is similar to but much larger than *Diceros* (S. Cote, personal communication, 2006), and several molar fragments that could not be serially identified (see Ambrose, Kyule, and Hlusko, 2007; Appendix 1). Three of these rhinocerotid specimens were definitely from the mudstones and the others were collected in the first few years before exact horizon was noted for each specimen.

Artiodactyla

The Artiodactyla assemblage consists of fossils attributable to the bovid, hippopotamid and suid families. As with the entire assemblage, these specimens are quite fragmentary, but they indicate the presence of at least four bovid tribes, one species of suid, and a large hippopotamid at LEM 1. Aepycerotini (*Aepyceros* aff. *A. premelampus*), Boselaphini and Neotragini have been recovered from the mudstones, and *Tragelaphus* sp. has been found in the underlying sandstones (Hlusko et al., 2007). Ecomorphological analysis of the bovid astragali and phalanges demonstrate a lack of open habitat forms in the assemblage, indicating that LEM 1 samples forest and/or light cover habitats (DeGusta and Vrba, 2003, 2005; Hlusko et al., 2007). The suid *Nyanzachoerus syrticus* is also represented, but primarily in the sandstone horizon (Hlusko and Haile-Selassie, 2007). Hippopotamid specimens are uncommon at LEM 1 and are usually

recovered as only isolated dental fragments from the sandstone horizon (Boisserie, 2007).
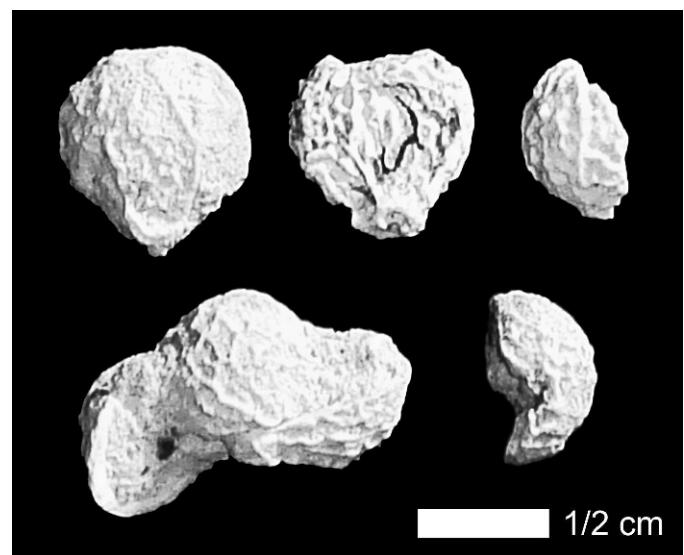
Ecology of Extant Related Taxa

Animal habitat preferences are to certain degrees flexible, although some taxa appear to maintain their habitat preferences consistently, even over several million years (Andrews, 1996). Therefore, extrapolations of paleoenvironment can be made by cautiously interpreting extant habitat preferences to extinct members of the same genera, or in some instances, families. Taxa with restricted ecological ranges are more useful in this endeavor than are more catholic taxa. Geraads (1994, p. 222) argues that paleoecological reconstructions are best made by considering only one family, due to taphonomic biases introduced through accumulation and diagenesis. However, all taxonomic levels are affected to different degrees by these processes. Fossil vertebrate assemblages may reflect accumulation by a variety of agents from a mosaic of nearby habitats whose characteristics and proximity can be best assessed by understanding taphonomic effects on all of the recovered fossil taxa, as well as their habitat preferences. Below, we will discuss some of the more relevant and diagnostic taxa that have been recovered from LEM 1.

Although few taxonomic groups provide an irrefutable paleoecological signal, there are trends within a faunal list, as the majority of genera may be suggestive of the same range of local habitats. Habitat preferences discussed below are from Nowak (1991) and Haltenorth and Diller (1980) except where noted. In the case of LEM 1, the strongest local habitat signal is for the presence of gallery forest and woodland trees in the mudstone levels, with woodland and somewhat more open habitats nearby. The lower sandstone fossils accumulated or were redeposited in a proximal lake-shore habitat, and reflect a relatively broader range of habitats. We focus our paleoecological discussion on the dominant mudstone assemblage.

Within the mudstones, several taxa require trees for roosting or nesting, or spend a majority of their time in an arboreal habitus. For example, owls and eagles often require trees in which to roost (Stidham, 2007). Of the reptiles recovered from LEM 1, the partial Chamaeleonidae skull suggests the presence of trees, as almost all extant chameleons are arboreal and found primarily in trees (Vitt et al., 2003, p. 49). The postcrania of *Paracolobus enkorikae*, the medium-sized and dominant colobine monkey, resemble those of extant arboreal colobines (Hlusko, 2007b). Extant *Dendrohyrax* have been described as sharing a niche with colobine monkeys and they shelter in cavities of partially dead trees (Milner and Harris, 1999a, b). *Dendrohyrax arboreus* in South Africa also prefer to shelter in partially rotted trees with multiple cavities (Gaylard and Kerley, 2001). Additionally, extant *Dendrohyrax* spend approximately 90% of their time in trees (Milner and Harris, 1999a, b; Gaylard and Kerley, 2001). Although they are found throughout tropical forests in Africa, the ranges of modern tree hyraxes and colobus monkeys extend into outlier patches of continuous canopy woodlands and riparian forests within mesic savanna environments. Within the rodent fauna, extant *Atherurus*, the brush-tailed porcupine, is only found in forests (Kingdon and Howell, 1993, p. 232), and provides the strongest faunal evidence for a closed forest habitat at LEM 1. The extinct large porcupine *Xenohystrix* has also been interpreted as forest-dwelling (Maguire, 1978, p. 144).

Fossil seeds of *Celtis zenkeri* (Ulmacae) occur in the speckled tuff at Lemudong'o (Figure 6). This tree species is currently found in rain forests at elevations between 250 and 1200 m in equatorial

Figure 6. Fossil seeds of *Celtis zenkeri*, from the speckled tuff. Identified by C. Kabuye at the East African Herbarium.

Africa east as far as Tanzania, and western Uganda (Polhill, 1966). It provides strong evidence for a closed canopy woodland or forest during deposition of the mudstones contemporary with the speckled tuff and microfauna breccia (Ambrose et al., 2003; Ambrose, Kyule, and Hlusko, 2007). *Thryonomys* and *Arvicanthis* suggest mesic to wet highland savanna habitats. None of the recovered small rodent specimens represent rainforest endemics.

The LEM 1 bovids are dominated by *Aepyceros* aff. *A. premelampus*, which is a small impala. The preferred habitats of modern impala are grassy woodlands to wooded grasslands near water. Tragelaphine bovids such as the lesser kudu (*Tragelaphus imberbis*) inhabit predominantly arid thicket and scrub as well as gallery forests. Bushbuck (*T. scriptus*) occupies predominantly wetter savanna woodland, bush and forest habitats, often sharing habitats with colobus monkeys and tree hyrax, and is almost always found near water. Sitatunga (*T. spekei*) prefer swampy habitats with tall grass and reeds, forests and gallery forests, and nyala (*T. angasi*) prefer non-swampy thicket, bush, savanna woodland and gallery forest. Small tragelaphines at most late Miocene sites are similar to lesser kudu and nyala in size and may have been similar in their ecological requirements (WoldeGabriel et al., 1994; Pickford and Senut, 2001; Haile-Selassie et al., 2004b). However they could resemble bushbuck or sitatunga in their diet and habitat preferences. Bushbuck and especially sitatunga-like tragelaphines would provide stronger evidence for closed tropical forests in the late Miocene. Carbon and oxygen-isotope analysis of their tooth enamel and limb-bone ecomorphological analysis could help resolve this question. Dik-dik (*Madoqua*), which are present at LEM 1, inhabit a wide range of dry bush to mesic woodland habitats.

An ecomorphological analysis of the bovid astragali and phalanges is consistent with the species-based habitat reconstruction. The results clearly indicate that open habitat forms are not represented in this assemblage, and suggest the presence of forest and/or light cover (Hlusko et al., 2007).

However, the mudstone assemblage does contain some taxa that are indicative of relatively more open habitats. Several taxa,

including *Tatera* (gerbils), *Aethomys*, *Arvicanthis*, *Xerus* (African ground squirrel), *Thryonomys* (cane rats), leporids, and aepycerotine bovids, indicate more open environments such as grassy woodlands, wooded grassland savanna and dry bush. *Tatera* prefers dry sandy soil for its burrows. The dry-habitat taxa *Acomys* and *Madoqua* both rely on brush for concealment but do not require access to a permanent source of water. Although *Eurygnathohippus* is an extinct equid lineage, its cursorial limb morphology indicates open habitat preferences, and its mesowear suggests a grazing adaptation (Bernor, 2007). The rarity and poor preservation of this hipparionine in the LEM 1 assemblage suggests that such open habitats were relatively far from the paleolake margin zone.

Several taxa from the mudstone assemblage are less habitat specific. The African bush squirrel genus *Paraxerus* includes a diverse range of species, only one of which is restricted to moist tropical forests. Modern viverrid carnivores are equally diverse, and occupy a spectrum of wet forests to dry bush habitats, so their catholic habitat preferences render them less informative for habitat reconstruction. Extant suids occur in a wide range of habitats including dense rainforest, swamps, gallery forest savanna woodlands, thickets and bush near water, but not in open grasslands. Carbon isotope analysis of *Nyanzachoerus syrticus* from Lothagam shows it consumed a substantial amount of C_4 grasses (Harris and Cerling, 2002; Cerling et al., 2003).

Taphonomy of LEM 1

As described above and in detail elsewhere (Ambrose, Nyami et al., 2007), there are two fossil horizons at LEM 1: 1) an upper mudstone and bioturbated tuff (the speckled tuff), and 2) underlying sandstone. The fossils from the sandstone horizon are typically rolled and abraded, and enamel is often manganese-stained. The number of identifiable specimens is small compared to the mudstones, comprising only ~3% of the total LEM 1 assemblage. Most of the fossils from LEM 1 derive from the upper mudstone horizon (~97%). These fossils demonstrate no evidence of fluvial transport, and sedimentation appears to have occurred in a frequently inundated distal lake margin zone. The high clay content of the mudstones causes extensive shrinking and swelling of the sedimentary matrix within and encasing the fossils, and results in intense fragmentation of the fossils during erosion. We focus our paleoecological discussion primarily on this upper horizon since fossils from the mudstones dominate the assemblage. However, it is important to keep in mind that there are two sedimentary facies that represent different time periods of the same lake-basin system, although radiometric dating indicates these layers were probably deposited closely in time.

A remarkable characteristic of the LEM 1 mudstone faunal assemblage is the rarity of large animals in comparison to other fossil assemblages such as Lothagam (Leakey and Harris, 2003). Most of the larger and more durable specimens recovered, such as the *Anancus* mandible and *Nyanzachoerus* molars, derive from the sandstone. As such, many of the large animals often found in lakeshore habitats, such as hippopotamids and crocodylids, are quite rare in this assemblage. This skewed representation and the high frequency of small animals that are usually biased against during deposition and diagenesis suggests that the assemblage may not fully sample one local habitat or ecology, or it may indicate the absence of these large aquatic terrestrial vertebrates during the time of mudstone deposition.

The largely unweathered and unpatinated surfaces of the majority of bones from the mudstone horizon indicate rapid

Figure 7. Representative carnivore damage at LEM 1. KNM-NM 41169, cercopithecoid distal humerus with arrows indicating carnivore-tooth puncture marks.

burial. The primary taphonomic agents for accumulation and modification of the relatively larger taxa in the mudstone assemblage are likely to be mainly small- and medium-sized mammalian carnivores. They have left high frequencies of gnawing, crushing and puncture marks on the bones, such as is shown in Figure 7. Additionally, it is likely that raptorial birds also contributed to the bone accumulation, especially that of the rodents (Manthi, 2007). The breakage patterns and skeletal elements of the relatively larger mammals are not characteristic of modern raptorial-bird bone assemblages (Stewart et al., 1999; Sanders et al., 2003; McGraw et al., 2006; Trapani et al., 2006).

Comparison to Penecontemporaneous Mio-Pliocene Sites

The paleoecology of LEM 1 can be compared with a number of penecontemporaneous late Miocene sites in eastern Africa (Figure 3), including the Nawata Formation of Lothagam (Leakey et al., 1996; Leakey and Harris, 2003), the Lukeino Formation of the Tugen Hills (Pickford and Senut, 2001), the Adu-Asa Formation of the western margin of the Middle Awash Valley (Haile-Selassie et al., 2004b), and Toros-Menalla in Chad (Vignaud et al., 2002), all of which contain the biochronologically diagnostic suid *Nyanzachoerus syrticus* (*tulotos*). However, comparisons to these sites are hindered by the differences in sample sizes between sites, and the taphonomic bias toward small body sizes at LEM 1.

The geomorphological setting of Toros-Menalla 266 is the margin of a fluctuating lake surrounded by a sandy desert. The strata are described as having an aeolian/lacustrine origin, reflecting the deposition and reworking of wind-blown desert sands that were deposited directly into paleolake Chad (Vignaud et al., 2002). The closest modern analog for such a depositional setting may be the Okavango delta in Botswana or modern Lake Chad. Despite the unusual depositional setting, the mammalian faunal assemblage has some overlap with that of LEM 1. Notable differences from LEM 1 include the presence of hominids, giraffids, reduncines, hippotragines, and antilopines, the absence of tragelaphines, and the abundance of crocodylids, fish, turtles, and semi-aquatic large artiodactyls (hippos and anthracotheres are approximately 25% of the fauna). There are very few colobines at TM266, but they may reflect a riparian forest context for the hominid *Sahelanthropus tchadensis* (Vignaud et al., 2002). Although the high-crowned bovids and other species suggest a mosaic of environments including gallery forest, woodland and grassland, and the fish fauna indicates a large and stable fresh-water lake, the overall terrestrial setting is likely to have been more open and drier than at LEM 1.

The Nawata Formation assemblage of Lothagam also contains numerous shellfish, fish, turtle, and crocodile species, reflecting a large, slow-moving river, and the terrestrial-mammal fauna suggests a mosaic of riverine gallery forest, woodlands, and grasslands (Leakey et al., 1996; Leakey and Harris, 2003). The overall paleoenvironmental setting of Lothagam is also apparently somewhat drier than LEM 1 and hominids are absent from the late Miocene Nawata Formation. Compared to Lemudong'o, many large-bodied species and larger and more complete skeletal elements and skeletons were recovered from Lothagam.

Lukeino has perhaps the greatest geomorphological and ecological similarity to LEM 1. The geomorphic setting was a small rift-lake sedimentary basin, but at Lukeino the fossils seem to have accumulated mainly in a shallow lake margin at the base of a lava scarp or cliff (Pickford and Senut, 2001). The fauna associated with the hominid *Ororrin tugenensis* includes a diversity of fish, crocodiles, and turtles, indicating a more stable permanent lake than at LEM 1. The presence of several colobine species, an aepycerotine, tragelaphines, reduncines, hipparions, *Nyanzachoerus*, and giraffids suggest a mosaic of environments that included gallery forest woodland and open grassy woodland (Pickford and Senut, 2001). The most notable difference between Lukeino and LEM 1 appears to be related to taphonomic biases: More skeletal elements of a variety of large species have been recovered at Lukeino.

The Adu-Asa formation of the Middle Awash Valley also samples a faulted rift-margin lake-basin setting as well as riverine fluvial depositional environments, as do LEM 1 and Lukeino (Haile-Selassie et al., 2004b). The Adu-Asa faunal assemblage has many taxa in common with LEM 1, but contains a more diverse artiodactyl community including reduncines, giraffids and several suid species. Additionally, though paleoecologically less revealing, the Adu-Asa Formation localities have also yielded remains of the hominid *Ardipithecus kadabba*, whereas no hominid has yet been recovered from LEM 1.

Implications of the Lemudong'o Paleobasin for Hominid Evolution

One of the primary foci for research in the late Miocene of Africa is to better understand the earliest ancestors of humans, the Hominidae (Hendey, 1976, 1983; Boaz et al., 1987; Hill, 1995; Harrison, 1997; Andrews and Banham, 1999; Pickford and Senut, 2001; Vignaud et al., 2002; Leakey and Harris, 2003; Haile-Selassie et al., 2004b; for taxonomy see White, 2002). As such, no paleoecological reconstruction from this time period is complete without a consideration of its implications for hominid evolution. Although hominid remains have not yet been recovered from LEM 1, our understanding of the paleoecology and paleolandscape of this area provides some insight to early hominid evolution. Understanding the environments that were not habitually occupied by our earliest hominid ancestors may provide insights into the nature of their habitat preferences and adaptations.

Late Miocene and early Pliocene hominids from several localities seem to have occupied wetter, more closed, forest and woodland portions of the mosaic of habitats available (WoldeGabriel et al., 1994; Pickford and Senut, 2001; Haile-Selassie et al., 2004b; Pickford et al., 2004). If further research confirms our interpretation of LEM 1 as close to the shoreline of a lake fed by slow-moving streams, then perhaps the absence of hominid remains indicates that hominids were not regularly spending a considerable amount of time in the wooded habitats at lake margins.

The absence of evidence, of course, is not evidence of absence. Moreover, this assemblage from LEM 1 appears to have resulted primarily from the accumulation of carcasses by carnivorous birds and/or mammals. This site has yielded very few bones of animals that were as large as late Miocene hominids. Therefore, the lack of hominids at LEM 1 may also result from taphonomic biases rather than, or, perhaps, in addition to habitat preferences of our earliest ancestors. If additional research in this paleobasin eventually produces hominid fossils, it will further support the hypothesis of a more forested habitat preference for the earliest bipedal hominids (Boesch-Achermann and Boesch, 1994; WoldeGabriel et al., 1994; Pickford et al., 2004).

Conclusions

The paleoecology of LEM 1 reflects a local environment of permanent gallery-forest near the fluctuating margin of a shallow lake in a small tectonically formed rift-valley basin. More open woodland to wooded grasslands occurred nearby. Its spectrum of terrestrial habitats resembles that of several penecontemporary fossil sites from the late Miocene of the Gregory Rift Valley in eastern Africa, including the Lukeino Formation in the Baringo Basin of northern Kenya, and the western margin of the Middle Awash Valley, Ethiopia. LEM 1 bears less similarity to other equatorial sites adjacent to large lakes and rivers that contain more arid-adapted terrestrial faunas and diverse aquatic faunas, such as Toros-Menalla in the Lake Chad paleobasin, the Nawata Formation of Lothagam in the Turkana basin, and the Manonga Valley paleobasin in Tanzania. Post-depositional taphonomic

effects of the high-energy beach depositional environment may account for the bias toward larger species in the lower sandstone. The bias toward smaller species in the upper mudstones may reflect the predominantly small prey sizes brought to this forested location by avian and small mammalian carnivores.

The broader paleoecological context of Lemudong'o can be viewed from the perspective of global paleoclimatic records. The Lemudong'o Formation sedimentary sequence includes early and late phases of predominantly lacustrine and peri-lacustrine deposition, reflecting wetter environments and climates. The middle phase of sedimentation apparently reflects a long period of drier climate. This is consistent with the fluctuating, often arid climates of the terminal Miocene Messinian period, 5–7 Ma, when large quantities of terriginous dust were blown from Africa into the oceans (DeMenocal and Bloemendal, 1995), and water stress-adapted C_4 grasslands expanded globally throughout the tropics (Cerling et al., 1997). Messinian climate changes may have played an important role in the paleobiogeography of Africa, promoting forest and savanna expansions and contractions, speciations, extinctions, and faunal interchanges between northern and southern savannas and between Africa, Arabia and Eurasia (Brain, 1981; Laporte and Zihlman, 1983; Vrba, 1987, 1988; Pickford, 2004). The unexplored paleolake basins in Narok that precede and follow the Lemudong'o Formation paleolake may make important contributions to understanding the local expressions of these global climate changes and for testing hypotheses about the evolution of various terrestrial vertebrates, including hominids.

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