

Current events

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A new evaluation of the significance of the Late Neogene Lusso Beds, Upper Semliki Valley, Zaire

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Introduction

Fieldwork was re-instituted in the Western Rift in 1982 by the Semliki Research Expedition, under the direction of Boaz (1990), after a hiatus of 22 years when the Ganda–Congo Expedition directed by de Heinzelin ceased operations (1962; Gautier, 1965). Most fieldwork has been on the fossiliferous sediments exposed in the Upper Semliki River Valley and along the northern shore of Lake Rutanzige (formerly termed Lake Edward or Lake Amin). Detailed stratigraphic profiling and correlation have revealed a measured aggregate thickness of primarily lacustrine, fossiliferous sediments of some 50 m. These sediments have been named the Lusso Beds (de Heinzelin & Verniers, 1987) to distinguish them from similar but as yet unreliably correlated sediments in Uganda, originally termed the Kaiso Beds (Bishop, 1969), and now known by a variety of recently coined formational names (Pickford *et al.*, 1988, 1989). We report here a fossil vertebrate fauna composed of 51 taxa, an invertebrate fauna composed of 28 taxa and a fossil woody-plant flora composed of 61 taxa. Biostratigraphic correlation indicates an age for the upper half of the Lusso Beds of 2·0 and 2·3 Ma. The palaeobotanical evidence demonstrates abundant savanna trees, such as *Acacia*, and the

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preponderance of open woodland/savanna-adapted taxa in the fauna indicates a proximal taphocenosis of open-canopied-woodland to grassland. Fossil wood also records the presence of dense lowland forest more distant from the depositional environment. The juxtaposition of these two habitats, as recorded in the Lusso Beds, is so far unique in the late Pliocene–early Pleistocene African fossil record. Stone tool occurrences at Lusso Bed localities attest to a hominid presence in the Western Rift in the late Pliocene.

The Semliki Valley of Zaire extends from latitude 0°30'S, the point at which the Semliki River issues from Lake Rutanzige, to latitude 1°30'N, where the river debouches into Lake Mobutu (formerly Albert) (Figure 1). During the river's 230 km course along the floor of the western section of the East African Rift Valley System, it falls from an elevation of 912 m at its source to 618 m at its termination. The river has cut into and exposed lacustrine and fluvial sediments of late Pliocene to Holocene age in the southern or Upper Semliki Valley, and lacustrine sediments of indeterminate Miocene to Pleistocene age in the Lower Semliki Valley.

Fossiliferous sites were located through surface survey and mapped on 1:34790 aerial photographs of the entire area. Most fossils are surface-collected and have been assigned to stratigraphic level based on the strata exposed at the locality. Because of the limited stratigraphic extent and low topographic relief of most localities, determination of stratigraphic provenance of surface fossils can be made in the field with a high degree of assurance. Extensive wet-sieving of Lusso Bed localities using fine mesh screen boxes was carried out over four field seasons to assess paleoecological conditions. Localities are numbered within named areas of the Upper Semliki region (Figure 1).

The Semliki Research Expedition has investigated the geology, palaeontology and palaeoanthropology of the Semliki Valley, most of which is contained within Virunga National Park. Most of the research has been concentrated on the Upper Semliki Valley and this will be reported here. Future work will focus on associated areas of outcrops in the Lower Semliki area, Zaire, and in western Uganda.

Geological context

De Heinzelin & Verniers (1987) named lacustrine sediments, typified by exposures at Lusso Point on the northern shore of Lake Rutanzige, the Lusso Beds. Fuchs (1934), Bishop (1969) and subsequently others, considered these deposits extensions of the Kaiso Beds of Uganda on the basis of lithostratigraphic similarity. Lepersonne (1949) termed these deposits the "Lake Edward Beds." The lacustrine Lusso Beds are stratigraphically the lowest exposures in the Upper Semliki and are overlain by the primarily fluvial sediments of the Semliki Beds and later terrace deposits (Verniers & de Heinzelin, 1990; Figure 2).

The Lusso Beds have an aggregate thickness of at least 50 m in the Lusso–Kanyatsi area (Figures 1 & 2). They are composed of lacustrine clays, lacustrine micaceous fine silts and alluvial/peri-lacustrine sands. Lusso Bed deposits outcropping along the Semliki River preserve more beach and near-shore sandy lacustrine facies. Oolitic ironstones occur at regular stratigraphic intervals and have been used as marker horizons. It has not been possible to trace out any marker beds between the Lusso–Kanyatsi area and the Semliki River outcrops of the Lusso Beds (Figure 2). However, it is possible to deduce that the Lusso–Kanyatsi deposits underlie those exposed along the Semliki River because the latter are in contact with the overlying Semliki Beds, which do not occur in the Lusso–Kanyatsi area. The molluscan fauna has also provided a basis for a tentative biostratigraphic correlation between these two areas (Figure 2).

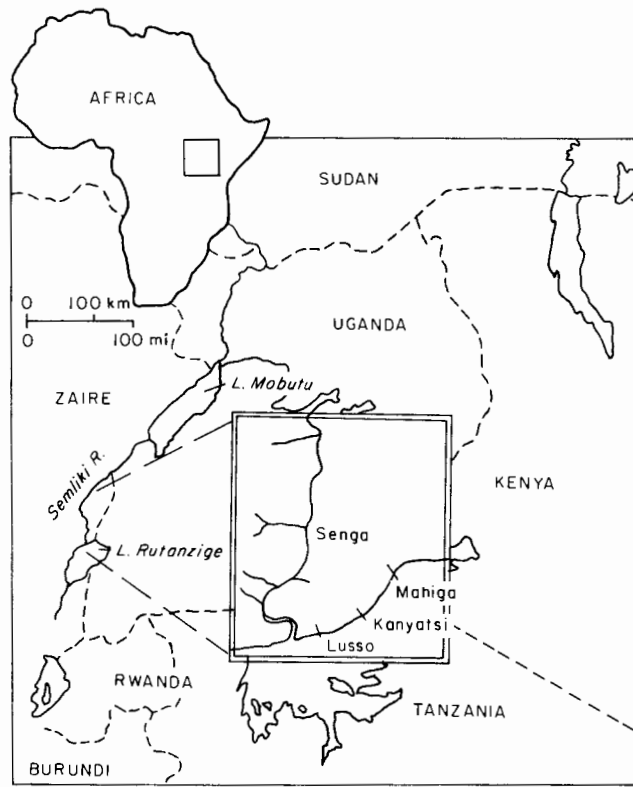


Figure 1. Map of the study area, Upper Semliki River Valley, eastern Zaire.

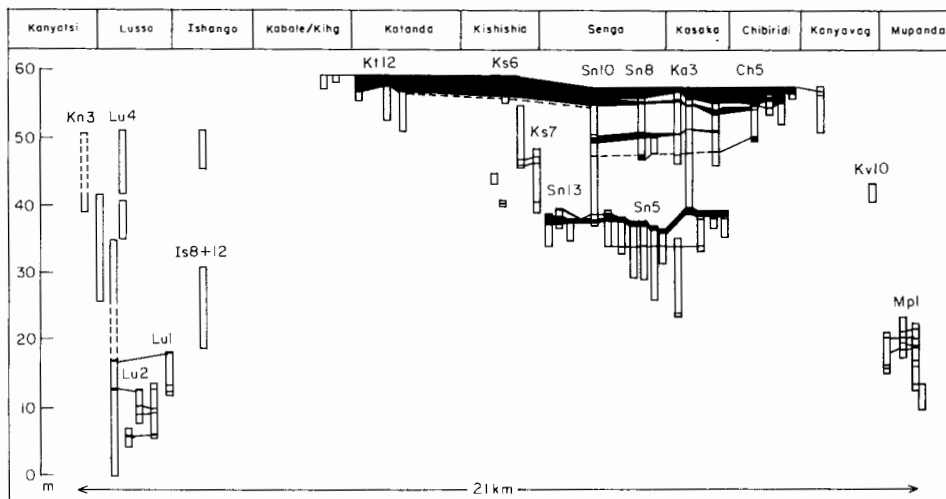


Figure 2. Summary stratigraphic section of the Lusso Beds, Upper Semliki, Zaire. Only ironstone levels used as marker beds for lithostratigraphic correlation are indicated. The stratigraphic relationship between lakeside and Semliki River Lusso Bed localities is tentative.

Fossils of vertebrates, molluscs and wood occur throughout the Lusso Beds, but are concentrated in the ironstone levels. Ironstones are typified by sediments coarsening upwards from clay to silt to sands, at the tops of the units. Iron content also increases towards the tops of these units, which are capped by pure iron oolites, indicating a regressive episode. Occasionally iron-free, alluvial gravels, indicating emersion, are present above the sands.

Opal sponge spiculae occur in abundance in some clay horizons, even to the point of forming pure spiculites. Molluscs are usually found in the medium grain sized sand and mixed sand-oooid levels. Vertebrate fossils occur most frequently in the uppermost, iron oolitic levels.

Deposition occurred in near-shore, shoreline, or beach lacustrine facies in those areas of outcrop immediately adjacent to the modern Semliki River (Figure 1). These westernmost sediments are more coarsely grained and show cross-bedding in some outcrops. The Lusso–Kanyatsi outcrops to the east are in general finer grained and were deposited under deeper water, except when lake regressions reached this area. The Lusso Beds in the easternmost portion of the study area, near Mahiga (Figure 1), are typified by only fine-grained sediments (clay, fine silts and clay-ironstones or “boxstones”) from deeper lacustrine depositional conditions. The lake that occupied the Semliki graben in late Pliocene times was oriented along the main north–south axis of the rift and shows an east-to-west gradient of facies. The fossil sites along the Semliki River are thus near-shore or beach facies, and those to the east, along the northern shore of Lake Rutanzige, represent more offshore lacustrine depositional environments. Further stratigraphic work is required to refine the relationships between these two regions of outcrop of the Lusso Beds.

Recent tuff correlations have been posited between Western Rift sites in Uganda and Eastern Rift sites in the Turkana basin, Ethiopia/Kenya and Afar area of Ethiopia (Pickford *et al.*, 1991). These tuffs seem to both pre-date the Zairean Upper Semliki Lusso Beds (3.4–3.6 Ma) and post-date them (1.5 Ma). No evidence of volcanic or volcanoclastic rocks has been found in the Lusso Beds, although a tuff has recently been recognized in the sediments of the Lower Semliki Valley, Zaire (F. H. Brown, pers. comm.), also pre-dating the Upper Semliki Lusso Beds. In the Upper Semliki Lusso Beds then, age has been determined by mammalian biostratigraphic comparisons with Eastern Rift sites.

Flora

Abundant and well-preserved fossil wood specimens from the Lusso Beds have been analysed (Dechamps & Maes, 1990). Most of the specimens are fossil twigs and branches and a few are pieces of larger trunks. Some 61 taxa of woody plants have been identified by thin-section study of their wood structure (Table 1). Floral taxa are indicative of six community types: dense lowland (“ombrophile”) forest, swamp forest, gallery forest, woodland savanna, savanna and steppe. These communities exist today within the Semliki–Lake Rutanzige Valley but are much more widely dispersed. In the Pliocene there apparently existed a close association of hydrophytic and xerophytic communities.

Tabulation of the habitat requirements (maximum and minimum temperatures and rainfall) of modern representatives of the species found in the Lusso Beds (Dechamps & Maes, 1990) indicates that there were marked dry and wet seasons. The presence of traumatic rings on samples of *Acacia* indicate the presence of dry season bush fires in the late Pliocene Upper Semliki. In four localities successively higher in the Lusso Beds, Kanyatsi 2, 3, 4 and 5, the fossil wood samples show a trend towards more forested conditions towards the top of this sequence. However, at locality Sn5A, stratigraphically situated above most if not all of the

Table 1 Taxa of fossil wood from the upper Pliocene Lusso Beds, Zaire

<i>Acacia</i> cf. <i>abyssinica</i>	<i>Cynometra alexandrii</i>
<i>Acacia albida</i>	<i>Dichapetalum acuminatum</i>
<i>Acacia ataxacantha</i>	<i>Dichapetalum</i> aff. <i>glandulosum</i>
<i>Acacia cilolota</i>	<i>Dichapetalum griseisepalum</i>
<i>Acacia</i> cf. <i>giraffae</i>	<i>Dichapetalum lokanduense</i>
<i>Acacia hockii</i>	<i>Dichapetalum lujae</i>
<i>Acacia nilotica</i> subsp. <i>adansoniae</i>	<i>Dichapetalum mombutuense</i>
<i>Acacia nilotica</i> subsp. <i>subalata</i>	<i>Dichapetalum mundense</i>
<i>Acacia nilotica</i> var. <i>tomentosa</i>	<i>Dichapetalum</i> spp.
<i>Acacia polycantha</i> subsp. <i>camphylacantha</i>	<i>Diospyros</i> sp.
<i>Acacia rocumae</i>	Gramineae sp. [?"bamboo"]
<i>Acacia seyal</i>	<i>Grewia flavescens</i>
<i>Acacia sieberiana</i>	<i>Grewia mollis</i>
<i>Acacia sieberiana</i> var. <i>woodii</i>	<i>Irvingia robur</i>
<i>Acacia</i> sp.	cf. <i>Juniperus</i> sp.
<i>Agelaea deweyrei</i>	<i>Leptadenia</i> cf. <i>hastata</i>
<i>Airyantha schweinfurthi</i>	<i>Encephalartos</i> sp.
<i>Antidesma membranacea</i>	<i>Loeseneriella clematiodes</i>
<i>Anthonota macrophylla</i>	Monocotyledon sp.
<i>Aphania senegalensis</i>	<i>Magnistipula butayei</i>
<i>Aptandra zenkeri</i>	<i>Ostryoderris gabonica</i>
<i>Baphia</i> sp.	<i>Phoenix reclinata</i>
<i>Baphiastrum boonei</i>	<i>Phoenix</i> sp.
<i>Brachystegia</i> cf. <i>laurentii</i>	<i>Podocarpus milanjanus</i>
<i>Brachystegia</i> cf. <i>microphylla</i>	<i>Raphiostylis beninensis</i>
<i>Brachystegia</i> cf. <i>utilis</i>	<i>Rothmannia urcelliformis</i>
<i>Byrsocarpus</i> cf. <i>orientalis</i>	<i>Roureopsis obliquifoliolata</i>
<i>Canthium</i> cf. <i>camphylacanthum</i>	<i>Salacia</i> sp.
<i>Cassipourea</i> aff. <i>malosana</i>	<i>Salix</i> sp.
<i>Combretum paniculatum</i>	<i>Sapium ellipticum</i>
<i>Combretum</i> sp.	

Kanyatsi sites (Figure 2), significantly drier conditions, extending even to "steppe" habitats, had appeared.

Fauna

Table 2 lists the invertebrate and vertebrate fauna found in the Lusso Beds. There are 27 taxa of molluscs currently known from the Lusso Beds. Fifteen of these are cosmopolitan taxa (*sensu* Williamson, 1979), occurring over wide temporal and geographic ranges in the Neogene of Africa. Molluscan endemics from the Neogene deposits of the North West African Rift represent two successive adaptive radiations, of earlier and later Pliocene age, respectively (Williamson, 1990). The 12 endemic taxa known from the Lusso Beds in the Upper Semliki area are representative of the upper radiation— all or most of these taxa are known from numerous other localities in eastern Zaire and Uganda. A small area of up-faulted deposits at the head of the Nyakasia Ravine (de Heinzelin, 1955), east of the main Semliki Lusso sites (Figure 1), has yielded members of the lower molluscan radiation. This molluscan assemblage is known from numerous other localities in eastern Zaire and Uganda (Gautier, 1970). The Nyakasia deposits clearly pre-date the Lusso Beds on the basis of the molluscan biostratigraphy (Williamson, 1990). The extinction of the upper radiation (Lusso-aged) mollusc community, and its replacement by an exclusively cosmopolitan fauna similar to that of the present-day lake, occurs within the upper Lusso Beds. The lower Lusso Beds have yielded six as yet undescribed new endemic gastropod and bivalve taxa (Table 2).

Table 2 Invertebrate and vertebrate taxa from the upper Pliocene Lusso Beds, Zaire

Mollusca	Pisces <i>continued</i>
“Cosmopolitan” taxa	Characidae indet.
Gastropoda	<i>Auchenoglanis</i> sp.
<i>Bellamyia unicolor</i>	<i>Bagrus</i> sp.
<i>Bulinus</i> sp.	<i>Clarotes</i> sp.
<i>Cleopatra bulimoides</i>	Bagridae indet.
<i>Gabbiella humerosa</i>	? <i>Clarias</i> sp.
<i>Melanoides tuberculata</i>	<i>Synodontis</i> sp.
<i>Pila ovata</i>	<i>Lates niloticus</i>
Bivalvia	<i>Lates</i> cf. <i>rhachirhynchus</i>
<i>Aspatharia cailliaudi</i>	Cichlidae indet.
<i>Aspatharia wissmanni</i>	Perciformes gen. et sp. indet. (A)
<i>Caelatura bakeri</i>	
<i>Corbicula consobrina</i>	Amphibia
<i>Etheria elliptica</i>	Anura gen. et sp. indet.
<i>Eupera</i> sp.	
<i>Mutela nilotica</i>	Reptilia
<i>Pleiodon ovatus</i>	Pleurodira gen. et sp. indet.
<i>Pseudobovaria mayana</i>	cf. <i>Pelusios sinuatus</i>
Endemic taxa	cf. <i>Cycloderma</i>
Gastropoda	Testudinidae indet.
<i>Bellamyia adami</i>	<i>Crocodylus</i> sp.
<i>Bellamyia cylindricus</i>	
<i>Bellamyia worthingtoni</i>	Mammalia
<i>Bellamyia</i> sp. nov. A	<i>Menelikia lyocera</i>
Gastropoda gen. et sp. nov. A	? <i>Kobus sigmoidalis</i>
Gastropoda sp. nov. B	<i>Kobus ancystrocera</i>
<i>Platymelania bifidicincta</i>	<i>Kobus kob</i>
<i>Platymelania brevissima</i>	<i>Syncerus</i> sp.
Bivalvia	<i>Tragelaphus nakuue</i>
<i>Caelatura</i> sp. nov. A	Alcelaphini spp.
<i>Pleiodon</i> sp. nov. A	<i>Kolpochoerus lunnetes</i>
<i>Pseudobovaria</i> sp. nov. A	<i>Notochoerus euilus</i>
<i>Pseudodiplodon sengae</i>	<i>Metridiochoerus jacksoni</i>
	Hipparioninae gen. et sp. indet.
	<i>Equus</i> sp.
	<i>Elephas recki</i>
	<i>Giraffa</i> sp.
	cf. <i>Ceratotherium</i> sp.
	<i>Hippopotamus</i> sp.
	<i>Hesperotodon imagunculus</i>
	Colobinae gen. et sp. indet. (A)
	<i>Theropithecus</i> sp.
	<i>Thryonomys</i> sp.
	<i>Otomys</i> sp.
	<i>Tachyoryctes</i> sp.
	Carnivora gen. et sp. indet.
Pisces	
<i>Protopterus</i> sp.	
? <i>Hyperopisus</i> sp.	
<i>Gymnarchus</i> sp.	
<i>Labeo</i> sp.	
<i>Barbus</i> sp.	
<i>Distichodus</i> sp.	
<i>Hydrocynus</i> sp.	
<i>Alestes</i> sp.	
<i>Sindacharax</i> ? <i>deserti</i>	
<i>Sindacharax</i> sp.	
Characidae gen. nov. A	

The fish fauna from the Lusso Beds consists of some 20 taxa, which are Nilo-Sudanian in their affinities. There is at least one newly discovered species [Osteichthyes gen. et sp. indet. (A)]. Another taxon, Characidae gen. nov. A, occurs elsewhere only in Plio-Pleistocene deposits in northeastern Kenya, as noted by Schwartz (1983). The lower part of the Lusso Beds around Lusso and Kanyatsi preserves an abundance of fish with dentitions adapted to crushing. Sixty per cent (based on minimum numbers of individuals) of the fish fauna is made

up of these species, which are interpreted to have been molluscivores. A significant decrease in molluscivores occurs higher in the Lusso Beds, where there is a greater diversity of fish, including piscivores, insectivores and detritivores.

The herpetofauna includes *Crocodylus*, four chelonians and a single anuran. Three of the chelonians are aquatic (cf. *Cycloderma* sp., cf. *Pelusios sinuatus* and a large unnamed pleurodire). The fourth chelonian is a large testudinid. The identified reptilian taxa are consistent with an attribution of Nilotic zoogeographic affinities.

Although fossil mammalian faunas of Plio–Pleistocene age have been well known for some years from the Ugandan side of the Western Rift (Bishop, 1963; Cooke & Coryndon, 1970) and some of these deposits were recently revisited (Senut *et al.*, 1987; Pickford *et al.*, 1988, 1989), the Plio–Pleistocene mammalian record of the Zairean side of the Rift has remained largely unknown. We report here a mammalian fauna consisting of 22 identified taxa from the Lusso Beds.

The primate fauna consists of the cercopithecine *Theropithecus* and a colobine monkey. No hominid fossils have yet been recovered from the Lusso Beds. Two lower molars from Senga 5 can be attributed to *Theropithecus* sp. indet. They are equivalent in size to fossils of *T. brumpti* and *T. oswaldi* from the Omo Shungura Member G level (Eck & Jablonski, 1987), but it is not now possible to distinguish between these two species on the basis of isolated teeth. The Senga specimens are also comparable in size to specimens from Kanjera and Swartkrans, perhaps intermediate in size between these two populations of *T. oswaldi*. The Senga specimens appear smaller than the few teeth from Olduvai Bed I. An age within the time range of Omo G (2.3 to 1.9 Ma) is reasonable, especially given the generally close relationship between tooth size and age in *Theropithecus* (Eck, 1987).

A single isolated upper molar from locality Lu2 can probably be referred to the as yet unnamed colobine species termed gen. et sp. indet. (A) by Leakey (1987). Colobines of this size range, larger than any living taxon but smaller than the large Plio–Pleistocene species of *Paracolobus*, *Rhinocolobus* or *Cercopithecoides*, are also known from the Hadar Formation and the nearby Leadu Beds (of less certain age), Laetoli, Omo Shungura upper B, G8 and especially C [where Colobinae gen. et sp. indet. (A) is the most common colobine according to Leakey, 1987] and perhaps from Koobi Fora. If all of these specimens represent a single species, which is not yet clear, the taxon would range in age from about 3.7 to 2.1 Ma.

Bovoid fossils predominate in numbers of individuals* recovered from surface collection and excavation (Figure 3). The bovinds, including the species *Tragelaphus nakuae*, ?*Kobus sigmoidalis*, *Kobus ancystrocerus* and *Menelikia lyrocera*, show closest morphological similarities to and indicate a biostratigraphic correlation with Omo Shungura Formation Members F and G, at an age of 2.0 to 2.3 Ma (Feibel *et al.*, 1989). Hippopotamids, mostly the large *Hippopotamus*, are the next most numerous mammalian group. Co-occurring with *Hippopotamus* is the “pygmy” *Hexaprotodon imagunculus*, consistent with a Shungura F to G biostratigraphic age. Three suid species, *Notochoerus euilus*, *Kolpochoerus limnetes* and *Metridiochoerus jacksoni* in the upper part of the Lusso Beds are most comparable in morphology to those from Omo Shungura Members F to G (cf. Cooke, 1976). The co-occurrence of *Equus*, first reported in Africa from Member G of the Shungura Formation (Eisenmann, 1985), and a hipparion similar to “*Hipparion albertense*” from the Kaiseo Formation of Uganda, is consistent with

*Unless specimens showed articulation or other taphonomic indicators of belonging to the same individual, they were counted as separate individuals, based on the very low density and the disarticulated nature of the bone assemblage. We eschewed a strict application of the methodology for determining “minimum number of individuals” based on the most common sided body parts present. This would have presented a distorted view of the true nature of the faunal composition by placing undue emphasis on rare elements of the fauna.



Figure 3. Traumatic rings in fossil wood of *Acacia* sp., Lusso Beds, indicating bush fire and savanna vegetation.

a correlation of Shungura Formations F and G. However, an apparent late-surviving hipparionine lineage at the earliest levels of Olorgesailie (Potts, 1989), at about 0.9 to 1.0 Ma, makes this biostratigraphic indicator less than definitive. The presence of *Elephas recki* is consistent with, but provides no further precision to, the biostratigraphic age indicated by the rest of the large mammal fossil record from the Lusso Beds.

Three rodent taxa are known from the Lusso Beds: *Thryonomys* sp., *Otomys* sp. and *Tachyoryctes* sp. (Figure 4), earlier thought to have represented a possible record of an anomalurid (reported in Boaz, 1990). *Thryonomys* is a widespread (although numerically rare) component of Pliocene–Holocene East African faunas. The genus is first reported in Africa from Kenya ca. 5 Ma (Winkler, 1990). The earliest East African record of *Otomys*, other than the Lusso Bed specimen, is from Olduvai Bed I (Denys, 1989). *Tachyoryctes* (and rhizomyid rodents in general) is poorly known in Africa from pre-Pleistocene deposits. The oldest *Tachyoryctes* is an extinct species, *T. pliocaenicus*, reported from Hadar, Ethiopia (2.6 to 3.3 Ma; Sabatier, 1978). The Semliki specimen is an important addition to the African record of the family Rhizomyidae.

Pending further refinement, we infer an approximate date of 2.0–2.3 Ma for the upper part of the Lusso Beds. The age of the lowest part (Nyakasia area) is not yet established but tentatively considered as early Pliocene.

Paleoecology

Initial studies of faunal similarity indicated that late Neogene Zairean localities in the Upper and Lower Semliki Valley were allied with Ugandan Plio–Pleistocene Kaiso Formation sites, and differed from penecontemporaneous sites in eastern Africa (Pavlakakis, 1987; Bernor & Pavlakakis, 1987). However, these studies were based on a less complete knowledge of the Zairean fauna and were carried out prior to renewed collection in the Ugandan Plio–Pleistocene by the Uganda Palaeontology Expedition (Pickford *et al.*, 1988, 1989). There now seem to be both temporal and possibly ecological differences between Zairean and Ugandan Western Rift localities.



Figure 4. Scanning electron photomicrograph of *Tachyoryctes* sp. (Ks2-19), a left lower first molar, anterior to upper left, from the Lusso Beds.

Andrews *et al.* (1979) have distinguished various ecological communities on the basis of taxonomic make-up. Forest communities (lowland and montane) are characterized by high taxonomic diversity of rodents, insectivores and primates, whereas floodplain, woodland/bushland and short grass plains communities are characterized by higher numbers of ungulate and carnivore taxa. To lessen the problem of preferential recovery of large vertebrates and to allow recovery of the small-bodied components of the fauna during surface survey and excavation, extensive wet-sieving for microfauna was systematically carried out in the Upper Semliki Lusso Beds. Nevertheless, the numbers of taxa of rodents ($n=3$), insectivores ($n=0$) and primates ($n=2$) are low, and the numbers of taxa of ungulates (bovids, $n \geq 7$; suids, $n=3$; equids, $n=2$; hippopotamids, $n=2$; others, $n=2$) are high, comprising over 70% of the mammalian taxonomic diversity (Table 2). Numbers of individuals within these taxonomic groupings reveal the same pattern of ungulate predominance (Figure 5). The relatively small sample size of this assemblage, however, suggests caution in accepting this conclusion based on these results alone.

Bovids have been shown to be sensitive paleoecological indicators in sub-Saharan African fossil sites (e.g., Kappelman, 1984; Vrba, 1985). Bovids from the Upper Semliki, which have been identified by one of us (A.W.G.), were tabulated to assess the relative percentages of numbers of individuals of savanna/grassland bovid tribes (alcelaphines and antilopines)

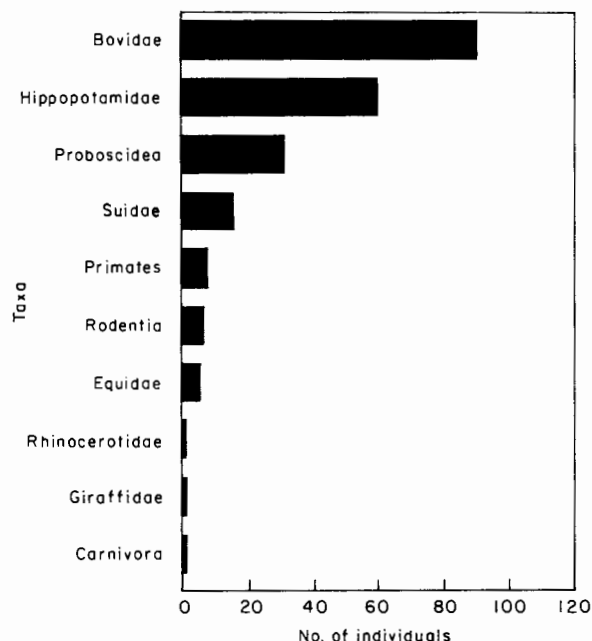


Figure 5. Histogram of numbers of individuals of mammalian taxa recovered from Lusso Bed contexts (Upper Semliki Pliocene fauna).

to woodland and bush-loving bovid tribes (tragelaphines and reduncines). Overall, alcelaphines (no antilopines are known) outnumber tragelaphines plus reduncines 22 individuals to 15 individuals (1.47 to 1). Alcelaphines make up 46% of the total identified bovid fauna by numbers of individuals, comparable to the value that Vrba (1985) obtained at Sterkfontein Member 4.

The preponderance of savanna-adapted mammals in the total surface-collected assemblage (Figure 5), as well as the excavated assemblages from localities Sn5A (Harris *et al.*, 1990) and Sn13B (Boaz *et al.*, in prep.), indicate that the predominant faunal representatives were not derived from forest or densely wooded habitats, but from more woodland, bush or grassland-dominated habitats. The small-mammal taxa are consistent with an aquatic setting, bordered by abundant grasses and/or a savanna habitat. The bulk of the fossil wood assemblage supports this reconstruction both by taxonomic make-up and by the presence of traumatic rings due to bush-fire. However, the presence of fossil wood taxa characteristic of dense lowland Central/West African forest, such as *Tessmannia anomala*, also indicates that forested and densely wooded habitats were not far distant. These communities may have occupied the well-watered rift shoulders, perhaps 5–10 km away. Only a few faunal elements, such as *Hexaprotodon imagunculus*, considered here to have had a similar adaptation to the extant pygmy hippopotamus, and the colobine, are possibly indicative of these or similar forested and heavily wooded habitats.

Fossiliferous outcrops in the Plio–Pleistocene Western Rift of Zaire are rarer than those in the Eastern Rift and, where found, they preserve fewer and frequently less complete fossil remains. Their presumed depositional environments, particularly forest acidic soils, were hypothetically much less conducive to fossil preservation than the savanna environments of eastern Africa. The Upper Semliki Lusso Bed fauna is dominated by bovids and

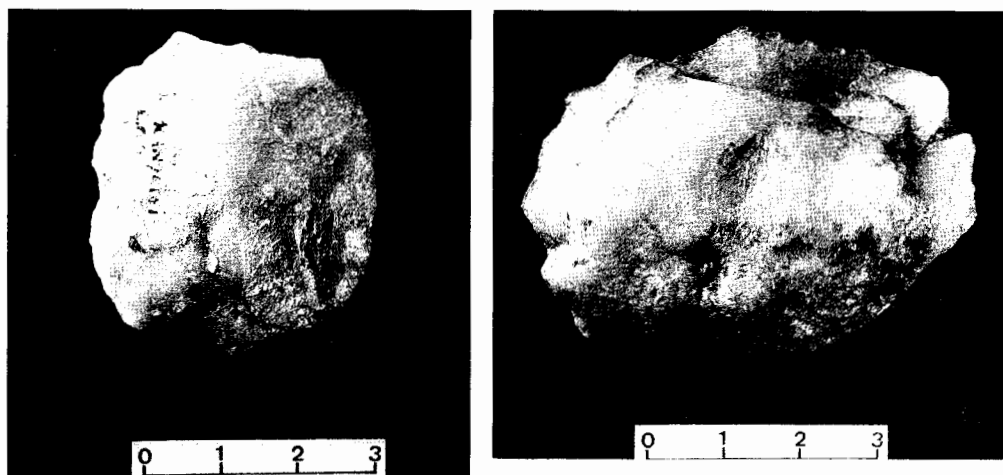


Figure 6. Quartz flakes of hominid manufacture recovered by de Heinzelin in excavation from the Lusso Beds at Kanyatsi 2, northern shore of Lake Rutanzige.

other primarily savanna species. We conclude that these Zairean localities are thus more representative of savanna than dense forest habitats, and are instead quite similar to penecontemporaneous fossil localities in eastern Africa, despite the documented nearby presence of dense forest. This conclusion is at variance with paleoenvironmental reconstructions of "humid" and forested environments in recently re-investigated western Ugandan sites of Pliocene and Pleistocene age (Pickford *et al.*, 1988, 1989). We suggest that the lower density of fossil land vertebrates in the Western Rift is due not to taphonomic destruction of bone in forested environments but to preservation of predominantly off-shore lacustrine sediments which preserve abundant fish and invertebrate remains, but only rarely preserve terrestrial species.

Archaeology

De Heinzelin (1955) first discovered stone flakes in a geological trench in Lusso Bed deposits at Kanyatsi on the northern shore of Lake Rutanzige. Excavations conducted by Harris *et al.* (1987, 1990) revealed abundant flake tools at the site of Senga 5A. A total of 723 stone artifacts of Oldowan character have been excavated from this locality, spatially associated with a Lusso-aged fauna, including *Notochoerus euilus*, *Metridichoerus jacksoni*, *Tragelaphus nakuae* and *Elephas recki*. The stone artifact assemblage comprises diverse cores and flakes made almost entirely of quartz, and is most comparable to the Pliocene-aged stone tool assemblage from Omo (Merrick & Merrick, 1976). The Omo assemblage is also characterized by the small size of tools, lack of cores and use of quartz as the primary raw material. The assemblage known from Olduvial Bed I on the other hand is comprised of large flake and core tools made on predominantly basalt and quartzite (Leakey, 1971). A chelonian xiphiplastron fragment shows evidence of cut-marks made by stone tools (Harris *et al.*, 1990; Meylan, 1990).

The fossil bone and stone artifactual occurrence at Sn5A, however, is a re-deposited unit in a much later deposit, the Semliki Lower Terrace of late Pleistocene age (Harris *et al.*, 1990), as evidenced by sedimentary inclusions of late Pleistocene age and the geometry of the site. However, fauna and artifacts excavated from Sn5A seem to be all of Lusso age, and Harris

et al. (1990) concluded that there was a basic integrity of fauna and archaeology at the site. Further work at Kanyatsi 2 by Harris, as well as reassessment of the artifactual material excavated in the 1950s, confirmed de Heinzelin's original discovery and identification of *in situ* stone flakes (Figure 6) at this locality.

The earliest fossil record of Hominidae in the Western Rift is a fragmentary cranium ascribed to *Homo* sp. at a level in the Ugandan Nyabusosi Formation estimated to be 0.7–1.8 Ma (Senut *et al.*, 1987). Fossil remains of hominids have not been recovered from Lusso Bed contexts, but the archaeological records at Senga 5A and Kanyatsi 2 indicate their presence.

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References

- Andrews, P., Lord, J. M. & Evans, E. M. N. (1979). Patterns of ecological diversity in fossil and modern mammalian faunas. *Biol. J. Linn. Soc.* **11**, 117–205.
- Bernor, R. L. & Pavlakis, P. (1987). Zoogeographic relationships of the Sahabi large mammal fauna (early Pliocene, Libya). In (N. T. Boaz *et al.*, Eds) *Neogene Paleontology and Geology of Sahabi, Libya*, pp. 349–383. New York: Alan R. Liss.
- Bishop, W. W. (1963). The later Tertiary and Pleistocene in eastern equatorial Africa. In (F. C. Howell & F. Boulière, Eds) *African Ecology and Human Evolution*, pp. 246–275. Chicago: Aldine de Gruyter.
- Bishop, W. W. (1969). Pleistocene geology in Uganda. *Geol. Surv. Ugan. Mem.* **No. 10**.
- Boaz, N. T. (Ed.) (1990). Evolution of environments and Hominidae in the African Western Rift Valley. *Virg. Mus. nat. Hist. Mem.* **1**.
- Boaz, N. T., Pavlakis, P., McDonell, M. & Gatesy, J. (in prep.) Analysis of the Senga 13B Excavation: early hominid environments in the late Pliocene of eastern Zaire. For *National Geographic Research & Exploration*.
- Cooke, H. B. S. & Coryndon, S. (1970). Pleistocene mammals from the Kaiso Formation and other related deposits in Uganda. In (L. S. B. Leakey & R. J. G. Savage, Eds) *Fossil Vertebrates of Africa 2*. London: Academic Press.
- Cooke, H. B. S. (1976). Suidae from Plio-Pleistocene strata of the Rudolf Basin. In (Y. Coppens *et al.*, Eds) *Earliest Man and Environments in the Lake Rudolf Basin*, pp. 251–263. Chicago: University of Chicago Press.
- de Heinzelin, J. (1955). Le fossé tectonique sous le parallèle d'Ishango. *Inst. Pares Nat. Congo Belge, Explor. Parc Nat. Albert, Mission J. de Heinzelin de Braucourt (1950)* **1**.
- de Heinzelin, J. (1962). Les formations du Western Rift et de la cuvette congolaise. *Ann. Mus. R. Afrique Centrale, Sci. Hum.* **40**, 129–243.
- de Heinzelin, J. & Verniers, J. (1987). Premiers résultats du Semliki Research Project (Parc National des Virunga, Zaire). I. Haute Semliki: Revision stratigraphique en cours. *Mus. R. afr. Cent. Rap. Ann. Geol.* **1985–86**, 141–144.
- Dechamps, R. & Maes, F. (1990). Woody plant communities and climate in the Pliocene of the Semliki Valley, Zaire. *Virg. Mus. nat. Hist. Mem.* **1**, 71–94.
- Denys, C. (1989). Phylogenetic affinities of the oldest East African *Otomys* (Rodentia, Mammalia) from Olduvai Bed 1 (Pleistocene, Tanzania). *N. Jb. Geol. Paläont. Mh.* **12**, 705–725.
- Eck, G. G. (1987). *Theropithecus oswaldi* from the Shungura Formation, Lower Omo Basin, southwestern Ethiopia. *Cahiers de Paléontologie. Travaux de Paléontologie est-africain. Les faunes Plio-Pleistocènes de la Vallée de l'Omo (Éthiopie). Vol. 3, Cercopithecidae de la Formation de Shungura*, pp. 123–140. Paris: Éditions du C.N.R.S.
- Eck, G. G. & Jablonski, N. G. (1987). The skull of *Theropithecus brumpti* compared with those of other species of the genus *Theropithecus*. *Cahiers de Paléontologie. Travaux de paléontologie est-africain. Les faunes Plio-Pleistocènes de la Vallée de l'Omo (Éthiopie). Vol. 3, Cercopithecidae de la Formation de Shungura*, pp. 11–122. Paris: Éditions du C.N.R.S.

- Eisenmann, V. (1985). Indications paléocologiques fournies par les *Equus* (Mammalia, Perissodactyla) pliocènes et pléistocènes d'Afrique. In (Fondation Singer-Polignac, Ed.) *L'Environnement des hominidés au Plio-Pleistocene*, pp. 57-78. Paris: Masson.
- Feibel, C. S., Brown, F. H. & McDougall, I. (1989). Stratigraphic context of fossil hominids from the Omo Group deposits: Northern Turkana Basin, Kenya, and Ethiopia. *Am. J. phys. Anthrop.* **78**, 595-622.
- Fuchs, V. (1934). The geological work of the Cambridge expedition to the East African lakes, 1930-1931. *Geol. Mag.* **71**, 97-112; **72**, 145-166.
- Gautier, A. (1965). *Geological Investigation in the Sinda-Mohari (Ituri, NE-Congo): A Monograph on the Geological History of a Region in the Lake Albert Rift*. Gent: Rijksuniversiteit te Gent.
- Gautier, A. (1970). Fossil freshwater mollusca of the Lake Albert-Lake Edward Rift. *Ann. Mus. R. Afr. Cent. Terr. Evol. Sci. Geol.* **67**, 1-144.
- Harris, J. W. K., Williamson, P. G., Morris, P. J., de Heinzelin, J., Verniers, J., Helgren, D., Bellomo, R. V., Laden, G., Spang, T. W., Stewart, K. M. & Tappen, M. J. (1990). Archaeology of the Lusso Beds. *Virg. Mus. nat. Hist. Mem.* **1**, 237-272.
- Harris, J. W. K., Williamson, P. G., Verniers, J., Tappen, M. J., Stewart, K., Helgren, D., de Heinzelin, J., Boaz, N. T. & Bellomo, R. V. (1987). Late Pliocene hominid occupation in Central Africa: the setting, context, and character of the Senga 5A site, Zaire. *J. hum. Evol.* **16**, 701-728.
- Kappelman, J. (1984). Plio-Pleistocene environments of Bed I and lower Bed II, Olduvai Gorge, Tanzania. *Palaeogeog. Palaeoclim. Palaeoecol.* **48**, 171-196.
- Leakey, M. D. (1971). *Olduvai Gorge, Volume 3. Excavations in Beds I and II, 1960-1963*. Cambridge: Cambridge University Press.
- Leakey, M. G. (1987). Colobinae (Mammalia, Primates) from the Omo Valley, Ethiopia. *Cahiers de Paléontologie. Travaux de paléontologie est-africain. Les faunes Plio-Pléistocènes de la Vallée de l'Omo (Éthiopie). Vol. 3, Cercopithecidae de la Formation de Shungura*, pp. 147-169. Paris: Éditions du C.N.R.S.
- Lepersonne, J. (1949). Le fossé tectonique du Lac Albert-Semliki-Lac Édouard. Résumé des observations géologiques effectuées en 1938, 1939, 1940. *Ann. Soc. Geol. Belg.* **72**, 1-92.
- Merrick, H. & Merrick, J. (1976). Archeological occurrences of earlier Pleistocene age, from the Shungura Formation. In (Coppens, Y. et al., Eds) *Earliest Man and Environments in the Lake Rudolf Basin*, pp. 574-584. Chicago: University of Chicago Press.
- Meylan, P. (1990). Fossil turtles from the Upper Semliki. *Virg. Mus. nat. Hist. Mem.* **1**, 163-170.
- Pavlakis, P. (1987). Biochronology, paleoecology and biogeography of the Plio-Pleistocene fossil mammal faunas of the Western Rift (East-Central Africa) and their implication for hominid evolution. Ph.D. Dissertation, New York University.
- Pickford, M. (1990). Uplift of the roof of Africa and its bearing on the evolution of mankind. *Hum. Evol.* **5**, 1-20.
- Pickford, M., Senut, B., Ssemmanda, I., Elepu, D. & Obwona, P. (1988). Premiers résultats de la mission de l'Uganda Palaeontology Expedition à Nkondo (Pliocène du Bassin du Lac Albert, Ouganda). *C.r. Séanc. Acad. Sci. Paris Ser. 2* **306**, 315-320.
- Pickford, M., Senut, B., Roche, H., Mein, P., Ndaati, G., Pbwona, P. & Tuhumwire, J. (1989). Uganda Palaeontology Expedition: résultats de la deuxième mission (1987) dans la région de Kisegi-Nyabusosi (bassin du lac Albert, Ouganda). *C.r. Séanc. Acad. Sci. Paris Ser. 2* **308**, 1751-1758.
- Pickford, M., Senut, B., Poupeau, G., Brown, F. H. & Haileab, B. (1991). Correlation of tephra layers from the Western Rift Valley (Uganda) to the Turkana Basin (Ethiopia/Kenya) and the Gulf of Aden. *C.r. Séanc. Acad. Sci. Paris Ser. 2* **313**, 223-229.
- Potts, R. (1989). Ologesailie: new excavations and findings in Early and Middle Pleistocene contexts, southern Kenya rift valley. *J. hum. Evol.* **18**, 477-484.
- Sabatier, M. (1978). Un nouveau *Tachyorcytes* (Mammalia, Rodentia) du bassin pliocène de Hadar (Éthiopie). *Geobios* **11**, 95-99.
- Schwartz, H. L. (1983). Paleocology of late Cenozoic fish from the Turkana Basin, Kenya. Ph.D. Dissertation, University of California, Santa Cruz.
- Senut, B., Pickford, M., Ssemmanda, I., Elepu, D. & Obwona, P. (1987). Découverte du premier Homininae (*Homo* sp.) dans le Pléistocène de Nyabusosi (Ouganda Occidental). *C.r. Séanc. Acad. Sci. Paris Ser. 2* **305**, 819-822.
- Verniers, J. & de Heinzelin, J. (1990). Stratigraphy and geological history of the Upper Semliki: a preliminary report. *Virg. Mus. nat. Hist. Mem.* **1**, 17-39.
- Vrba, E. S. (1985). Ecological and adaptive changes associated with early hominid evolution. In (E. Delson, Ed.) *Ancestors: The Hard Evidence*, pp. 63-71. New York: Alan R. Liss.
- Williamson, P. G. (1979). Evidence of the major features and development of Rift palaeolakes in the Neogene of East Africa from certain aspects of lacustrine mollusc assemblages. In (W. W. Bishop, Ed.) *Geological Background to Fossil Man*, pp. 507-527. Edinburgh: Scottish Academic Press.
- Williamson, P. G. (1990). Late Cenozoic mollusca faunas from the North West African Rift (Uganda-Zaire). *Virg. Mus. nat. Hist. Mem.* **1**, 125-139.
- Winkler, A. J. (1990). Systematics and biogeography of Neogene rodents from the Baringo District, Kenya, Ph.D. Dissertation, Southern Methodist University.