

12. Fauna, taphonomy, and ecology of the Plio-Pleistocene Chiwondo Beds, Northern Malawi

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Abstract

The vertebrate fauna of the Chiwondo Beds in Northern Malawi is heavily biased towards the preservation of large terrestrial mammals, the majority being ungulates. The faunal diversity resembles an African short-grass plains assemblage. The taxonomic diversity is nevertheless low, emphasizing an incomplete fossil record. Based on modern bovid representation in African game parks, statistical tests show that the Chiwondo bovid assemblage consists of a mixture of species found in the Somali-Masai and the Zambezian ecozones. The composition of the terrestrial fauna is similar to Swartkrans 1 and the Upper Ndolanya Beds. The fossil assemblages can be assigned to three biostratigraphic time intervals that date from older than 4.0 Ma to less

than 1.5 Ma. The occurrence of *Paranthropus boisei* at a lake margin site in the Chiwondo Beds corresponds to robust australopithecine-bearing localities near Lake Turkana, Kenya. A case study showed that the investigated death assemblage on a delta plain in the Malema region was subject to heavy modification after deposition. This has affected the size distribution, the frequencies of skeletal elements, and thus the taxonomic composition. High-density skeletal elements such as molars and partial mandibles dominate the assemblage. The *Homo rudolfensis* locality at Uraha has a different faunal composition, the preservation in a paleosol points to a different taphonomic history and the Uraha area encompasses a longer time span.

Introduction

Due to an interest in the paleobiogeography of southeastern Africa, the Hominid Corridor Research Project (HCRP) began its long-term study in the Malawi Rift in 1983. The research agenda is focused on the understanding of the ecological differences, migration events, and the origin and dispersion of Plio-Pleistocene faunas between eastern and southern Africa (Schrenk et al., 1993; Bromage et al., 1995; Kullmer et al., 1999).

Dixey (1927) first recognized the Chiwondo and Chitimwe Beds, which he attributed to the Pliocene and Pleistocene, respectively. J.D. Clark and colleagues' (Clark et al., 1966, 1970; Coryndon, 1966; Clark and Haynes, 1970; Mawby, 1970) explorations into the Chiwondo Beds of the northern Malawi Rift led to the first major contributions to the knowledge of the paleoecology and paleobiogeography of that area. Kaufulu et al. (1981) reinvestigated the deposits considering the high potential of the Chiwondo Beds for paleoanthropology.

Geology

The sedimentology and geology was described by Ring and Betzler (1995) and Betzler and Ring (1995). Lake-beds and fluvial deposits have been subdivided into five depositional units, which are bounded by unconformities (angular and erosional unconformities, paleosols) reflecting sedimentary breaks (Figure 1).

Unit 1 overlies the Mesozoic Dinosaur Beds with an angular unconformity. The sediments consist of reddish to grayish braided stream deposits. After a perennial lake was established around 4.5–4 Ma, the sedimentary system was lake dominated throughout Unit 2. A general flooding of the depositional area marks the lower limit of this unit.

The base of Unit 3 is marked by a change of the type in depositional system above an angular unconformity. Biostratigraphic data and facies repartition suggest that two subunits can be differentiated (Betzler and Ring, 1995).

A predominance of fluvial processes was established in Unit 3A. Subunit 3A occurs throughout the Karonga-Chilumba area. Meandering rivers and minor lagoons developed in the proximal parts. Lake-ward, the sediment accumulated in the stream-mouth bars of deltas. Subunit 3B is restricted to the southern part of the Karonga-Chilumba area. It is a condensed section containing a series of calcimorphic paleosols. Pronounced lake regressions took place between 2.3–2 Ma and 1.6–1.5 Ma (= paleosol in Unit 3B), correlating with the Mbamba sequence of the offshore seismic record and the second magmatic pulse of the Rungwe volcanics, southern Tanzania (Ring and Betzler, 1995).

Deposition of Unit 4, which is bound to the southern part of the Karonga-Chilumba area, occurred following minor tectonic activity, allowing a transgression after 1.5 Ma. The lower part of Unit 4 consists of aeolian sands, while the upper part corresponds to a lake high stand, which is documented by open lake

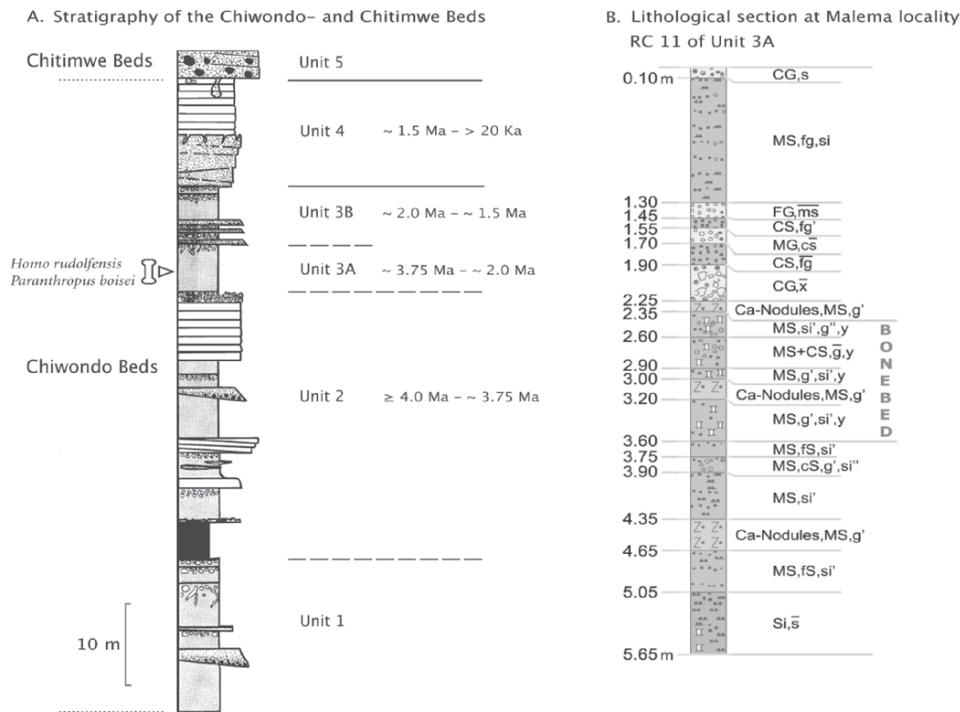


Figure 1. A. Generalized stratigraphic profile of Chiwondo and Chitimwe Beds Units 1–5 including their age ranges. Solid lines mark major unconformities; dashed lines mark minor unconformities. B. Lithological section of Malema hominin locality RC 11 of Unit 3A. The thickness refers to locality RC 11 only. The RC 11 bone bed extends from 2.35 to 3.6m depth. Abbreviations: Si = silt, si = silty; fs = fine sand; ms = middle sand; cs = coarse sand; s = sandy; fg = fine gravel; mg = middle gravel; cg = coarse gravel; g = gravelly; x = stone; y = boulder; quantity of sediment fraction ‘= slight, “ = very slight, — = strong.

limestones with abundant diatoms (Ring and Betzler, 1995). The alluvial fan deposits of the Chitimwe Beds, Unit 5, indicate a lake level lowering and are evidence of the changing sedimentary character.

Biostratigraphy

The age of the Chiwondo Beds relies on faunal correlation with radiometrically dated biostratigraphic units in eastern Africa. The age range refers to radiometrically well-dated volcanic tuffs in the Koobi Fora and Shungura Formations as described by Brown et al. (1985), Brown and Feibel (1986), and Feibel et al. (1989).

Most of the Late Pliocene fossil localities are attributed to stratigraphic Unit 3A (e.g., Uraha, Mwimbi, Malema, and Mwenirondo localities), few are located in stratigraphic Unit 3B (Uraha), while some older Middle Pliocene localities occur in stratigraphic Unit 2 (Uraha and Mwimbi). The age of Unit 2 of the Chiwondo Beds ranges between >4 Ma and circa 3.75 Ma, the age of Unit 3A ranges between circa 3.75 and 2 Ma, the age of Unit 3B ranges between circa 2 and 1.5 Ma (Schrenk et al., 1993; Bromage et al., 1995). Stratigraphic Unit 3A is the longest time-aggregated deposit within the Chiwondo Beds. Short-term sedimentary unconformities exist, but none are significant enough to discriminate individual subunits. Nevertheless, localities

approximating one another within survey areas tend to be similar in age, while those localities further apart tend to become more disparate in their biochronology (Bromage et al., 1995). Fossils recovered from Unit 2 and Units 3A and B correspond to three biochronologic

intervals and age ranges (Table 1) (Bromage et al., 1995).

Interval I. Circa 4–3.75 Ma (Unit 2 of the Uraha and Mwimbi areas): e.g., *Nyanzachoerus jaegeri*. White (1995) provides a first appearance for *N. jaegeri* (FAD)

Table 1. List of identified mammal taxa at fossil areas of the Chiwondo Beds (modified after Bromage et al., 1995). "X" marks the presence of a taxon, the ones in parentheses refer to Kaufulu et al. (1981)

Stratigraphic unit 2	Uraha	Mwimbi	Malema	Mwenirondo	Mwamberu	Sadala
<i>Nyanzachoerus jaegeri</i>	X	X				
<i>Anancus</i> aff. <i>kenyensis</i>	X					
early <i>Loxodonta</i> sp.		X				
<i>Mammuthus subplanifrons</i>	X					
Stratigraphic Unit 3A						
<i>Damaliscus</i> sp.	X	X	X	X		
Alcelaphini, medium-sized	X		X			
<i>Connochaetes</i> sp.	X	X				
<i>Megalotragus</i> sp.	X	X	X	X		
<i>Megalotragus kattwinkeli</i>	X	(X)		(X)		
<i>Gazella</i> sp.	X	X	X			
<i>Gazella</i> sp. aff. <i>vanhoepeni</i>						(X)
Antilopini gen. indet.	X			X		
<i>Tragelaphus</i> sp.	X		X			
<i>Tragelaphus</i> cf. <i>angasi</i>	X			(X)		
<i>Tragelaphus</i> cf. <i>strepsiceros</i>	X	X				
Tragelaphini gen. indet.		X				
<i>Kobus</i> sp.	X	X	X	X		
<i>Kobus</i> aff. <i>patulicornis</i>		(X)			(X)	
Reduncini sp.			X			
<i>Oryx</i> aff. <i>gazella</i>	X					
<i>Hippotragus</i> sp.	X		X	X		
<i>Hippotragus</i> aff. <i>gigas</i>			X			
<i>Syncerus</i> sp.	X	X	X	X		
<i>Ugandax</i> sp.			X	X (X)		
Bovini gen. indet.		X				
<i>Aepyceros</i> sp.	X (X)	X	X	X (X)	(X)	
<i>Madoqua</i> sp.	X					
Neotragini gen. indet.			X			
<i>Giraffa</i> aff. <i>pygmaea</i>	X		X			
<i>Giraffa</i> aff. <i>stillei</i>	X	X	X	X		
<i>Giraffa</i> aff. <i>jumae</i>			X			
<i>Sivatherium</i> sp.			X			
<i>Hippopotamus</i> sp.	X	X	X	X		
<i>Metridiochoerus andrewsi</i>	X	X (X)				
<i>Notochoerus euilus</i>	X	X		X		
<i>Notochoerus scotti</i>	X	X	X	X		
early <i>Notochoerus scotti</i>			X			
<i>Notochoerus capensis</i>		X (X)			(X)	
<i>Diceros bicornis</i>	X					
<i>Ceratotherium simum</i>	X		X	X		
Rhinocerotidae gen. indet.		X				

(Continued)

Table 1. List of identified mammal taxa at fossil areas of the Chiwondo Beds (modified after Bromage et al., 1995). "X" marks the presence of a taxon, the ones in parentheses refer to Kaufulu et al. (1981)—cont'd

Stratigraphic unit 2	Uraha	Mwimbi	Malema	Mwenirondo	Mwamberu	Sadala
<i>Hipparion</i> sp.	X	X	X	X		
<i>Elephas</i> sp.	X	X				
<i>Elephas recki</i>			X			
<i>Elephas recki atavus</i>	X					
<i>Elephas recki shungurensis</i>			X			
<i>Deinotherium</i> sp.	X		X			
<i>Parapapio</i> sp.	X		X	X		
<i>Theropithecus</i> sp.			X			
Papionini gen. indet.				X		
<i>Homo rudolfensis</i>	X					
<i>Paranthropus boisei</i>			X			
Stratigraphic Unit 3B						
<i>Metridiochoerus compactus</i>	X					

at 5.0–6.0 Ma at Lothagam 1C, with a quality score 2 (= date possibly actual FAD) and a last appearance (LAD) at 3.75 Ma in the eastern Central Awash Complex (with quality score 0 = arbitrary split of lineage). The VT-3 Tuff with an age of 3.75 Ma (White et al., 1993) occurs in the Aramis subunit of Kalb et al. (1982), where *N. jaegeri* was discovered (Kalb et al., 1982).

An age of older than 4 Ma for parts of Unit 2 is further indicated by the occurrence of *Anancus* aff. *kenyensis*. This taxon occurs in the Adu-Asa Formation (WoldeGabriel et al., 2001; Haile-Selassie et al., 2004), the Kuseralee Member of the lower Sagantole Formation (Kalb and Mebrate, 1993; Kalb, et al. 1995; Renne et al., 1999), and in the Mursi Formation (Beden, 1976) at an age of >4 to <4.15 Ma (Brown and Nash, 1976; Brown et al., 1985; Feibel et al., 1989).

An early *Loxodonta* sp. occurs at Mwimbi. *L. adaurora* is known from the Mursi Formation (Beden, 1987) and Hadar Formation (Kalb et al., 1982; Kalb, 1995). *Mammuthus subplanifrons* is identified at Uraha. Maglio (1973) also reported its occurrence in the Chiwondo Beds. *M. subplanifrons* from Kalb et al. (1982) Aramis subunit occurs between the VT-1 and CT tuffs and is dated to <4.1–3.75 Ma respectively (White et al., 1993).

Interval II. Between 3.75 and 1.8 Ma and younger (Unit 3A of Chiwondo Beds): e.g., *Notochoerus euilus*. The FAD of the taxon derives anagenetically and falls coincident with the LAD of *Nyanzachoerus jaegeri* at 3.75 Ma (with quality score 0 = arbitrary split of lineage) (White, 1995). A reliable LAD for *Notochoerus euilus* is 2.0 Ma (Shungura upper Member G) (Harris and White, 1979; Feibel et al., 1989) and for *Notochoerus scotti* an age of 1.8 Ma (Koobi Fora, just above the KBS tuff) (with quality score 3 = date probably actual LAD) (White, 1995).

The third molars from Interval II of the early *Notochoerus scotti* types are slightly more advanced than the early specimens from Shungura C, but less progressive than specimens from Shungura G, the correlation therefore suggests Shungura D–F age of 2.52–2.33 Ma (Feibel et al., 1989). Their occlusal length is shorter than advanced *N. scotti* specimens recognized from Shungura G. The number of lateral pillar pairs is relatively low (six pairs) indicating an early stage of *N. scotti*, since younger specimens tend to increase their occlusal length by adding lateral pillar pairs to the distal end of the tooth crown (Kullmer, 1999).

Elephas recki shungurensis specimens are identified in Chiwondo Beds Unit 3A. The

taxon occurs in the upper Hadar and Matabaietu Formations between ~3.0 and ~2.0 Ma (Kalb, 1995) and from Shungura Member C to lower Member F (Beden, 1987), indicating an age of 2.85–~2.35 Ma.

Interval III. 1.6 Ma and younger (Unit 3B of the Uraha area): e.g., *Metridiochoerus compactus* is encountered from 1.6 Ma (correlation with Koobi Fora, just below the Okote Tuff) to 0.78 Ma (correlation with Olduvai Bed IV). So, Unit 3B has a correlation of 1.6–0.8 Ma.

Other taxa fall in age ranges I–III⁽⁺⁾, II–III^(o), or II^(*) (the FADs and LADs refer to Behrensmeyer et al., 1997): *Giraffa pygmaea*⁽⁺⁾ (FAD 4.35–LAD 1.39 Ma; E. Turkana), *Sivatherium marusium*⁽⁺⁾ (FAD 4.10–1.33 Ma; W. and E. Turkana), *Giraffa stillei*^(o) (FAD 3.50–LAD 1.39 Ma; E. Turkana), *Megalotragus isaaci*^(o) (FAD 2.52–LAD 1.39 Ma; E. Turkana), *Ceratotherium simum*^(o) (FAD 3.40–LAD 0.70 Ma; W. and E. Turkana, Omo), *Diceros bicornis*^(o) (FAD 3.40–LAD 0.70 Ma; W. and E. Turkana, Omo), *Ugandax* sp. nov. WT^(*) (FAD 3.36–LAD 1.88 Ma; W. Turkana), *Hippotragus gigas*^(*) (FAD 3.36–LAD 1.6 Ma; W. and E. Turkana).

Most of the equids can be referred to species of *Hipparion* sp. One isolated molar of *Equus* sp. from northern localities derives from a layer of upper Unit 3A just below the contact of the Chiwondo and Chitimwe Beds (Bromage et al., 1995).

The *Homo rudolfensis* locality at Uraha is situated in Unit 3A within a ferruginous, calcimorphic paleosol, 5.5 m above an oncolid layer of Unit 2, and circa 6 m below the boundary of Unit 3 to 4 (Figure 7; Betzler and Ring, 1995). Equids that derive from the same lithologic unit as *H. rudolfensis* are referred to *Hipparion* sp. (Bromage et al., 1995). One equid molar fragment from Uraha may tentatively be assigned to *Equus* sp. (Ray Bernor, pers. comm.). It derives from the upper part of Unit 3A above the ferruginous paleosol-yielding *Homo rudolfensis*.

According to Table 1 and information given above, Uraha, Malema, Mwimbi, and Mwenirondo share certain taxa, which co-occur in biostratigraphic Unit 3A.

Fauna

The sample of vertebrates recovered from Units 2 and 3 of the Chiwondo Beds consists of about thousand identifiable vertebrate specimens from areas between the towns of Karonga in the north and Chilumba in the south, a distance of over 70 km (Figure 2). Three major fossiliferous areas can be distinguished within the Chiwondo Beds: Uraha, Mwimbi, and Malema.

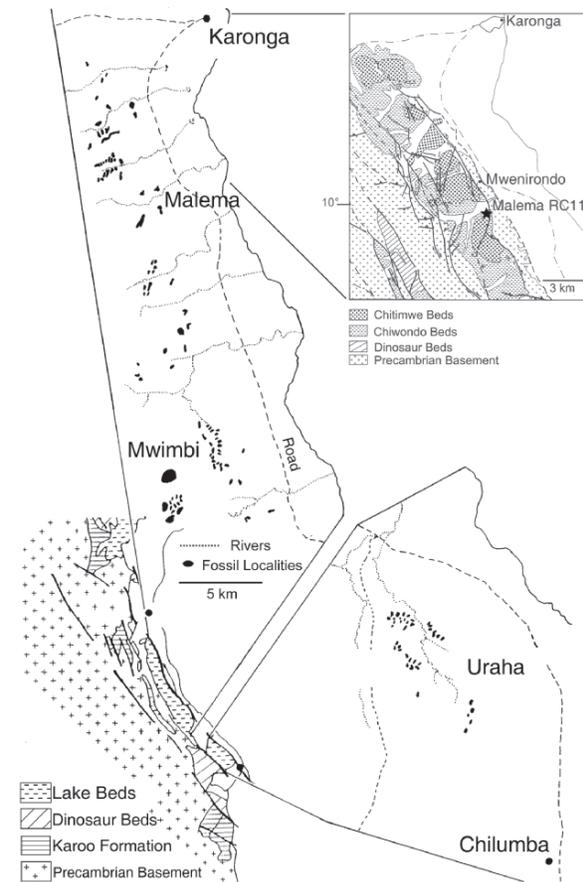


Figure 2. Topographical and geological setting of the Chiwondo Beds, Northern Malawi.

Most of the fossil specimens have been collected from the erosional surface by systematic surveys. Bovids, followed by equids, suids, hippopotamids, and giraffids, dominate the fauna of the Chiwondo Beds (Figure 3). The recovered skeletal elements are mostly isolated molars, mandible fragments, or high-density limb bones. Because of the very low fossil density in the Chiwondo Beds, only a few systematic excavations were conducted during years of fieldwork, until a fossil-rich horizon containing also *Paranthropus boisei* was discovered at Malema locality RC 11, which considerably enlarged the collection (Bromage and Schrenk, 1986; Sandrock et al., 1999).

Taking a closer look at the fauna of the Uraha, Malema, and Mwimbi regions, it is evident that bovids dominate the faunal assemblages (Figure 4a–c). Equids have about the same relative abundance at Uraha and Malema. However, there are some differences between the regions in their suid proportions: at Malema only early *Notochoerus scotti* specimens are found, whereas at Uraha remains of *Nyanzachoerus jaegeri*, *Notochoerus euilus*, *Notochoerus scotti*, *Metridiochoerus andrewsi*, *Metridiochoerus compactus* were discovered. The latter species occurs only at Uraha. Mwimbi is the only area where specimens attributable to *Notochoerus capensis* are found. Giraffes are more common in the

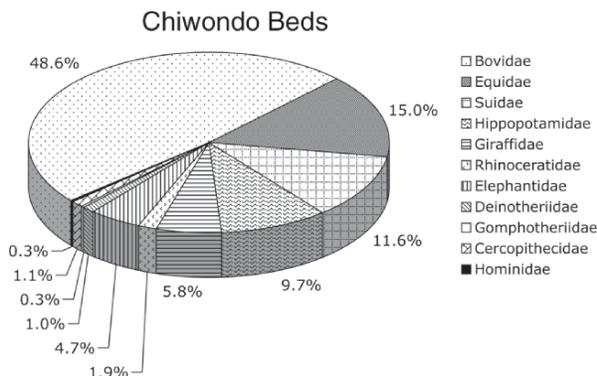


Figure 3. The mammal fauna of the Chiwondo Beds.

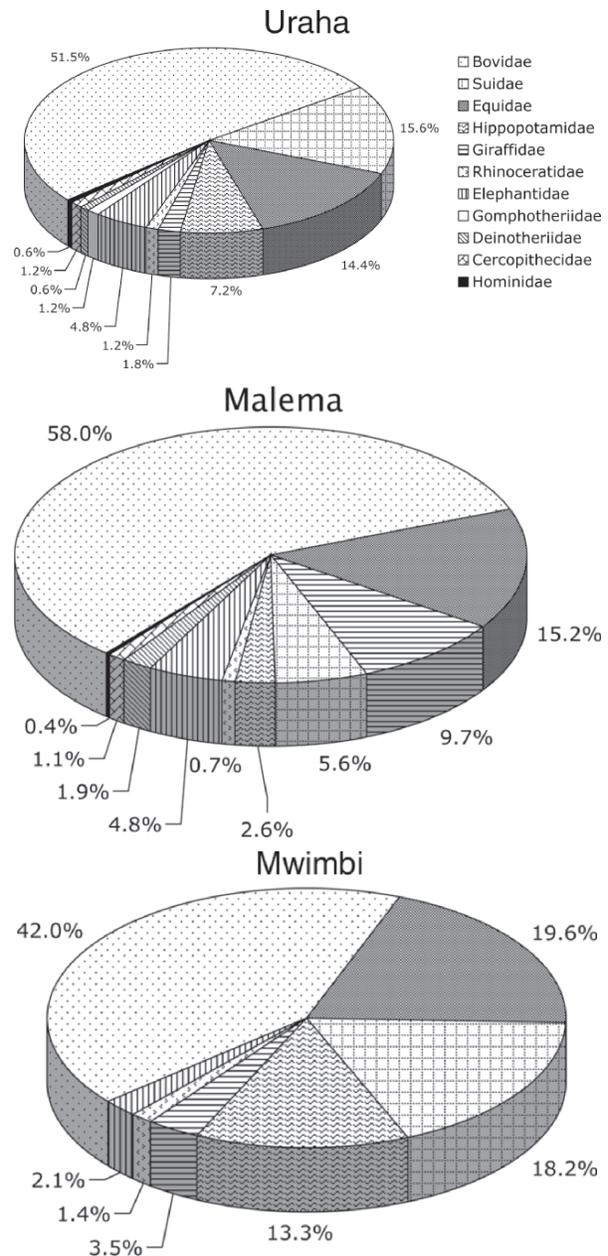


Figure 4a–c. The mammal fauna at Uraha (a), Malema (b), and Mwimbi (c) localities.

Malema region. Three size groups (i.e., large, similar to the extant species, medium size species, and a smaller one) can be distinguished at Malema and are tentatively attributed to *Giraffa* aff. *jumaea*, *Giraffa* aff. *stillei*, *Giraffa* aff. *pygmaea* respectively. *Sivatherium* sp. remains are represented only at Malema.

Bovoid specimens are identified as *Syncerus* sp. or *Ugandax* sp. The *Ugandax* sp. specimens from Malema share morphological affinities with specimens of the Mwenirondo region that are curated at the University of California Museum of Paleontology (UCMP) (Kaufulu et al., 1981). Gentry and Gentry (1978) mentioned a right mandible with P₄-M₃ from Mwenirondo and identified it as *Syncerus* sp. Hippotragins are common at Malema; they may be referred to *Hippotragus* aff. *H. gigas*. Coryndon (1966) assigned two mandibles from Mwenirondo to *Oryx*, but Gentry and Gentry (1978) thought these specimens likely belonged to *Syncerus*. Gentry and Gentry (1978) attributed a broken right mandible with P₄-M₃ to *Hippotragus gigas*. Kaufulu et al. (1981) identified two size groups of hippotragins without further distinguishing them. Alcelaphins make up the majority of the bovid fauna. They comprise large-, medium- and small-sized specimens. The largest is *Megalotragus* sp., and the smallest *Damaliscus* sp. *Megalotragus* is recognized by its huge well-rounded lobes and its very simple central cavity. Especially the upper molars of *Megalotragus* sp. at Malema are extremely hypsodont.

As very rare elements, specimens of the cercopithecoid *Parapapio* occur at northern and southern localities, while *Theropithecus* sp. is only found in the Malema region.

The Malawi Rift faunas include representatives from three geographically based assemblages: some species represent eastern African endemics, a smaller group consists of southern African endemics, and many species are shared between eastern and southern Africa. Interesting is the substantial occurrence of *Aepyceros* sp. at Uraha, which marks the southernmost distribution of this genus in the Late Pliocene.

It is striking that the abundance of mammalian families within the Chiwondo Beds differs significantly from that of East and South Africa fossil sites. This is especially highlighted by the apparent absence of micromammals and carnivores (Schrenk et al., 1995).

It is important to note, that the fossil sample of the main fossiliferous Unit 3A is likely spanning approximately 1.7 Ma, but this cannot be demonstrated based on the current taxonomic content. Only species like *E. recki shungurensis* and early *Notochoerus scotti* give some localities a more precise age range.

More fine-scaled stratigraphic subunits within Units 2 and 3A cannot be defined. Consequently, the fossil occurrences within these units might represent a longer time span, but adjacent localities within laterally extensive areas agree in their biochronologic range estimation (Bromage et al., 1995).

The faunal data from the excavation site of the Malema RC 11 bone bed diminishes large-scaled time averaging. The early *Notochoerus scotti* specimens at this locality give a more precise chronological control (Kullmer, 1999), making these deposits readily correlated with other East African strata between 2.6 and 2.4 Ma.

Taphonomy

Malema site RC 11 excavations were undertaken over several field seasons. The sedimentary sequences in Unit 3A at Malema can be referred to fine- to medium-grained fluvial sediments of a delta plain. Due to a slow lake level lowering and increased sediment input by rivers, the fluvial deposits became dominant after 3.7- to 2.0-Ma ago in the Malema sequence (Betzler and Ring, 1995). The emerging picture is a stable north-south directed land corridor bordered by the rift shoulder to the west and the lake to the east. Meandering rivers with minor lagoons developed proximally, lake-ward prograding river deltas with stream mouth bars developed (Betzler and Ring, 1995). The sedimentological and taphonomical study indicates that the Malema bone assemblage was deposited at the lake margin, probably on a delta plain (Sandrock, 1999) (see Figure 1).

Lacustrine transgressions were minor occurrences during this time and only inter-fingered with the delta front. Small-scaled lake bottom layers with gastropods, which can be found in almost the entire Malema valley, derive from minor transgressive phases of paleolake Malawi, while the overlying sand units represent fluvial sequences. Geological sections indicate that this system consisted of quite shallow distributaries. These channels eroded into fine to middle sand units of previously formed overbank deposits (Sandrock, 1999).

Sudden and gradual abandonment of channels are evident by fine-grained channel fills and mixed-grained fills fining upward. Coarse bed-load sediments are entirely missing within the sequences. The angular to subangular rounding of the mineral components suggests a proximate source area for the sediment (Sandrock, 1999).

The features of the RC 11 case study may serve as a good example for the Chiwondo Beds assemblages as a whole. The observed taphonomic variables indicate a mixture of an attritional and hydraulically winnowed assemblage (Figure 5; after Behrensmeyer, 1991). The representation of the skeletal parts is strongly linked to the sedimentary environment. The most obvious feature is the dominance of high-density elements, especially teeth and half mandible fragments that fall into the Voorhies Group II–III range. The removal of the lighter skeletal elements of Voorhies Group I and the much greater amount of dental material than postcranial elements is evidence for hydraulic transport (Behrensmeyer, 1975, 1991). It is reasonable to conclude that more postcranial material existed at RC 11, which was subsequently destroyed and is now a part of the large fraction of indeterminate fragments. A hydraulic sorting is overprinted by the destruction of many skeletal elements, apparently biasing the assemblage to those that are dense and towards a classic channel lag deposit.

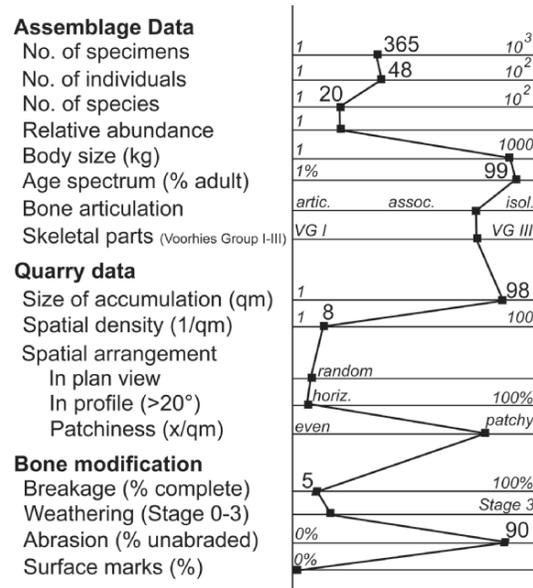


Figure 5. Taphonomic variables at Malema locality RC 11. The excavation area has a size of 22m × 10m; the fossiliferous layer has a thickness of 1.3m. Regular numbers refer to the locality, italicized numbers are underlining the graphic.

The relative abundance was measured by using the MNI. Using the NISP would have overestimated the number of individuals due to unrecognized matches among the large amount of broken specimens and unrecognized association among specimens (Badgley, 1986).

The mixed features of an autochthonous-attritional assemblage and an allochthonous-sorted assemblage are the best analogues to describe site RC 11. Sorting, the dominance of Voorhies Groups II–III elements, the lack of association, lower stages of weathering, and overrepresentation of adults indicate allochthony. Autochthony is indicated by at least a few Voorhies Group I elements and a random orientation of the skeletal elements. Abrasion cannot really be inferred from the RC 11 assemblage, since it is heavily overprinted, if this was minimal it would also suggest autochthony. The same is true for associated skeletal elements that are obviously lacking at Malema.

The Malema site is similar to the late Miocene Tonopah quarry, Nevada, (Henshaw, 1942) in that the fossils are preserved in a relatively fine-grained matrix. The fossils consist of only teeth and limb bones. Skeletal associations and abrasion are lacking.

Persistent but weak currents were likely responsible for the deposit. The currents likely operated over a considerable time to create this lag deposit. In contrast, the early Pliocene Verdigre quarry of Voorhies (1969) was characterized by strong currents acting over a shorter time resulting in the fossil elements showing abrasion and no associations.

The Malema bone assemblage shows that *Hipparion* sp. and alcelaphins like *Megalotragus* sp. and *Damaliscus* sp. are the most common fossils from the lake margin area in Unit 3A. This leads to two potential scenarios: one scenario suggests that fluvial processes brought in all mammals representative of open habitats, being allochthonous in this sense. But this does not yet explain the scarcity of water-dependent reduncins in a deltaic deposit. The other scenario is that the Malema bone bed samples only the fauna of a microhabitat on the flat delta plains of the drier lake margin areas where rivers are an only minor constituent and water dependent taxa are few or absent.

The majority of the animals in the assemblage are adult animals, just 1% being juvenile. Due to their earlier destruction, the juvenile individuals of RC 11 probably share the same destiny as the micromammals. A bias against their survival potential could possibly be reworking in channels or leaching. Despite special sieving efforts, no micromammals were discovered. The lack of micromammals is striking since even in case of a “category 5 predator” (Dauphin et al., 1997) with felids or canids and the most destructive effects commonly observed to operate, at least a few bones should be preserved.

Paleoecology

Terrestrial species range between 22% and 57% in 15 modern environments (Kovarovic et al., 2002). In contrast, the Chiwondo Beds sample contains nearly 90% terrestrial species – fossorial, scansorial, and (semi-) arboreal animals are absent. This places them towards modern tropical grassland or semi-arid bushland and to Swartkrans 1 and the Upper Ndolanya Beds, which also have high percentages of terrestrial taxa. In the Chiwondo Beds small animals are underrepresented or absent altogether. Again, in modern ecosystems, species of 1g to 10kg range between 53% and 82%: the African tropical grassland and bushland faunas exhibit the smallest percentage (Kovarovic et al., 2002), but the Malawi fauna corresponds neither to the observed weight pattern of Swartkrans 1 nor to the East African localities of Kanapoi, Aramis, Laetolil Beds, or the Ndolanya Beds.

The fauna is dominated by medium- to large-sized species, the latter being large bovids, proboscideans, and hippopotamuses. Consequently an overrepresentation of herbivorous species exists. Grazers and browsers make up the majority, but especially alcelaphin grazers dominate like in Swartkrans 1 and the Ndolanya Beds.

A correspondence analysis was applied to a contingency-table data set of modern bovid genera from 29 African game parks using data derived from Shipman and Harris (1988). Variable 1 consists of the game parks, and variable 2 of the bovid genera. In addition, the bovid genera of Malema and Uraha have been included (Figure 6, Table 2). The resulting cluster of points on two axes allow the interpretation of the relations between the variables. Distances between points within a variable do have a meaning, but proximity between points only *can* indicate a consistent association.

The results share strong resemblance to the existing phytochorions in Africa today

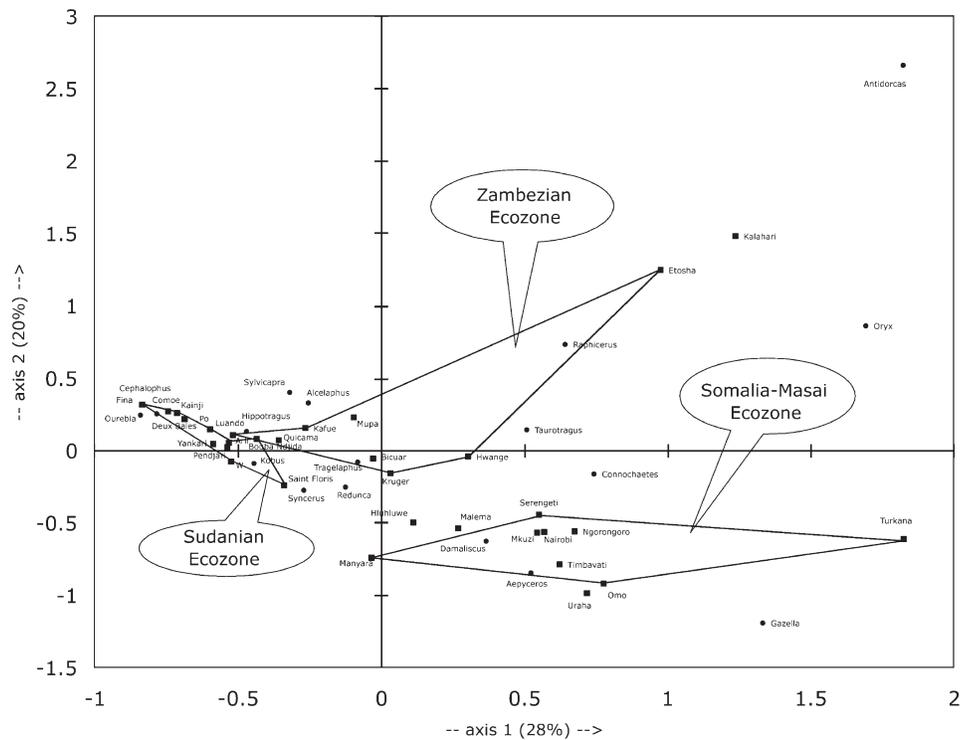


Figure 6. Correspondence analysis of game parks and bovid genera on axes 1 and 2. Chi-square distance on data = 876.6201 ~ degrees of freedom = 480, corresponding probability: 0.0000, limit Chi square for the chosen confidence range = 532.0753. Using this test one should reject the hypothesis of independence. Variable 1 (rows) consists of 29 African parks and Pliocene sites Uraha and Malema. Variable 2 (columns) consists of modern bovid genera living in the parks and bovid genera discovered at Uraha and Malema (variables 1 and 2 from Table 2).

(Sandrock, 1999). Axis 1 and 2 separate the Zambezian and Sudanian ecozones from the Somalia-Masai ecozone. Axis 1 shows increasing aridity to the right side of the plot towards the habitats of the Somalia-Masai ecoregion, which consists mainly of dry woodlands and scrub, with a gradation to grasslands (White, 1983). Turkana, Serengeti, Nairobi, Ngorongoro, Omo, and Manyara parks belong to the Somalia-Masai (SM) domain and plot separately from the Zambezian (Z) phytochorion including the parks Hwange, Kruger, Kafue, Quiçama, Luando, Etosha, Bicuár, and Mupa. All other parks but Hluhluwe, Mkuzi

(both referring to the Tonga-Pondoland ecozone), Timbavati, and Kalahari belong to the Sudanian (S) phytochorion.

The Zambezian ecozone as a whole is close to the center of gravity of the multivariate cloud, which reflects that most bovids live in this ecozone in different proportions, while in the Somalia-Masai ecozone, tribes like Antilopini and Alcelaphini dominate the assemblages. The antilopin *Antidorcas* only occurs at Etosha and Kalahari game parks; today it is a southern African endemic. The antilopin *Gazella*, on the other hand, only occurs in the Somalia-Masai domain. Members of the cephalophins, neotragins, reduncins, and *Hippotragus* on the left side of the plot are clearly separated from

Table 2. Logarithmic abundances of bovid genera in 29 African parks plus Pliocene localities Malema and Uraha

	Alcela.	Conno.	Dama.	Anti.	Gaz.	Aepy.	Tauro.	Tragel.	Kobus	Redun.	Syn.	Hippotr.	Oryx	Oureb.	Raphi.	Cephalo.	Sylvi.
Malema	0	1.47	1.44	0	0.47	0.6	0	0.3	0.9	0	1.25	1.39	0	0	0.3	0	0
Uraha	0	1	1.11	0	1.14	1.07	0	0.84	0.3	0	0	0.69	0	0	0	0	0
Kruger	0	3.97	2.8	0	0	5.18	2.62	4.02	3.5	3.17	4.38	3.14	0	2	3.69	2.47	3
Luando	0	0	0	0	0	0	2.3	2.84	3.24	2.69	2.17	3.47	0	2.39	0	2	3
Hwange	0	3.39	2.11	0	0	3.9	3.25	3.56	3	2.39	4.11	3.39	2.07	0	3.47	0	3.3
Nairobi	3.03	2.4	0	0	2.92	2.8	1.76	1.3	1.95	1.17	0	0	0	0	0.3	0	0.3
Turkana	0	0	3.3	0	3.02	0	0	0	0	0	0	0	3.12	0	0	0	0
Serengeti	4.25	5.61	4.43	0	5.27	4.81	3.84	3.39	3.47	3.39	4.69	3.39	3.39	0	0	0	0
Ngorongoro	2	4.13	0	0	3.69	0	2.6	0	1.77	1.77	1.77	0	0	0	0	0	0
Etosha	2.77	3.6	0	4.07	0	0	2.69	3.3	0	0	0	2.47	3.65	0	2.69	0	2.39
Bouba Ndjida	3.84	0	2.15	0	0	0	2.97	2.92	3.14	3.75	3.24	3.63	0	4.06	0	1.7	3.73
Quicama	0	0	0	0	0	0	3.39	3.47	0	3.17	3.9	3.17	0	0	0	3.39	3
Hluhluwe	0	3.54	0	0	0	3.68	0	3.5	2.91	2.27	3.34	0	0	0	0	0	1.17
Kafue	1.95	2	0	0	0	0.3	0.3	1.6	1.89	2.07	1.92	1.49	0	1.69	1.6	1.47	1.6
Pendjari	3.94	0	2.77	0	0	0	0	0	4.27	2.91	3.54	3.7	0	3.89	0	0	3.39
Comoé	3.9	0	0	0	0	0	0	3	3.87	0	2.69	2	0	4.23	0	3.81	3.81
Omo	0	0	3.32	0	2.81	0	2.97	0.47	0	0	2.54	0	0	0	0	0	0
Kalahari	4.15	3.8	0	4.38	0	0	3.81	0	0	0	0	0	4.2	0	3.21	0	2.85
Manyara	0	0	0	0	0	2.84	0	1.39	1.17	1.6	3.17	0	0	0	0	0	0
Bicuar	0	2.69	0	0	0	2.17	2.39	2.3	2	1.69	2	2.69	0	1.69	1	0	2.69
Mupa	0	2.39	0	0	0	0	2.3	2.74	2.77	3	0	2.3	0	2.69	2.69	0	2.69
Mkuzi	0	3.14	0	0	0	3.97	0	2.74	0	1.83	0	0	0	0	0.77	0	0.47
Arli	2	0	1.95	0	0	0	0	1.9	3.07	1.74	1.81	3.27	0	3	0	0	3.33
Deux Bales	2.65	0	0	0	0	0	0	2.29	2.24	1.7	1.6	3.07	0	2.81	0	2.18	2.69
Po	2.73	0	0	0	0	0	0	2.03	1.99	2.27	2.39	2.89	0	2.7	0	0	2.68
Saint Floris	2.95	0	3.32	0	0	0	0	0	3.5	0	3.25	2.7	0	0	0	0	0
Yankari	2.82	0	0	0	0	0	0	0	2.81	0	2.82	2.55	0	0	0	0	0
Fina	3.47	0	0	0	0	0	0	0	3.1	0	0	3.59	0	3.66	0	0	0
Kainji	3.8	0	0	0	0	0	0	2.74	3.68	0	2.07	3.76	0	3.44	0	2.19	3.09
W	3	0	2.62	0	0	0	0	2.38	3.78	0	3.61	3.45	0	3.32	0	0	0
Timbavati	0	3.09	0	0	0	3.66	0	1.89	0	1.51	0	0	0	0	0	0	0

Alcela. = *Alcelaphus*, Conno. = *Connochaetes*, Dama. = *Damaliscus*, Anti. = *Antidorcas*, Gaz. = *Gazella*, Aepy. = *Aepyceros*, Tauro. = *Taurotragus*, Tragel. = *Tragelaphus*, Redun. = *Redunca*, Syn. = *Syncerus*, Hippotr. = *Hippotragus*, Oureb. = *Ourebia*, Raphi. = *Raphicerus*, Cephalo. = *Cephalophus*, Sylvi. = *Sylvicapra*.

antilopins and alcelaphins to the right side. The analysis clearly shows the association of open arid-adapted Alcelaphini–Antilopini and *Oryx* to the parks of the Somalia-Masai ecozone. These results coincide with previous analyses (Greenacre and Vrba, 1984; Shipman and Harris, 1988; Alemseged, 2003).

Due to the difficulties to identify all Chiwondo bovids to species level, the correspondence analysis was applied to generic level – for both the fossils and the modern taxa. Furthermore, it is not necessary in this case to work at the species level, because it is well known that species of Alcelaphini and Antilopini are living in open arid environments (Vrba, 1975, 1976, 1980; Shipman and Harris, 1988).

Based on bovid proportions, Late Pliocene Malema and Uraha seem to share more affinities with the arid grassland of the Somalia-Masai than with the Zambezan phytochorion. Today Malawi belongs to the Zambezan phytochorion.

In agreement with the site comparison presented above is another fact: the micromammals of the Upper Ndolanya Beds at Laetoli show a Somalia-Masai composition (Denys, 1999). This suggests that similar ecological conditions are represented in the two regions, disregarding the lack of small mammals in the Chiwondo Beds.

A second correspondence analysis refers to the 29 game parks, once again as variable 1, but this time variable 2 refers to modern bovid tribes plus the Chiwondo and Upper Ndolanya Beds' bovid tribes (Figure 7, Table 3; data for the Ndolanya Beds derive from Gentry, 1987). It shows a similar ecological dispersion to the previous graph, separating the Zambezan and Sudanian from the Somalia-Masai ecozone. The Chiwondo and Ndolanya Beds plot between the Somalia-Masai and Zambezan ecozones. The Ndolanya Beds plot closer to the arid parks of the Zambezan ecozone. This may be explained by the frequent occurrences of Neotragini and *Antidorcas* sp. at Etosha, Kalahari and the Ndolanya Beds.

Limitations of the analyses are, first, the use of only bovids, and second, the combined application of modern and fossil data, but due to the incomplete fossil record we believe it is both useful and important to gain this large-scaled ecological information.

A closer look at the bovid distribution of Malema and Uraha may reveal different habitats within the Chiwondo Beds. Although more antilopins were discovered in Uraha, these together with the alcelaphins suggest general grassland conditions. These tribes dominate in both areas. Nevertheless more Aepycerotini and Tragelaphini specimens were discovered in the Uraha region, which imply a closed/dry habitat for at least some parts of the environment, that was apparently less significant in the Malema area.

Shipman and Harris (1988, p. 375) state that there is a “strong taphonomic bias in habitat representation dictated by the mode of deposition.” The lake margin sites (Olduvai) represent open to wet habitats, the riverine settings (Koobi Fora, W. Turkana, and Omo) sample closed/wet and closed/dry habitats, and the South African cave localities only sample the open arid spectra. Reed (1997) did not find strong support for *P. boisei* favoring dry or preferred closed habitats. Instead her analysis shows that *P. boisei* occupied habitats with abundant water and edaphic grasslands. Reed's study supports the interpretation by Behrensmeyer (1978) of *P. boisei* living in delta environments at Koobi Fora. This implies a preference for the vicinity of lake margins or rivers in the habitat of this early robust hominin. *Paranthropus boisei* KNM-ER-406 was recovered in a tributary on the delta plain (Behrensmeyer, 1978).

The sedimentary environment of the maxillary fragment RC-911 is thus similar to its East African analogue. Furthermore in both hominin localities the large alcelaphin *Megalotragus* dominates at the lake margin. The comparison with Koobi Fora shows that the Malema alcelaphins and *Hipparion* do not contradict a lake margin setting.

Table 3. Logarithmic abundances of bovid tribes in 29 African parks plus Pliocene Chiwondo Beds and Ndolanya Beds

	Alcelaphini	Antilopini	Aepycerotini	Tragelaphini	Reduncini	Bovini	Hippotragini	Neotragini	Cephalophini
Ndolanya Beds	1.81	1.6	0	0.95	0.3	0.3	0.95	1.56	0
Chiwondo Beds	2.03	1.5	1.27	1.14	1.17	1.39	1.51	0.6	0
Kruger	4	0	5.18	4.04	3.67	4.38	3.14	3.7	3.11
Luando	0	0	0	2.95	3.35	2.17	3.47	2.39	3.04
Hwange	3.41	0	3.9	3.73	3.09	4.11	3.41	3.47	3.3
Nairobi	3.12	2.92	2.82	1.89	2.02	0	0	0.3	0.3
Turkana	3.3	3.02	0	0	0	0	3.12	0	0
Serengeti	5.65	5.27	4.81	3.97	3.74	4.68	3.69	0	0
Ngorongoro	4.13	3.69	0	2.6	2.07	1.77	0	0	0
Etosha	4.22	4.07	0	3.39	0	0	3.68	2.69	2.39
Bouba Ndjida	3.85	0	0	3.25	3.84	3.24	3.63	4.06	3.73
Quicama	0	0	0	3.74	3.17	3.9	3.17	0	3.54
Hluhluwe	3.54	0	3.68	3.5	3	3.34	0	0	1.17
Kafue	2.27	0	0.3	1.62	2.29	1.92	1.49	1.95	1.84
Pendjari	3.97	0	0	0	4.29	3.54	3.7	3.89	3.39
Comoe	3.9	0	0	3	3.87	2.68	2	4.23	4.11
Omo	3.32	2.81	0	2.97	0	2.54	0	3.21	0
Kalahari	4.31	4.38	0	3.81	0	0	4.2	0	2.85
Manyara	0	0	2.84	1.39	1.74	3.17	0	0	0
Bicuar	2.69	0	2.17	2.65	2.17	2	2.69	1.77	2.69
Mupa	2.39	0	0	2.87	3.2	0	2.3	3	2.69
Mkuzi	3.14	0	3.97	2.74	1.83	0	0	0.77	0.6
Arlı	2.27	0	0	1.9	3.09	1.81	3.27	3	3.33
Deux Bales	2.65	0	0	2.29	2.35	1.6	3.07	2.81	2.81
Po	2.73	0	0	2.03	2.45	2.39	2.89	0	2.68
Saint Floris	3.32	0	0	0	3.5	3.25	2.7	0	0
Yankari	2.82	0	0	0	2.81	2.82	2.55	0	0
Fina	3.47	0	0	0	3.1	0	3.59	3.66	0
Kainji	3.8	0	0	2.74	3.68	2.07	3.76	3.44	3.15
W	3.15	0	0	2.38	3.78	3.61	3.45	3.32	0
Timbavati	3.09	0	3.66	1.89	1.51	0	0	0	0

locality of Malema RC 11 indicates a mixture of an attritional and hydraulically winnowed assemblage. The sediments of the Malema bone assemblage consist of fine- to medium-grained fluvial sediments that accumulated at the lake margin, likely on a delta plain. Isolated molars, half mandible fragments, and high-density postcranial elements dominate at the site. The fauna is dominated by large terrestrial herbivores. Juvenile specimens and small mammals are underrepresented. Large bovids, proboscideans, and hippopotamuses rule the Chiwondo Beds assemblages. Especially alcelaphin grazers dominate like in Swartkrans 1 and the Ndolanya Beds, pointing towards grass-bushland habitats.

Throughout the Chiwondo Beds the tribes Alcelaphini and Antilopini make up the majority of the bovid assemblage. Species of Aepycerotini and Tragelaphini, that are adapted to a closed dry habitat, are more common in the Uraha region than in the northern deposits. Correspondence analysis of African bovid generic abundances shows that the Chiwondo Beds bovid assemblage show more affinities to the more arid Somalia-Masai ecozone, than to the Zambezian ecozone to which the Malawi Rift belongs today.

Interpretation of the paleoenvironments represented by the Chiwondo Beds is limited by the incomplete preservation of the fossils, the limited number of localities, and the discontinuous stratigraphic sequence. But, its geographic position between the classic East and South African vertebrate fossil sites and the recovery of two hominins demonstrate its important potential for the understanding of faunal distribution in Africa during the Late Pliocene.

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