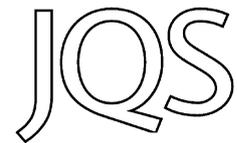# Quaternary fossil fauna from the Luangwa Valley, Zambia

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LAURA C. BISHOP,[1]* LAWRENCE BARHAM,[2] PETER W. DITCHFIELD,[3] SARAH ELTON,[4]
WILLIAM E. H. HARCOURT-SMITH[5] and PETER DAWKINS[1]
[1]Research Centre in Evolutionary Anthropology and Palaeoecology, School of Natural Sciences and Psychology, Liverpool John
 Moores University, Byrom Street, Liverpool L3 3AF, UK
[2]School of Archaeology, Classics and Egyptology, University of Liverpool, UK
[3]Research Laboratory for Archaeology and the History of Art, University of Oxford, UK
[4]Department of Anthropology, Durham University, UK
[5]Department of Anthropology, Lehman College, Bronx, NY, USA

ABSTRACT: This paper describes a large collection of Quaternary fossil fauna from the Luangwa Rift Valley, Zambia. Stone Age artefacts have been recovered from stratified fluvial contexts, but no *in situ* fossil faunas have yet been recovered. We report on 500 fossil specimens collected from the surface of point bars exposed seasonally along the banks of the main Luangwa River channel. We used non-destructive X-ray fluorescence analysis of the fossils' chemical signatures to determine whether they derive from one or many primary contexts, and the relationship between chemical signature and state of preservation. Specimens are identified to taxon (genus) to reconstruct palaeoenvironments and biochronology. A relatively wide range of taxa is identified, including a fossil hominin talus, described here. None of the fossils is positively attributable to extinct species, except a femur of an extinct *Theropithecus* reported in 2003. Although no additional extinct taxa were identified, some of the remains were attributable to genera that are not currently found in this region. The results suggest that most of the assemblage derives from sediments which are Middle Pleistocene or later, and that past environments in the Luangwa Valley may have differed from the habitat availability found today. Copyright © 2016 The Authors. *Journal of Quaternary Science* Published by John Wiley & Sons Ltd.

KEYWORDS: fauna; palaeoenvironment; Stone Age; XRF; Zambia.

Introduction

The Luangwa Valley of eastern Zambia is an extension of the East Africa Rift System (EARS) (Fig. 1a), but it lacks the tectonic activity that has been critical for the preservation, exposure and dating of palaeoanthropological sites along the eastern arm of the rift from Tanzania northwards (Barham and Mitchell, 2008). As a result, the Stone Age archaeological record is poorly known (Barham *et al.*, 2011) and Quaternary fossil faunas are notable for their rarity (Elton *et al.*, 2003). This paper summarizes briefly the geological background of the Luangwa Valley before describing a surface collection of 500 specimens from eight localities along the banks of the Luangwa River and its tributaries. We analyse their preservation (bone chemistry, surface modification), and describe the only specimen that can be attributed to a hominin – a talus. Principal components analyses of hominoid and modern human tali are used to determine the taxonomic affinity of the Luangwa specimen. The faunal identifications are used to examine past environments and we discuss the biostratigraphic implications of the collection and make suggestions for future research in the valley.
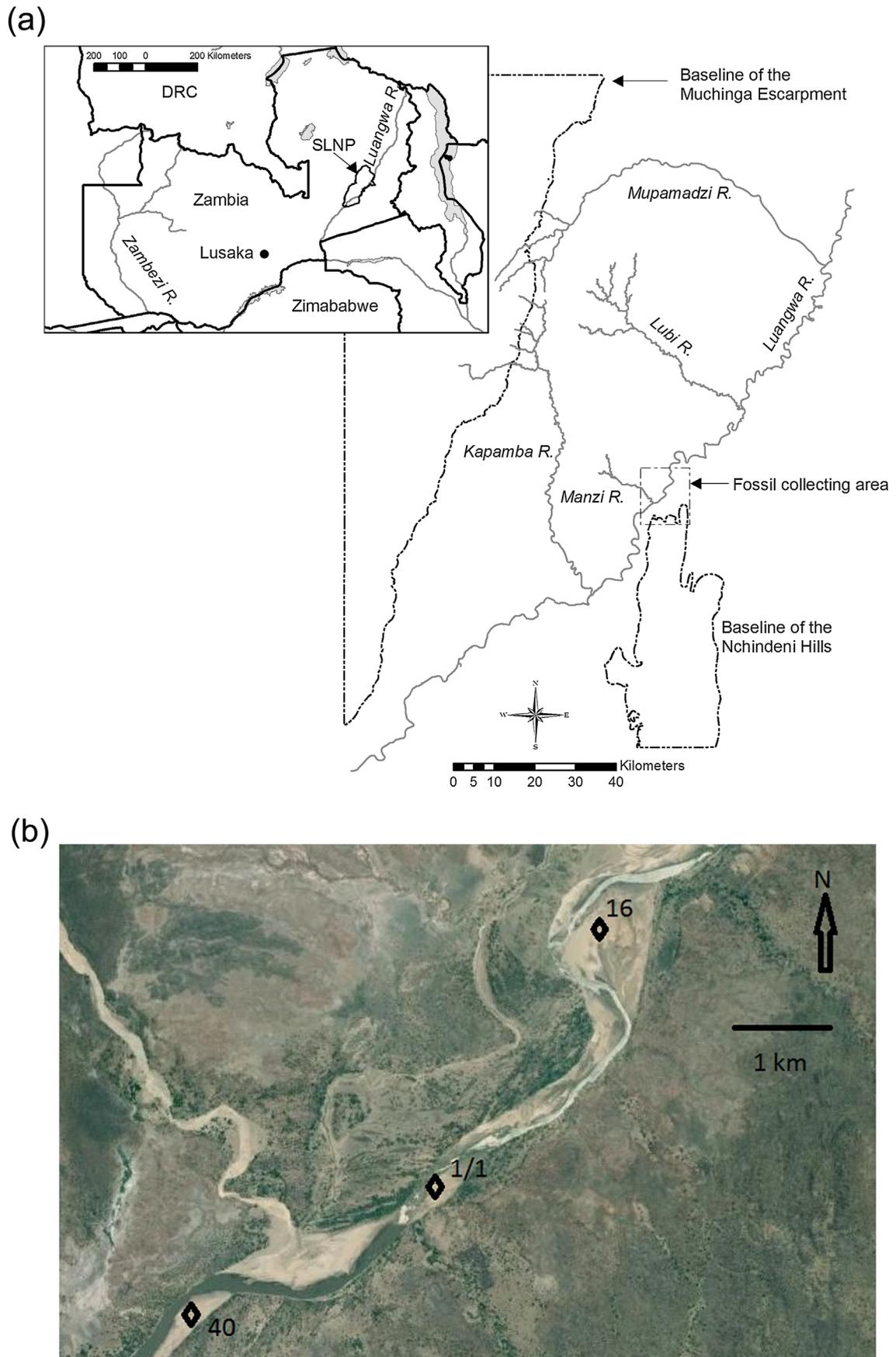
The Luangwa Valley context

The Luangwa River valley extends 700 km south-west across eastern Zambia from its source in the highlands of northern Malawi to its confluence with the Zambezi (Fig. 1a). The river system meanders over an area of relatively low topographic relief within the confines of an elongated trough formed by a series of en echelon half-grabens that form a SW–NE-trending extension of the western branch of the EARS (Astle *et al.*, 1969; Utting, 1976; Sepulchre *et al.*, 2006). It is bounded by

*Correspondence: L. C. Bishop, as above.
E-mail: l.c.bishop@ljmu.ac.uk

steep escarpments to the west and east (Dixey, 1937), with the western Muchinga escarpment forming the boundary with the high plateau that characterizes much of Zambia's geography (Trapnell, 1996). The modern vegetation of the valley falls within the Zambesian woodland savanna that spans much of south-central Africa from Angola to Mozambique (White, 1983). This broad ecozone is characterized by thornless deciduous woodland with an extended dry season that lasts from 4 to 7 months. In the Luangwa Valley, the higher, wetter elevations (>1000 mm of rainfall per annum) are covered by *miombo* woodland dominated by legumes of the genera *Brachystegia*, *Julbernardia* and *Isoberlina* (Smith and Allen, 2004). The drier valley floor (<500 mm of rainfall per annum) is characterized by mopane woodland (*Colophospermum mopane*), with nutritious grazing and riverine forests and thickets (Smith and Allen, 2004). The valley floor vegetation supports dense concentrations of large mammals that are otherwise normally dispersed in the *miombo* woodland including elephant, buffalo, wildebeest and zebra (East, 1984, p. 113).

The Luangwa Valley is tectonically quiescent by comparison with the EARS to the north in Malawi and Tanzania (Delvaux *et al.*, 2012). There is no active volcanism, there are no rift lake basins and large earthquakes are relatively rare (Foster and Jackson, 1998). The lithology of the valley fill is characterized by deep Karoo sediments (Carboniferous–Early Jurassic) overlain unconformably by a comparatively thin mantle of Quaternary deposits rarely more than a few metres thick (Dixey, 1937; Utting, 1988). The valley's geologically recent record of tectonic activity is not well known and is assumed to have been affected by regional trends linked to formation of the western arm of EARS as early as 25 Ma (Roberts *et al.*, 2012) or as recently as 12 Ma (Sepulchre *et al.*, 2006), and the Malawi Rift 5–2 Ma (Ebinger, 1989). The evolutionary history of local fish populations indicates

Figure 1. (a) Location map of the Luangwa Valley and the fossil fauna collecting area in the South Luangwa National Park (SNLP). (b) The key fossil collecting areas along the Luangwa River: locality 16, (Kopje Bar), 1/1 (Chowo Beach) and 40 (Fisherman's Beach 2).

that there may have been more recent regional uplift in the Pleistocene (Schwarzer et al., 2011; Moore et al., 2012).

The geological context of the valley, in particular its lack of volcanism and lake basin formations, restricts the extent to which fossils are preserved and limits the application of radiometric dating methods with which to anchor the palaeoanthropological record. The nearest source of volcanism with the potential for developing a tephra-based chronology is the Rungwe volcanic province of south-central Malawi (Ebinger, 1989), but the depositional contexts for preserving tephra are lacking in the Luangwa Valley. The impact of uplift on the preservation and exposure of archaeological sites in the Luangwa Valley is being investigated, with evidence emerging of large-scale dissection and erosion of former land surfaces (D. Colton et al., unpubl. data). The only dated Stone Age succession in the valley comes from the Manzi River, a tributary of the Luangwa River. Excavations along the Manzi exposed Early Stone Age artefacts in secondary fluvial contexts associated with a palaeomagnetic reversal correlated with an age of 1.1 Ma (Barham et al., 2011). An upper deposit containing Middle Stone Age tools was dated radiometrically (optically stimulated luminescence) to 70–40 ka. The discontinuous succession of the Manzi section typifies the depositional context of sites exposed along the Luangwa and its tributaries. Erosion rates are high with marked seasonal differences in river flow (Gilvear et al., 2000) with channel migration of up to $60\,m\,a^{-1}$ (Colton, 2009). In this context, sites are readily eroded and artefacts and fossil fauna carried as clasts in the wet season peak flow then re-deposited on point bars as the rivers subside in the dry season. This is the geomorphological setting for the faunal material described below. Away from the floodplain and the influence of the modern river system, Stone Age artefacts are common surface finds, but fossil faunas of the Quaternary are notable for their absence.

The faunal remains and their preservation

Between 1999 and 2006, over 500 fossil faunal specimens were collected from a series of secondary point bar deposits in the meandering Luangwa and Manzi Rivers. These fossils are seasonally deposited on point bars following periods of high water flow. Their primary context remains unclear; no excavations have recovered bones of similar preservation. Bones recovered from eight point bars were examined; some of the sites had been given names previously: Chowo Beach, Threequarters Baobab, Luangwa Beaches, Kopje Bar, Chamilandu Beach, Fisherman's Beach and Fisherman's Beach 2. The largest collections were from two sites, Chowo Beach (Site 1/1) and Kopje Bar (Site 16) (Fig. 1b), that yielded approximately 150 and 250 remains, respectively. Approximately 40% of the bones examined were identifiable to zoological family or below ($n = 184$ from all sites). Table 1 shows the faunal list from the Luangwa Valley collection localities.

Preservation of bones varies considerably, and their appearance ranges from fresh to highly mineralized. Bones are variably coloured, and a subsample from Chowo Beach demonstrated coloration ranging from light brown and grey through red brown and black, with none of these being dominant in the assemblage. Many bones exhibit partial to

Table 1. Faunal taxa and numbers of identifiable specimens (NISP) recovered from numbered point bar localities in the Luangwa and Manzi River Valleys. See Fig. 1 for positions of these localities.

		Chowo Beach 1/1	Threequarters Baobab 5	Luangwa Beaches 8	Kopje Bar 16	Fisherman's Beach 17	— 19	Chamilandu Beach 34	Fisherman's Beach 2 40
Pisces		2			2				
Crocodylia		4	1		5		1		1
Chelonia		2			2				
Aves		1							
Mammalia indet.		109	3	12	155	1		2	2
Hominidae		1							
	Theropithecus				1				
Canidae		1							
Suidae		2							
	Phacochoerus			1	1				
	Potamochoerus								1
Hippopotamidae		11	2	2	43				1
Giraffidae					1				
Bovidae	Size 1				1				
	Size 2	5		1	11				
	Size 3	4			16			1	
	Size 4	1			8				
	Size indet.	5			8				
	Tragelaphini size 4	2			2				
	Bovini size 4	2		1	2				
	Reduncini size 2	3							
	Kobus				2				
	Alcelaphini size 3	2		1					
	Antelopini size 2	2			1				
	Antidorcas				1				
	Aepycerotini	2		1	1				
Equidae		1			4				
Proboscidea					1				1
	Loxodonta				1				
Rodentia	*Thryonomys*	1							

complete dark staining by manganese and/or vivianite. Observation of recent carcasses in the river valley suggests that this can occur very quickly, sometimes even before soft tissues have decayed. Bones recovered from every point bar site exhibit a range of preservations, which probably correspond to multiple geological provenances, diagenetic histories and potentially a range of ages.

Bone chemistry was analysed using combustion elemental analysis to determine whether faunal material was suitable for radiocarbon dating. Crushed, dried ca. 3-mg bone samples in clean tin capsules were analysed for total nitrogen in a Carlo Erba 1108 CHN analyser having a helium carrier gas flow of $80 \, mL \, min^{-1}$ as in Brock et al. (2012). Thirty-nine samples from two sites were processed (Site 1/1, $n = 11$; site 16, $n = 28$). Results showed that, with the exception of one bone with very fresh appearance from site 16, the faunal remains showed no evidence of any collagen preservation, precluding dating by radiocarbon (Table 2). Analysis revealed a lack of preserved nitrogen with none of the samples reaching the level of 0.75% by weight nitrogen, which has been identified as a useful indicator of collagen preservation (Brock et al., 2012). The samples also showed only trace amounts of carbon (up to 2% by weight), which is likely to represent the inorganic carbonate fraction in combination with diagenetic carbonates (Table 2). In general, the term 'fossil' can be applied to the remains recovered from the Luangwa Valley point bars due to the high degree of mineralization observed. This is not necessarily indicative of age, however, because carbon and nitrogen from organic molecules degrade very quickly after early burial under hot, wet conditions, which have existed in the Luangwa Valley for thousands, if not millions, of years. Similarly, the rapid manganese staining observed on modern carcasses from the valley suggests that mineralization can occur very quickly under local conditions.

Because the bones showed a high degree of mineralization, we also attempted to examine their elemental content using non-destructive, energy dispersive X-ray fluorescence (EDXRF) using the methods outlined by Plummer et al. (1994). We investigated the range and variability of elemental composition in fossils recovered from Chowo Beach ($n = 4$) and Kopje Bar ($n = 14$). The analysis was performed using a Princeton Gammatech Joel-JSM-840 scanning electron microscope having a silicon–lithium drifted detector. An optimum accelerating voltage of 20 kV was used at a working analysis distance of 20 mm. Spirit System software supplied by the manufacturer was used for elemental analysis of the fossils (Table 2). Plummer et al. (1994) used EDXRF to identify the chemical structure of fossils collected from surface deposits of the Homa Peninsula, Kenya. They compared these to subsets of fossils having known, in situ provenance. Similarities between the elemental composition of surface-collected and in situ specimens allowed them to ascertain the likely provenance of the former. For the Luangwa Valley fossils, there are no in situ fossil-bearing deposits to act as a comparative dataset. Thus, the purpose of this analysis was to determine the extent to which the chemical composition of the fossils might reveal a shared taphonomic or diagenetic history for subsamples of the Luangwa fossils. However, our preliminary analysis showed that variability in within-collection locality chemical composition was as variable as between-collection locality variation. When sampled at multiple loci, individual bones also demonstrated within-sample variation in chemical composition. There was no discernible clustering or pattern to the chemical compositions of the fossils studied, so the utility of this approach was limited in the absence of comparative in situ material.

The bones all exhibit signs of rolling; they vary from almost fresh in appearance with fractured surfaces showing slight damage, to highly rounded, polished and smoothed. This is unsurprising given that all faunal remains studied had been recovered from the seasonal point bars within and near the river channel, but the wide range of damage from rolling may signify that they derived from a range of contexts and distances from their ultimate place of recovery. Some faunal remains showed signs of etching which may also have been a result of their time in water or may be due to the activity of insects or damage from plant roots during burial before movement in the fluvial system. The level of surface damage made assessment of potential hominin modification difficult; under the circumstances no unequivocal indications of intentional damage were observed. Appendicular skeletal portions were more common than axial. Chowo Beach, for example, yielded 35 mammalian remains that could be identified to skeletal part, of which 14 were axial fragments (40%) and 21 (60%) appendicular fragments. Craniodental remains were surprisingly rare considering their higher potential survivorship following fluvial transport (Turner et al., 2002). Axial-derived skeletal parts are also easier to identify owing to their often less linear shape and, in the case of horn cores and teeth, tissue morphology.

Forty-five mammalian specimens recovered from Chowo Beach (Site 1/1) and 105 specimens from Kopje Bar (Site 16; Fig. 1b) were identifiable to family level or below. The dominant family from both recovery areas was Bovidae, followed closely by Hippopotamidae in both cases. Equidae and Suidae (Phacochoerus) were represented by a handful of specimens from each sample. Rarer taxa had different representation at each of the main collection areas; Chowo Beach yielded a mineralized hominin talus (see below), cane rat (Thryonomys) and canid mandibles, while Kopje Bar preserved a femur attributed to Theropithecus cf. darti, a giraffid, and two proboscidean fossils, one of which is attributed to Loxodonta.

Although the sample sizes are small, there is a high level of antelope diversity represented in the samples recovered from both sites. Both samples show a wide range of antelope sizes (size classes 2–4 from Chowo and 1–4 from Kopje Bar), with size classes 2 and 3 most common (Klein and Cruz-Uribe, 1984). Antelopini, Reduncini, Bovini, Aepycerotini and Tragelaphini have been identified from both samples, while Alcelaphini are present only in the Kopje Bar sample. The habitat preferences demonstrated by species of these tribes vary from grassland to more intermediate waterside and swamp habitats. This corresponds well with interpretations of past environments in the Luangwa Valley.

One additional collection area, Fisherman's Beach 2 (Site 40; Fig. 1b) has yielded two unusual and highly mineralized fossils – one a well-preserved mandible of Potamochoerus and the other a juvenile proboscidean. Potamochoerus is unknown from other collection areas and Proboscidea are rare, suggesting that this collection locality may be accumulating fossils which derive from a different part of the sequence. Potamochoerus is a species with a 4-Myr time range and useless for biostratigraphic purposes; however, the preservational state of these fossils and their taxonomic rarity in the sample suggest that this collection area holds promise for future research.

Theropithecus femur

One of the best-preserved fossils from the Luangwa Valley, a complete femur, has been assigned to Theropithecus cf. darti, a Pliocene cercopithecid (Elton et al., 2003). The bone has

Table 2. Analysis of bone samples from the Luangwa Valley showing %N and %C (by weight) data and EDAX data showing per cent elemental composition.

	Data measured by combustion EA				Data measured by EDXRF																			
Specimen no.	C (wt%)	N (wt%)	Processing no.	Subsample area	C	O	Na	Mg	Al	Si	P	S	Cl	K	Ca	Ti	Mn	Fe	Sb	I	Ba	W	Pt	Ce
16.22	1.489	0.028	1	a	7.67	36.76		0.24	0.44	0.67	12.55				27.5		6.34	7.86			1.13	0.84		
			1	b	7.76	28.43			0.44	1.03	12.08				31.63		7.33	9.83			1.47			
16.44	1.643	0.087	2	a		47.53					8.51				17.87		15.83	4.85			2.04			
			2	b		49.73				1.27	7.84				14.72		19.48	4.69	3.36		2.26			
16.39	1.712	0.066	3	a		47.57		0.85	1.97	5.13	6.16				14.47	0.84	14.33	8.68						
			3	b	5.06	45.87	0.75	0.87	1.14	2.67	7.09				14.84	0.55	12.22	6.64	2.29					
			3	c		44.74			3.49	9.13	3.95			0.78	9.51		16.55	9.61			2.23			
16.25	1.811	0.055	4	a		37.2			0.93	1.98	13.54	1.55			29.94		2.34	6.86	4.25		1.41			
			4	b		43.11				1.25	12.66	1.6			25.57	0.53	4.32	7.75	3.2					
16.31B	2.296	0.108	5	a	5.04	41.53		0.24	1.37	0.52	13.92				28.57		1.69	5.89			0.59	0.87		
			5	b	6.43	40.46			1.23	0.39	13.93				28.53		1.45	6.58				0.77		
16.12	1.765	0.079	6	a		41.83		0.78	3.04	4.32	6.95			0.46	16.23	0.8	13.83	12.56						
			6	b		43.55		0.54	2.21	1.96	11.16				23.59		5.68	11.84						
			6	c		39.73		0.39	3.38	5.6	5.92			0.56	13.31	0.79	15	15.71						
16.23	1.687	0.047	7	a		46.73			1	3.08	10.64				20.52		3.53	14.49						
			7	b		44.76				1.65	16.1				27.93		0.96	8.6						
16.46	1.528	0.052	8	a	4.16	33.22			0.08	1.6	14.42				38.96		2.88	3.97						
			8	b	5	43.66			1.86	3.77	11.26			0.38	25.7	0.34	3.64	4.38						
16.31A	1.852	0.094	9	a	5.43	43.49	0.27		4.95	10.64	3.46			1.21	8.4	0.6	12.81	7.95			1.66			
			9	b	12.5	44.66			3.46	7.03	3.09			0.67	6.13		10.75	9.54			1.55			
			9	c	12.8	41.32			2.68	5.44	3.87			0.43	8.3		10.97	12.35						
16.47	1.533	0.083	10	a	3.5	45.62		0.84	8.16	20.84				1.15	2.82	0.89	2.01	14.17						
			10	b	2.47	31.72		0.61	7.74	20.51				1.36	2.46	1.06	3.66	28.41						
			10	c	7.57	40.33		0.69	7.74	20.84				0.93	2.35	0.92	2.41							
None	n/a	n/a	11	a	3.84	35.41		0.24	1.49	3.27	7.62			0.31	20.06		16.12	11.12		2.02				1.85
			11	b	3.36	35.05		0.22	1.49	3.27	7.46			0.3	20.79		15.15	10.82		2.09				
				c	3.52	38.78		0.24	0.84	1.67	9.95			0.25	22.5	0.38	9.93	10.8						
16.7	1.725	0.049	12	a		38.29			3.14	13.96				1.05	1.21	1.42	23.34	17.59				0.93		
			12	b		32.13			3.56	13.18				0.9	1.1		22.25	22.54			4.34			
				c		33.1	0.22		4.1	18.25				1.68	1.13	0.93	8.39	32.43						

continued

Table 2. (Continued)

Specimen no.	Data measured by combustion EA				Data measured by EDXRF																			
	C (wt%)	N (wt%)	Processing no.	Subsample area	C	O	Na	Mg	Al	Si	P	S	Cl	K	Ca	Ti	Mn	Fe	Sb	I	Ba	W	Pt	Ce
16.35	1.527	0.057	13	a		45.5				5.03	12.64				26.15		6.94	3.75						
			13	b		49.72			1.81	4.44	11.71				20.98		7.9	1.34						
16.28	1.644	0.052	14	a	7.49	44.85		0.35	3.65	9.34	6.17			0.9	12.09	0.45	1.28	13.44						
			14	b	3.91	45.61		0.45	3.42	10.22	7.24			0.98	13.56	0.44	1.12	11.08			2.1	1.97		
1/1.54A	1.781	0.064	15	a	24.8	36.85	0.46	0.18	1.02	1.59	10.05	0.29		0.42	20.15		0.49	1.87						
			15	b	24.7	41.54	0.43		1.6	2.28	8.58	0.29	0.41	0.32	18.42			1.84				0.95		
1/1.40	1.508	0.052	16	a		35.37					14.52				38.28		1.46	6.92	3.46					
			16	b		30.49			0.69	1.4	12.61	32.8					3.16	14.39	4.5					
				c		26.56			0.78	1.47	11.59				33.12		2.27	19.11	3.17	1.94				
1/1.52	1.749	0.011	17	a	6.58	35.89	0.32		0.89	1.85	11.05	1.14			28.44	0.44	9.61	3.78						
			17	b	5.13	34.93					13.85	2.59			30.81		2.09	7.25					2.16	
No. C			18	a	9.8	41.89		0.33	2.83	5.9	8.04			0.64	20.22		5.47	4.88				1.2		
			18	b	9.76	40.61		0.49	1.71	3.15	11.09			0.42	23.35		3.38	4.01			0.83	1.21		
1/1.15	4.542	0.211			Not analysed by EDXRF																			
1/1.54	1.486	0.021																						
1/1.48	2.059	0.015																						
1/1.72	1.289	0.085																						
1/1 no #	1.872	0.102																						
1/1 no #	1.56	0.084																						
1/1.73	1.664	0.047																						

pronounced distolateral splay (a 'reverse' carrying angle) and anterior convexity, both features indicative of *Theropithecus* (Fig. 2). The gracility of the specimen, along with the relatively long femoral neck that lacks a ridge on the anterior aspect and an oval fovea capitis, aligns the fossil more closely with *T. darti* than with *T. oswaldi* or other members of the genus. Of all the cercopithecids, *Theropithecus* has a distinctive postcranial skeleton, due in part to its unusual squatting and shuffling behaviour when foraging (Krentz, 1993). This significantly increases the likelihood that the specimen has been identified correctly to genus level. Craniodental material, however, is most diagnostic for many cercopithecids, *Theropithecus* included, and to date no cercopithecid crania or teeth have been recovered. The femur has traces of manganese deposits and also shows acid etching.

Hominin talus

Specimen LZH-01 is a fairly complete, heavily mineralized left talus from an adult individual. The minimal damage is post-mortem and is limited to some areas of surface abrasion of cortical bone that exposes the underlying cancellous bone (Figs 3 and 4; see below). The specimen is brownish black reflecting at least partial fossilization. Chemical analysis showed that there was insufficient organic material preserved to allow direct radiocarbon dating of this specimen; this was also true of all but one Luangwa Valley specimen examined.

The trochlear surface is almost complete with some abrasion along the anterior, lateral and posteromedial edges. The abrasion is most extensive along the lateral edge and extends onto the lateral side of the body. Thus, much of the periphery of the lateral malleolar facet is missing. The trochlear surface is slightly grooved and does not extend onto the talar neck. The medial malleolar facet is slightly abraded inferodistally and this abrasion extends onto the medial surface of the talar neck, most of which displays exposed cancellous bone. The radii of curvature of the medial and lateral edges of the trochlea are subequal.

Superiorly, the talar neck appears slightly grooved for the anterior edge of the tibia in dorsiflexion, and it also displays some vascular foramina. The lateral, inferior and medial surfaces of the neck are abraded. Indeed, albeit minimally, all the edges of the head are abraded. Thus, it cannot be determined if there were separate or continuous anterior calcaneal (subtalar) facet(s) on the inferior surface of the neck. The talar groove is deeper and broader laterally, partly due to a proximal extension of the calcaneal facet of the neck. The posterior calcaneal facet (of the body of the talus) is slightly abraded medially and laterally, but fairly complete proximally and distally. The facet is moderately concave. The
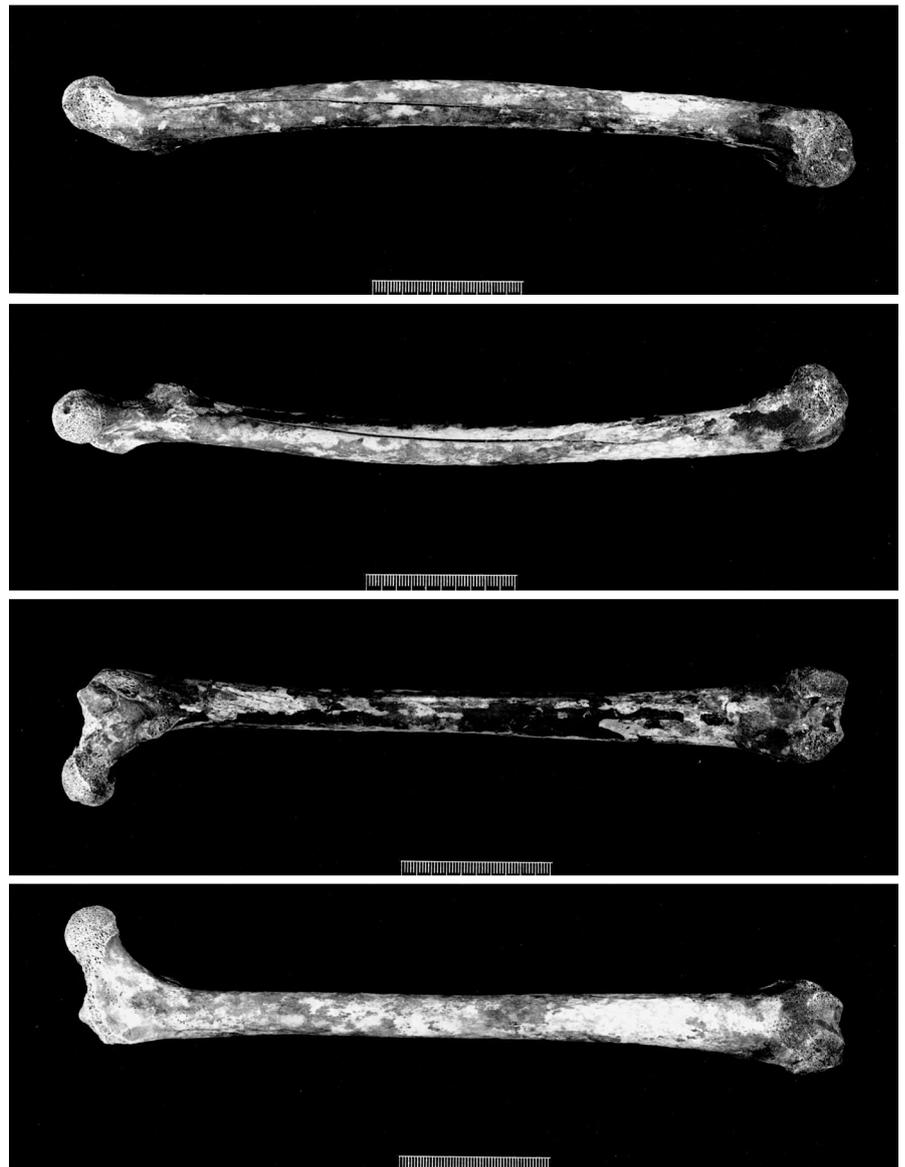
Figure 2. The *Theropithecus* cf. *darti* right femur. From top: lateral, medial, posterior and anterior views. Reproduced from Elton *et al.* (2003) with permission from Elsevier, licence no. 3738290102930.

(a)

(b)
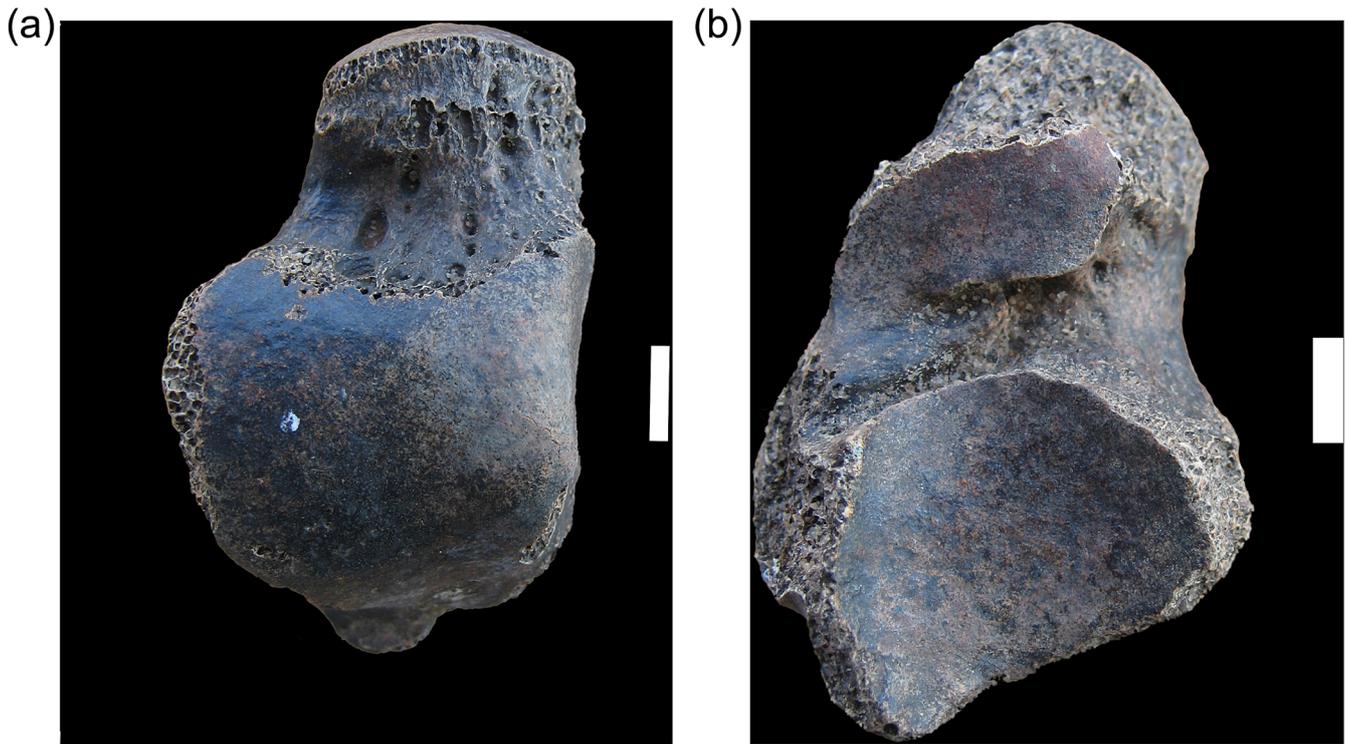
Figure 3. Dorsal (a) and plantar (b) views of the Luangwa talus illustrating damage and state of preservation. Scale bar = 1 cm.

lateral tubercle is missing. Due to abrasion laterally, and more extensively medially, only a small amount remains of the groove for flexor hallucis longus.

The conformation of the trochlea with its subequal medial and lateral edges, as well as the two malleolar surfaces, reflect a talocrural joint that belonged to a habitual biped (Latimer *et al.*, 1987; Latimer and Lovejoy 1990). Overall LZH-01 can thus confidently be assigned to the hominini. Its flat and mildly grooved trochlea is very similar to that of *Homo sapiens*, *Homo neanderthalensis*, *Homo erectus* and *Australopithecus afarensis*, but distinct from the heavily grooved and mediolaterally sloped trochlea found in the Olduvai foot (OH 8) and tali from Koobi Fora (KNM-ER 813a, 1464a & 1476) and Sterkfontein (StW 88). Indicative linear measurements of the talus are presented in Table 3. Given this morphology and the indications of a relatively recent age of the specimen through its associated fauna, it is reasonable and parsimonious to assign LZH-01 to the genus *Homo*.

We conducted a three-dimensional morphometric analysis of the hominin talus to examine the relationship of its shape and morphology within a comparative context. Talar *x*, *y*, *z* landmarks were collected using a Microscribe digitizer following the protocol of Harcourt-Smith (2002). Due to damage on the Luangwa specimen, not all possible landmarks could be taken. No landmarks on the anterior calcaneal facet were possible, and most of those on the head and posterior calcaneal facet had to be estimated using clay to reconstruct missing edges of the facets. Thus, most landmarks that could be directly taken come from the trochlea and malleolar facets.

A comparative dataset of extant great ape genera (*Pongo*, *Pan*, *Gorilla*), *H. sapiens* and several fossil hominins (AL288-1 – *Australopithecus afarensis*, StW 88 – *Au. africanus*, OH 8 – *H. habilis*) was used. The *Pan*, *Gorilla* and *Pongo* samples consist of entirely wild-shot adult individuals free of noticeable pathologies. The *H. sapiens* sample consists of modern South African Zulu, Xhosa and Khoi-San, Native American Arikara and 4th century AD Romano-British.

Landmark data were subjected to a generalized procrustes analysis followed by a principal components analysis. Both the generalized procrustes analysis and the principal components analysis were performed in *morphologika* 2.5 (O'Higgins and Jones, 1998). Analyses were formed on two datasets, those with and those without the estimated landmarks. Results were virtually identical. The analysis of the reduced dataset shows the Luangwa talus clearly clustering with the modern *H. sapiens* on PC1, to the exclusion of the great apes, which each form their own, distinctive clusters (Fig. 5). Modern human tali separate from the great apes mainly due to their relatively flat and ungrooved trochlea and more vertical malleolar facets (Harcourt-Smith, 2002). Analysis of just modern human tali reinforces this result by showing that the Zambian specimen clusters comfortably with those of modern populations from southern Africa (Fig. 6). This demonstrates that the talus, like the vast majority of the fauna from the Luangwa River localities, is likely to represent an extant taxon, although it must be noted that most Middle–Late Pleistocene *Homo* tali are very similar to that of *H. sapiens* (Harcourt-Smith, 2002).

Biostratigraphy and age

As mentioned above, with the exception of the *Theropithecus* specimen, all the fauna which can be identified are not distinguishable from extant species, and derive from extant genera. Some of these (e.g. *Antidorcas* and *Potamochoerus*) are now rare or unknown in the valley and in the Zambesian ecozone more generally (Klein, 1984a: table 1; IUCN SSC Antelope Specialist Group, 2008; Seydack, 2008). At some African localities, Middle Pleistocene (1.2–0.13 Ma; Head and Gibbard, 2005) faunas can have completely modern taxa occurring in geographical ranges that do not reflect their modern distributions (Potts *et al.*, 1988; Potts and Deino, 1995; Bishop and Turner, 2007; Faith *et al.*, 2012). There is no evidence to contradict a hypothesis that the Luangwa Valley fauna, with the exception of the *Theropithecus*

Figure 4. Dorsal view of the Luangwa talus (a) compared to modern *Homo sapiens* (b), OH 8 *Homo habilis* (c) and *Pan troglodytes* (d).
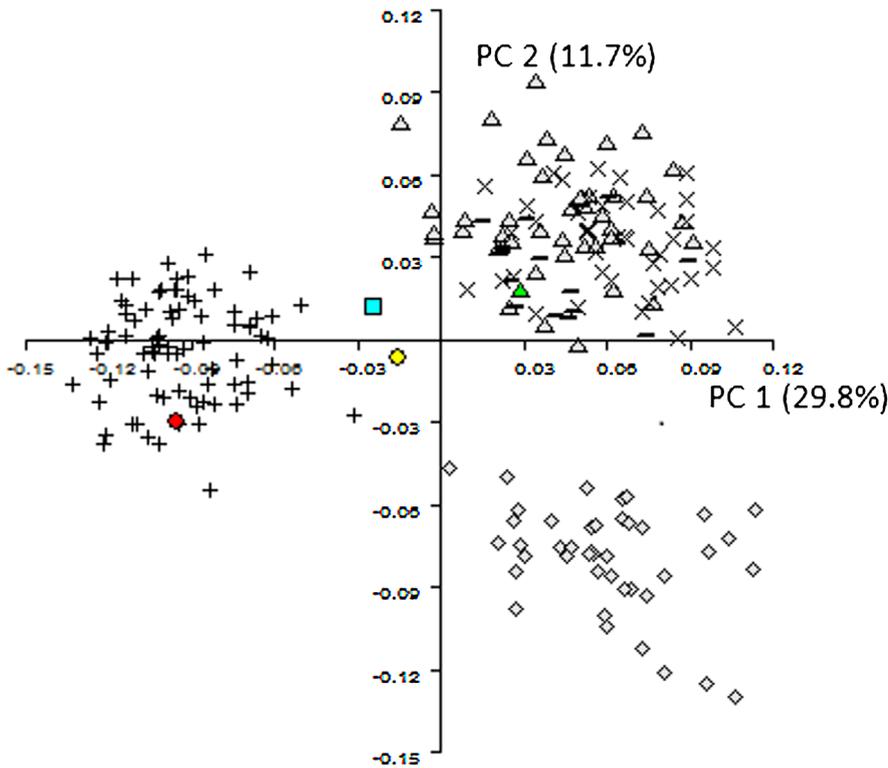
specimen, is of Middle Pleistocene age or potentially more recent. Some specimens examined for this study were of very recent origin, as was evinced by their less mineralized and unaltered appearance when compared to recent remains in the landscape.

The wider regional fossil faunal record for southern Africa is patchy in its distribution and poorly dated, but it provides tentatively corroborative evidence of the pattern seen in the Luangwa sample of few extinct species and some evidence of exotic species suggestive of past shifts in vegetation, possibly linked to environmental change. Essentially modern faunas

Table 3. Measurements of adult hominin left talus LZH-01.

Maximum anteroposterior length (mm)	58.5
Maximum mediolateral breadth (mm)	39.4
Maximum superoinferior height (mm)	35.6
Estimated maximum trochlear width (mm)	33.0

are reported from the Middle Pleistocene cave deposits at Kabwe (Cooke, 1950a,b), Twin Rivers (Bishop and Reynolds, 2000) and in the Late Pleistocene sequences at Mumbwa Caves (Barham, 1996; Klein and Cruz-Uribe, 2000) and Redcliff Caves (Cruz-Uribe, 1983). The distinctiveness of one extinct species recorded in the Victoria Falls area (*Leptailurus hintoni*. Cooke 1950b) has been disregarded subsequently (cf. *Leptailurus* sp. in Werdelin and Lewis, 2005). Leopard's Cave also preserves taxa found outside their current geographical range (e.g. *G. thomsoni*. Klein 1984b) and potentially *Megalotragus*, an extinct mega-Alcelaphine which is known until the Late Pleistocene from many localities (Cooke, 1950b). At Mumbwa, the presence of antilopine (springbok or gazelle) in the basal deposits (>180 ka) suggests a drier, less wooded habitat than today (Klein and Cruz-Uribe, 2000, p. 56). Gazelle and springbok are not recorded in the historical fauna of the Zambesian ecozone, but are found in Holocene deposits in Zambia and Malawi (Voigt, 1973; Phillipson, 1976; Crader, 1984). With the exception of springbok/

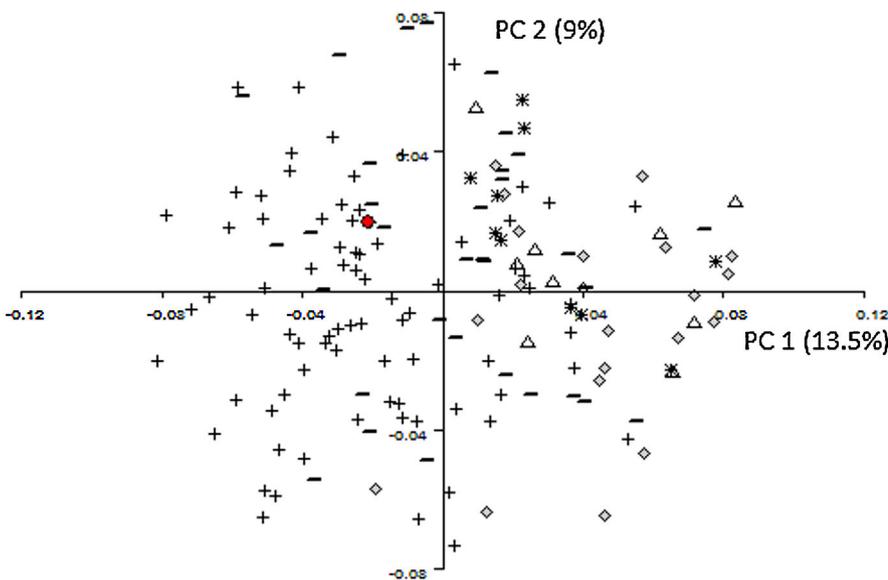**Figure 5.** Principal components analysis of Procrustes registered x, y, z coordinates of hominoid tali, including the Luangwa specimen [grey diamonds, *Pongo*; plus signs, *Homo sapiens*; dashes, *Pan paniscus*; grey triangles, *Gorilla gorilla*; X marks, *Pan troglodytes*; red circle, Luangwa specimen; yellow circle, *Australopithecus* afarensis (AL288-1); blue square, *Homo habilis* (OH 8); green triangle, *Australopithecus africanus* (Stw 88)]. Note: this analysis was performed on a subsample of available landmark coordinates, due to the fragmentary nature of the Luangwa specimen. For more details see the section on the talus.

gazelle, the Holocene faunas from the Zambesian ecozone show continuity in taxa with their Middle and Late Pleistocene predecessors (Klein and Cruz-Uribe, 2000).

There is the additional possibility that extinct taxa are underreported in the sample. Our analysis could not distinguish to the species level due to the rarity of definitive diagnostic material within the recovered assemblage. Several of the genera identified from the Luangwa Valley contain extinct as well as extant species, and examples of the latter are known from other southern African Middle Pleistocene localities. *Aepyceros* includes a South African form, *A. helmoedi* (Brink *et al.*, 2012), and a hypsodont unnamed species from Kenya (Faith *et al.*, 2014). Several unnamed, potentially new Alcelaphini species have been noted at Middle Pleistocene sites (Klein *et al.*, 2007; de Ruiter *et al.*, 2008; Faith *et al.*, 2011). Extinct species of the genus *Antidorcas* are known, for example at Redcliff Cave

(*A. bondi*, Cruz-Uribe, 1983) and from South Africa's Western Cape (*A. australis*. Klein *et al.*, 2007). The limited craniodental sample from Luangwa most closely resembles the modern taxon, but it is difficult to rule out *A. bondi* given geographical and ecological considerations (Brink and Lee-Thorp, 1992).

The *Theropithecus darti* femur tells a more straightforward story. The femur is unlikely to be an example of Middle Pleistocene *Theropithecus oswaldi*, which shows considerably greater shaft robusticity, as well as a shorter neck with a ridge on the anterior aspect. The combination of distolateral splay, anterior convexity, relatively long total length, lack of robusticity and long neck in the Luangwa Valley femur make it unlikely to be a representative of any of the cercopithecids currently found in the Luangwa Valley or indeed Zambia. Eight modern monkey species are found in Zambia today: three species of *Papio* (Kingdon *et al.*, 2008a; Hoffmann and

Figure 6. Principal components analysis of Procrustes registered x, y, z coordinates of *Homo sapiens* tali, including the Luangwa specimen (grey diamonds, Romano British; plus signs, Zulus; dashes, Xhosa; stars, Arikara; white triangles, Khoi-San; red circle, Luangwa specimen). Note: this analysis was performed on a subsample of available landmark coordinates, due to the fragmentary nature of the Luangwa specimen. For more details see the section on the talus.

Hilton-Taylor, 2008), two *Cercopithecus* species (Kingdon *et al.*, 2008b; Oates *et al.*, 2008), two *Chlorocebus* (Butynski, 2008; Kingdon *et al.*, 2008c) and one *Colobus* (Kingdon *et al.*, 2008d). The largely forest-dwelling and relatively small-bodied cercopithecine *Cercopithecus ascanius* (<5 kg; Smith and Jungers, 1997) and colobine *Colobus angolensis* (<10 kg; Smith and Jungers, 1997) are found only in the far north (north-west, and north-west plus north-east, respectively) of the country, well away from the Luangwa Valley (Kingdon *et al.*, 2008d; Oates *et al.*, 2008). The fossil femur shares two features with colobine monkeys, an incomplete intertrochanteric crest and modest robusticity. However, it is also considerably larger than the femora of modern *Colobus* (Elton *et al.*, 2003), including *C. angolensis*, and although there was a radiation of large-bodied, terrestrial colobines in East and southern Africa in the Plio-Pleistocene, they were extinct by about 1.8 Ma (Leakey, 1982), before the Middle Pleistocene. The femur is also well outside the range of size variation seen in the other relatively small-bodied modern primate taxa within the Luangwa Valley and environs, *Chlorocebus cynosuros* west of the Luangwa River, *C. pygerythrus* east of the Luangwa River, and *Cercopithecus mitis* (also west) (Jansson, 2006; Butynski, 2008, Kingdon *et al.*, 2008b,c).

If the femur is not Pliocene *Theropithecus*, the most obvious modern or Middle Pleistocene candidate genus is *Papio*. Three *Papio* species are found in Zambia, *P. ursinus*, *P. cynocephalus* and *P. kindae*, with a three-taxon hybrid zone evident in the Lower Luangwa Valley (Jolly *et al.*, 2011). Along with having the distolateral splay and anterior convexity characteristic of *Theropithecus*, the fossil femur lacks the complete intertrochanteric crest, robusticity and shorter neck of *Papio* species. It is worth noting that most postcranial reference collections have very poor representation of *P. kindae*, which is smaller than the other two *Papio* species found in Zambia, and little is documented about its femur. It thus cannot be discounted that the femur belongs to *P. kindae*, as its range extends into the Luangwa Valley. However, as behavioural observations of *P. kindae* do not document the extensive sitting and shuffling that result in the characteristic *Theropithecus* femoral distolateral splay, and because the specimen is too gracile to be *T. oswaldi*, the balance of evidence still supports the attribution of the fossil femur to *Theropithecus* cf. *darti*.

Theropithecus darti is a time-sensitive species, so its presence in an area that is otherwise dominated by fauna from the Middle Pleistocene or later indicates either misidentification of the specimen or the presence of earlier horizons that have not yet been fully documented. The recovery of Oldowan-like tools (chopper-cores) near the femur points to deposition of archaeological material during the Plio-Pleistocene, although these tools (Mode 1) continue to be made well into the Pleistocene in the valley (Barham *et al.*, 2011). Thus, it is possible that the faunal assemblage in the Luangwa Valley samples a range of time periods. Nonetheless, the emerging chronology of the Luangwa Valley deposits currently spans the past 1.1 Ma, supporting a Middle Pleistocene or more recent age for much of the fauna recovered.

Conclusions

Abundant fossil faunal remains have been recovered from surface contexts in the Luangwa Valley. Numerous taxa have been identified, including *Loxodonta*, *Hippopotamus*, several genera of bovid, *Phacochoerus*, *Potamochoerus*, *Equus* and *Homo*. A *Theropithecus darti* femur (Elton *et al.*, 2003) is the only example of an extinct taxon identified from the currently available collection of fossils. Several of the taxa identified in the surface-collected assemblage are not known to occur in the Luangwa Valley today, which is a further indicator of antiquity. Thus, biostratigraphic indicators are mixed, suggesting that Pliocene to Middle Pleistocene and later deposits are being sampled, and may be mixed together, within the surface collections. This conclusion is further supported by the previous finds and excavations of Early Stone Age artefacts which document the presence of older sediments within the valley (Barham *et al.*, 2011).

As the fossils are all surface collected from various locations within the modern Luangwa River valley, we attempted geochemical studies to determine the extent to which fossil chemistry might provide insight into provenance and age. No significant patterns linked fossils to collection locality and the variability of preservation was very high. Furthermore, there is no preservation of collagen in these faunal remains, making them unsuitable for radiocarbon dating. The lack of collagen may be an indication of antiquity, diagenetic processes or, most probably, both. The fauna generates a palaeoenvironmental signal similar to modern environments in the valley today, albeit with a slightly different community profile. Future work will concentrate on further collections and on identifying the primary contexts of these faunal remains. Hydrodynamic studies of the fossils may also shed light on their provenance, suggesting the extent of transport before their recovery.

Abbreviations. EARS, East Africa Rift System; EDXRF, energy dispersive X-ray fluorescence.

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