

## Bats (Chiroptera) from Olduvai Gorge, Early Pleistocene, Bed I (Tanzania)

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### ABSTRACT

Olduvai Gorge in Tanzania is most famous for producing some of the first discoveries of fossil hominins in East Africa. *Zinjanthropus* (= *Paranthropus*) *boisei* was initially discovered in 1959 from Olduvai Bed I. During screen-washing operations to search for more hominin material at Olduvai, an associated faunal assemblage was accumulated including 40 numbered specimens of fossil bats. Except for seven dental specimens, this collection consists entirely of postcrania, almost exclusively complete or fragmentary humeri representing both proximal and distal ends. Although briefly discussed in preliminary reports, these specimens have remained undescribed for over 50 years and have never been comprehensively compared to extant species. Our analyses indicate that the Olduvai bat fossils represent five families and nine genera, and include four new species: *Myzopoda africana*, n. sp., *Cardioderma leakeyi*, n. sp., *Scotoecus olduvensis*, n. sp., and *Nycticeinops serengetiensis*, n. sp. The Olduvai bat fossils come from the FLK North 1 and FLK NN1 levels, both of early Pleistocene age, and ranging between 1.80 and 1.85 Ma based on <sup>40</sup>Ar/<sup>39</sup>Ar dating techniques, respectively. Compared to the meager Pleistocene bat record from elsewhere on mainland Africa, the Olduvai bat assemblage, although richer, is similar in the predominance of vespertilionids. The East African Olduvai bat fauna differs from Pleistocene faunas from South Africa in including both *Myzopoda* and *Cardioderma* but lacking both hipposiderids and rhinolophids. These taxonomic differences are likely the result of differential sampling due to variation in roosting site preferences (cave-dwelling vs. non-cave-dwelling taxa) and foraging habitats (open vs. forested) in East and South Africa.

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## INTRODUCTION

Pleistocene bat assemblages from mainland Africa remain poorly documented. Such assemblages exist, but fossil bats recovered in excavations focused on other taxa (e.g., primates) have rarely been adequately studied or described (Gunnell and Simmons, 2005; Gunnell, 2010), sometimes sitting untouched in museum drawers for decades. African Pleistocene bats have been reported from South Africa including from the sites of Swartkrans (Avery, 1998) and Kromdraai B (Pocock, 1987) as well as from Twin Rivers Cave in Zambia (Avery, 2003). In East Africa, preliminary reports of Pleistocene bats from the famous Olduvai Gorge site were published by Butler (1978) and Butler and Greenwood (1965). Pleistocene bats have also been reported from the Okote Member of the Koobi Fora Formation in Kenya (Black and Krishtalka, 1986). Late Pleistocene bat occurrences additionally have been reported from Madagascar (Sabatier and Legendre, 1985; Samonds, 2007).

Herein we describe an assemblage of fossil bats from Olduvai Gorge in Tanzania (fig. 1) and compare it to known bat faunas from other Pleistocene sites in Africa and Madagascar. The Olduvai bat assemblage includes seven dental specimens, two complete humeri, 35 humeral fragments, seven proximal radii, one proximal femur, and a broken metacarpal fragment. All specimens come from the FLK North 1 and FLK NN1 levels, both of early Pleistocene age, and dating between 1.80 and 1.85 Ma, respectively (Werdelin, 2010; Deino, 2012; McHenry, 2012; Stanistreet, 2012).

## MATERIALS AND METHODS

**ABBREVIATIONS:** **AMNH**, American Museum of Natural History, New York; **FLK N**, Frida Leakey Korongo North fossil locality (**Tr.** followed by a Roman numeral or number indicates a specific trench within the locality), Olduvai Gorge, Tanzania; **FMNH**, Field Museum of Natural History, Chicago; **NHMUK**, Natural History Museum, United Kingdom, London; **NMT**, National Museum of Tanzania, Dar es-Salaam. A dagger (†) in front of a genus and species name the first time it appears in the text indicates that the designated species is extinct.

**DENTAL NOMENCLATURE AND MEASUREMENTS:** Lower teeth are indicated with a lower case letter and a number; for example, p2 designates the lower second premolar. Upper teeth are indicated with an upper case letter and number; for example, M2 designates the upper second molar. We employ the traditional premolar numbering system of p2, p3, p4 for bats that retain three lower premolars following most recent authors (e.g., Hooker, 2010; Smith et al., 2012; Ravel et al., 2014; Hand et al., 2015) rather than the p1, p4, p5 system advocated by O’Leary et al. (2013). Occlusal morphological terminology follows Gunnell et al. (2011).

Measurements of humeri are presented in table 1. These measurements were taken with digital calipers, and include total humerus length (L, where possible), total distal width (Distal W), width of trochlea and capitular tail (Trochlea W), midshaft greatest width (Midshaft W), width from trochiter to lesser trochanter (Proximal W), maximum height of head (Head H), and length of deltopectoral crest (DPC L). Tooth measurements are presented in table 2. These were taken using a binocular microscope fitted with an ocular micrometer and followed the measuring protocol of Maitre (2014). All measurements are recorded in millimeters.

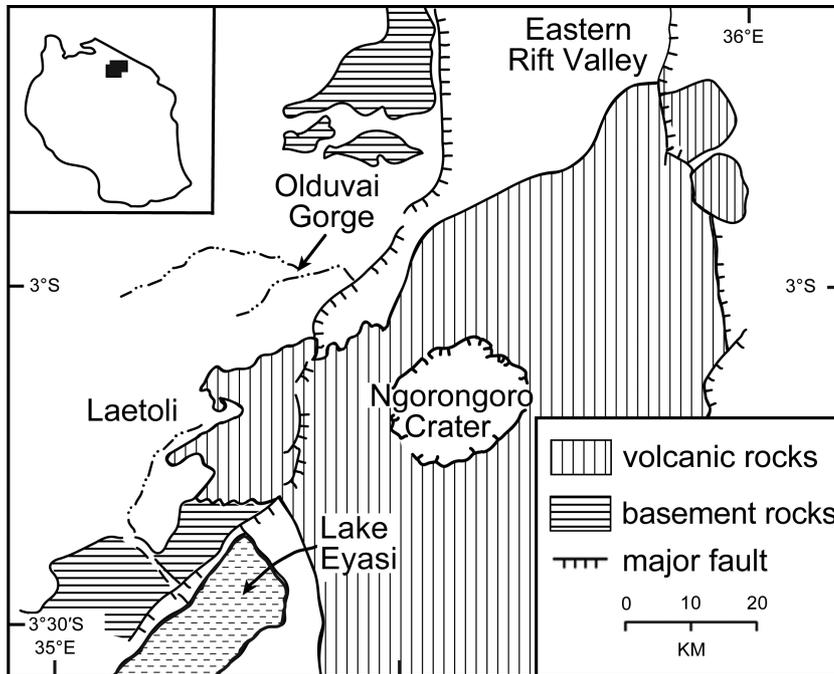


FIGURE 1. Map showing the general location of the Olduvai Gorge area in northern Tanzania (rectangle within country boundary shown in inset) and the location of Olduvai in relation to some geographic and geologic features in the Great Rift Valley.

COMPARATIVE MATERIAL: Extant bat specimens used for comparative taxonomic purposes are listed in appendix 1 and include representatives of Myzopodidae (2 species), Megadermatidae (1 species), Molossidae (19 species), Vespertilionidae (18 species), and Miniopteridae (3 species).

#### SYSTEMATIC PALEONTOLOGY

Order CHIROPTERA Blumenbach, 1779

Family MYZOPODIDAE Thomas, 1904

*Myzopoda* Milne-Edwards and Grandidier, 1878

†*Myzopoda africana*, new species

Figures 2, 3

*Myzopoda* sp., Butler, 1978: 65; Gunnell, 2010: 586.

HOLOTYPE: NMT.010/Bat, complete left humerus (see table 1 for measurements).

ETYMOLOGY: The species name is given for the African continent, since the new species represents the only known occurrence of the genus *Myzopoda* on continental Africa; extant species are restricted to Madagascar.

Table 1. Olduvai and extant bats humerus measurements. Abbreviations: **L**, total humerus length; **Distal W**, total distal width; **Trochlea W**, width of trochlea and capitular tail; **Midshaft W**, midshaft greatest width; **Proximal W**, width from trochiter to lesser trochanter; **Head H**, maximum height of head; **DPC L**, length of deltopectoral crest.

Taxon	Number	L	Distal W	Trochlea W	Midshaft W	Proximal W	Head H	DPC L
<i>Myzopoda africana</i>	NMT.010/Bat	26.5	4.86	3.38	1.77	4.36	1.89	5.11
<i>Myzopoda africana</i>	NMT.008/Bat	—	—	—	1.57	4.02	1.89	5.79
<i>Myzopoda africana</i>	NMT.009/Bat	—	4.65	3.15	1.59	—	—	—
<i>Myzopoda schliemanni</i>	FMNH 187668	23.7	3.67	2.38	1.28	3.09	1.47	4.28
<i>Myzopoda aurita</i>	BMNH 1899	23.5	3.53	2.34	1.23	3.11	1.54	3.75
<i>Mops</i> cf. <i>M. thersites</i>	NMT.014/Bat	—	2.97	2.53	1.42	—	—	—
<i>Mops</i> cf. <i>M. thersites</i>	NMT.028/Bat	—	3.2	2.6	1.59	—	—	—
<i>Mops</i> cf. <i>M. thersites</i>	NMT.029/Bat	27.1	3.33	2.48	1.51	4.49	2.15	5.18
<i>Mops</i> cf. <i>M. condylurus</i>	NMT.031/Bat	—	3.67	2.94	—	—	—	—
<i>Mops</i> cf. <i>M. thersites</i>	NMT.033/Bat	—	3.27	2.51	1.7	—	—	—
<i>Molossus rufus</i>	AMNH 267273	34.3	3	2.5	1.7	3.75	1.65	5.8
<i>Molossus rufus</i>	AMNH 268595	35.5	2.9	2.5	1.65	4.5	2.35	6.3
<i>Eumops trumbulli</i>	AMNH 97328	36.9	3.55	2.95	1.85	5.15	2.25	5.85
<i>Tadarida mexicana</i>	AMNH 145485	23.2	2.4	1.85	0.95	2.9	1.15	3.5
<i>Scotoecus olduvensis</i>	NMT.024/Bat	—	2.6	2.14	1.29	—	—	—
<i>Scotoecus olduvensis</i>	NMT.024/Bat	—	—	—	1.34	3.06	1.77	4.43
Cf. <i>Eptesicus isabellinus</i>	NMT.032/Bat	—	3.37	2.81	1.58	—	—	—
<i>Eptesicus furinalis</i>	AMNH 278332	23	2.15	1.7	1	3	1.15	4.15
Cf. <i>Myotis</i> sp.	NMT.012/Bat	—	3.26	2.63	1.48	—	—	—
<i>Myotis thysanodes</i>	AMNH 145487	25.2	2.55	2.05	0.95	2.95	1.1	4.6
Cf. <i>Pipistrellus</i> sp.	NMT.030/Bat	—	2.15	1.81	0.86	—	—	—
Cf. <i>Pipistrellus</i> sp.	NMT.040/Bat	—	2.48	2	1.08	—	—	—

Taxon	Number	L	Distal W	Trochlea W	Midshaft W	Proximal W	Head H	DPC L
<i>Pipistrellus subflavus</i>	AMNH 208193	20.7	1.95	1.35	0.75	2.4	0.95	3.55
<i>Nycticeinops serengetiensis</i>	NMT.013/Bat	—	2.36	2.22	1.03	—	—	—
<i>Nycticeinops serengetiensis</i>	NMT.015/Bat	—	2.49	2.13	1.05	—	—	—
<i>Nycticeinops serengetiensis</i>	NMT.016/Bat	—	2.47	2.09	1.04	—	—	—
<i>Nycticeinops serengetiensis</i>	NMT.023/Bat	—	2.47	1.9	1.1	—	—	—
<i>Nycticeinops serengetiensis</i>	NMT.025/Bat	—	2.24	1.83	1.01	—	—	—
<i>Nycticeinops serengetiensis</i>	NMT.034/Bat	—	—	—	1.1	2.84	1.47	3.37
<i>Nycticeinops serengetiensis</i>	NMT.035/Bat	—	2.4	1.88	1.02	—	—	—
<i>Nycticeinops serengetiensis</i>	NMT.036/Bat	—	2.42	1.86	1.04	—	—	—
<i>Nycticeinops serengetiensis</i>	NMT.037/Bat	—	2.43	1.88	1.02	—	—	—
<i>Miniopterus</i> cf. <i>M. schreibersi</i>	NMT.011/Bat	—	3.05	2.56	1.38	—	—	—
<i>Miniopterus</i> cf. <i>M. schreibersi</i>	NMT.017/Bat	—	—	2.46	1.38	—	—	—
<i>Miniopterus</i> cf. <i>M. schreibersi</i>	NMT.019/Bat	—	—	—	—	—	1.76	4.56
<i>Miniopterus</i> cf. <i>M. schreibersi</i>	NMT.022/Bat	—	2.89	2.27	1.29	3.72	1.56	4.92
<i>Miniopterus</i> cf. <i>M. schreibersi</i>	NMT.038/Bat	—	2.9	2.33	1.4	—	—	—

TYPE LOCALITY: Tanzania: Arusha Province, Olduvai Gorge, Bed I, FLK NI, Layer 123.

DIAGNOSIS: Differs from living *Myzopoda schliemanni* and *M. aurita* in having a larger humerus (mean dimensions 21% larger) that is more robust and has a relatively longer deltopectoral crest, a more rounded humeral head, a more robust lesser tubercle, a more distinct and elongate lateral capitular tail, a more distinct and laterally compressed capitulum, and a relatively broader epitrochlea with a more distally extended epitrochlear process.

REFERRED SPECIMENS: NMT.008/Bat, left proximal humerus from Olduvai Bed I, FLK NI, layer 123; NMT.009/Bat, right distal humerus, Olduvai Bed 1, FLK NI, layer 4 (collected 1960).

DESCRIPTION: Three humeri from Olduvai can be assigned to *Myzopoda* based on the presence of the following combination of characters: round, bulbous capitulum, extended capitular tail with flaring lip, a broad epicondyle with two distinct processes, and a humeral head placed distal to the trochiter (greater tubercle). The proximal humerus (fig. 2) of *M.*

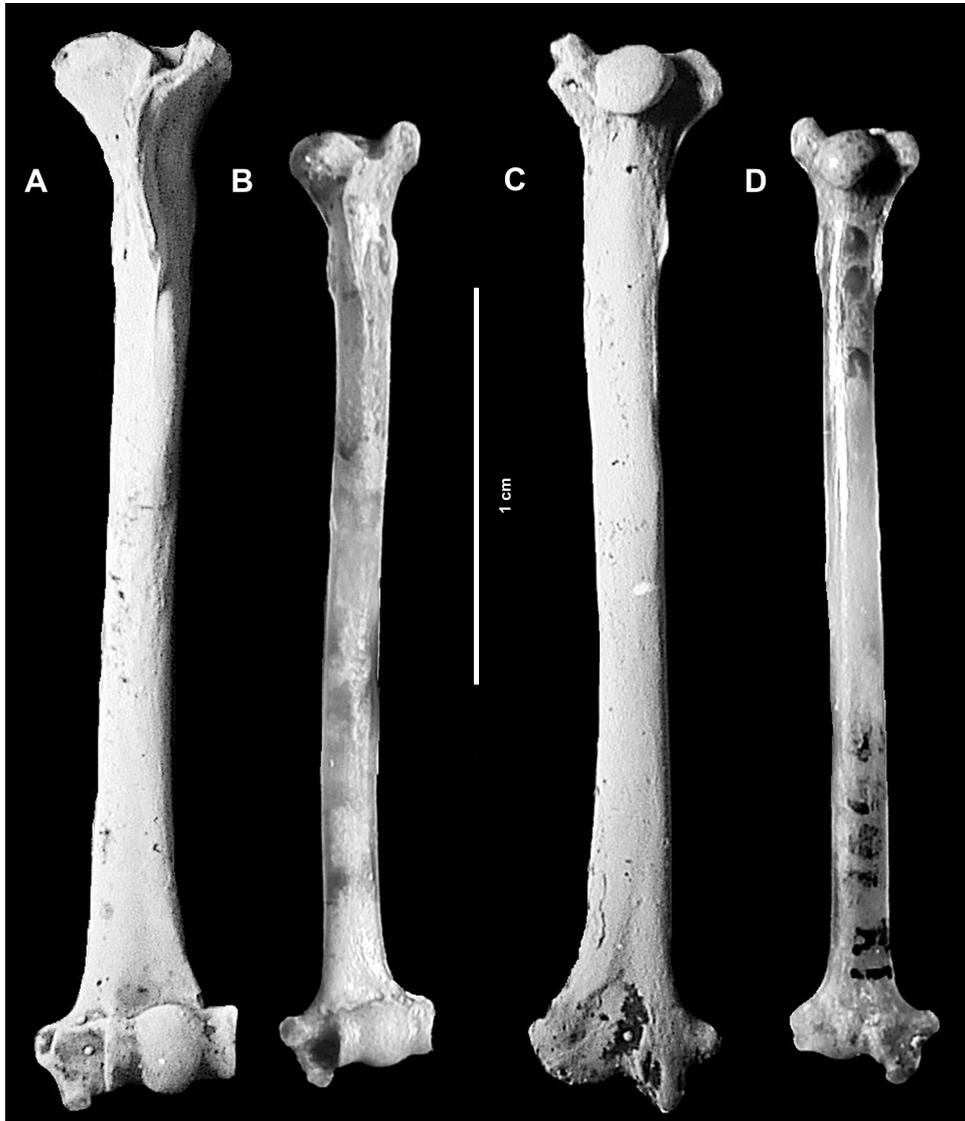


FIGURE 2. A, C, Left humerus of *Myzopoda africana*, n. sp. (NMT.010/Bat, holotype) compared with B, D., *Myzopoda schliemanni* (FMNH 187668), in anterior (A–B) and posterior (C–D) views.

*africana* has a semi-rounded, distolaterally slightly flattened head. The proximal extent of the head does not extend as far proximally as the trochiter and is even slightly below the proximal extent of the lesser tubercle. The deltopectoral crest is elevated anteriorly, is relatively long and curving, and has a sharply defined anterior margin with a slight overhanging lip developed medially. Distally (figs. 2, 3), the humerus of *M. africana* has a rounded and slightly laterally compressed capitulum that is robust and not offset from the long axis of the humeral shaft. The lateral capitular tail is as broad as the trochlear surface. The trochlear groove is distinct but not deeply invaginated and with a sharply defined trochlear lip. The

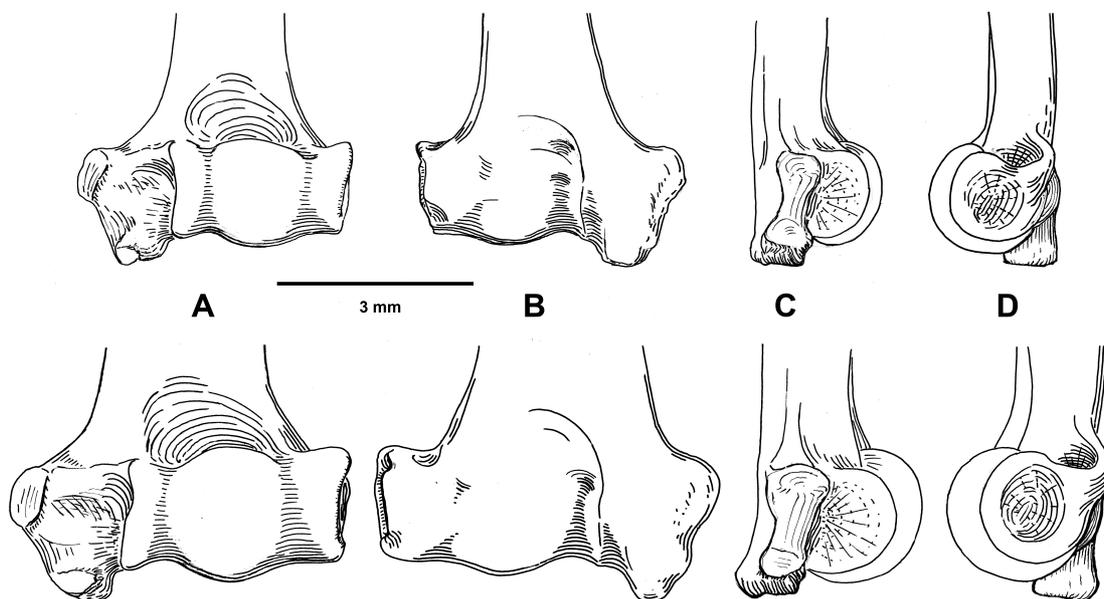
***Myzopoda aurita* (NHMUK 1849.11.3.5)*****Myzopoda africana* (holotype, NMT.010/Bat)**

FIGURE 3. Left distal humerus of *Myzopoda aurita* (NHMUK.1849.11.3.5) compared with *Myzopoda africana*, n. sp. (NMT.010/Bat, holotype), in **A**, anterior, **B**, posterior, **C**, medial and **D**, lateral views.

medial epicondyle is robust with a relatively elongate process that extends distally beyond the trochlear ridge and is developed as two rounded surfaces aligned anteroposteriorly. There is a small but distinct groove on the lateral surface of the epicondyle.

Other fossil material of *Myzopoda* is unknown from both Africa and Madagascar, although more ancient myzopodids referred to another genus have been described from Egypt (Gunnell et al., 2014).

Family MEGADERMATIDAE H. Allen, 1864

*Cardioderma* Peters, 1873

†*Cardioderma leakeyi*, new species

Figures 4, 5

Megadermidae Butler and Greenwood, 1965: 14.

*Cardioderma* sp., Butler, 1978: 65; Gunnell, 2010: 586.

HOLOTYPE: NMT.003/Bat, left maxilla with P4–M3 (fig. 4), from the 1960 Olduvai Collection (see table 2 for measurements).

REFERRED SPECIMEN: NMT.002/Bat, right dentary with m1–3, FLK NI, Layer 3.

ETYMOLOGY: Named in honor of L.S.B. Leakey who was instrumental in initiating and leading the search for vertebrate fossils, especially fossil humans, in East Africa.

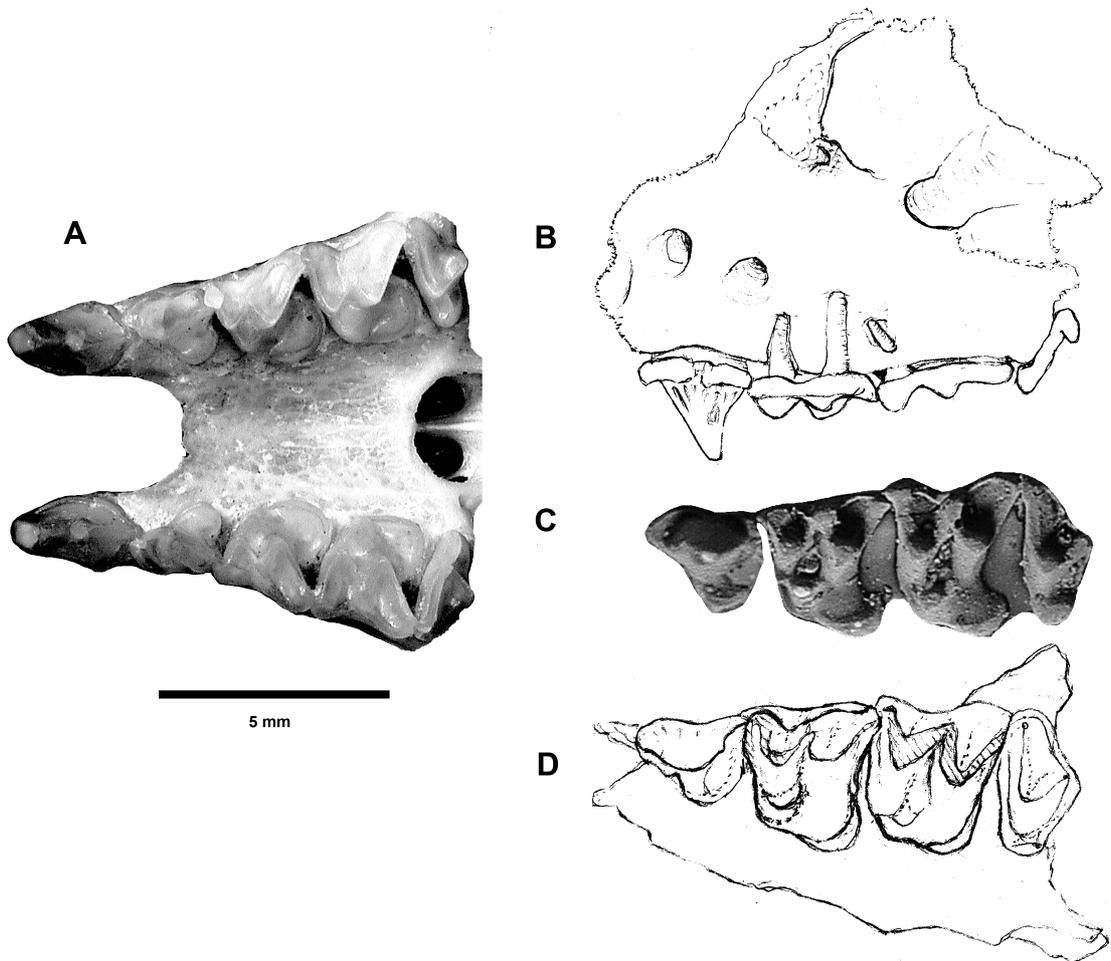


FIGURE 4. Upper dentition of *Cardioderma cor* (A) compared with *Cardioderma leakeyi*, n. sp. (B–D). A, AMNH 184338, palate (photograph). NMT.003/Bat (holotype) left maxilla with P4–M3 in B, C lateral (drawing and photograph of cast, respectively) and D occlusal (drawing) views.

**TYPE LOCALITY:** Tanzania: Olduvai Gorge, Bed I, FLK NI, Layer 2.

**DIAGNOSIS:** Differs from extant *Cardioderma cor* in averaging 18%–20% larger in tooth dimensions; P4 with relatively larger parastyle and metastyle and better developed labial cingulum; M1–2 with relatively more robust mesostyle, deeper parafoossa and metafoossa, and deeper trigon basin; less reduced M3/m3; m1 and m2 with relatively broader talonid basin and more robust metaconid; m3 with broader trigonid and less reduced talonid.

**DESCRIPTION AND COMPARISONS:** The specimens referred to *Cardioderma leakeyi* can be recognized as megadermatids based on the robust nature of the cusps and crests on upper and lower cheek teeth, the large hypocone shelves and the narrow and labiolingually restricted profossae on M1–2, the broadly open trigonid on m1 and the high and short lower molar talonids. The holotype maxilla (NMT.003/Bat, fig. 4) has a maxillary foramen that opens over the anterior root of P4 as in the extant species of *Cardioderma*, *C. cor*. There is a secondary

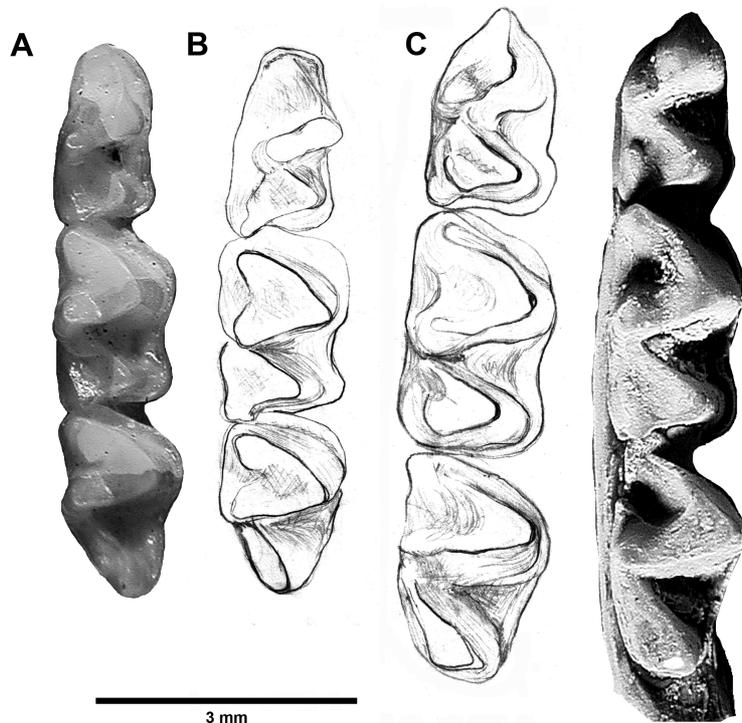


FIGURE 5. Lower dentition of *Cardioderma cor* (A–B) compared with *Cardioderma leakeyi*, n. sp. (C). A, AMNH 184338, photograph of right m1–3; B, NHMUK 36.11.4.4, drawing of right m1–3; C, NMT.002/Bat, right m1–3 (drawing on left, photograph of cast on right).

and smaller foramen that opens more ventrally on the maxilla over the posterior root of P4 (this foramen is slightly more posteriorly placed in the extant species). In lateral view, the anterior labial root of M1 is exposed through the bony surface of the maxilla, as is often the case in *C. cor*. The root of the zygomatic arch is dorsal to M2 as in the living form, but it is much more robust in *C. leakeyi*, as is the anterior orbital process. The optical foramen is the same size and in the same position in both species of *Cardioderma*.

The P4 of *Cardioderma leakeyi* has a robust paracone, relatively large parastyle and metastyle, and a relatively heavy labial cingulum. The lingual cingulum is relatively broad anteroposteriorly and extends lingually farther than is seen in *C. cor*. M1–2 each have a prominent hypocone shelf, an anteroposteriorly narrow but labiolingually extended and deep protofossa, a robust mesostyle, and parastylar and metastylar foveae that are nearly equivalent in size (whereas in *C. cor* the metastylar fovea is typically larger). M3 has a relatively robust parastyle and a labiolingually short lingual shelf and is less anteroposteriorly compressed than seen in *C. cor*.

The horizontal ramus of the dentary (NMT.002/Bat) is relatively deep in *Cardioderma leakeyi* (3.0 mm beneath m1) compared to *C. cor* (2.0 mm below m1). The lower molars of *C. leakeyi* (fig. 5) are all quite similar to those of extant *C. cor*. The m1 is broken anteriorly, making it impossible to tell whether *C. leakeyi* had a small, low, and centered paraconid as seen in *C. cor*. All three lower molars of *C. leakeyi* have a prominent protoconid and a somewhat lower,

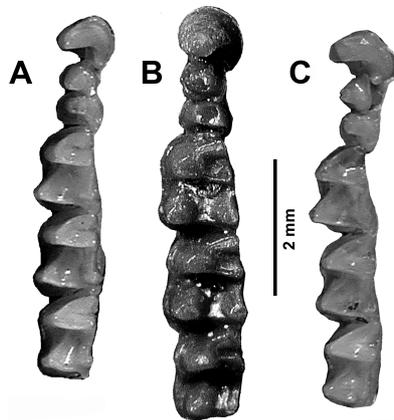


FIGURE 6. Left lower dentitions of *Scotoecus* in occlusal view. **A**, *S. albofuscus* (AMNH 241054); **B**, *S. olduvensis*, n. sp. (NMT.004/Bat, Holotype, cast); **C**, *S. hindei* (AMNH 241055).

but distinct, metaconid. Lower m2 and m3 have distinct paraconids that are placed somewhat lower than the metaconids. The hypoflexid is deep and the cristid obliqua is angled and joins the postvallid of the trigonid well lingual of center on all molar teeth. The hypoconid on m1–2 is distinct, but it is less so on m3; the entoconid is distinct only on m1. Molar talonids are broader than those seen in *C. cor*, but the talonid is not as broad as the trigonid on any tooth. All molars have moderate and complete labial cingulids.

The only other published record of a fossil *Cardioderma* species (Louchart et al., 2009) is from the early Pliocene in Ethiopia. However, the material upon which that assignment is based has never been described or figured making comparisons impossible at this time.

#### Family VESPERTILIONIDAE Gray, 1821

##### *Scotoecus* Thomas, 1901

##### †*Scotoecus olduvensis*, new species

##### Figures 6, 7

Cf. *Pipistrellus (Scotozous) rueppelli*, Butler and Greenwood, 1965: 15; Butler, 1978: 65; Gunnell, 2010: 588.

**HOLOTYPE:** NMT.004/Bat, left dentary with c1–m3 (fig. 6B; see table 2 for measurements).

**REFERRED SPECIMEN:** NMT.024/Bat, left distal humerus (also includes right proximal humeral fragment), FLK Main Dig 1, Z level (see table 1 for measurements).

**ETYMOLOGY:** Named for Olduvai Gorge, Tanzania.

**TYPE LOCALITY:** Tanzania: Olduvai Gorge, Bed I, FLK NI, Layer 3.

**DIAGNOSIS:** Similar to extant *Scotoecus albofuscus* (fig. 6A) and *S. hindei* (fig. 6C) but differs from both in being, on average, 12% larger in tooth dimensions; *S. olduvensis* further differs from *S. hindei* in having: c1 lacking a buccal cingulid and anterolingual and posterolingual

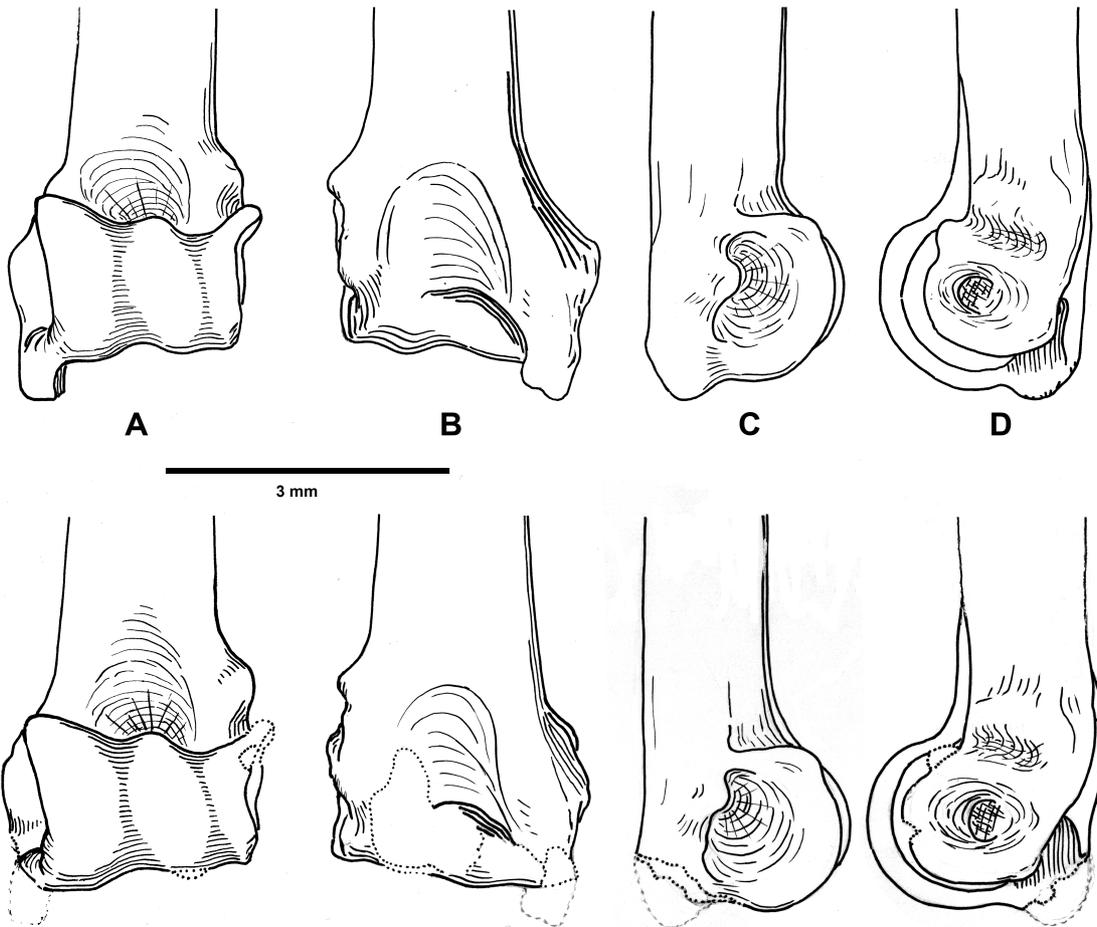
***Scotoecus hindei* (NHMUK 63.1151)*****Scotoecus olduensis* (NMT.023/Bat)**

FIGURE 7. Left distal humerus of *Scotoecus hindei* (NHMUK 63.1151) compared with *Scotoecus olduensis*, n. sp. (NMT.023/Bat), in A, anterior, B, posterior, C, medial, and D, lateral views.

basal cuspules; a relatively longer posterior shelf that is not notched; p2 relatively larger compared to p4; p4 more similar in size to p2 (not larger as in extant taxa); p4 with a buccal cingulid lacking or very weak, a more robust cusp, and a lingual cingulid lacking an anterolingual extension. *S. olduensis* further differs from *S. albofuscus* in having: c1 more robust, lacking a heavy lingual cingulid, with a more posteriorly extended posterior shelf that is not notched; p4 more similar in size to p2 (not larger as in extant taxon), lacking a lingual crest off the posterior part of the cusp that terminates in a posterior lingual extension of the lingual cingulid, which lacks an anterolingual extension, but has a better developed posterior shelf; *S. olduensis* further differs from both extant taxa in having: p2 lacking a distinctive anterior extension of the anterolingual cingulid that forms a protrusion that fits into the notch of the canine posterior shelf; m3 with a somewhat lower hypoconid and entoconid and lacking a hypoconulid.



DESCRIPTION: The lower canine of *S. olduvensis* is robust and relatively broad with a convex anterior surface, a flat posterior surface, and a lingual cingulid continuous with a low, moderate posterior shelf. The posterior shelf is overlapped by p2, which is single rooted and slightly wider than long but essentially circular in occlusal view. Anteriorly p2 overlaps the posterior shelf of the canine and has a continuous cingulid that is heaviest buccally. Lower p4 is similar to p2 but is slightly larger and relatively wider than long. It has a developed lingual cingulid, but the buccal cingulid is very weak. Like p2 there is only a single cusp developed on p4 that is slightly more robust than that found in p2. The lower molars are very similar to those of *S. hindei* and *S. albofuscus*: in having very tall and prominent talonid cusps and high entocristids, in being nyctalodont with well-developed crests, and in having relatively strong buccal cingulids. The lower molar trigonids are nearly as wide as talonids, in contrast to the living species in which the trigonid is noticeably more restricted buccolingually. The bases of the hypoconid and entoconid are inflated producing a relatively narrow and restricted talonid basin compared to the extant taxa.

The distal end of NMT.024/Bat, the left distal humerus that we refer to *S. olduvensis* (fig. 7, bottom row), has a narrow but robust capitulum that is slightly angled and not offset from the shaft. The lateral capitular tail, even though somewhat broken, appears to have been much less broad than trochlear surface and is essentially continuous with the capitulum (shallow to absent groove). The trochlear groove is weak and the trochlear surface is relatively wide and robust with a sharply defined trochlear lip. The medial epicondylar process is broken and the groove on lateral surface of epicondyle is weak to absent.

Also included with NMT.024/Bat is a potentially associated right proximal humerus. The head of this specimen is ovate and somewhat angled. The proximal margin of the head does not extend beyond the proximal extent of trochiter and is about at the same height as the proximal extent of the lesser trochanter. There is a high (anteriorly) deltopectoral crest. It is relatively long and sharply defined with a slight overhanging lip developed medially. The deltopectoral crest curves toward base of trochiter and anteriorly encloses a moderately deep fossa.

No other fossils of *Scotoecus* have been described or figured (Simmons and Gunnell, in prep.).

*Cf. Eptesicus isabellinus*

Figure 8

*Eptesicus cf. hottentotus*, Butler, 1978: 65.

REFERRED SPECIMEN: NMT.032/Bat, right distal humerus, FLK NI, layer 6, 1964 (see table 1 for measurements).

DESCRIPTION AND DISCUSSION: Olduvai specimen NMT.032/Bat represents a vespertilionid humerus very similar in size and morphology to that of extant *Eptesicus isabellinus*. NMT.032/Bat (fig. 8, bottom row) has a narrow but robust capitulum that is not angled or offset from shaft. The lateral capitular tail is much less broad than the trochlear surface, and is separated from the capitulum by a shallow groove. A trochlear groove is absent and the

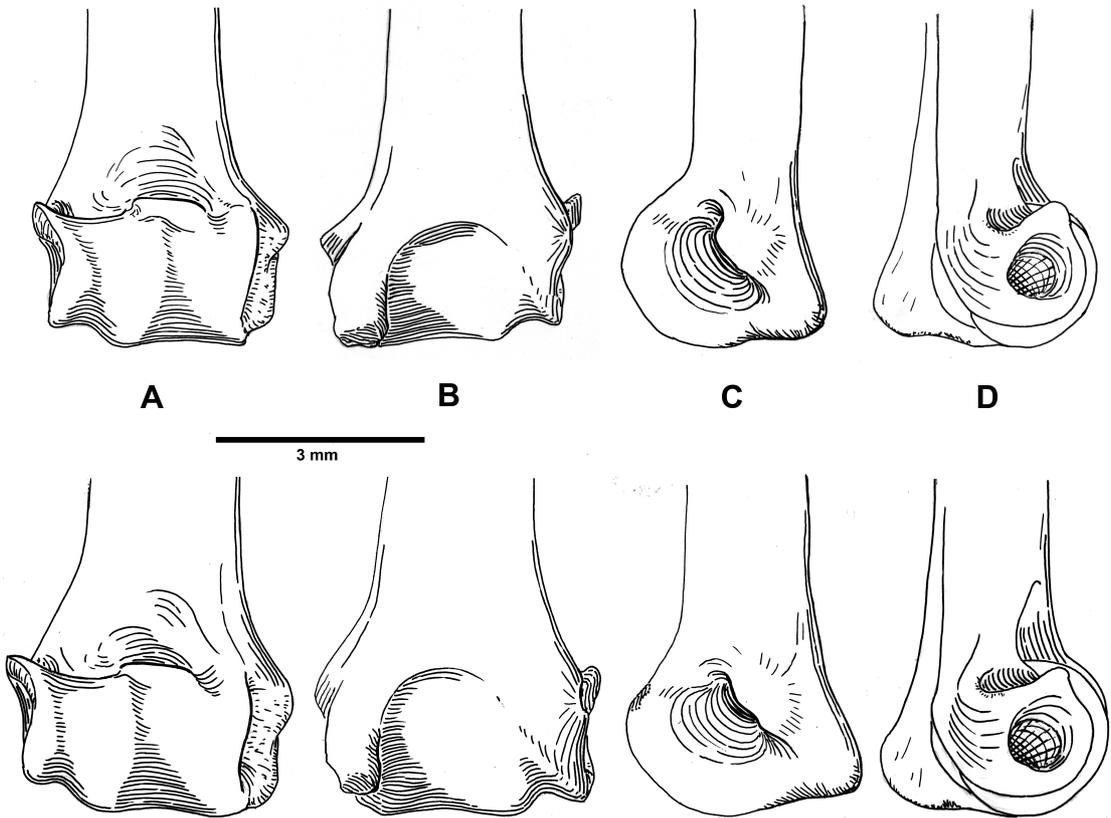
***Eptesicus isabellinus* (NHMUK 19.7.7.1160)****Cf. *Eptesicus isabellinus* (NMT.032/Bat)**

FIGURE 8. Right distal humerus of *Eptesicus isabellinus* (NHMUK 19.7.7.1160) compared with cf. *Eptesicus isabellinus* (NMT.032/Bat) in A, anterior, B, posterior, C, medial, and D, lateral views

trochlear surface is relatively wide and robust with a sharply defined trochlear lip. The medial epicondylar process is low and robust and does not extend distally beyond the trochlear ridge. Groove on the lateral surface of epicondyle is weak to absent. These are all features typical of *Eptesicus*.

The taxonomy of *Eptesicus isabellinus* is unresolved at the moment, but it appears to be the North African representative of the *Eptesicus serotinus* radiation sensu lato (Simmons, 2005). However, it is not clear whether *E. isabellinus* can be maintained as a species separate from *E. serotinus* (Simmons, 2005). We have chosen to retain it as distinct subject to revision of circum-Mediterranean *Eptesicus* species.

NMT.032/Bat very closely resembles *E. isabellinus* (NHMUK 19.7.7.1160, fig. 8, top row) in nearly every detail of size and morphology. The fossil specimen has a slightly less distally extended epicondylar process and the distal end is slightly deeper anteroposteriorly. NMT.032 differs from *Eptesicus furinalis* (AMNH 278332) only in being relatively larger with a slightly

broader capitulum and lacking any groove between the capitulum and trochlea. The lateral ridge is slightly broader than in the extant taxon but otherwise similar.

The only records of *Eptesicus* fossil material from Africa all come from southern Africa (Hendey, 1981; Pocock, 1987; Avery, 1998), mostly from the early to late Pliocene deposits, and they are based on teeth and jaws that are not directly comparable to the specimen described here. *Eptesicus* is a common element of other Plio-Pleistocene faunal communities and is widespread across the northern continents during this time period (Simmons and Gunnell, in prep.).

Cf. *Myotis* sp.

*Myotis* sp., Butler, 1978: 65; Gunnell, 2010: 588.

REFERRED SPECIMEN: NMT.012/Bat, left damaged distal humerus, FLK NI, layer 3 (see table 1 for measurements).

DESCRIPTION AND DISCUSSION: NMT.012/Bat is the only specimen in the Olduvai sample that may represent *Myotis*. The distal end of the humerus of NMT.012/Bat has typical *Myotis* features including having a relatively narrow capitulum that is not offset from shaft, a lateral capitular tail that is less broad than trochlear surface and proximolaterally extended into a distinct lip, a trochlear groove that is essentially absent, and a trochlear surface that is relatively broad with a trochlear lip that is not sharply defined. Additionally, the medial epicondyle has a small process that does not extend distally beyond the trochlear ridge and the groove on the posterolateral surface of the epicondyle is deep, narrow, and distinct.

Of the 12 *Myotis* species living in Africa today (Simmons, 2005), only *M. dieteri* (Democratic Republic of Congo), *M. morrisoni* (Ethiopia, Nigeria), *M. scotti* (Ethiopia), *M. tricolor* (sub-Saharan Africa), *M. bocagii* (western and southern Africa), and *M. welwitschii* (sub-Saharan Africa) are found south of the Sahara, and of these only *M. welwitschii* lives in Tanzania today. NMT.012/Bat represents a relatively large species of *Myotis*, such as *M. welwitschii*, and may well be related to, or even represent, that species.

*Myotis* is poorly represented in the fossil record of Africa in the Plio-Pleistocene and is restricted to southern Africa (Broom, 1948; Pocock, 1987) outside of the record from Tanzania and an occurrence in Morocco (Gunnell et al., 2011). *Myotis* is a common element of other Plio-Pleistocene faunal communities and is widespread across the northern continents during this time period (Simmons and Gunnell, in prep.).

Cf. *Pipistrellus* sp.

REFERRED SPECIMENS: NMT.030/Bat, right distal humerus, FLK NNI, layer 2 or 3; NMT.040/Bat, left distal humerus, FLK NI, layer 3, Tr. IV, 1964 (see table 1 for measurements).

DESCRIPTION: Two fragmentary distal humeri from Olduvai represent pipistrelles, similar in size and morphology to *Pipistrellus nanulus* and *P. rueppelli*, the former known today from equatorial Africa and the latter from much of the African continent (Simmons, 2005).

In anterior view the distal end of NMT.030/Bat has a narrow capitulum that is slightly angled and not offset from shaft. The lateral capitular tail is much less broad than the trochlear

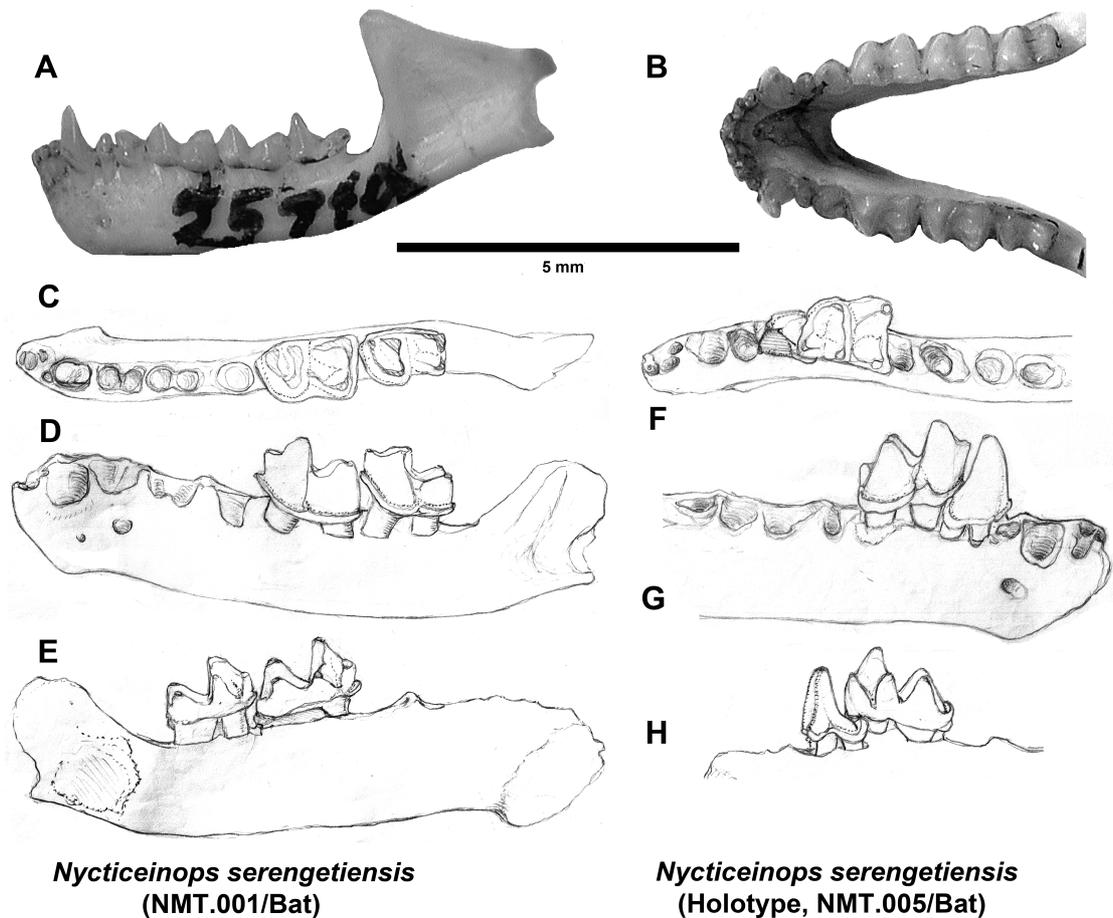
***Nycticeinops schlieffeni* (AMNH 257406)**

FIGURE 9. Mandible of *Nycticeinops schlieffeni* (AMNH 257406, photographs) in **A**, lateral and **B**, occlusal views compared with *Nycticeinops serengetiensis*, n. sp. (drawings). **C–E**, *N. serengetiensis*, left dentary with m1–2 and all anterior alveoli (NMT.001/Bat) in **C**, occlusal, **D**, lateral and **E**, medial views. **F–H**, Holotype of *N. serengetiensis*, right dentary with p4–m1 with all other alveoli (NMT.005/Bat) in **F**, occlusal, **G**, lateral, and **H**, medial views.

surface and is not separated from capitulum by a groove. The trochlear groove is moderately deep, the trochlear surface is relatively wide and robust, and the trochlear lip not sharply defined. The medial epicondylar process is small and extends distally only slightly beyond trochlear ridge. In posterior view, the groove on the lateral surface of the epicondyle is weak to absent. NMT.040/Bat differs slightly from NMT.030/Bat in lacking the slight angulation of the capitulum and in having a more sharply defined trochlear lip. Otherwise the two humeri are nearly identical.

Pipistrelles are unknown from the fossil record in Africa outside Olduvai (Butler, 1978; Simmons and Gunnell, in prep.).

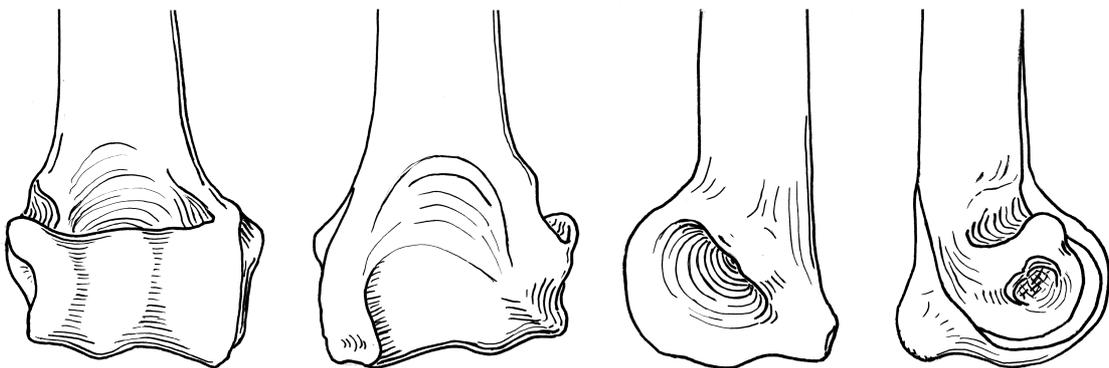
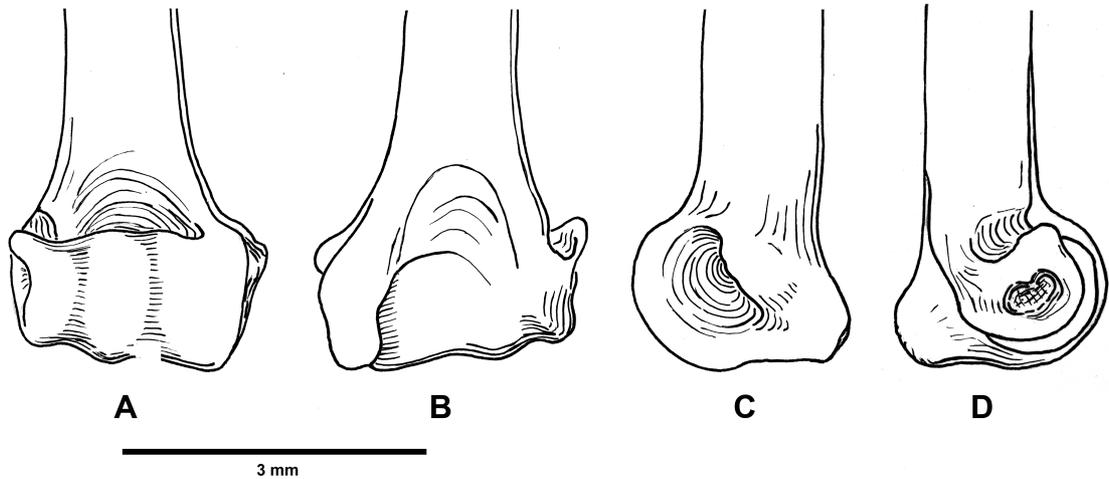
***Nycticeinops schlieffeni* (NHMUK 32.7.463)*****Nycticeinops serengetiensis* (NMT.015/Bat)**

FIGURE 10. Right distal humerus of *Nycticeinops schlieffeni* (NHMUK 32.7.463) compared with *Nycticeinops serengetiensis*, n. sp. (NMT.015/Bat), in **A**, anterior, **B**, posterior, **C**, medial, and **D**, lateral views.

*Nycticeinops* Hill and Harrison, 1987

†*Nycticeinops serengetiensis*, new species

Figures 9, 10

Cf. *Nycticeius* (*Scoteinus*) *schlieffeni*, Butler and Greenwood, 1965: 15; Butler, 1978: 65; Gunnell, 2010: 588.

**HOLOTYPE:** NMT.005/Bat, right dentary with p4–m1 and alveoli for all other teeth (fig. 9F–H; see table 2 for measurements).

**REFERRED SPECIMENS:** NMT.001/Bat, left dentary with m2–3 and alveoli for all anterior teeth, from FLK NI, layer 123; NMT.006/Bat, left edentulous dentary preserving all tooth alveoli, from FLK NI, layer 1; NMT.013/Bat, left distal humerus, from FLK NI, layer 2; NMT.015/Bat, right

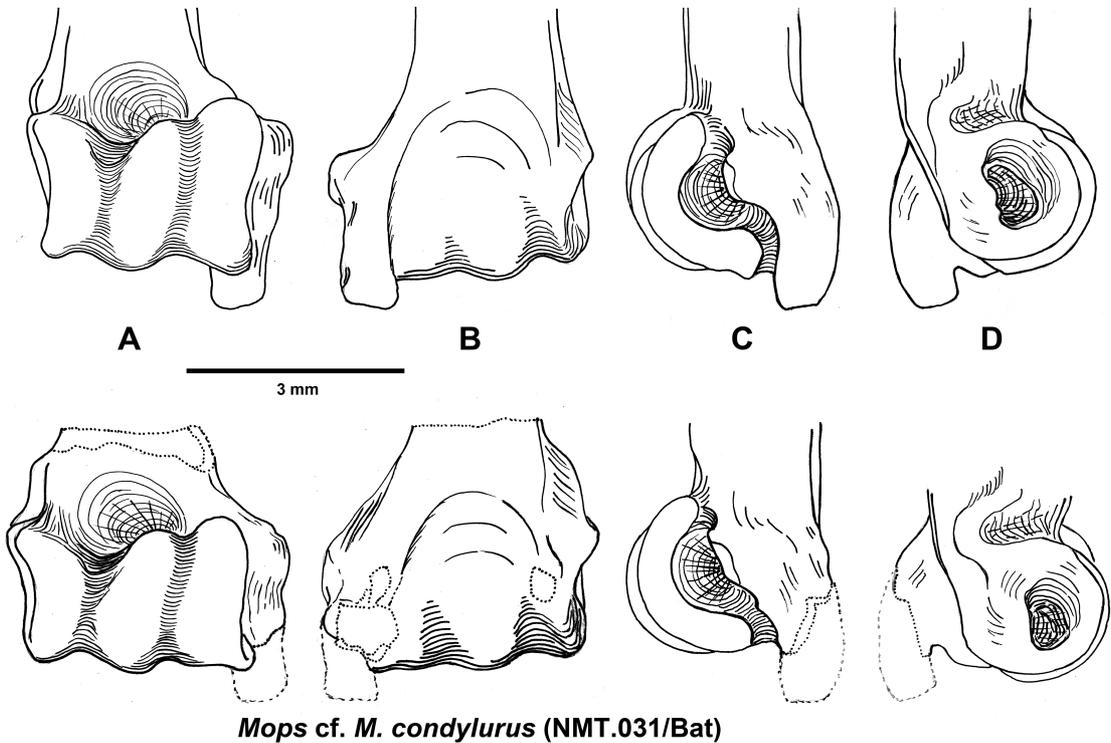
***Mops condylurus* (NHMUK 20.6.13.1)*****Mops cf. M. condylurus* (NMT.031/Bat)**

FIGURE 11. Right distal humerus of *Mops condylurus* (NHMUK 20.6.13.1) compared with *Mops cf. M. condylurus* (NMT.031/Bat) in A, anterior, B, posterior, C, medial, and D, lateral views.

distal humeri (3), from FLK NI, layer 123; NMT.016/Bat, left and right distal humeri, from FLK NI, layer 3; NMT.023/Bat, right distal humerus (and most of shaft), from Main Dig, FLK 1, Z level; NMT.025/Bat, left distal humerus, from FLK1, Z level; NMT.034/Bat, left proximal humerus, from FLK NI, layer 1, Tr. IV, 1964; NMT.035/Bat, right distal humeri (2), from FLK NI, layer 5, Tr. IV, 1964; NMT.036/Bat, left distal humerus, from FLK NI, layer 2, Tr. V; NMT.037/Bat, left and right distal humeri, from FLK NI, layer 1, Tr. III (see table 1 for measurements).

**ETYMOLOGY:** Named for the famed Serengeti region in northern Tanzania where Olduvai Gorge is located.

**TYPE LOCALITY:** Tanzania: Olduvai Gorge, Bed I, FLK NI, layer 5, Tr. IV.

**DIAGNOSIS:** Differs from extant *Nycticeinops schlieffeni* (the only other recognized species of the genus) in having teeth on average 20% larger; p4 relatively taller and labiolingually narrower with a relatively longer talonid shelf; m1 with more curved paracristid and more angled entocristid, hypoconulid relatively lower and talonid basin more deeply excavated; m2 with relatively lower hypoconulid; and m3 with heavier anterolabial cingulid.

**DESCRIPTION AND DISCUSSION:** All three of the known fossil jaws have slightly different arrangements of their incisor alveoli. The holotype of *N. serengetiensis* (NMT.005/Bat) has a

small i3 alveolus directly in front of the canine alveolus while a slightly larger i2 alveolus is anteromedial to that of i3 and directly posterior to an equally large i1 alveolus. NMT.001/Bat has a similar arrangement except that the i1 alveolus is noticeably larger than either the i2 or i3 alveoli and is placed somewhat more laterally, producing a triangular arrangement of alveoli. The edentulous dentary of *N. serengetiensis* (NMT.006/Bat) is more similar to the holotype except that the alveoli of i2 and i3 are nearly mediolaterally opposite one another and the i2 alveolus is smaller. The arrangement of incisors in extant *Nycticeinops schlieffeni* (e.g., AMNH 257406) is somewhat different in that the i2 alveolus is not as far medial but instead forms part of a non-arcuate row of incisors running from the canine to the midline of the jaw with i1 most anterior and i3 most posterior. The offset arrangement found in *N. serengetiensis* may, in part, be due to the larger teeth of the fossil form and subsequent crowding of teeth in the jaw (although certain other extant vespertilionids also have a similar arrangement of incisor alveoli to those seen in *N. serengetiensis*; N.J. Czaplewski, personal commun.). As further evidence of this crowding, the p4 of NMT.005/Bat is very closely appressed to the m1 with the m1 overlapping the p4 talonid shelf.

The dentaries of *N. serengetiensis* are all broken posteriorly but preserve enough of the ascending ramus to show that it rose dorsally at a shallower angle than that in *N. schlieffeni*, in which the ramus rises more steeply and then turns anteriorly (fig. 9A). Like in the extant taxon, there is typically a single mental foramen located beneath the area of contact between c1–p3, but it is relatively larger in *N. serengetiensis*, which occasionally has a smaller foramen located more anteriorly as well (fig. 9D). The dentaries of *N. serengetiensis* also differ from the modern species by having their ventral borders gently sloping dorsally from posterior to anterior and then ending anteriorly by turning dorsally. In *N. schlieffeni* the dorsal border of the dentary angles dorsally from posterior to anterior and forms a continuous surface with no angulation producing a jaw that is deeper beneath p4 than it is beneath m3.

The Olduvai collection includes 13 distal humeri and one proximal humerus that we refer to *N. serengetiensis* based on their similarity to those of extant *N. schlieffeni*. NMT.034/Bat is a left proximal humerus that has a semi-rounded and slightly angled head that does not extend quite as far proximally as the trochiter but does extend slightly past the lesser trochanter. The deltopectoral crest is high anteriorly and fairly long, and has a sharply defined edge with a slightly overhanging lip developed medially. The crest curves toward the base of the trochiter and anteriorly encloses a moderately deep intertrochanteric fossa.

The distal humerus of *N. serengetiensis* is characterized by a relatively narrow capitulum that is neither angled nor offset from the shaft. The lateral capitular tail is much less broad than the trochlear surface and is separated from the capitulum by a very shallow groove. The trochlear groove is weak and the trochlear lip is sharply defined. The medial epicondyle has a small process that extends distally only slightly beyond trochlear ridge. The groove on lateral surface of epicondyle is moderately developed.

Other than the specimens described here no other fossils of *Nycticeinops* are known (Simmons and Gunnell, in prep.).

## Family MOLOSSIDAE Gervais, 1856

*Mops* Lesson, 1842*Mops* cf. *M. condylurus*

## Figure 11

Molossidae indet. (in part), Butler, 1978: 66; Gunnell, 2010: 587.

REFERRED SPECIMEN: NMT.031/Bat, right distal humerus from FLK NI, layer 3, Tr. III.

DESCRIPTION AND COMPARISONS: The humeral specimens described below can all be recognized as molossids based on the presence of a relatively small and rounded humeral head that is positioned well below the trochiter, a bilaterally narrow and angled (proximomedially to distolaterally) capitulum, a bilaterally narrow trochlea separated from the capitulum by a moderate to distinct trochlear groove, an extended and robust capitular tail that is separated from the capitulum by a deep groove, and a well-developed and distally extended epitrochlear process.

The specimen referred here to *Mops* cf. *M. condylurus* (as well as those referred to *Mops* cf. *M. thersites* below) resembles those of extant species of *Mops* in having an angled capitulum that is separated from the trochlea by a shallow yet distinct groove and from the lateral capitular tail by a deeper and well-formed groove. The epicondylar process is distinct but does not extend very far beyond the distal edge of the trochlea. *Molossus* differs from the Olduvai molossids in having: a less distinct groove between the capitulum and trochlea, a shallower groove between the capitulum and capitular tail, and a much more distally extended epitrochlear process (see Simmons and Geisler, 1998: fig. 33). The Olduvai molossids resemble *Eumops* in possessing a shallow groove between the capitulum and the trochlea but differ in having a narrower (proximodistally) lateral capitular tail that is separated from the capitulum by a shallower groove. The Olduvai molossids also are similar to *Tadarida*, *Otomops*, *Myopterus*, and *Chaerephon* in sharing a relatively broader and angled capitulum but differ in having a relatively more elongate trochlea (proximodistally). Additionally, the Olduvai molossids have a more robust and more distinctly separated capitular tail than either *Myopterus* or *Otomops* do.

Olduvai specimen NMT.031/Bat represents a molossid very similar in size (see table 1 for comparative measurements) and morphology to extant *Mops condylurus*, which is today known from most of Africa south of the Sahara (Simmons, 2005). In anterior view, the distal end of NMT.031/Bat shows a narrow, medially angled capitulum that is not offset from the shaft. The lateral capitular tail is not as broad as the trochlea but is nearly as deep and is separated from the capitulum by a relatively deep groove. The trochlear surface is relatively broad and well defined, is separated from the capitulum by a weak groove, and has weakly defined medial trochlear lip. The medial epicondyle is not wide but is robust. The epicondylar process on NMT.031/Bat is broken so it is not possible to determine its extent. Posteriorly, the groove on the lateral surface of the epicondyle is very weak to absent. NMT.013/Bat differs from *M. condylurus* in having a relatively less deep trochlea and a somewhat wider capitulum, especially at its distal extent.

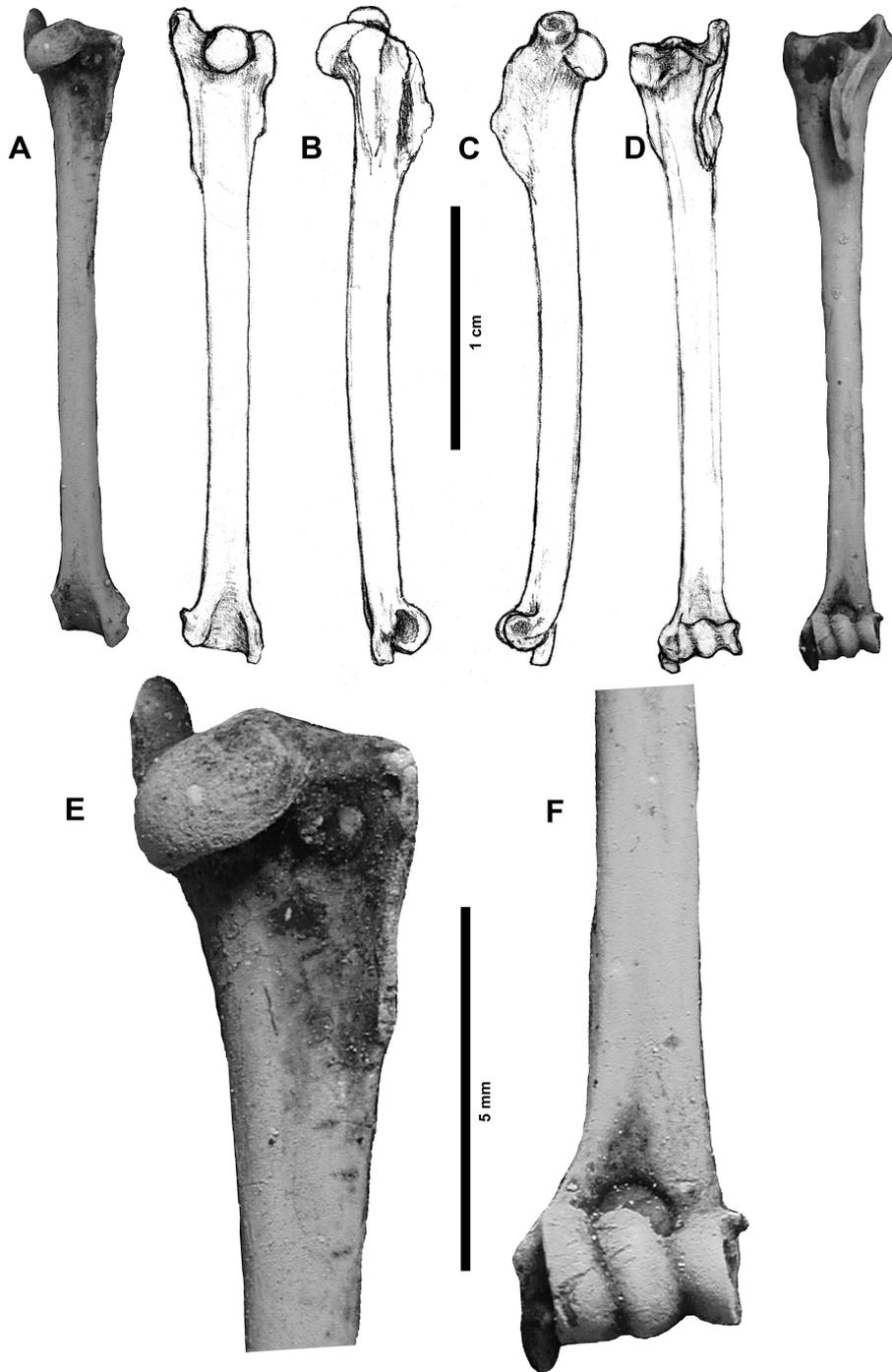


FIGURE 12. Left complete humerus of *Mops* cf. *M. thersites* (NMT.033/Bat). A, photograph and drawing in posteromedial view; B, drawing in medial view; C, drawing in lateral view; D, photograph and drawing in anterior view; E, close-up photograph of proximal end in posteromedial view; F, close-up photograph of distal end in anterior view.

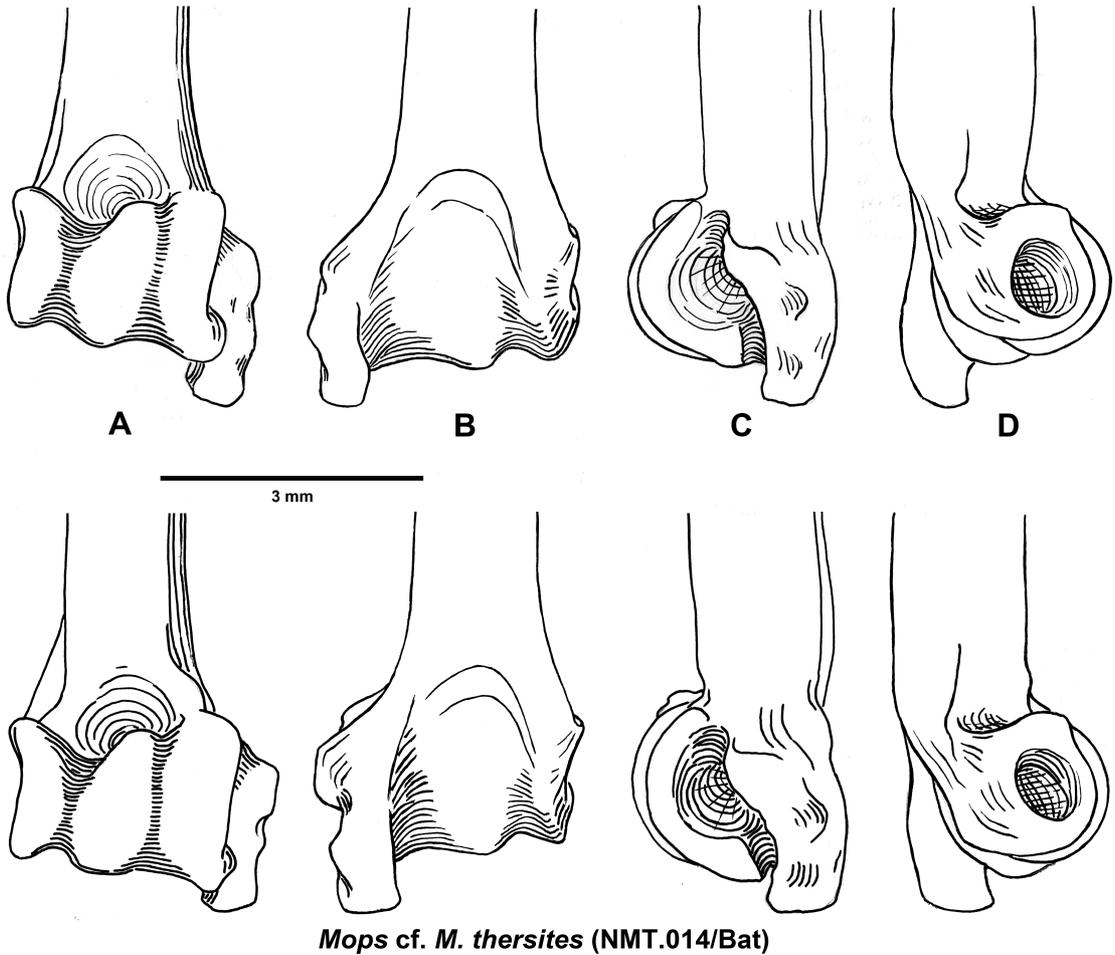
***Mops thersites* (NHMUK 53.114.119)**

FIGURE 13. Right distal humerus of *Mops thersites* (NHMUK 53.114.119) compared with *Mops cf. M. thersites* (NMT.014/Bat) in A, anterior, B, posterior, C, medial, and D, lateral views.

*Mops cf. M. thersites*

Figures 12, 13

Molossidae indet. (in part), Butler, 1978: 66; Gunnell, 2010: 587.

REFERRED SPECIMENS: NMT.014/Bat, right distal humerus, FLK N1, layer 3, no. 4; NMT.028/Bat, right distal humerus, FLK NNI, layer 2; NMT.029/Bat, left complete humerus, FLK NNI, layer 2; NMT.033/Bat, left distal humerus, FLK NI, layer 3, Tr. III (see table 1 for measurements).

**DESCRIPTION AND DISCUSSION:** The Olduvai specimens referred above are very similar in size and morphology to the humeri of extant *Mops thersites*, which is today known from western and central equatorial Africa south and east to Mozambique and Zanzibar (Simmons, 2005). The proximal end of NMT.029/Bat (fig. 12E) is similar in shape and proportions to all extant molossids except that head on the Olduvai specimen is relatively larger, especially proximodistally. The head is ovate with the long axis oriented slightly proximomedially to distolaterally. The proximal margin of the head is situated well below the proximal extent of the trochiter, but is even with the proximal extent of lesser tubercle. The deltopectoral crest is high anteriorly and relatively long. It is a very sharply defined crest with a well-developed overhanging lip developed medially, a crest that curves laterally toward the trochiter at its proximal end and forms the anterior border of a deep intertubercular fossa.

The distal end of the humerus is preserved in four specimens of *Mops* cf. *M. thersites* (figs. 12, 13). The capitulum is narrow, angled, and not offset from shaft. The lateral capitular tail is slightly less broad than the trochlear surface, and is separated from capitulum by a moderate groove. The trochlear groove is weak, the trochlear surface is relatively broad, and the trochlear lip is not sharply defined. The medial epicondylar process in NMT.029/Bat extends a short distance past the trochlear ridge and only slightly less far distally than is seen in *Mops thersites*. The groove on lateral surface of epicondyle is either absent or only weakly developed.

In general, molossids are rare in the African fossil record. There is an early Miocene *Tadarida* recorded from Kenya (Arroyo-Cabrales et al., 2002) and a late Pleistocene or Holocene record of *Mormopterus* (Sabatier and Legendre, 1985) from Madagascar and nothing else outside of the occurrences from Olduvai.

Family MINIOPTERIDAE Dobson, 1875

*Miniopterus* cf. *M. schreibersi* (Kuhl, 1817)

Figures 14, 15

*Miniopterus* cf. *schreibersi*, Butler, 1978: 65; Gunnell, 2010: 588.

**REFERRED SPECIMENS:** NMT.007/Bat, right dentary p3–4 (p4 now lost but shown in drawings of MG), from FLK NI, layer 5, Tr. IV; NMT.011/Bat, left and right distal humeri, from FLK NI, layer 3; NMT.017/Bat, right distal humerus, from FLK NI, layer 2; NMT.019/Bat, right proximal humerus, FLK NI, layer 2 (maybe not *Miniopterus*, poorly preserved); NMT.022/Bat, left proximal humerus, right distal humeri (2), humeral shaft, from FLK, Main Dig Z level; NMT.038/Bat, right distal humerus, from FLK NI, layer 3, Tr. IV (see tables 1 and 2 for measurements).

**DESCRIPTION AND DISCUSSION:** One dental specimen representing *Miniopterus* cf. *M. schreibersi* is known from the Olduvai sample, a right dentary (NMT.007/Bat) that originally had p3–4 and the alveoli for all other teeth preserved. The p3 is double rooted with a single, lingually placed cusp that has a sloping, convex buccal surface and straight, flat lingual surface. A continuous, weakly developed cingulid is present that is developed into a tiny posterolingual

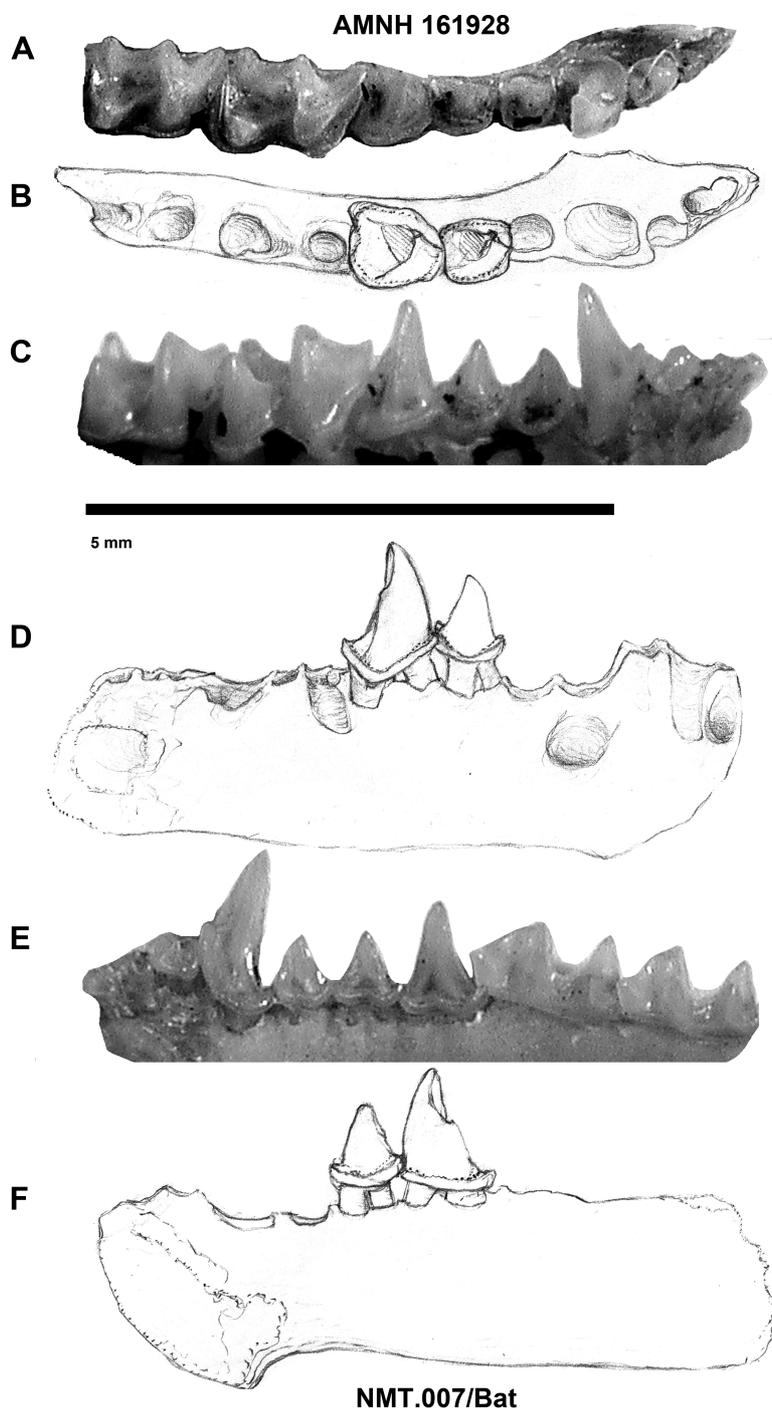


FIGURE 14. Comparison of extant *Miniopterus schreibersi* (A, C, E – AMNH 161928, right i1–m3, photographs) and extinct *Miniopterus* cf. *M. schreibersi* (B, D, F – NMT.007/Bat, right p4–m1, drawings) in A–B, occlusal, C–D, lateral, and E–F, medial views.

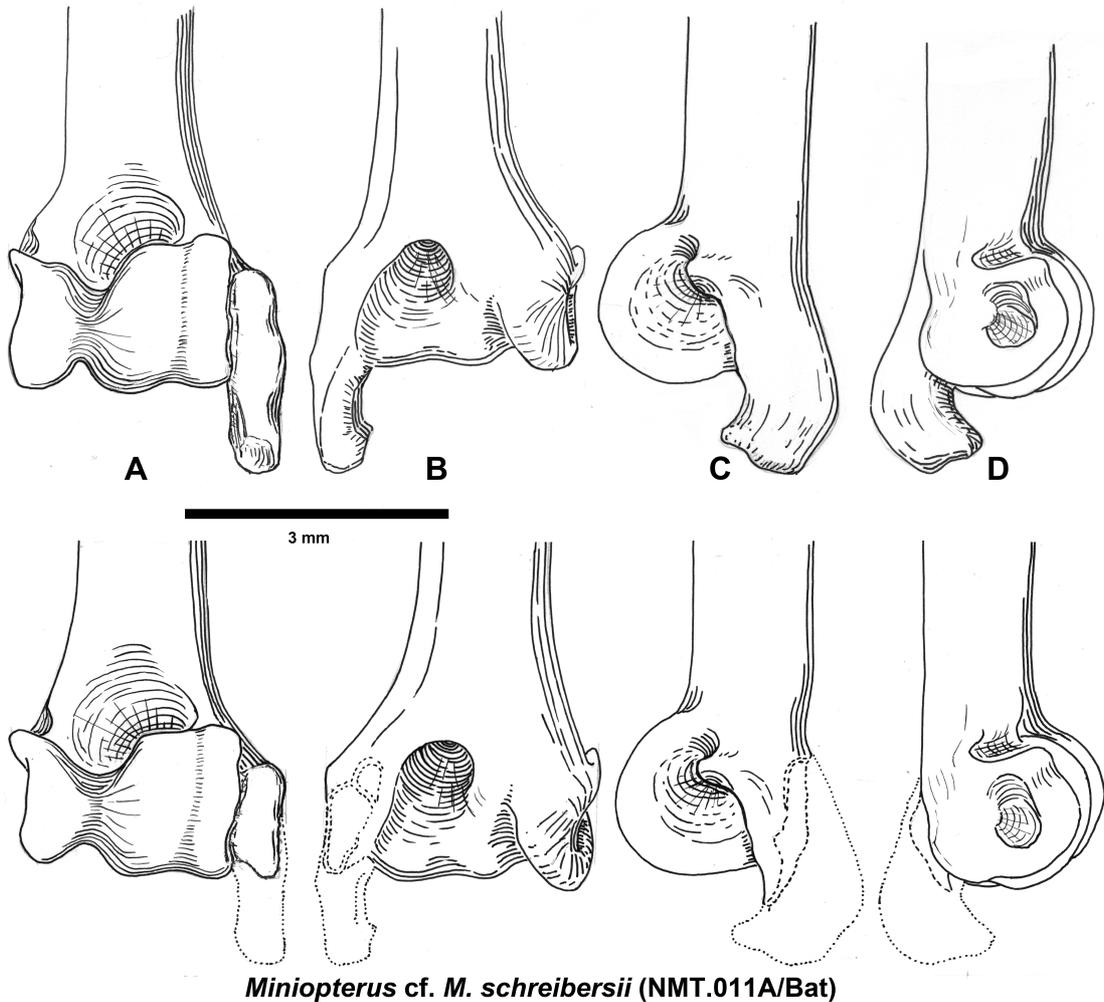
***Miniopterus schreibersii* (NHMUK 19.7.7.2417)**

FIGURE 15. Right distal humerus of extant *Miniopterus schreibersii* (NHMUK 19.7.7.2417) compared with fossil *Miniopterus* cf. *M. schreibersii* (NMT.011A/Bat) in A, anterior, B, posterior, C, medial, and D, lateral views.

extension. In detailed morphology this p3 is quite similar to that of extant *M. schreibersii* (fig. 14). The p4 was originally in place in this specimen and based on the available drawings (see fig. 14) it was very similar to p4 of extant *M. schreibersii*. It shared the presence of a tall, pointed protoconid and a broad but short talonid shelf formed by the distal cingulid with the extant taxon. Both extinct and extant specimens lack any indication of a para- or metaconid and both have well-developed labial and lingual cingulids that join anteriorly with the labial cingulid sloping ventrally from anterior to posterior.

The dentary has a large mental foramen beneath the c1–p2 roots. Based on alveoli, p2 was single rooted as in living *M. schreibersii*. The i3 alveolus is slightly separated from the conjoined i1–2 alveoli and is larger than either of the other incisor alveoli as in extant *Miniopterus* species,

Table 3. Geographic distribution of African Pleistocene bats (including late Holocene of Madagascar) based on number of species per family (Gunnell, 2010).

Taxon/Locality	Olduvai	Koobi Fora	South Africa	Madagascar
Pteropodidae	—	1	—	2
Emballonuridae	—	—	—	1
Rhinolophoidea	—	—	5	4
Miniopteridae	1	—	1	—
Myzopodidae	1	—	—	—
Nycteridae	—	1	—	—
Vespertilionidae	5	1	3	1
Megadermatidae	1	—	—	—
Molossidae	2	—	—	1

and all incisor alveoli are aligned mesiodistally. There is a smaller mental foramen below the i1 alveolus on anterior surface of dentary.

The humeral fragments of the Olduvai *Miniopterus* specimens are very similar in size and morphology to the humerus of extant *Miniopterus schreibersi*. The proximal end of the humerus in Olduvai *Miniopterus* specimens has a moderately high (anteriorly) deltopectoral crest that is relatively long and sharply defined. It has a distinct, overhanging medial lip. The crest curves to the base of the trochiter and anteriorly encloses a relatively deep intertrochanteric fossa. The head of the humerus is ovate and angled. The proximal margin of the head does not extend as far proximally as the trochiter, instead extending proximally about the same distance as the lesser trochanter.

The distal end of the *Miniopterus* humerus has a narrow, rounded capitulum that is slightly angled and is not offset from shaft. The lateral capitular tail is somewhat broader than the trochlear surface and is separated from the capitulum by a deep and distinct groove. In contrast, the trochlear groove is faint and the trochlear surface is relatively narrow with a sharply defined trochlear lip. The medial epicondylar process is broken in all Olduvai specimens, but, judging by what remains, it would have been distinct and would have extended well beyond the trochlear ridge as it does in extant *Miniopterus* (fig. 15). The groove on the lateral surface of the epicondyle is absent, but there is a distinct fossa that occurs on the lateral surface below the root of the epicondylar process. Like all other *Miniopterus* species, the specimens from Olduvai have well developed and deep olecranon fossae (see fig. 15B, top and bottom), a feature not commonly found in bats.

These Olduvai specimens are assigned to *Miniopterus* cf. *M. schreibersi* because they are very similar in morphological detail to the humerus of the living taxon. However, *Miniopterus schreibersi* is not the only similar-sized *Miniopterus* species to occupy sub-Saharan Africa today. Therefore it is possible that the Olduvai species might be more closely related to one of the other species, especially *M. africanus* or *M. inflatus*, given that both of these species have been confused with *M. schreibersi* in the past (Simmons, 2005). We have chosen to follow Butler's (1978) original assignment of these specimens to *Miniopterus* cf. *M. schreibersi* but acknowl-

Table 4. Bat genera known from Pleistocene localities in Africa, with habitat and roosting behavior of related extant species,

Genus	Fossil Locality	Species: Habitat/Roosting Behavior	Sources
<i>Cardioderma</i>	Olduvai (East Africa)	<i>C. cor</i> : dry and coastal woodlands/forage along river valleys/roost in baobab trees/rock shelters	Vaughan, 1976; Varty and Hill, 1988; Csada, 1996)
<i>Myzopoda</i>	Olduvai (East Africa)	<i>M. aurita</i> / <i>M. schliemanni</i> : arid and humid forests/roost in trees and tree leaves	Schliemann and Maas, 1978
<i>Mops</i>	Olduvai (East Africa)	<i>Mops</i> sp., dry or moist savannah/open woodland/roost in trees/rock crevices	Rosevear, 1965; Kingdon, 1974; Smithers, 1983
<i>Nycticeinops</i>	Olduvai (East Africa)	<i>N. schlieffeni</i> : riverine forests and savannah/forages over open water/roost in trees/rock crevices	Fenton and Thomas, 1980; Johnston, 2006
<i>Pipistrellus</i>	Olduvai (East Africa)	<i>P. nanus</i> : arid and semiarid savannah/roosts in trees and leaves, culverts/other species in wide range of habitats	Kingdon, 1974; Lausen and Barclay, 2005
<i>Myotis</i>	Olduvai (East Africa)	<i>M. welwitschii</i> : open woodland and savannah/roosts dense vegetation/trees/rock crevices and caves	Kingdon, 1974; Ratcliffe, 2002
<i>Eptesicus</i>	Olduvai (East Africa)	<i>E. serotinus</i> : dry forest/semi-desert/open woodlands and park lands/roosts in rock crevices/tree holes/seldom if ever in caves	Hutson et al., 2008
<i>Scotoecus</i>	Olduvai (East Africa)	<i>S. albofuscus</i> : woodlands/dry savannah/roosts in tree holes/crevices	Hill, 1974; Jacobs, 2008
<i>Miniopterus</i>	Olduvai (East Africa)	<i>M. schreibersi</i> : open woodlands/many other habitats/migratory/roosts in caves/crevices	Van der Merwe, 1975; Nowak, 1994
<i>Nycteris</i>	Koobi Fora (East Africa)	<i>N. thebaica</i> : moist open woodland and dry savannah/roost in caves/trees/burrows	Smithers and Labao Tello, 1976; Taylor, 1998; Mickleburgh et al., 2008b
<i>Scotophilus</i>	Koobi Fora (East Africa)	<i>S. dinganii</i> : dry and moist savannah/roost in caves, seldom in trees but often in artificial habitats	Happold, 1987; Nowak, 1994
<i>Hipposideros</i>	Twin Rivers Cave (South Africa)	<i>H. megalotis</i> : dry dense forest edges/forages between forest edges/roosts in caves and hollow trees/often in large colonies	Hayman, 1954; Nowak, 1994
<i>Miniopterus</i>	Twin Rivers Cave (South Africa)	<i>M. schreibersi</i> : habitats/migratory/roosts in caves/crevices	Van der Merwe, 1975; Nowak, 1994
<i>Rhinolophus</i>	Swartkrans (South Africa)	<i>R. darlingi</i> : savannah woodlands and shrublands/roost in caves/mines/rock crevices	Skinner and Chimimba, 2005
<i>Eptesicus</i>	Swartkrans Kromdraai (South Africa)	<i>E. hottentotus</i> : woodlands/grasslands/marshlands/forage along river banks/roost in caves and mines	Skinner and Chimimba, 2005
<i>Myotis</i>	Swartkrans (South Africa)	<i>M. tricolor</i> : dry to moist savannah with shrub vegetation/roost in large caves	Herselman and Norton, 1985
<i>Hipposideros</i>	Anjohibe Cave (Madagascar)	<i>H. commersoni</i> : dry dense forest edges/gallery forest/forages between forest edges/roosts in caves/often in large colonies/also in large trees	Goodman, 2006; Goodman et al., 2005

Genus	Fossil Locality	Species: Habitat/Roosting Behavior	Sources
<i>Rousettus</i>	Anjohibe Cave (Madagascar)	<i>R. madagascariensis</i> : dense forests and edges/agricultural lands/roosts in caves	MacKinnon et al. 2003
<i>Eidolon</i>	Many localities (Madagascar)	<i>E. helvum</i> : arid to humid forests/wide range of habitats/roosts in tall trees/caves	Mickleburgh et al., 2008c
<i>Tadarida</i>	Many localities (Madagascar)	<i>T. aegyptiaca</i> : warm, semiarid regions/open savannah/humid valleys/roost in rock shelters/crevices	Mickleburgh et al., 2008a
<i>Mormopterus</i>	Tsimanampetsotsa (Madagascar)	<i>M. jugularis</i> : forages in open agricultural areas/roosts in man-made structures/trees/caves	Goodman et al. 2005
<i>Triaenops</i>	Anjohibe Cave (Madagascar)	<i>T. furculus</i> : dry forest and spiny thicket/roosts in caves	Goodman et al., 2005; Olsson et al., 2006
<i>Emballonura</i>	Tsimanampetsotsa (Madagascar)	<i>E. atrata</i> : humid forest/roosts in caves/crevices	Goodman et al, 2005, 2006

edge that more complete specimens are needed to assess the precise relationship of the Olduvai *Miniopterus* species to living members of that genus.

The African fossil record of *Miniopterus* is limited to the record from Olduvai, two Pliocene records from South Africa (Pocock, 1987) and a late Pliocene record from Morocco (Gunnell et al., 2011). The South African Pliocene occurrences are recorded in faunal lists, but the specimens upon which the assignments are based have never been described or figured.

#### THE OLDUVAI BAT ASSEMBLAGE

The Olduvai bat assemblage is dominated by vespertilionids (five species) whereas this family is rarer in other Pleistocene assemblages (Black and Krishtalka, 1986; Pocock, 1987; Avery 1998, 2003; Samonds, 2007; Gunnell, 2010); table 3 summarizes the known geographic distribution of African Pleistocene bats (including late Holocene bats from Madagascar as well). Other members of the Olduvai bat assemblage are similarly rare elsewhere; megadermatids and myzopodids are absent from other Pleistocene African sites, and molossids are known only from late Pleistocene and Holocene localities in Madagascar (Sabatier and Legendre, 1985). Only the ubiquitous extant bat *Miniopterus schreibersi* is known from Pleistocene sites in both Olduvai and South Africa (Pocock, 1987; Avery, 1998). The most prominent group *not* present at Olduvai is rhinolophoids, which are well known from South African and Madagascar Pleistocene sites, represented by multiple species of *Hipposideros* and *Rhinolophus* from the former and by *Triaenops* and *Hipposideros* from the latter (Sabatier and Legendre, 1985; Avery, 2003; Samonds, 2007). Nycterids are represented by a single specimen from Koobi Fora but are unknown from other Pleistocene sites in Africa (Black and Krishtalka, 1986). Pleistocene fruit bats are represented at Koobi Fora (by a single tooth) but are otherwise unknown from mainland Africa, and are represented only on Madagascar (Samonds, 2007) in late Pleistocene and Holocene sites (*Eidolon* and *Rousettus*).

Many of the distributional differences noted above probably reflect habitat differences between sampling localities in East and South Africa; table 4 summarizes habitat and roosting

behavior of extant relatives of Pleistocene taxa. Most of the Olduvai bats represent taxa that today live in dry to moist savannah and open woodlands developed along watercourses. Most prefer roosting in trees and vegetation, although some seek out rock crevices as well. Very few of the extant relatives of the Olduvai bats (other than *Miniopterus* and occasionally *Cardioderma* and *Myotis*) make use of caves as roosting sites. Open savannah habitats with riverine dry open forests and shrub-lands are the predominant habitats reconstructed for East African Pleistocene sites (Reed, 1997) and the bat assemblage at Olduvai Gorge fits well with this interpretation. More specifically, Olduvai FLK North sites have been interpreted as representing forest and shrub-woodland habitats fed by freshwater springs and developed on a lake margin flat (Ashley et al., 2010; Barboni et al., 2010). Most of the Olduvai bat taxa could be expected to live in such habitats and do not contradict this paleoecological interpretation. However, the presence of *Pipistrellus*, *Eptesicus*, and *Scotoecus*, taxa that often inhabit dry or semiarid open forests and woodlands, does suggest that there may have been drier and more open habitats nearby.

All of the Pleistocene bat assemblages known from South Africa are found in two cave deposits, Kromdraai B and Swartkrans. The taxa found in these sites are those that today often roost in caves. The habitats reconstructed for Kromdraai B and Swartkrans are open savannah with patches of riparian woodland nearby (Reed, 1997). *Hipposideros commersoni* forages in open areas near forest but typically roosts in caves, often in large colonies. *Eptesicus hottentotus* also prefers to forage near forest along riverbanks and roosts in caves. Both *Rhinolophus mehelyi* and *R. clivovosus* forage in more open savannah areas but roost in caves and rock shelters as do *Miniopterus schreibersi* and *Myotis tricolor*. The bat fauna known from the South African Pleistocene caves do not contradict the paleoecological reconstructions proposed for these areas.

Similarly, the late Holocene bats of Madagascar are often found in cave deposits and represent taxa that typically roost in caves today. Taxa that prefer denser forested areas in Madagascar include *Hipposideros commersoni*, *Rousettus madagascarensis*, and *Emballonura atrata*, and all of these taxa roost in caves or rock shelters. Extant bats that prefer to forage in more open country include *Tadarida aegyptiaca*, *Triaenops furculus*, and *Eidolon helvum*, with the two former species preferring caves as roosting sites while *Eidolon* prefers to roost in tall trees.

In summary, it appears that differences in taxonomic representation between Olduvai and other Pleistocene/late Holocene bat assemblages can be best interpreted as habitat and sampling driven. Bats that prefer cave roosting sites are more common in southern Africa and Madagascar fossil bat faunas, while bats that represent lineages known to prefer trees and foliage as roosting sites are more common at Olduvai, where caves were less prevalent features of the landscape.

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## APPENDIX 1

### COMPARATIVE SPECIMENS EXAMINED

#### MYZOPODIDAE

*Myzopoda aurita*: NHMUK 1849.11.3.5, left humerus, Madagascar

*Myzopoda schliemanni*: FMNH 187668, left and right complete humeri, Madagascar

#### MEGADERMATIDAE

*Cardioderma cor*: AMNH 184338, skull and mandible, female, Kibwezi, Kenya; NHMUK 36.11.4.4, skull and mandible, Turkwell River, Uganda

#### MOLOSSIDAE

*Chaerephon ansorgei*: NHMUK 71.2457, skeleton, female, Addis Ababa, Ethiopia

- Chaerephon major*: NHMUK 32.7.4.1, skeleton, female, Timbuktu, Mali; NHMUK 62.445, skeleton, male, Igbetti, Nigeria; NHMUK 66.6041, skeleton, Nigeria
- Chaerephon nigeriae*: NHMUK 47.14, skeleton, female, Kampala, Uganda; NHMUK 57.434, skeleton, Kinke, Elizabethville, Democratic Republic of Congo
- Chaerephon pumilus*: NHMUK 36.3.16.21, skeleton, male, Rwenzori Mountains, Uganda; NHMUK 61.52, skeleton, male, Kigoma, Tanzania; NHMUK 64.221, skeleton, female, Entebbe, Uganda; NHMUK 66.5573, skeleton, Aldabra, Seychelles
- Eumops trumbulli*: AMNH 97328, skeleton, female, Brazil
- Molossus rufus rufus*: AMNH 267273, skeleton, female, French Guiana; AMNH 268595, skeleton, male, French Guiana
- Mops annulus*: NHMUK 46.242, skeleton, Oda, Ghana
- Mops brachypterus*: NHMUK 54.916, skeleton, male, Sierra Leone
- Mops condylurus*: NHMUK 20.6.13.1, skeleton, male, Mongala, Sudan; NHMUK 64.1948, skeleton, male, Liwale, Tanzania; NHMUK 64.1949, skeleton, male, Liwale, Tanzania; NHMUK 64.1950, skeleton, female, Liwale, Tanzania; NHMUK 72.4467, skeleton, Ethiopia; NHMUK 51.392, skeleton, male, Kílwa, Tanzania
- Mops demonstrator*: NHMUK 66.4137, skeleton, male, Gulu, Uganda
- Mops midas*: NHMUK 1.10.19, skeleton, Fashoda, Sudan
- Mops thersites*: NHMUK 53.114.119 (= 53.115), skeleton, Newton, Sierra Leone
- Mops trevori*: NHMUK 63.1154, skeleton, female, West Madi County, Uganda
- Myotis whitleyi*: NHMUK 23.4.12.52, skeleton, female, Entebbe, Uganda; NHMUK 67.1735, skeleton, male, Mayuka, Cameroon
- Otomops martiensseni*: NHMUK 70.2538, skeleton, male, Kenya
- Tadarida aegyptiaca*: NHMUK 61.1086, skeleton, West Nicholson (= Tshabezi), Zimbabwe; NHMUK 65.3429, skeleton, female, Mianga Road, Nigeria; NHMUK 4.1.4.2, skeleton, Angola
- Tadarida lobata*: NHMUK 70.727, skeleton, male, Cherangi Hills, Kenya
- Tadarida mexicanus*: AMNH 145485, skeleton, male, New Mexico
- Tadarida teniotis*: NHMUK 3.4.1.3, skeleton, male, Giza, Egypt

#### VESPERTILIONIDAE

- Eptesicus furinalis*: AMNH 278332, skeleton, female, Lamanai, Belize
- Eptesicus isabellinus*: NHMUK 19.7.7.1160, skeleton, locality uncertain
- Eptesicus serotinus*: NHMUK 19.7.7.1409, skeleton, St. Camerano, Italy
- Glauconycteris variegata*: NHMUK 52.1319-29, skeleton, Tanzania
- Kerivoula argentata*: NHMUK 62.987-989, skeleton, Uramba, Tanzania
- Kerivoula lanosa*: NHMUK 70.725, skeleton, Cherangi Hills, Kenya
- Kerivoula smithii*: NHMUK 62.1845, skeleton, Kalehe Province, Democratic Republic of Congo
- Myotis bocagei*: NHMUK 54.854, skeleton, Moba, Democratic Republic of Congo; NHMUK 30.12.1.22, skeleton, Entebbe (Daniba Island), Uganda
- Myotis daubentonii*: NHMUK 28.1951, skeleton, Surrey, UK
- Myotis nattereri*: NHMUK 19.7.7.929, skeleton, St. Paterne, France
- Neoromicia capensis*: NHMUK 62.2051, skeleton, male, Kyagwe District, Uganda
- Neoromicia tenuipinnis*: NHMUK 63.1044, skeleton, Dundo Lunda, Angola
- Nycticeinops schlieffeni*: AMNH 257406, skull and mandible, female, Transvaal, Kruger National Park, South Africa; NHMUK 32.7.463, skeleton, locality uncertain

*Pipistrellus annulus*: NHMUK 69.215, skeleton, Lokori, Kenya

*Scotoecus albofuscus*: AMNH 241054, skull and mandible, female, Obala, Cameroon

*Scotoecus hindei*: AMNH 241055, skull and jaws, female, Ngaoundere, Cameroon

*Scotophilus leucogaster*: NHMUK 64.159, skeleton, female, West Madi County, Uganda

*Scotophilus* sp.: NHMUK 7.6.2-18-20, skeleton, Beira, Mozambique

#### MINIOPTERIDAE

*Miniopterus inflatus*: NHMUK 70.2530, skeleton, Suswa Caves, Kenya

*Miniopterus natalensis*: NHMUK 36.3.16.13-20, skeleton, Mount Elgon, Uganda

*Miniopterus schreibersi*: AMNH 161928, skull and mandible, female, Nyasaland, Zambia; NHMUK 19.7.7.2417, skeleton, female, Zimbabwe; NHMUK 68.647, skeleton, Buea, Cameroon

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