

Chapter 2 Rodents

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Abstract New rodent specimens collected at Laetoli between 1998 and 2005 are described here. The material allows an updating and refinement of the previously published taxonomic lists, especially those for the Lower Laetolil Beds and the Upper Ndolanya Beds. The increased number of well-preserved cranial specimens allows the description of several new species and a better appreciation of the size and morphology of some Laetoli taxa compared to their southern and eastern African counterparts. This is especially the case for *Saccostomus*, for which the fossil record has recently been much improved. The new species described here include a small sciurid, two Gerbillinae, and a thryonomyid. Some species are newly recognized at certain localities, and *Aethomys* and *Petromus* are recorded for the first time at Laetoli. The distribution and stratigraphic range for *Pedetes laetoliensis* is extended, and it is now recorded in the Upper Ndolanya Beds. Similarly, *Xerus janenschii* is now identified in the Laetolil Beds. As in the previous study of the Laetoli rodents, important differences in species composition and diversity between the Upper Laetolil Beds and the Upper Ndolanya Beds are confirmed. These probably reflect differences in landscape. Compared to other Pliocene assemblages, the Laetolil Beds are characterized by a very unusual diversity of sciurids and the dominance of *Saccostomus* and *Pedetes*, but otherwise they compare well with other East African Mio-Pliocene rodent assemblages, such as those from the Omo Valley and Lemudong'o. The Laetoli assemblages are distinct from those of Lukeino, Chorora and Harasib 3, but could belong to the same faunal unit as Ibole (Manonga Valley). They also differ in some respects from those from Hadar and Pliocene South African sites. Few species are shared in common between the Laetolil Beds and Upper Ndolanya Beds, but it is uncertain whether this turnover is due to taphonomic or paleoclimatic factors. This contribution highlights the importance of Laetoli for

understanding rodent evolution, as well as for its geographic position at the crossroads between East and South Africa.

Keywords Mammalia • Rodentia • East Africa • Pliocene • Pleistocene • Taxonomy

Introduction

In Africa, small mammals represent about 80% of the modern biodiversity, and rodents alone constitute about the half of it. Their role as primary consumers and forest regenerators make them important in ecosystems, and they are considered good indicators of habitat. Due to their relatively small size, fossil rodents occur only in localized bone concentrations, and among the Pliocene sites of Africa there are few rodent faunas known. The Laetoli rodents were initially collected during the 1938–1939 Kohl-Larsen expedition to the southern Serengeti, which formed the basis for Dietrich's (1942) initial taxonomic study. Subsequent collections by Mary Leakey (1974–1979) allowed a better documentation of rodent paleodiversity (Denys 1987a; Davies 1987) and situated the faunas in a well-constrained geochronological and stratigraphic context for the first time. This led to an improved knowledge of rodent evolution during the Plio-Pleistocene of East Africa, including a better appreciation of their relationships with South African faunas (Denys 1999; Denys et al. 2003; Winkler et al. 2010).

Due to the peculiar sedimentary nature of the site, Laetoli is characterized by remarkably well-preserved material, which allows the description of cranial and postcranial characteristics of the rodents. Laetoli provides records of the first appearance data (FAD) of several rodent genera and, being located at the southern end of the Rift Valley, it is biogeographically important. Moreover, rodents are known both from the Laetolil Beds (lower and upper units) and the Upper Ndolanya Beds, which allows biostratigraphical comparisons between the main stratigraphic units.

We present here the results of a systematic study of new fossil rodent material recovered by Terry Harrison's teams during

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the 1998–2005 field seasons at Laetoli. The study includes the description of new taxa and a reinterpretation of the evolutionary relationships of the fossil rodents from Laetoli.

Material and Methods

Specimens were examined and illustrated using a Wild Microscope fitted with a camera lucida. Cranial and dental dimensions were measured with Mitutoyo calipers (0.01 mm precision). Some specimens were prepared by R. Vacant (Palaeontology Laboratory at the MNHN) and by the author. SEM images of the teeth were taken by C. Chancogne-Weber with a JEOL 45 at the Palaeontology Laboratory. Univariate statistics were performed using XLSTAT Software version 9 (Addinsoft).

Comparisons were made with the following reference mammal collections: Paris, France (MNHN); Natural History Museum, London, England (NHM); Zoologische Museum, Berlin, Germany (ZMB); Zoologische Museum für Naturkunde, Bonn, Germany (ZFMK); Durban Science Museum, South Africa (DM); Namibian Museum, Windhoek, Namibia (NM).

Tooth nomenclature follows Denys (1987a), and rodent taxonomy follows that of Wilson and Reeder (2005).

Systematics

Suborder Anomaluromorpha Bugge, 1974
Family Pedetidae Gray, 1825
Pedetes laetoliensis Davies, 1987
(Fig. 2.1, Table 2.1)

Springhares are quite numerous at Laetoli, with well-preserved skeletal material. The specimens collected by Mary Leakey led Davies (1987) to describe a new species. Among the diagnostic characters were its small size, enlarged infraorbital foramen and the absence of cusps on the molars (Fig. 2.1). The original type description did not list the provenance of the specimens, but Davies (personal communication) listed 35 individuals of *Pedetes* occurring at Locs. 1, 2, 3, 4, 5, 6, 7, 8, 9, 9N, 9S, 10, 10W, 10E, 11, 13, 14, 15, 16, 19, 21 and 22. Davies (1987) mentions the occurrence of *Pedetes* cf. *surdaster* from the Late Pleistocene Upper Ngaloba Beds at Loc. 2, but none from the Upper Ndolanya Beds. However, Harris (1987) lists the species as occurring in the Upper Ndolanya Beds.

Here, 75 additional specimens add to the number of localities at which *Pedetes* occurs (see Appendix 2.1). The new remains come from Locs.1, 2, 4, 5, 6, 8, 9, 10E, 11, 13, 15, 21 and 22, and are derived from all horizons throughout

Table 2.1 Upper and lower tooththrow length (mm) for the new Laetoli Beds specimens of *Pedetes laetoliensis* Davies, 1987, compared with the dimensions of the holotype (after Davies 1987) and representatives of the two extant species

Specimen	P/4-M/3	P4/-M3/
EP 1089/05	12.38	
EP 714/00	12.94	
EP 1509/98	13.04	
EP 1235/98	13.15	
EP 2914/00		13.02
Holotype	14.05	13.5
<i>P. capensis</i>	17.9	19.1
<i>P. surdaster</i>	18.5	18.0
<i>P. capensis</i>	Mean 17.26	Mean 17.42
N=4	Range 16.67–17.38	Range 16.60–18.94



Fig. 2.1 New specimens of *Pedetes* from Laetoli. (a) right maxilla with DP4-M3/ of *P. laetoliensis* (EP 1994/00, Loc. 5, Upper Laetoli Beds); (b) right mandible with DP4-M3/ of *P. laetoliensis* (EP 1867/00,

Loc. 2, Upper Laetoli Beds); (c) mandible of *Pedetes* sp. with DP4-M2 (EP 2196/00, Loc. 7E, Upper Ndolanya Beds). Scale bar in mm

the Upper Laetolil Beds. The dimensions of the upper and lower toothrows of the new specimens are close to those of the type series, but they display a great range of variability (Table 2.1). This may be due to the difficulty in measuring some isolated molars that have convex crowns and because the occlusal surface of hypsodont molars changes in dimensions during the course of wear. The shape of the molars is similar to the previously recovered material described by Davies (1987: fig. 6.29, p. 176) (Fig. 2.1). The molars are characterized by bilobate crowns of nearly equal size and proportions, which makes identification of serial position difficult. They all have high crowns and flat occlusal surfaces. No traces of cusps are visible.

The only other extinct species of *Pedetes*, *P. gracilis*, comes from Taung (Broom 1934: fig. 5, p. 476). *Pedetes gracilis* has a longer molar row (12 mm) and is very similar to the modern *Pedetes caffer*. According to Broom (1934), the differences between the species are the smaller size of the fossil teeth, and the plates of the infolded enamel are nearly parallel and less deeply folded than those in modern *P. caffer*. Molars of *P. laetoliensis* display deep folds and are not fully parallel in comparison to *P. gracilis*. A pedetid indet. is mentioned briefly as occurring at Harasib, and probably constitutes a new genus of the family (Mein et al. 2000a). In addition, a single incisor from Lukeino (Mein and Pickford 2006) is attributed to an indeterminate Pedetidae.

Pedetes sp.

Only one specimen has been recovered from the Upper Ndolanya Beds at Loc. 7E during renewed fieldwork, while Davies (personal communication) recorded its presence at Loc. 14. It is represented by a mandible with DP/4-M/2 (EP 2196/00) in a poor state of preservation (Fig. 2.1). The length of the DP/4-M/2 reaches 10.06 mm in EP 2196/00, which, based on its small size, indicates the possible presence of *P. laetoliensis* in the Upper Ndolanya Beds. Up to now no *Pedetes* has been recovered from the Upper Ndolanya Beds at Loc. 18. The molars display no link between the two lobes of the molars, and the first lobe of the P4 shows two well-individualized and oblique cusps, which is considered a juvenile feature.

Family Sciuridae Fischer de Waldheim, 1817

Sciurid remains are quite abundant at Laetoli. From the Laetolil Beds three different taxa of sciurid were recognized by Denys (1987a), a small *Paraxerus* sp. (Locs. 11 and 12), a larger *Xerus* sp. (Loc. 9S), and *Xerus* cf. *janenschii* (Loc. 2). The Upper Ndolanya Beds at Locs. 7E and 18 have yielded well-preserved remains of *Xerus janenschii*. Newly recovered cranial material allows us to refine the taxonomy of the Laetoli squirrels, which can be distinguished on their molar row size and dental criteria.

Genus *Paraxerus* Forsyth Major, 1893

This taxon is characterized by a short zygomatic plate, complex upper molars with three clear re-entrant folds, lower teeth with central depression non-isolated and well-developed ectolophid. When the lower molars have strongly marked cusps and non-flattened crowns during wear, one can attribute the molars to *Paraxerus* rather than to *Funisciurus*. Both genera have a P3/.

Paraxerus meini sp. nov.

(Fig. 2.2)

Holotype: EP 2816/00, left mandible with P/4-M/3 (Fig. 2.2).

Type locality: Laetoli Loc. 5, Upper Laetolil Beds between Tuffs 3 and 5, Tanzania.

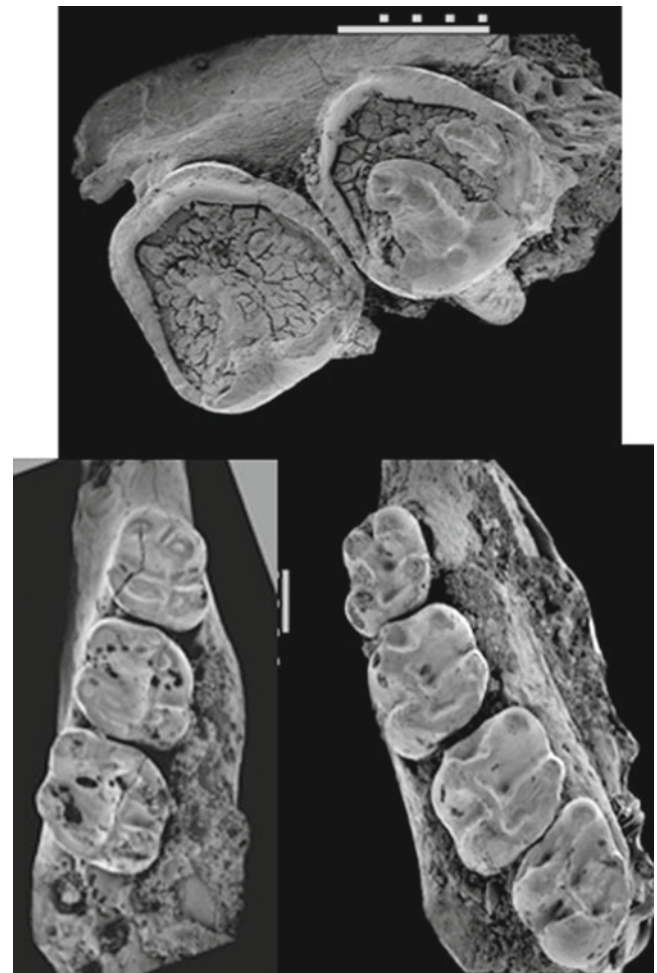


Fig. 2.2 *Paraxerus meini* sp. nov. upper and lower molars. Top, EP 881/03 (paratype) (Loc. 10E, Upper Laetolil Beds), left maxillary fragment with P4/M1; below, EP 1250/03 (Loc. 7E, Upper Ndolanya Beds), right mandible with P/4-M/2 and EP 2816/00 (holotype) (Loc. 5, Upper Laetolil Beds)

Age and Horizon: Mid-Pliocene, Upper Laetolil Beds (between Tuffs 3 and 7) and Upper Ndolanya Beds.

Paratypes: EP 881/03 (Loc. 10E), maxillary fragment with P4-M1 (Fig. 2.2). EP 2815/00 (Loc. 5), right mandibular fragment with P4-M/2. EP 1000/01 (Loc. 11), mandible with P4-M/3. EP 4152/00 (Loc. 8), right and left hemi-mandibles with M/1-3. EP 1250/03 (Loc. 7E), right mandible with P4-M/2.

Referred material from Laetolil Beds (previously identified as *Paraxerus* sp. indet. by Denys 1987a): LAET 76-4121A, lower P4; LAET 74-304, upper P4-M3/ (figured in Denys 1987a, plate 6.2-1 p. 123); LAET 76-4178, lower P4-M/1; LAET 76-4170, right mandible fragment with P4-M/3 (figured in Denys 1987a: plate 6.2-2, p. 123).

Distribution: Localities 5, 8, 10E, 11, and 12 of the Upper Laetolil Beds, and Loc. 7E of the Upper Ndolanya Beds.

Repository: National Museum of Tanzania, Dar es Salaam.

Etymology: Named in honor of Pierre Mein, who has described many new rodent species from the Miocene of Europe and Africa.

Measurements: Tables 2.2 and 2.3.

Diagnosis: One of the smallest species of the genus compared to modern *Paraxerus*. Smaller than extant *P. ochraceus*, which is the smallest East African species, but larger than *P. boehmi* from Central Africa. Bunodont, with many supplementary cusplets in all parts of the molars, more than in *P. ochraceus*. Less bunodont than modern *P. ochraceus*, *P. palliatus*, *P. flavovittis*, *P. cepapi*. Characterized by lower molars with a very rectilinear, long ectolophid associated with a mesoconid on M/1-2. Characterized by a transverse entolophid connected directly to the anterior part of the hypoconid. Differs from *Heteroxerus karsticus* in its smaller size, and the absence of a direct link between the entoconid and hypoconulid. Differs from *P. ochraceus* from the Omo in the larger size of the lower molars.

Description and comparisons: During Mary Leakey's expeditions of 1975–1976 *Paraxerus* was recovered only from

Locs. 11 and 12, and was represented by only three mandibular fragments and one maxillary fragment. Here we add and figure additional material from Locs. 5, 8 and 7E. This rare squirrel at Laetoli is represented by a few mandibles and incomplete maxillae, but no other cranial fragments.

The P3/ occurs in all specimens, but only an alveolus is found, so that the morphology of the tooth cannot be described. All the preserved upper molars are heavily worn (Fig. 2.2; see Plate 6.2 in Denys 1987a), but one can distinguish an anteroloph and a small posteroloph on P4/. A paraloph and metaloph are visible with the development of a faint metaconule on the metaloph. The hypocone is hardly visible and no mesostyle is seen in specimen LAET 74-304, but one is found in specimen EP 881/03. On the upper M1 and M2 there are two well-developed parallel lophs. A small anteroloph exists, but the conules are not visible due to wear. The M3/ is present only on specimen LAET 74-304, but it is worn. It has a triangular shape and it is smaller than M1-2/. Two lophs are visible on M3/; the metaloph being reduced to a cusp in comparison to the protoloph.

On P4 the cusps are bunodont and the protoconid and metaconid are nearly the same height. The two cusps are united by a small crest issuing from the posterior part of the protoconid. There is an ectolophid linking the protoconid to the hypoconid, and a small posterolophid. No anterolophid is observed on P4. On M/1-2 there is a small anterolophid and posterolophid with supplementary cusps (anteroconulid and hypoconulid). The ectolophid is well developed and longitudinal, with a slight mesoconid on M/1-2. The entolophid is well-developed and connects the hypoconid to the entoconid transversely with a very rectilinear crest. On the entolophid of M/1-2 there is one or two supplementary cusps. On M/2 the entolophid is smaller than on M/1 and the anteroconulid and hypoconulid are less visible. On M/3, which is narrow and elongated, the same structures are visible and the cusps are still distinguishable. The anteroconulid is low and small. The hypoconulid and posterolophid is absent on M/3. The

Table 2.2 Upper (UPTR) and lower (LTR) tooththrow lengths (mm) for *Paraxerus meini* nov. sp. compared to modern *Paraxerus* species

Species	Country/site	N	UPTR mean	SD	Range	N	LTR mean	SD	Range
<i>P. meini</i>	Laetoli (this work; Denys 1987a)	2	6.63	0.53	6.25–7.00	4	6.88	0.69	5.96–7.58
<i>P. flavovittis</i>	Tanzania	12	7.60	0.316	7.03–8.18	14	7.41	0.213	7.02–7.76
<i>P. cepapi</i>	Tanzania	10	7.93	0.52	7.08–8.43	10	7.66	0.55	6.8 – 8.29
	Zimbabwe								
	South Africa								
<i>P. boehmi</i>	Uganda	2	6.13		5.48–6.79	2	5.60		5.57–5.64
	DR Congo								
<i>P. ochraceus</i>	Kenya	4	7.09	0.57	6.32–7.72	4	6.88	0.49	6.25–6.97
	Somalia								
	Tanzania								

N number of specimens, SD standard deviation

Table 2.3 Fossil and modern *Paraxerus* spp. lower P4 and molar dimensions (mm)

	P/4L	P/4W	M/1L	M/1W	M/2L	M/2W	M/3L	M/3W
<i>P. meini</i>								
LAET 4121A	1.95	1.65						
LAET 4178	1.78	1.50	1.85	1.74				
LAET 4170	1.70		1.75	1.68	1.82	1.75	2.02	1.70
EP 2815/00	1.52	1.38	1.90	1.76	1.71	1.90		
EP 2816/00	1.52	1.29	1.71	1.57	1.71	1.71	2.00	1.62
EP 4152/00	1.76	1.62	1.76	1.67	1.81	1.90	2.10	1.81
EP 1000/01	1.67	1.52	1.67	1.67	1.71	1.76	1.71	1.71
Mean	1.70	1.49	1.77	1.68	1.75	1.80	1.96	1.71
<i>P. ochraceus</i>								
26.5.12.50	1.57	1.29	1.62	1.48	1.62	1.66	1.86	1.48
<i>P. flavovittis</i>								
2007-1236	1.52	1.52	1.57	1.62	1.72	1.86	2.05	1.62
<i>Paraxerus</i> sp.								
KNM-NK 44920	2.08	2.0						
KNM-KP 46313			2.0	2.2	2.0	2.6	3.0	2.5
<i>P. cepapi</i>								
DM521	1.81	1.76	1.91	1.91	1.95	2.05	1.91	1.86
<i>P. ochraceus</i> Omo B								
	1.5	1.45	1.765	1.61–1.86	1.8	1.7–1.87	2.16 1.85–2.3	1.97 1.8–2.04
<i>H. karsticus</i>								
Mean	1.44	1.45	1.81	1.82	1.99	1.88	2.06	1.85
Minimum	1.34	1.36	1.66	1.73	1.77	1.70	1.89	1.72
Maximum	1.54	1.55	1.97	1.92	2.24	2.06	2.23	2.03
Standard deviation	0.074	0.059	0.083	0.056	0.11	0.093	0.1	0.103

L length, W width

Sources: *P. ochraceus*, Omo Member B, Wesselman (1984); *H. karsticus*, Mein et al. (2000a); *Paraxerus* sp., Kanapoi and Lemudong'o, Manthi (2006, 2007). Modern species (*P. ochraceus*, *P. flavovittis* and *P. cepapi*) from museum collections

entoconid is small and oblique, delimiting the distal border of the molar.

Comparisons of molar size with various modern East and South African *Paraxerus* species shows that *Paraxerus meini* nov. sp. clearly has a smaller toothrow length compared to modern *P. flavovittis*, *P. cepapi* and *P. ochraceus*, but larger than *P. boehmi*. There is marked individual variability of molar size in the modern species (Tables 2.2 and 2.3).

Comparison of the morphological features of the molars with modern *P. ochraceus* shows that *P. meini* shares well-developed lophs on the upper molars, the presence of a metaconule on P4/, and no hypocone on M3/. Lophs are less well developed in *P. palliatus* and *P. flavovittis*, especially the ectolophid. On the lower molars one can see the anteroconulid and posteroconulid on M/1-2 of *P. palliatus* and *P. ochraceus*, and the M/3 is narrow and lacks a hypoconulid and discrete entoconid. It seems that *P. meini* can be distinguished from *P. palliatus* and *P. flavovittis* in having numerous supplementary cusplets, less bunodont molars, and a better-developed ectolophid. Compared to *P. ochraceus* there are fewer supplementary cusplets and a more rectilinear ectolophid

with a mesoconid. *Paraxerus meini* differs from *P. flavovittis* in the presence of a hypoconulid and entoconulid on M/1 and M/2. From a morphological point of view the molars of *P. meini* display some similarities with *P. ochraceus* from Tanzania, being characterized by the development of numerous cusplets, but they are expressed to a greater extent in *P. meini*. This group is characterized by marked molar size and shape variability, but cusp variability is not well known. From the MNHN, NHM, ZMB and DM voucher specimens examined, *P. meini* has upper and lower toothrows intermediate in size between *P. boehmi* and *P. ochraceus* (Table 2.3).

The fossil record for this taxon is poorly known. Only an isolated tooth (left P/4) of *Paraxerus* sp. has been discovered at Lemudong'o (~6 Ma), which displays some similarity with *P. palliatus* (Manthi 2007). Compared to *P. meini*, the Lemudong'o P/4 has the same bunodont pattern with the two anterior cusps well separated. Based on the published images of the Lemudong'o specimen there is no ectolophid, contrary to *P. meini*, and no evidence of a posterolophid. Another lower molar attributed to *Paraxerus* sp. was described from Tabarin (4.5–4.4 Ma) (Winkler 2002). Manthi (2006) mentions a single mandible of *Paraxerus* sp. from Nzube's mandible

site at Kanapoi, which has larger molars, similar to the specimen from Lemudong'o (Table 2.3). From Omo Members B, C and F, Wesselman (1984) described some molars that he attributed to modern *P. ochraceus*. They display the same pattern as *P. meini*: longitudinal rectilinear ectolophid, presence of an entolophid on M/1-2, and existence of an anterolophid or an anteroconulid. The difference between the Omo *P. ochraceus* and the modern species relates to the oblique disposition of the proto-loph originating from the protocone in the fossil, while it is more transverse and originates from the back of the molar in the modern form. The specimens from Omo and Laetoli probably belong to the same lineage, and may be the ancestors of modern *P. ochraceus*. The *P. meini* specimens have larger molars compared to modern representatives of the genus (Table 2.3).

The late Miocene site of Harasib in Namibia has yielded the remains of a sciurid that is attributed to the extinct European genus *Heteroxerus* (Mein et al. 2000a). The reasons why the Harasib squirrel is not attributed to *Paraxerus* is not well justified, except for the smaller size of the unicuspid P3/ in the Harasib material. However, there is extensive variability in the modern representatives, and such a character is not adequate to reject a close relationship between *P. meini* and *H. karsticus*. The hypocone is absent or small in *H. karsticus* and there is some variability described by the authors in the metaloph orientation and disposition. *Heteroxerus karsticus* has larger molars than *P. meini*. The figured holotype of *H. karsticus* displays a very longitudinal rectilinear ectolophid and there is an anteroconulid on M/1-2 as in *P. meini*. The entolophid is better developed and more transverse than in the Laetoli specimens, while it is very reduced or absent in *H. karsticus* (Mein et al. 2000a). When the entolophid is figured, as in Fig. 2.3, one observes that it is oblique and joins the

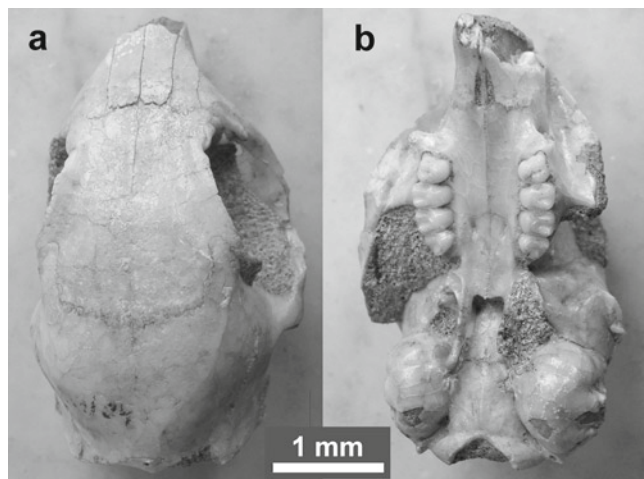


Fig. 2.3 Dorsal and ventral views of *Xerus janenschi* cranium, EP 219/04 from Loc. 15 (Upper Ndolanya Beds)

posterolophid midway along its length. The genus *Heteroxerus* was created by Stehlin and Schaub (1951) for the Miocene European *H. hurzeleri* based upon the existence of a direct link between the entoconid and hypoconulid, a feature that we do not find in *Paraxerus meini* or modern *Paraxerus* spp., but present on *H. karsticus* at Harasib (Mein et al. 2000a). Stehlin and Schaub (1951) also mentioned the existence of the little arm of the protoconid, which is also found in modern *Xerus* spp., but not in the *Paraxerus* we examined. *Heteroxerus karsticus*, as described by Mein et al. (2000a), also displays an anteroconulid on M/1-2 that is found in *P. meini* and in modern *P. ochraceus* and *P. cepapi*. The diagnostic characters provided by Mein et al. (2000a) indicate some differences between the two species and they probably represent distinct lineages. Further revisions of *Heteroxerus* and *Paraxerus* species composition and diagnoses are required to answer these questions.

Genus *Xerus* Hemprich and Ehrenberg, 1833

Xerus janenschi Dietrich, 1942

(Figs. 2.3–2.6)

The largest sciurid from Laetoli is found as a common taxon in the Upper Ndolanya Beds, but it is represented only by a single specimen from the Upper Laetoli Beds (Denys 1987a). Dietrich (1942) described it for the first time from Garusi, but the stratigraphic provenance and age is not known. Denys (1987a) recognized the same species from Locs. 18 and 7E from the Upper Ndolanya Beds.

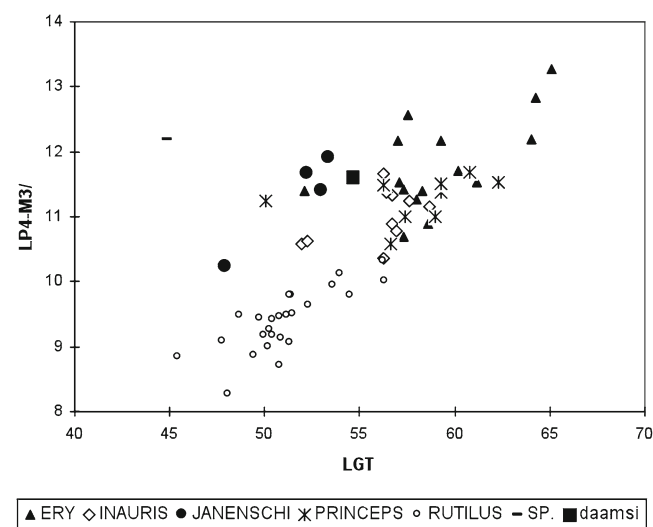


Fig. 2.4 Scatter plot of modern and fossil *Xerus* specimens. LP4-M3/: upper tooth row length. LGT: total length of the cranium (axis scales in mm). ERY: modern *Xerus erythropus* from East and Central Africa. INAURIS: modern *X. inauris* from South Africa. JANENSCHI: Laetoli fossils, *X. janenschi*. PRINCEPS: modern *Xerus princeps* from south-west Africa. RUTILUS: modern *X. rutilus* from Ethiopia. SP: Laetoli *Xerus* sp. DAAMSI: Fossil Chad KB, *X. daamsi*

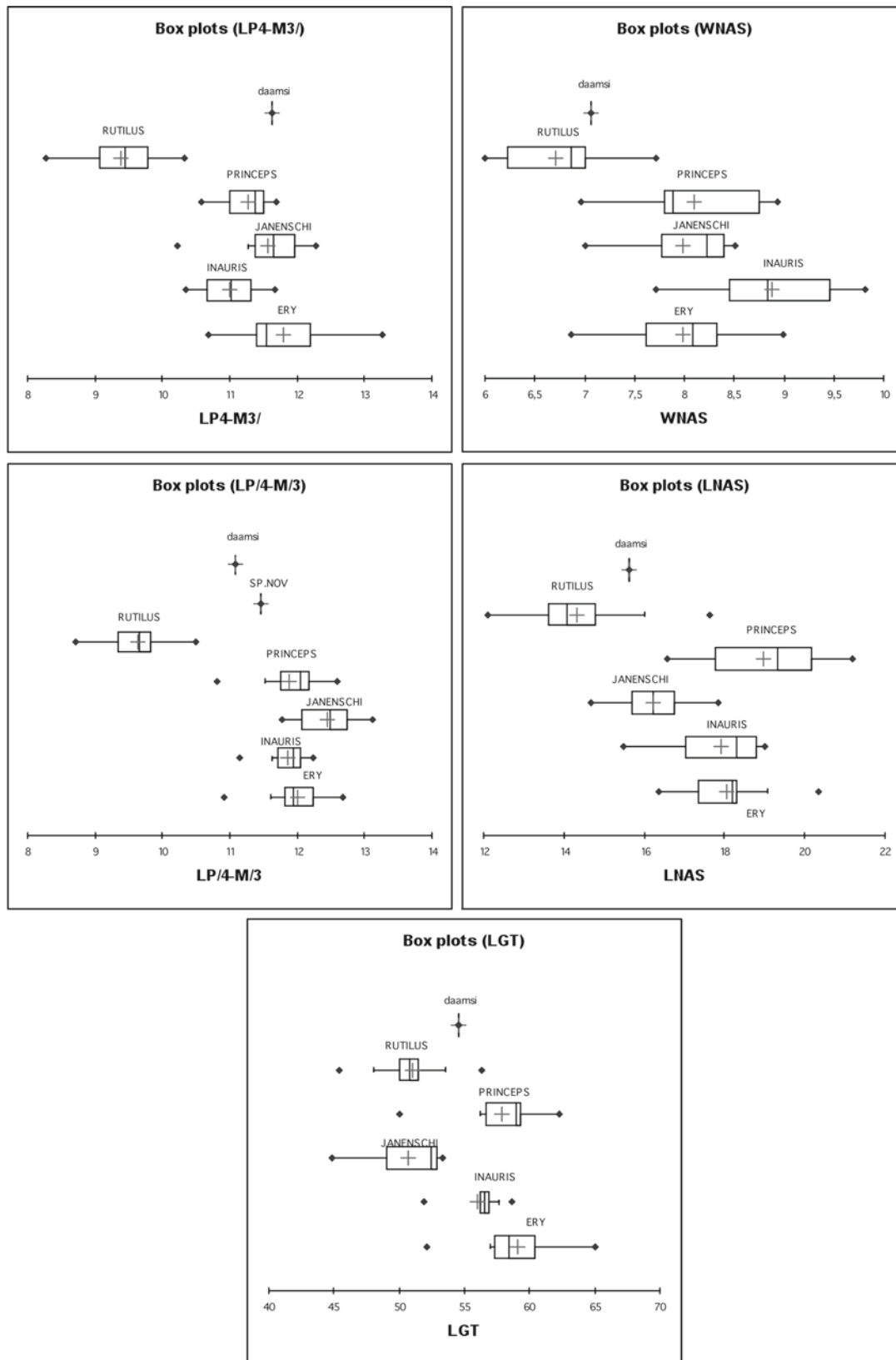


Fig. 2.5 Box plots for the different modern and fossil *Xerus* spp. for different cranial measurements (LP4-M3/: Upper tooth row length. WNAS: Nasal width. LP/4-M/3: Lower tooth row length. LNAS: Nasal length. LGT: Total cranium length) in mm. ERY: modern *Xerus erythropus* from

East and Central Africa. *INAURIS*: modern *X. inauris* from South Africa. *JANENSCHI*: Laetoli fossils, *X. janenschi*. *PRINCEPS*: modern *Xerus princeps* from southwest Africa. *RUTILUS*: modern *X. rutilus* from Ethiopia. *SP*: Laetoli *Xerus* sp. *DAAMSI*: Fossil Chad KB, *Xerus daamsi*



Fig. 2.6 Lower (left) and upper (right) tooththrows of *Xerus janenschi*. EP 292/04 (mandible with P4-M2) from Loc. 18 (Upper Ndolanya Beds) and EP 2356/98 (maxilla with P4-M3) from Loc. 18 (Upper Ndolanya Beds). Scale bar indicates 1 mm

Lacking P3/, no ectolophid and quite bunodont cusps, *Xerus janenschi* shares dental and cranial characters with *X. daamsi* (Denys et al. 2003) from the early Pliocene KB site in Chad and with *X. erythropus* from the Omo (Wesselman 1984). The absence of P3/ distinguishes the Laetoli fossils from the late Miocene *Xerus* sp. from Alayla Vertebrate Locality 2 in the Middle Awash of Ethiopia (Wesselman et al. 2009). A cladistic analysis comparing the Laetoli fossil to modern Xerini indicates that its closest affinities are with *X. rutilus* (Denys et al. 2003).

The new Laetoli material increases the sample of *X. janenschi* by 37 specimens (see Appendix 2.2) and establishes its presence for the first time in the Upper Ndolanya Beds at Loc.15 and Silal Artum, as well as in the Upper Laetoli Beds at Loc. 9S. The new specimens display the same skull characteristics previously described for *X. janenschi*, including a short nasal, trace of three transbulbar septa, rather bunodont molars, the absence of P3/, inflated tympanic bullae, and a wide braincase (Fig. 2.3). These characters allow *X. janenschi* to be grouped closest to the South African *X. inauris* and *X. princeps*. However, *X. janenschi* is also characterized by distinctive skull proportions (Table 2.4, Fig. 2.4). At an equivalent cranial

Table 2.4 Skull and molar dimensions (mm) in fossil and modern *Xerus* spp.

Species	LGT	LNAS	WNAS	LP4/-M3/	LP4-M/3
<i>Xerus daamsi</i>					
Chad (KB)	54.59	15.64	7.06	11.62	11.08
<i>X. erythropus</i>					
Mean	59.13	18.07	7.91	11.84	12.01
SD	3.26	1.21	0.6	0.73	0.46
Min	52.11	16.38	6.86	10.69	10.92
Max	65.06	20.33	8.99	13.27	12.68
<i>X. rutilus</i>					
Mean	51.07	13.26	6.74	9.39	9.65
SD	2.48	5.59	0.5	0.48	0.42
Min	45.44	12.86	6	8.27	8.71
Max	56.36	17.64	7.72	10.32	10.5
<i>X. inauris</i>					
Mean	55.65	17.35	8.44	10.97	11.89
SD	2.86	1.31	0.62	0.32	0.4
Min	51.91	15.47	7.72	10.58	11.14
Max	58.67	18.97	9.45	11.33	12.24
<i>X. princeps</i>					
Mean	58.5	19.89	7.74	11.16	12.01
SD	1.87	1.56	0.2	0.48	0.45
Min	56.6	17.82	7.44	10.57	11.52
Max	60.75	21.19	7.88	11.69	12.6
<i>X. janenschi</i>					
N	5	4	5	7	6
Mean	51.86	16.24	7.98	11.48	12.44
SD	0.99	0.65	0.28	0.24	0.21
Min	47.96	14.66	7	10.23	11.77
Max	53.4	17.83	8.51	12.28	13.12
<i>Xerus</i> sp.					
Berlin Gadj.	44.8			12.2	
100, Laetoli					

N number of molars, SD standard deviation, min-max minimum and maximum values, LGT greatest length of the skull, LNAS and WNAS nasal length and width, LP4/-M3/ upper tooth row length, P4-M/3, lower tooth row length. Modern *X. inauris*, *X. princeps*, *X. rutilus*, *X. erythropus* specimens have been measured in museum collections. Data for *X. daamsi* from Denys et al. (2003)

size to *X. rutilus*, *X. janenschi* has longer upper and lower molar rows. It is smaller than *X. daamsi*, *X. princeps*, *X. inauris* and *X. erythropus*. The nasals of *Xerus janenschi* are intermediate in length-width proportions between the smallest *X. rutilus* and *X. daamsi* and the other modern species, which are larger (Table 2.4, Fig. 2.5).

There is great variability within this species in terms of size, but the dental morphology of the newly collected fossils is similar to the type material and displays a very bunodont pattern (Fig. 2.6). The new material confirms that *X. janenschi* has larger molars than *X. daamsi* from Chad and *Xerus* sp. from Kanapoi, and smaller molars than those of *X. cf. inauris* from Olduvai Bed I (Table 2.5). However, they fall within the lower end of the range of variability for the Olduvai and Omo samples (Table 2.5).

Table 2.5 Tooth dimensions (*N* number of specimens, *SD* standard deviation) for fossil and modern *Xerus* spp. Laetoli UNB 1987 and this work relates to *X. janenschii*

Tooth	Locality	Length				Width			
		N	Mean	SD	Range	N	Mean	SD	Range
P4/ or DP4/	Laetoli UNB 1987	4	3.13	0.4	2.49–3.77	4	2.65	0.62	1.66–3.63
	Laetoli UNB this work	4	2.63	0.12	2.29–2.86	4	2.9	0.23	2.24–3.29
	Olduvai	1	2.75			1	2.28		
	Omo F	1	2.55			1	2.98		
	KB-97-162	1	2.50			1	2.80		
M1/	Laetoli UNB 1987	3	3.08	0.4	2.39–3.78	3	3.72	0.26	3.08–4.37
	Laetoli UNB this work	4	2.88	0.06	2.95–3.67	4	3.31	0.15	2.95–3.57
	Olduvai ^a	5	3.49		3.40–3.60	5	3.36		3.2–3.6
	KB-97-162	1	2.86			1	2.86		
M2/	Laetoli UNB 1987	2	3.08	0.28		2	3.55		
	Laetoli UNB this work	5	3.03	0.13	2.81–3.36	5	3.40	0.11	3–3.68
	KB-97-162	1	2.76			1	3.05		
M3/	Laetoli UNB 1987	2	2.83			2	3.10		
	Laetoli UNB this work	3	2.81	0.17	2.52–3.1	3	3.13	0.05	3.05–3.23
	KB-97-162	1	2.76			1	3.05		
P/4 or DP/4	Laetoli UNB 1987	6	2.76	0.36	2.38–3.14	6	2.68	0.36	2.30–3.06
	Laetoli UNB this work	7	2.43	0.15	1.86–3.10	7	2.27	0.18	1.71–3.10
	LB <i>Xerus</i> sp. this work	2	2.14		2.04–2.24	2	2.15		1.91–2.38
	Olduvai	6	3.13	0.42	2.30–3.40	6	3.07	0.51	2.05–3.45
	Omo B, C	2			2.50–2.60	2			2.76–2.88
	KB-97-162	1	2.41			1	2.31		
M/1	Laetoli UNB 1987	8	3.13	0.16	2.99–3.26	8	3.21	0.3	2.96–3.46
	Laetoli UNB this work	9	2.93	0.07	2.62–3.3	9	2.87	0.08	2.52–3.19
	LB <i>Xerus</i> sp. this work	3	2.46		2.38–2.5	3	2.56		2.5–2.62
	Olduvai	9	3.48	0.14	3.30–3.65	9	3.51	0.19	3.30–3.80
	Omo B, C ^a	2			3.12–3.46	2			3.60–3.70
	KB-97-162	1	2.62			1	2.9		
	Kanapoi	2	2.54		2.54–2.55	2	2.85		2.84–2.86
M/2	Laetoli UNB 1987	3	3.32	0.16	2.92–3.72	3	3.47	0.12	3.47–3.77
	Laetoli UNB this work	7	3.03	0.07	2.76–3.29	7	2.99	0.09	2.62–3.3
	LB <i>Xerus</i> sp. this work	2	2.52		2.38–2.65	2	2.66	2	2.60–2.71
	Olduvai	6	3.63	0.15	3.45–3.80	6	3.57	0.13	3.57–3.7
	KB-97-162	1	2.76			1	3.17		
	Kanapoi	2	2.57			2	2.98		2.94–3.01
M/3	Laetoli UNB 1987	2	3.78			2	3.3		
	Laet. UNB this work	4	3.1	0.1	2.86–3.33	4	2.98	0.06	2.81–3.1
	Olduvai	3	3.55	0.09	3.45–3.6	3	3.5	0.17	3.4–3.7
	Omo F	2			3.25–3.5	2			2.6–2.77
	KB-97-162	1	2.97			1	2.66		
	Kanapoi	2	2.49		2.49–2.5	2	2.78		2.76–2.79

Data sources: Olduvai Bed I, *X. cf. inauris*, Denys (1990); Omo B, C, *Xerus erythropus*, Wesselman (1984); Omo F, *Xerus* sp., Wesselman (1984); KB-97-162, Chad, *Xerus daamsi*, Denys et al. (2003); Kanapoi, *Xerus* sp., Manthi (2006). Abbreviations: UNB, Upper Ndolanya Beds; LB, Laetolil Beds

^a Attribution to M1 or M2 is ambiguous. DP/4 and P/4 have been pooled, which may explain the high variability observed for these teeth

Xerus sp.
(Fig. 2.4, Table 2.5)

The Upper Laetolil Beds have also yielded the remains of a smaller sciurid. This species is very bunodont and was described and figured by Denys (1987a) from Loc. 9S (LAET 75-1562, Plate 6.2) and possibly includes the

Gadjingero 100 skull (from the Kohl-Larsen collection in Berlin). New specimens from Loc. 9 (EP 1089/98) and Loc. 9S (EP 1215/04) can be attributed to this same species. The entoconid and posterolophid are very crestiform on P/4, M/1, and M/2, and they make a continuous distal wall on M/2. There is no prominent entoconid and the cusp relief is low. These features are similar to modern

X. rutilus (Denys et al. 2003). The specimens display a shorter skull length, relatively longer upper molar row (Fig. 2.4) and smaller lower molars than *X. janenschi* (Tables 2.4 and 2.5), although measurements of some teeth fall in the low end of the range of *X. janenschi*.

Family Nesomyidae Major, 1897

Subfamily Cricetomyinae Roberts, 1951

Tribe Saccostomurini Roberts, 1951

Genus *Saccostomus* Peters, 1846

Saccostomus major Denys, 1987

(Figs. 2.7–2.12)

Many new specimens from the Upper Laetolil Beds (Locs. 1, 2, 3, 4, 5, 6, 7, 8, 9S, 10, 10E, 10W, 11, 15, 17 and 22) are attributed to *S. major* (see Appendix 2.3). They display the same morphological characteristics of the teeth as the previously recovered material (Fig. 2.7). The initial description of the species included nearly complete skulls, and there are no new skeletal elements to describe here. However, with the recovery of 173 new *Saccostomus* individuals from the Upper Laetolil Beds we have been able to study the population at a finer scale. M/1 length and wear stages were analyzed to assess the variability among the species and to detect biostratigraphic differences.

The following wear stages can be defined (Fig. 2.8):

Stages 0–1: Presence of two isolated cusps on the prelobe of M1/1 or M3/ unerupted.

Stages 2–4: Cusps visible on all the molars, no large longitudinal links between cusps visible.

Stages 5–6: Wide links between the lobes and cusps hardly visible on the M3/ and the whole tooth row.

Among the newly collected material of *S. major* one finds a good proportion of juveniles (stages 0–1: 33.3%) and old adults (stages 5–6: 21.6%) compared to prime adults (stages 2–4: 45.1%).



Fig. 2.7 Left maxillary tooththrow of *Saccostomus major* from the Upper Laetolil Beds. EP 1738/04 from Loc. 2 (left) and EP 1326/03 (right M1/) from Loc. 11 (right). Scale bar indicates 1 mm

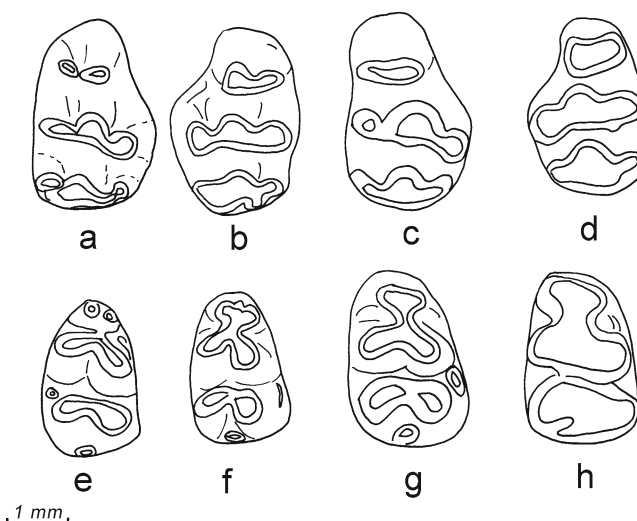


Fig. 2.8 Wear stages of the M1/ and M1/ *Saccostomus major* from the Upper Laetolil Beds. Top row, M1/. (a) stage 1, EP 1375/00; (b) stage 2, EP 160/03; (c) stage 3, EP 3904/00; (d) stage 4, EP 998/05. Bottom row, M1/. (e) stage 1, EP 162/03; (f) stage 2, EP 1424/03; (g) stage 3, EP 2434/03; (h) stage 4, EP 1065/03. Scale bar indicates 1 mm

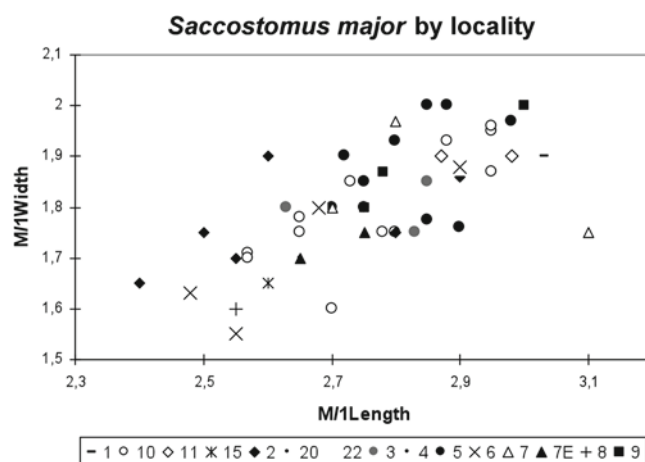


Fig. 2.9 Scatterplot of the M/1 dimensions (mm) of *Saccostomus major* by locality. The specimens from Loc. 7E (black triangles) come from the Upper Ndolanya Beds

The scatter plot of M/1 length by width, organized by locality, does not provide a clear pattern of size differences (Fig. 2.9). Specimens from the pooled Loc. 10 complex of localities encompass the full range of variation, while it appears that specimens from Locs. 1, 3, 5, 9, and 11 are slightly larger than those from Locs. 6, 8 and 15. When the data are sorted by stratigraphic level (i.e., below Tuff 2, below Tuff 3, between Tuffs 3–5, between Tuffs 5–7, between Tuff 7 and the Yellow Marker Tuff) one observes a slight

decrease in size between the lower levels and upper levels (Fig. 2.10). However, the sample is too small to reach a definitive conclusion about the biostratigraphic variation of *Saccostomus* M/1 through the Upper Laetolil Beds. Specimens from the Upper Ndolanya Beds fall in the middle of the distribution.

We confirm the presence of *S. major* in the Upper Laetolil Beds and add it to the faunal list of Loc. 15. However, it is still absent from Locs. 12, 13 and 21, as Denys (1987a) previously observed. It is not yet found in the Lower Laetolil Beds, although it is recorded at older eastern and southern African sites. *Saccostomus major* is described from the Manonga Valley (Winkler 1997), while *S. geraadsi* was named by Mein et al. (2004) from Ch'orora (Ethiopia) and Harasib 3a (Namibia). Finally, Mein and Pickford (2006) recognized *S. cf. geraadsi* based on molars from Lukeino in Kenya, dated to around 6.1–5.8 Ma.

Saccostomus major from Laetoli is similar in size to that from the Manonga Valley (Table 2.6, Fig. 2.11). *Saccostomus geraadsi* from Lukeino and Harasib have smaller molars compared to *S. major*, and their molar size fits within the variability of *S. cf. mearnsi* from Olduvai Bed I (Fig. 2.11).

Saccostomus cf. major (Figs. 2.9–2.12)

Denys (1987a) described a single mandibular fragment (LAET 75-862) from Loc. 18 (Upper Ndolanya Beds) and left it unattributed at the species level due to the small size of the M/2-3. New remains of *Saccostomus* have been recovered from the Upper Ndolanya Beds at Loc. 7E and are described here.

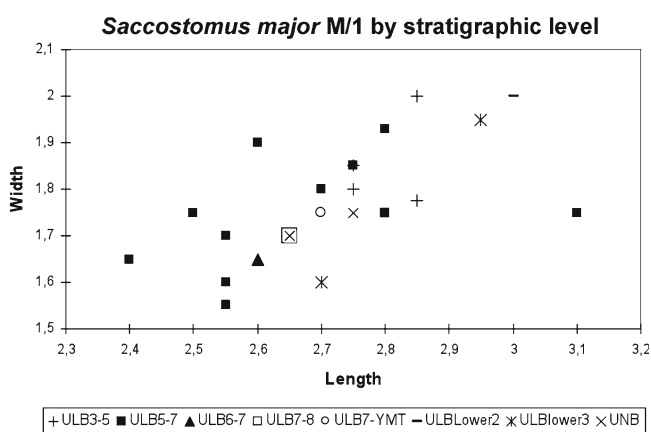


Fig. 2.10 Scatter plot of *Saccostomus major* M/1 grouped by stratigraphic level: ULB, Upper Laetolil Beds; 3-5=between Tuffs 3 and 5; 6-7=between Tuffs 6 and 7; 7-8=between Tuffs 7 and 8; 7-YMT=between Tuff 7 and Yellow Marker Tuff; Lower 2=below marker tuff 2; Lower 3=below Tuff 3, UNB, Upper Ndolanya Beds

Referred material: Loc. 7E. EP 1247/03 (Fig. 2.12), isolated right M/1. EP 1248/03, associated mandibles. EP 1249/03, left mandible fragment with M/1-2.

The isolated lower molar belongs to a young individual (wear stage 2) with the two cusps of the prelobe still visible (Fig. 2.12). It is comparable in size to specimens from the Upper Laetolil Beds (Fig. 2.9). Because it shows dentine and enamel corrosion we cannot describe the specimen in detail, except to mention that it has a link between the prelobe and the first lobe and a tiny cingular cV5 on the labial side of the molar. The mandibular fragment with M/1-2 also fits within the size variation of other Laetoli *S. major* specimens, and can be attributed to wear stage 1 (Fig. 2.9). The main differences distinguishing the Laetoli material from *S. cf. mearnsi* of Olduvai are the large prelobe of M/1 and the presence of an anterolabial crest (absent in the Olduvai Bed I specimens). Consequently, the new *Saccostomus* specimens from Loc. 7E can be attributed to *S. cf. major* pending additional finds from the Upper Ndolanya Beds. Because no new material was recovered from Loc. 18 we retain here *Saccostomus* sp. for the unique specimen from the Mary Leakey collection.

Saccostomus cf. major

A single mandibular fragment (EP 2075/03) with a broken M/1 (with trace of two roots) and a well-preserved M/2 is known from Emboremony 1 (Lower Laetolil Beds). This molar is of wear stage 4 and displays two relatively transverse lobes with fused cusps and an anterolabial cingulum. Its size (1.72×1.81 mm) falls within the range of the M/2s of *S. major* from the Upper Laetolil Beds.

Family Muridae Illiger, 1811 Subfamily Gerbillinae Gray, 1825

The Upper Laetolil Beds have already yielded two different species of Gerbillinae (Denys 1987a). One (Gerbillinae sp.) was not attributed to any genus due to the low number of specimens and the limited availability of characters. The other was attributed to *Gerbilliscus cf. inclusa* and was characterized by wide molars, very transversely aligned cusps, and mesially open prelobe on M/1. The new collections allow a more detailed description of the Gerbillinae sp. of Denys (1987a). Recent molecular revisions have changed the genus nomenclature, so we follow Wilson and Reeder (2005) in retaining *Gerbilliscus* for the Laetoli specimens in place of the old name *Tatera*.

Genus *Gerbilliscus* Thomas, 1897

Gerbilliscus satimani sp. nov. (Figs. 2.13–2.16)

Holotype: EP 147/01, nearly complete cranium with associated mandibles. Nasal region missing (Fig. 2.13).

Type locality: Loc. 6, Laetoli, Tanzania.

Age and horizon: Mid-Pliocene, Upper Laetolil Beds.

Table 2.6 Molar dimensions (mm) of *Saccostomus* spp. from Laetoli and from other Plio-Pleistocene sites

Tooth	Locality	Length			Breadth				
		N	Mean	SD	Range	N	Mean	SD	Range
M1/	Laetoli this work	16	3.00	0.03	2.86–3.19	16	1.93	0.03	1.67–2.14
	Laetoli (Denys 1987a)	21	3.00		2.83–3.38	21	2.08		1.80–2.40
	Olduvai Bed I	43	2.66		2.52–2.81	46	1.77		1.63–1.91
	Manonga					3	2.19		2.16–2.25
	Harasib 3	40	2.51	0.02	2.30–2.79	40	1.68	0.01	1.53–1.81
M2/	Lukeino	3			2.24–2.40	3			1.57–1.65
	Laetoli this work	8	1.86	0.04	1.68–2.00	8	1.81	0.03	1.71–2.00
	Laetoli (Denys 1987a)	13	2.01		1.80–2.37	13	1.9		1.78–2.07
	Olduvai Bed I	61	1.63		1.53–1.87	61	1.67		1.57–1.84
	Manonga	3	1.96		1.88–2.04	3	2.05		2.00–2.12
M3/	Harasib 3	44	1.68	0.01	1.44–1.83	44	1.65	0.01	1.47–1.83
	Lukeino	2			1.56–1.60	2			1.58
	Laetoli this work								
	Laetoli (Denys 1987a)	4	1.27	0.03	1.22–1.35	4	1.48	0.13	1.30–1.85
	Olduvai Bed I	5	1.13	0.04	1.00–1.22	5	1.24	0.02	1.18–1.29
M1/	Harasib 3	20	1.11	0.02	0.93–1.29	20	1.16	0.02	0.93–1.28
	Laetoli this work	56	2.78	0.02	2.40–3.10	56	1.81	0.01	1.55–2.00
	Laetoli (Denys 1987a)	38	2.78		2.48–3.03	38	1.83		1.63–2.00
	Olduvai Bed I	139	2.35		2.19–2.57	140	1.57		1.42–1.77
	Manonga	3	2.71		2.60–2.83	5	1.83		1.75–1.92
M2/	Harasib 3	42	2.22	0.01	2.05–2.40	42	1.51	0.01	1.36–1.69
	Lukeino	7	2.23	0.04	2.09–2.35	7	1.46	0.02	1.41–1.54
	Laetoli this work	20	1.86	0.02	1.67–2.00	20	10.83	0.02	1.57–2.00
	Laetoli (Denys 1987a)	34	2.06		1.85–2.33	34	1.93		1.75–2.15
	Olduvai Bed I	135	1.69		1.54–1.89	134	1.65		1.49–1.78
M3/	Manonga	2			1.84–1.88	2			1.84–1.96
	Harasib 3	41	1.67	0.01	1.49–1.85	41	1.56	0.01	1.43–1.70
	Laetoli this work	12	1.48	0.04	1.33–1.76	12	1.39	0.03	1.19–1.57
	Laetoli (Denys 1987a)	4	1.64	0.04	1.55–1.72	4	1.59		1.48–1.80
	Olduvai Bed I	17	1.28	0.02	1.16–1.41	17	1.24	0.02	1.16–1.37
	Lukeino	1	1.26			1	1.32		
	Harasib 3	30	1.3	0.02	1.18–1.46	30	1.19	0.01	1.08–1.39

N number of molars, *SD* standard deviation

Data sources: previous study of Laetoli (Denys 1987a), *S. cf. mearnsi*, Olduvai Bed I (Denys 1992), *S. major*, Manonga (Winkler 1997), *S. geraadsi*, Harasib 3 (Mein et al. 2004), *S. cf. geraadsi*, Lukeino (Mein and Pickford 2006)

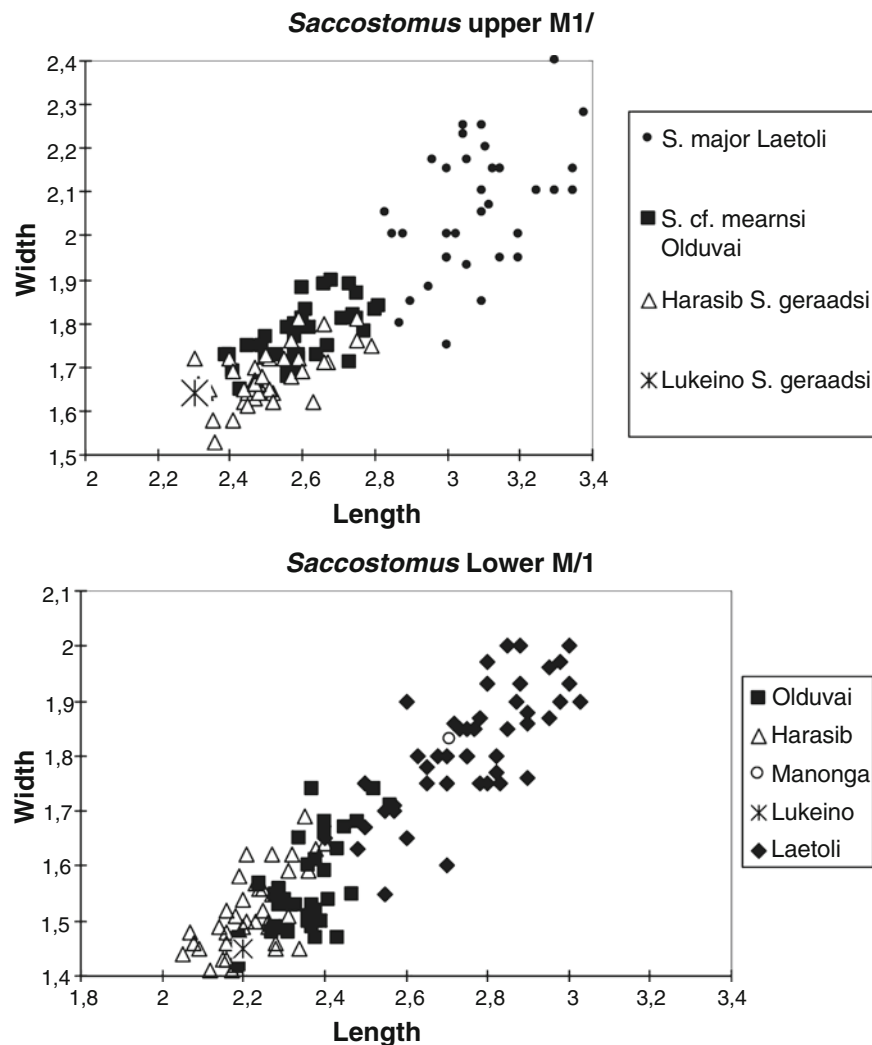


Fig. 2.11 Comparison of fossil *Saccostomus* spp. M1/ and M/1 from different localities. Length and width in mm. After Winkler (1997), *S. major* Ibole, Manonga Valley; Mein et al. (2004), *S. geraadsi*, Harasib;

Mein and Pickford (2006), *S. geraadsi*, Lukeino; Denys (1987a, this study) *S. major*, Laetoli; Denys (1992), *S. cf. mearnsi*, Olduvai Bed I

Type series: EP 782/03, left mandible with M1-2, Loc. 9. EP 999/01, left maxilla with M1/, Loc. 11. EP 1075/04, left mandible with M/1 (Fig. 2.16), Loc. 1. EP 1981/03, anterior cranial fragment with right maxilla with M1-2/, Loc. 7 (Figs. 2.14 and 2.16). EP 1889/03, left mandible with M/1-3, Loc. 1 (Fig. 2.14).

Referred material: LAET 75/A17, M1/, Loc. 6. LAET 75-3492, M1/, Loc. 10W (Plate 6.2 in Denys 1987a). LAET 79/A02, M1/, Loc. 6 (Plate 6.2 in Denys 1987a). LAET 79/A3761, M/1, Loc. 6. LAET 79/A13B, M/1, Loc. 6. LAET 79/A5B1, M/1, Loc. 5. LAET 79/A5B2, M/1, Loc. 5. LAET 79/A13, mandibular fragment with M/1-2, Loc. 6.

Distribution: Locs. 1, 5, 6, 7, 9 and 11 of the Upper Laetolil Beds.

Measurements: Table 2.7 and 2.8, Fig. 2.16

Repository: National Museum of Tanzania, Dar es Salaam

Etymology: Named after Satiman, the volcano probably responsible for producing the volcanic ash at Laetoli that allowed such exceptional preservation.

Diagnosis: A *Gerbilliscus* with quite narrow molars, cusps distinguishable, simple rounded prelobe of M1/1 open anteriorly on M/1 when unworn. No longitudinal link between the prelobe and first lobe of the M/1. Long palatal foramen (from the first lobe of M1/ to the front of the second lobe of M2/). No posterior cingulum visible on M/1. Small bilobed M3/. Well-developed tympanic bullae.

Differs from *G. gentryi* from Olduvai Bed I by its much smaller size (Fig. 2.15), the anterior opening of the M/1

prelobe, and well-individualized cusps. Differs from *Gerbillus* spp. from Olduvai Bed I and from Late Miocene site of Asakoma (Middle Awash, Ethiopia) by the absence of a longitudinal link between the prelobe and the first lobe of the M1/ and by the transversely aligned cusps. Differs from *Gerbillus* sp. from Omo Members B and F by a more rounded and larger prelobe of M1/, less fused cusps and by the anterior opening of the prelobe. Differs from *Gerbillus* sp. of Lemudong'o and Kanapoi by its much larger-sized molars.

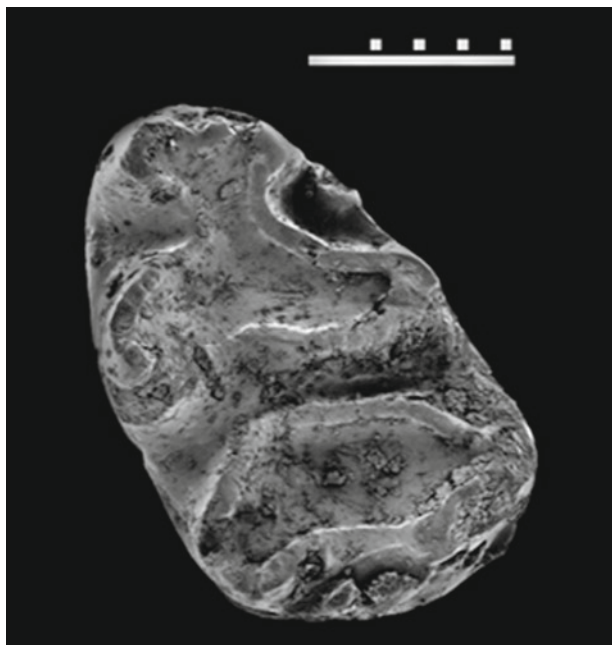


Fig. 2.12 *Saccostomus* cf. *major* from the Upper Ndolanya Beds (Loc. 7E), EP 1247/03. Scale bar in mm

Description: The holotype consists of a well-preserved cranium, but the rostrum is broken and the upper incisors are absent (Fig. 2.13). Another specimen (EP 1981/03, Loc. 7) displays the premaxilla, maxillary tooththrows and nasal bones with *in situ* incisors that show a median groove. The interorbital constriction is poorly marked. The right tympanic bulla is nearly complete. The latter is inflated in both tympanic and mastoid regions, as in modern *Gerbilliscus* (ex *Tatera*) and *Gerbillus*. The incisive foramen is short and stops far from the anterior root of the M1/, while the palatal foramen, which is long, begins at the level of the first lobe of the M1/ and ends at the front of the second lobe of M2/ (Fig. 2.13).

The holotype is an old individual and its molars are quite worn, but the cusps are still visible. The prelobe of M1/ is round or composed of two cusps separated by a deep anterior groove (the so-called anterior opening). The M1/ displays a round and narrow prelobe, with a distal crest not related to the first lobe. There is also the trace of a distal crest on the first lobe of M1/ with the two cusps not well aligned in a transverse lamina (Figs. 2.14 and 2.16). There is no distal cingulum on the type specimen and only one specimen displays a trace. Similarly, there is no anterocone on the M2/. The M3/ is composed of two lobes of nearly equal size and the crown is not very reduced in overall size.

Gerbilliscus satimani sp. nov. is slightly smaller than extant *G. leucogaster* from South Africa and has narrower molars (Table 2.7). The two species share the prelobe anterior opening on M1/. The disposition of the incisive and palatal foramina is similar. The cranial proportions are comparable between the two species for molar row length and interorbital constriction, but the tympanic bullae of *G. satimani* sp. nov are more developed than in *G. leucogaster* and

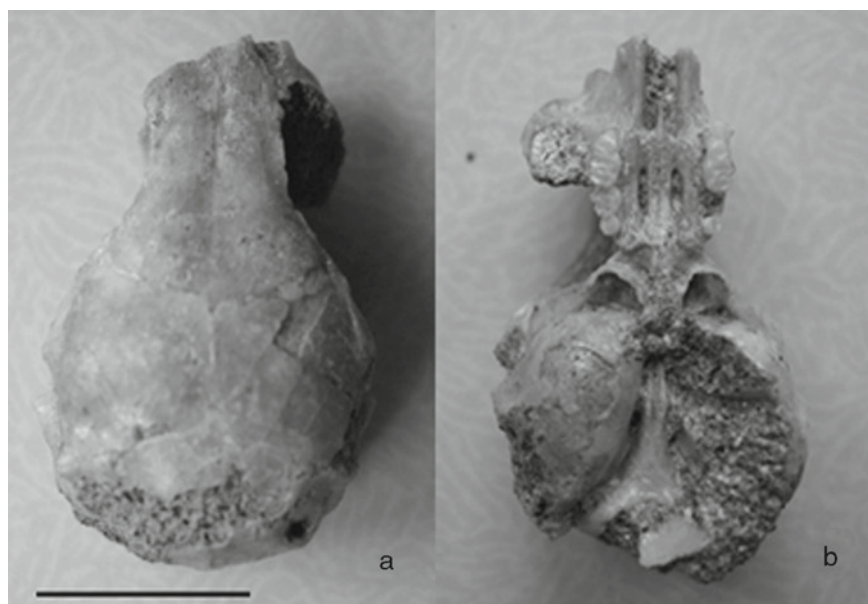


Fig. 2.13 Dorsal (a) and ventral (b) view of the holotype of *G. satimani* nov. sp. Cranium EP 147/01 from Loc. 6, Laetolil Beds. Scale bar 1cm



Fig. 2.14 SEM images of *G. satimani* specimens. *Left*, EP 1981/03 from Loc. 7 (left M1-2/). *Right*, EP 1889/03 from Loc. 1 (left mandible with M1/1-3). Scale bar in mm

equivalent in size to those of the extant South African *Gerbillurus vallinus* (Table 2.7). However, the modern South African *Gerbillurus* has a much shorter molar row than *G. satimani* (Table 2.7). *Gerbilliscus satimani* is smaller than *G. cf. inclusus* from the Upper Laetoli Beds and the new *Gerbilliscus* species from the Upper Ndolanya Beds (Figs. 2.15 and 2.16). *Gerbilliscus satimani* differs from *G. gentryi* from Olduvai bed I in being slightly smaller in size, and having narrower molars, a prelobe opening anteriorly, and the retention of a slight trace of a longitudinal crest on the upper molars (Figs. 2.15 and 2.16). *Gerbilliscus satimani* also differs from *Tatera* sp. (= *Gerbilliscus* sp.) from the late Miocene of Asakoma, Middle Awash (Ethiopia) by its larger molars, the absence of a longitudinal crest, well-individualized transverse cusps, and a prelobe with two unfused cusps of unequal size (Wesselman et al. 2009).

Mein and Pickford (2006) described a new species of *Abudhabia* from Kapsomin in the Lukeino Formation, mentioning that it may be intermediate between *Abudhabia* and *Tatera* sensu stricto (= *Gerbilliscus*) and similar in size and morphology to the Gerbillinae indet. of Laetoli of Denys (1987a). By comparing the new specimens to the figured one, we find that the size is similar, but there are a lot of morphological differences, which prevent one from recognizing a close affinity between the two species. Among these differences are the absence of anterocone and anteroconid on M2/2 and the quasi absence of a posterior cingulum on M1/, the absence of a groove between the two cusps on the M1/ prelobe and their fusion with a rounded aspect (which is a *Gerbilliscus* character). The main difference concerns the prelobe of M1/, which displays an anterior opening on poorly worn specimens of *G. satimani*

or simply a rounded prelobe that is very different from the specimens figured by Mein and Pickford (2006).

The Laetoli specimens also do not fit well with the *Gerbilliscus* sp. material from Hadar described by Sabatier (1982) because of the M1/ prelobe opening, which is located posteriorly in the latter specimens. The Hadar specimens also retain a trace of a posterior cingulum on M1/ and a small anteroconulid on M2/, as well as distinct cusps. Modern representatives of *Gerbilliscus* (*G. leucogaster* and *G. nigricauda*) may display traces of a posterior cingulum on M1/, so this cannot be taken as a valid character to distinguish *Abudhabia* from *Gerbilliscus* (= *Tatera*).

Wesselman (1984) described *Tatera* sp. indet. (= *Gerbilliscus*) from Omo Members B and F. The specimens from Omo Member B share with *G. satimani* the relatively well-individualized cusps of the first lobe of the M1/, but the former have a prelobe on the M1/ with an anterior depression in the middle, and traces of the two cusps that constitute it. The size of the molars is similar to those of *G. satimani*, but the M3/ is bilobed, whereas it is small in the Laetoli fossils (Table 2.8). The lower molars from Omo Member B are also like those figured from Omo Member F, and they display a different shaped prelobe on M1/ (posterior opening) and are nearly equal in size to *G. gentryi* specimens from Olduvai Bed I. Manthi (2007) described a *Gerbilliscus* (*Tatera*) sp. from Lemudong'o and the figured specimens display worn molars. The size of M1/ (Table 2.8) is much smaller than those of *G. satimani*. The M1/ of *Gerbilliscus* sp. from Kanapoi described by Manthi (2006) displays a round prelobe and a trace of cusps on the first row. They are also small, being similar in size to those from Lemudong'o (Table 2.8). These specimens may fit within the *G. satimani*

Table 2.7 Skull measurements for modern and fossil *Gerbilliscus* and *Gerbillurus* species

		A	B	C	D
<i>G. satimani</i>					
EP 147/01		5.11	5.28	6.33	11.7
EP 1889/03		5.51			
<i>G. cf. inclusus</i>					
EP 1372/98		7.2			
LAET 75-3588		7.2			
<i>G. gentryi</i>					
Olduvai Bed I	N	13	1		
	Min	5.30			
	Max	5.91			
	Mean	5.61	5.4		
	SD	0.21			
<i>G. leucogaster</i>					
Tanzania &	N	48	46	48	48
South Africa	Min	4.94	5.28	5.64	9.07
	Max	6.38	6.54	6.94	11.20
	Mean	5.55	5.91	6.10	10.19
	SD	0.32	0.24	0.32	0.57
<i>G. vallinus</i>					
Namibia & SW Africa					
NHM95-331		3.83	4.12		11.89
NHM25-1-2-87			4.02		11.75
NHM25-1-2-85		4.14	4.28		11.63
<i>G. afra</i>					
Angola					
NHM29-10-1-19		5.2	6.1		10.5
<i>G. paeba</i>					
South Africa					
NHM3-1-4-27		4.04	4.05		8.32
NHM49-345		3.97	4.22		9.39
<i>G. swalius</i>					
SW Africa					
NHM25-12-4-110		3.86	4.12		7.92

Data from the literature for Olduvai Bed I (Denys 1989a) and modern specimens from museum collections

A LI13, length of the lower molar row

B LS13, length of the upper molar row

C CIO, interorbital constriction width (taken in dorsal view)

D LBT, length of the tympanic bulla

lineage or belong together in a new smaller species as yet undescribed.

Gerbilliscus winkleri nov. sp.

(Figs. 2.15–2.17)

Additional specimens from the Upper Ndolanya Beds (Locs. 18 and 15) allow attribution of the previously so-called *Gerbilliscus* (*Tatera*) sp. from Laetoli and Hadar to a newly recognized species.

Holotype: EP 3320/00, left mandible with M/1 and associated right maxilla with M1-2/ (Fig. 2.16)

Type locality: Loc. 18, Laetoli, Tanzania.

Age and horizon: 2.66 Ma, mid-Pliocene, Upper Ndolanya Beds.

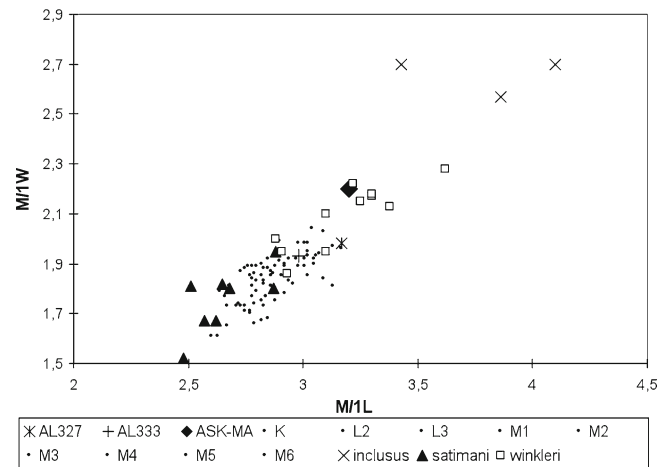


Fig. 2.15 Size comparisons of M/1 between Olduvai Bed I *Gerbilliscus gentryi* (Levels K, L2, L3, M1, M2, M3, M4, M5, M6 after Denys 1989a), *Gerbilliscus* spp. from Hadar (A.L. 333 and A.L. 327, mean value after Sabatier 1982) and Asakoma (ASK-MA after Wesselman et al. 2009), with *G. cf. inclusus*, *G. satimani* sp. nov., *G. winkleri* sp. nov. of Laetoli

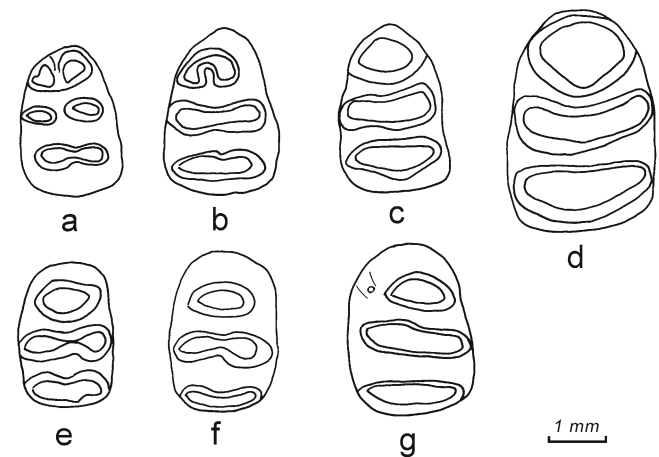


Fig. 2.16 Comparison of the upper and lower M1 of the different species of *Gerbilliscus* from Laetoli. Upper row, M1/1. (a) *G. satimani*, EP 1075/04; (b) *G. winkleri*, EP 3319/00; (c) *G. winkleri*, EP 3500/00, (d) *G. cf. inclusus*, EP 1372/98. Lower row, M1/1. (e and f) *G. satimani* EP 1981/03 and EP 999/01; (g) *G. winkleri*, EP 3320/00. Drawn to the same scale; the scale bar indicates 1 mm

Etymology: in honor of Alisa Winkler who has described numerous fossil rodents from East African Neogene sites.

Type series: Loc. 18, Upper Ndolanya Beds: EP 3319/00, left mandible with M/1-2. EP 817/01, left mandible with M/1 (Fig. 2.17). EP 3520/00, left maxillary fragment with M1-2/ and lower left M/1. Loc. 15, Upper Ndolanya Beds: EP 3500/00, left mandible with M/1.

Referred material: Previous *Tatera* sp. collections from Locs. 7E and 18, Upper Ndolanya Beds (after Denys 1987a):

Table 2.8 (continued)

Table 2.8 (continued)									
Tooth	Locality	Length			Breadth				
		N	Mean	SD	Range	N	Mean	SD	Range
M/2	G. <i>satimani</i> this work	4	1.50	0.06	1.43–1.57	4	1.61	0.11	1.52–1.76
	G. <i>satimani</i> Denys, 1987a	1	1.55			1	1.70		
	G. <i>winkleri</i> this work	1	1.71			1	1.95		
	G. <i>winkleri</i> Denys, 1987a	5	2.05	0.17	1.9–2.35	5	2.11	0.04	2.05–2.15
	G. sp. Lemudong'o	3	1.07	0.07	1.00–1.20	3	1.30	0.06	1.20–1.40
	G. cf. <i>inclusus</i>	1	2.12			1	2.52		
	G. <i>gentryi</i> Denys, 1989a	10	1.74	0.09	1.57–1.87	10	1.90	0.08	1.76–2.00
	G. sp. Hadar	19	1.85	0.05	1.75–1.96	19	1.92	0.07	1.79–2.05
	G. sp. Omo G	1	1.87			1	1.90		
	G. sp. Kanapoi	3	1.27		1.20–1.40	3	1.27		1.20–1.40
M/3	G. <i>satimani</i> this work	3	0.56	0.4	0.57–0.91	3	1.11	0.12	1.00–1.24
	G. <i>gentryi</i> Denys, 1989a	3	1.06	0.1	0.96–1.15	3	1.25	0.09	1.16–1.33
	G. sp. Hadar	2	0.96		0.93–1.00	2	1.29		1.27–1.32
	G. sp. Omo F	1	1.10				–		
	G. cf. <i>inclusus</i>	1	1.20			1	1.78		

N number of molars, *SD* standard deviation

Data sources: Hadar (Sabatier 1982), Omo Shungura B, F, G (Wesselman 1984), Lemudong'o (Manthi 2007), Middle Awash (Asa Koma) (Wesselman et al. 2009), Kanapoi (Manthi 2006)

LAET 75-728 (Plate 6.2 in Denys 1987a), LAET 75-899, LAET 75-673, LAET 76/71-72, LAET 75-862, LAET 75-602, LAET 74-36, LAET 75-636, LAET 74-35, LAET 75-661, and LAET 75-894 (Plate 6.2 in Denys 1987a).

Diagnosis: Well-aligned transverse cusps poorly individualized (fused into transverse laminae), prelobe of M/1 rounded or open distally. Oval-shaped prelobe of M1/, with no trace of cusps. Larger molars than *G. gentryi* and *G. satimani*. Same size as modern *G. leucogaster* from South Africa, but with much more fused and transverse laminae and a longer palatal foramen. In *G. winkleri* the palatal foramen starts at the level of the second lobe of the M1/ and ends at the back of the M2/, while in *G. leucogaster* the palatal foramen is situated between the first and second lobes of the M2/.

Differs from *G. gentryi* Denys, 1990 from Olduvai Bed I and *Gerbilliscus* sp. from Omo Members B and F in the larger size of M1/. Differs from *Gerbilliscus* sp. from Hadar in the smaller M1/. Differs from *Gerbilliscus* sp. from Asakoma (Middle Awash, Ethiopia) by the prelobe of the M/1 displaying two cusps of unequal size and more fused cusps. Differs from *G. satimani* sp. nov. in the larger size of the molars and M/1 prelobe with well fused cusps and distal opening of the M/1 prelobe.

Measurements: Table 2.8, Fig. 2.15.

Description: In the Upper Ndolanya Beds one finds a somewhat larger *Gerbilliscus*, which has more transversely aligned cusps than in *G. satimani*. It has quite large molars with generally well-fused cusps in transverse laminae, especially the first lobe of M1/1 (Fig. 2.17). Either the prelobe of the M/1 is rounded (55% of cases) or, on one unique unworn specimen (EP 3319/00), it is composed of two cusps of equal size, linked anteriorly and separated by a deep posterior groove, giving a horseshoe-shaped configuration (27%) (Figs. 2.16 and 2.17). Only 9% of specimens have a prelobe open distally, compared with 26% in *G. gentryi* from Olduvai. No M3/3s are yet known for this species. The M1/1s are larger on average than those of *G. gentryi* and *Gerbilliscus* sp. from Omo Members B and F, with which they may be related (Table 2.8, Fig. 2.15). The Hadar specimens (A.L. 333 and A.L. 327 localities) are very similar to the Laetoli *G. winkleri* in the shape of the M/1 prelobe, and fall just at the size limit between *G. gentryi* and *G. winkleri* (Fig. 2.15). We only used the average value provided in Sabatier (1982). Further knowledge of the range of variability of the A.L. 327 sample should help resolve whether or not the Hadar specimen can be placed in synonymy with *G. winkleri*. The Middle Awash ASK-VP1 unique M/1 fits within the range of variability of *G. winkleri* (Fig. 2.15). It belongs to an unworn molar and in contrast to *G. winkleri* specimens it exhibits the trace of two unequal size cusps (unfused) on the M/1, which prevents synonymy with either the Laetoli or Hadar taxa.

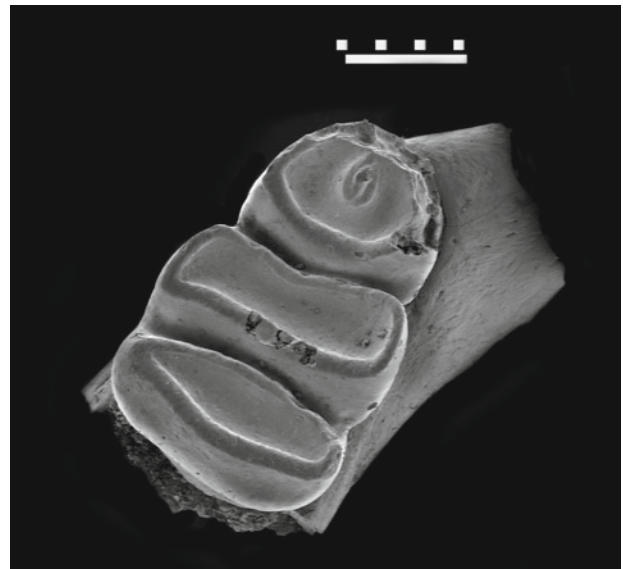


Fig. 2.17 *Gerbilliscus winkleri* sp. nov. EP 817/01 (paratype) from Loc. 18 (Upper Ndolanya Beds), left mandibular fragment with M/1. Scale bar indicates 1 mm

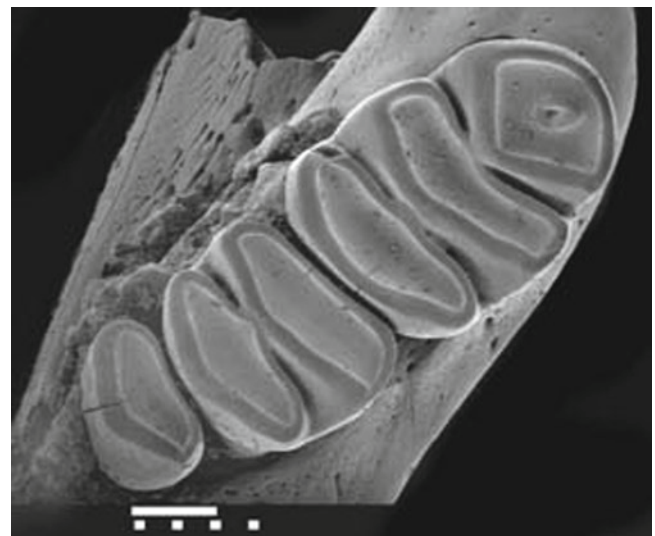


Fig. 2.18 *Gerbilliscus* cf. *inclusus* (EP 1372/98) from Loc. 13. Mandible fragment with M/1-3. Scale bar indicates 1 mm

Gerbilliscus cf. *inclusus*
(Figs. 2.15–2.18)

One new mandible fragment with M/1-3 (EP 1372/98), distinguished by its larger size (Fig. 2.15), has been recovered from Loc. 13 in the Upper Laetoli Beds (Fig. 2.18). Its large dimensions fit with those of Denys (1987a) specimens LAET 75-2726 (Loc. 3) and LAET 75-3588 (Loc. 8), and we add one new taxon to the faunal list of Loc. 13 (Fig. 2.15, Table 2.8). This new specimen has an M/1-3 length of 7.2 mm, which is the same as that for LAET 75-3588 (Table 2.7). The prelobe of M/1, which is a key character for species identification, was not well

preserved on specimens from the old Laetoli material, but on the new specimen it is rounded in its anterior part and distally elongated. The M/3 has only one lobe and is very reduced. Cusps are well fused and transverse, and there is no trace of cingular cusplets, but on the M/2 one still recognizes a trace of a longitudinal link between first and second lobe. The prelobe of M/1 of the Upper Laetoli *Gerbilliscus* cf. *inclusus* is different from that in *Gerbilliscus winkleri* sp. nov. from Laetoli, *G. gentryi* from Olduvai Bed I or *Gerbilliscus* sp. of Asakoma site (Middle Awash). Denys (1987a) compared these specimens with various modern *Gerbilliscus* representatives and found similarities with *G. inclusus*, due to the disposition of the prelobe of the M/1 (open anteriorly) and the relatively small proportions of M/3. Among *Gerbilliscus* of large size (*afra* group of Meester et al. 1986) one also finds *G. afra* and *G. brantsi*, which display a prelobe open anteriorly and with well-aligned cusps. *Gerbilliscus brantsi* displays a wider M/1 compared to *G. inclusus* and *G. afra*, but molar variability is not well known, so pending further taxonomic revisions of this complex we prefer to keep these rare fossils at Laetoli unassigned and retain the initial attribution of Denys (1987a).

Subfamily Murinae Illiger, 1811

Thallomys laetolilensis Denys, 1987

(Fig. 2.19)

Localities and horizons: Locs. 2, 4, 5, 6 and 9. Upper Laetoli Beds up to Tuff 7.

Referred material: EP 148/01, left mandible with M/1-3, Loc. 6. EP 2034/03, right mandible with M/2, Loc. 6. EP 2033/03, left mandible with M/1-3, Loc. 6 (Fig. 2.19). EP 1039/05, right mandible with M/2, Loc. 2. EP 244/05, right mandible with M/1-2 (very worn), Loc. 9. EP 243/05, right mandible with M/1-2, Loc. 9. EP 397/03, right mandible with M/1-3, Loc. 5 (Fig. 2.19). EP 1065/03, right mandible with M/1-3 (very worn), Loc. 10W. EP 187/03, right mandible with M/3, Loc. 4. EP 655/03, right mandible with M/1, Loc.

2. EP 654/03, right mandible with M/1, Loc. 2. EP 1783/03, right mandible with M/1, Loc. 22. EP 996/05, left mandible with M/1-2, Loc. 2. EP 2239/00, left mandible with M/1-3, Loc. 7. EP 1739/04, right mandible with M/1 and a broken M/2, Loc. 2. EP 1871/03, left mandible with M/3, Loc. 4. EP 243/05, left mandible with M/1, Loc. 9.

This small stephanodont murid is quite easy to identify with its stephanodont molars, its small size, and the presence of accessory roots on the M/1. It is rather abundant in the new collections and is found, as in the previous collections, at Locs. 5, 6 and 9. It is also found for the first time at Locs. 2, 4, and 22, but this time was not recorded at Locs. 10, 11 and 21. The new specimens comprise only lower molars and they fit well with the dimensions of the previously collected material (Table 2.9). There is a large size variation within this species that is not explained by locality

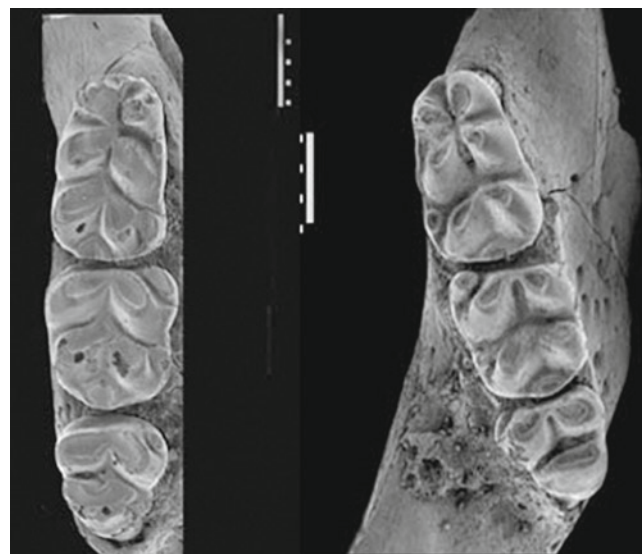


Fig. 2.19 *Thallomys laetolilensis*. Left, EP 397/03 from Loc. 5; right, EP 2033/03 from Loc. 6. Scale bars indicates 1 mm

Table 2.9 Length of M/1-3 and length and width dimensions of M/1 (mm) of the new specimens of *Thallomys laetolilensis* compared to the mean values of the type series (Denys 1987a)

Material	Specimen	LM/1-3	M/1L	M/1W
New specimens	EP 148/01	5.32		
	EP 397/03	4.84		
	EP 2033/03	4.82		
Previous Laetoli collections (type series) (Denys 1987a) (N=11)	Mean	4.98		
	Range	(4.65–5.20)		
New specimens (N=7)	Mean		2.02	1.24
	Range		(1.91–2.19)	(1.14–1.38)
	SD		0.04	0.03
Previous Laetoli collections (type series) (Denys 1987a, Table 6.5, p.137) (N=25)	Mean		2.15	1.34
	Range		(2.00–2.30)	(1.20–1.47)
	SD		0.12	0.08

N number of specimens, SD standard deviation

of origin or stratigraphic horizon of the specimens, because, for instance, EP 148/01 and EP 2033/03 both come from Loc. 6 and the same horizons. They are very different in size, but similar in cusp morphology. One can also observe variability in the disposition of the prelobe cusps on M/1 (Fig. 2.19).

Aethomys sp.
(Fig. 2.20)

One large murid mandible with M/1-2 (EP 1648/00) has been recovered from Loc. 3 in the Upper Laetolil Beds between Tuffs 7 and 8 (Fig. 2.20). By its large size, the absence of a link between the prelobe and second lobe of the M/1, the existence of a large Cv5, the absence of cusplike Cp on M/1 and better developed on M/2, and the trace of a longitudinal crest on the second lobe, this specimen can unambiguously be attributed to *Aethomys*. It is the first record of this genus at Laetoli, but this taxon has already been identified at various East African sites, such as Olduvai Bed I (Jaeger 1976), Natron (Denys 1987b), East Turkana (Black and Krishtalka 1986), the Omo (Wesselman 1984), and Kanapoi (Manthi 2006), and it is possibly present at Lemudong'o (Manthi 2007). It is also recorded from Langebaanweg (Denys 1990) and other South African cave sites (Pocock 1987).

This specimen differs from *A. lavocati* from Olduvai Bed I and from *A. modernis* of Langebaanweg by the absence of a longitudinal crest linking the prelobe to the first lobe of

M/1. Such a cusp prelobe disposition recalls *A. deheinzellini* from Omo Members F and G (Wesselman 1984). It also recalls the large *A. adamanticola* from Langebaanweg, with the same cusp prelobe disposition (no link of the prelobe and first lobe, no tma, presence of cv1 and cv5, a small Cp on M/1 and the presence of a strong cv1 and cv5 on M/2). Among the modern *Aethomys* species, East African forms of the *A. kaiseri-hindei* group correspond in morphology to the Laetoli specimens (with less developed cingular margin and cusps), but not the modern *A. chrysophilus*, which displays a longitudinal link on the M/1, or *A. namaquensis*, which has a tma. The M/1 dimensions of *Aethomys* sp. from Laetoli (2.33×1.52 mm) are much smaller than those of *A. adamanticola* (ranging between 3.00 and 3.15 mm long), *A. deheinzellini* and *A. lavocati* (greater than 2.5 mm in length) (see data in Jaeger 1976; Wesselman 1984; Denys 1990). Comparisons cannot be made with the Lemudong'o and Kanapoi specimens, which only have the M1/ figured and measured (Manthi 2006, 2007). The scarcity of the Pliocene remains attributed to *Aethomys* prevents further identification of the Laetoli *Aethomys* to a known or to a new species.

Mastomys cinereus Denys, 1987
(Fig. 2.21)

In addition to a large *Aethomys* and a medium-small *Thallomys laetolilensis*, there is a small Murinae from Locs. 8 and 11 (from between Tuffs 7 and 8), represented by a right mandible with M/1-2 (EP 1485/03 from Loc. 8) and a mandible with M/2 (EP 2592/00 from Loc. 11) (Fig. 2.21). The M/1 is very worn and broken, but displays the remains of two

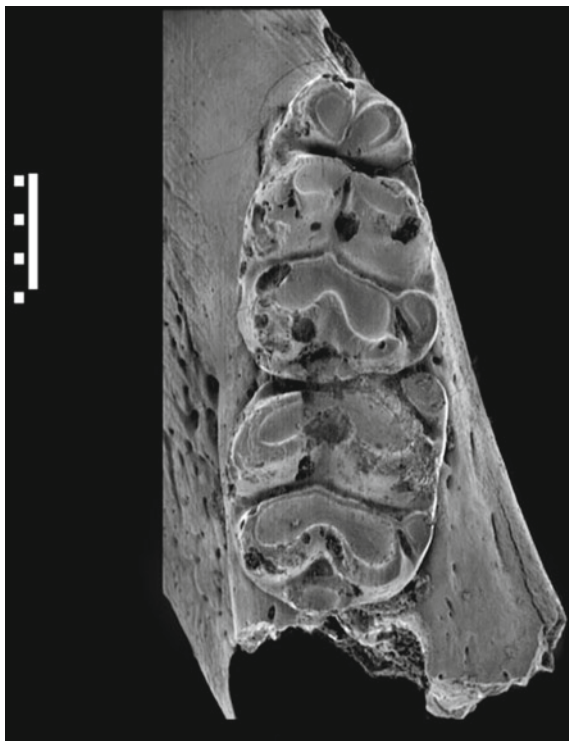


Fig. 2.20 SEM images of *Aethomys* sp. EP 1648/00 from Loc. 3, Upper Laetolil Beds. Scale bar indicates 1 mm

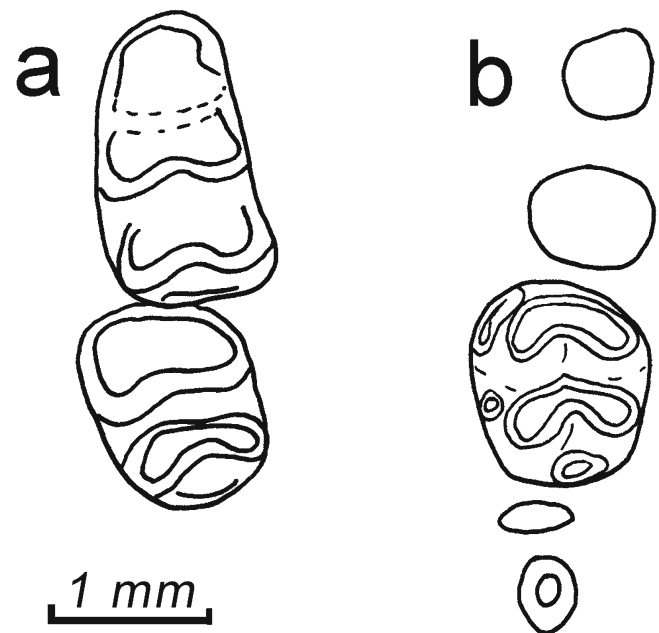


Fig. 2.21 *Mastomys cinereus* from the Upper Laetolil Beds. (a) EP 1485/03 (Loc. 8), left mandible with M/1-2; (b) EP 2592/00 (Loc. 11), left mandible with M/2 and roots of M/1 and M/3

anterior cusps, relatively well fused cusps with poorly marked synclinals, a small posterior cingulum, and the absence of a cingular margin that all characterize the species (Plate 6.4 in Denys 1987a). This molar measures 1.76×1.00 mm, which corresponds to the dimensions of the *M. cinereus* material of the previous collections (Denys 1987a: table 6.6). The M/2 of the specimen EP 1485/03 is also very worn and has nearly the same size as that of EP 2592/00 (1.29×1.05 mm and 1.23×1.05 mm respectively). The less worn M/2 displays a cv1 and cv5, a small posterior and two lobes with a large tC or tD (labial one), as in the isolated M/2 (79/A6108) figured in Denys (1987a: plate 6.4). Moreover, the root pattern on this mandible confirms that M/1 and M/3 each have two roots. In the previous records, *Mastomys cinereus* was known only from Locs. 5 and 6, and was not identified from Locs. 8 and 11 (Denys 1987a).

Infraorder Hystricognathi Brandt, 1855

Family Thryonomyidae Pocock, 1922

Genus *Thrynomys* Fitzinger, 1867

Some hystricognathous mandibles and four-lophed isolated molars were attributed by Denys (1987a) to *Thrynomys* sp. They all came from the Upper Ndolanya Beds (Locs. 7E and 18). The new material allows refinement of the descriptions and a better assessment of the relationship to modern and fossil representative.

Thrynomys wesselmani sp. nov.

(Figs. 2.22–2.25)

Holotype: EP 1324/05, maxillary fragment with P4-M3/ (Figs. 2.22 and 2.24)

Paratypes: EP 814/01, right mandible with M/1-3 (Fig. 2.25), associated with left mandible with M/2-3, Loc. 18. EP 464/05, left mandible with M/2-3 and incisor, Loc. 18. EP 1251/00, left mandible with M/1 and broken M/2 (very damaged), Loc. 22S (Fig. 2.22). EP 1252/00, isolated upper incisors, Loc. 22S (Fig. 2.23).

Type locality: Loc. 22S, Upper Ndolanya Beds, Laetoli.

Age and horizon: Mid-Pliocene (2.66 Ma), Upper Ndolanya Beds at Laetoli Locs. 7E, 18 and 22S.

Etymology: in honor of Hank Wesselman who described the Omo rodents.

Referred material: LAET 76-32 DP/4 (Fig. 2.25), LAET 76-700, M/1-2 (Plate 6.8 in Denys 1987a), LAET 76-117, DP/4-M/2, LAET 73-73, DP4-M/1 (Plate 6.8 in Denys 1987a).

Diagnosis: Intermediate-sized *Thrynomys*, smaller than *T. swinderianus* and slightly larger than *T. gregorianus*. It has a less straight lingual part of the posteroloph on M1/, more elongated DP/4, low crowns and roots visible. The DP/4 has four lophs and is narrow. The upper incisor exhibits three grooves, not equally distributed along the buccal surface of the incisors as in *T. gregorianus*, but grouped on the lingual side of the incisor as in *T. swinderianus* (Fig. 2.23). Distinct from the



Fig. 2.22 SEM images of *Thrynomys wesselmani* sp. nov. from the Upper Ndolanya Beds. Left, EP 1324/05 (holotype) from Loc. 22S (P4-M3/). Right, EP 1251/00 from Loc. 22S (left mandible with M/1-2)

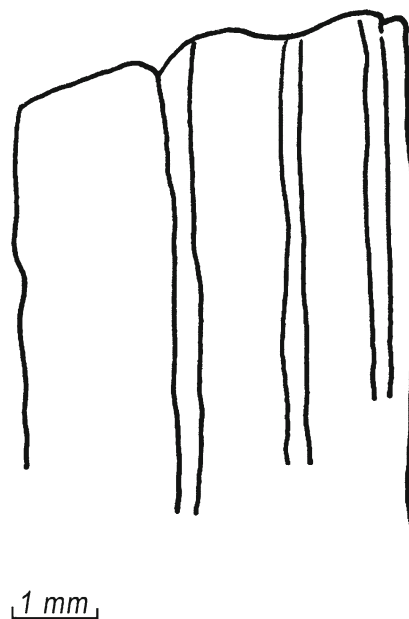


Fig. 2.23 Buccal side of the upper incisor of *Thrynomys wesselmani* sp. nov. (EP 1251/00). Scale bar indicates 1 mm

extinct Miocene *Paraphiomys* in lacking a mesoloph (*Thrynomys* has only three lophs on the upper molars) and relatively similar to fossil *Paraulacodus* and modern *Thrynomys* species.

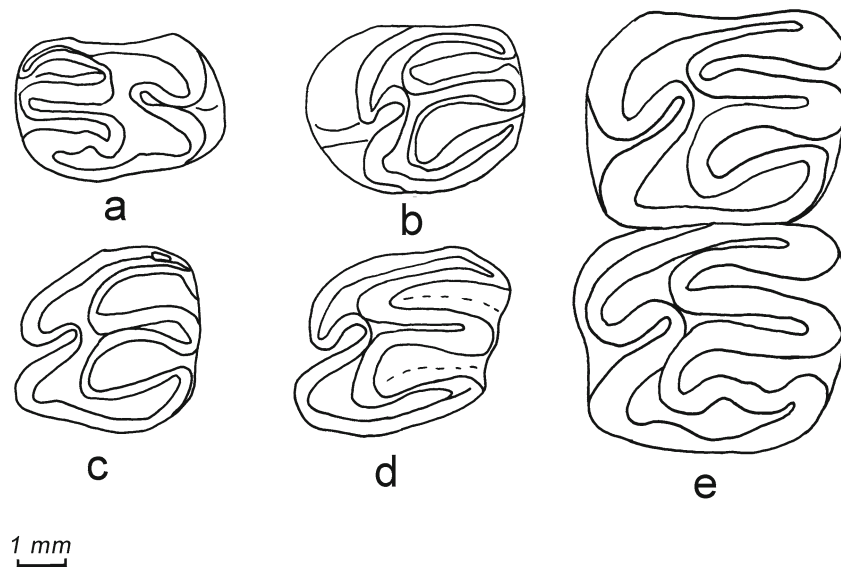


Fig. 2.24 Drawings of upper molars of *T. wesselmani* sp. nov. compared with other fossil and modern *Thryonomys* spp. (a) holotype, M1/, *T. wesselmani* sp. nov.; (b) LAET 73A, M1/, *T. wesselmani* sp. nov.; (c) right M1/ *Thryonomys gregorius* Omo L1-374, Member B;

(d) left M1/ of a young modern *T. gregorius*, BM(NH) 32.864, Kenya; (e) M1-2/ of modern *T. swinderianus*, MNHN 1892-1608 from the Congo

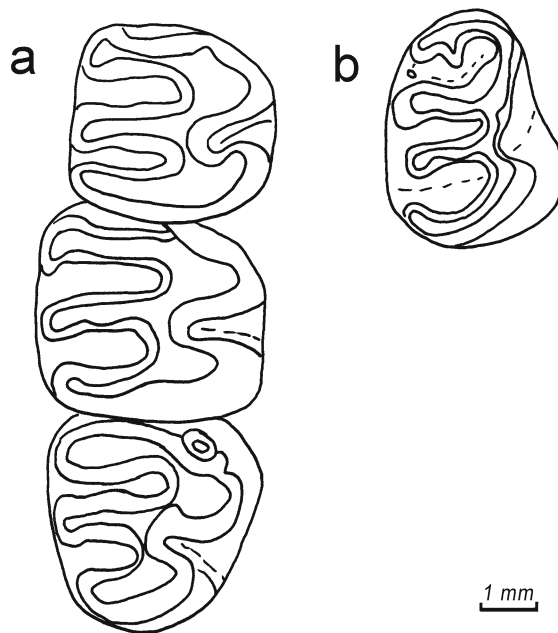


Fig. 2.25 Lower molar row of *T. wesselmani* sp. nov. (a) EP 814/01, right mandible with M1-3; (b) LAET 7E-32, right DP/4

Differs from the modern *T. swinderianus* by the lower hypsodonty (lower crowns with visible roots), and smaller size. Differs from *T. gregorius* by the groove disposition on the upper incisor and larger size of the molars. It is distinct from *Paraulacaudus* by having less oblique lophs on the M1/, the presence of three versus two grooves on the

upper incisors and by its larger size. It is distinguished from the Middle Awash late Miocene *Thryonomys asakomae* (Wesselman et al. 2009) by the presence of three grooves on the upper incisors instead of two and by its larger size.

Measurements: Tables 2.10 and 2.11

Description: The holotype has quite broken and worn molars, but on these one can distinguish the presence of three lophs on the upper molars as in modern *Thryonomys* (Figs. 2.22 and 2.24). The crowns are very low. The upper incisors are much narrower than in modern *Thryonomys* (Table 2.11) and display three grooves placed along the lingual half of the buccal surface (two large grooves of equal size and a small one, Fig. 2.23). This disposition is similar to *T. swinderianus* incisors, which also display three grooves grouped on the internal part of the surface, and the first groove is much deeper than in the fossil (figured in Kingdon 1974).

The DP4/ of *T. wesselmani* is in a bad state of preservation and none was previously recorded in the old Laetoli collections, but one can distinguish three lophs on a small, squared crown with an anteroloph running obliquely toward the anterior wall of the tooth and three oblique parallel lophs. The posteroloph (loph III of Denys 1987a) is relatively transverse and long, not convex distally. On the upper dental row, the protocone and hypocone are large, the hypocone being much more developed than the protocone, and they are relatively transverse as in modern *Thryonomys* spp. The labial valley (or sinus) separating these two cusps is oblique as in modern species. On the M1/ and M2/ of the holotype there is a little

Table 2.10 Tooth dimensions (mm) for fossil and modern *Thryonomys* spp. *Thryonomys wesselsmani* includes material from this work and Denys (1987a)

Specimen	LTR	DP/4	M1/	M2/	M3/	UTR	M1/	M2/	M3/
<i>T. wesselsmani</i>									
EP 1251/00			4.55×3.85						
EP 464/05				4.89×4.17	4.71×4.18				
EP 814/01			5.00×4.66	4.81×4.96	4.52×4.56				
EP 1324/05						15.45+	3.79×4.53	3.89×5.9	4.32×6
LAET 74-32		4.9×3.1							
LAET 75-700		(4.8)×3.1	4.7×4.8						
LAET 75-117		4.8×3.6	4.2×4.8	4.4×5.2					
LAET 74-31									
Mean		4.83×3.27	4.61×4.53	4.85×4.57	4.62×4.37				
<i>T. asakomae</i>			3.25–4.24× 3.40–4.30	4.00–4.10× 3.73–4.27	4.14–4.32× 3.84–4.07		3.56–3.63× 4.92–4.93	3.18–3.89× 3.44–5.13	3.14–3.69× 3.73–4.61
<i>Thryonomys</i> sp. Manonga									
Lemudong'o 45945			1.50×1.20	1.50×1.40			3.07×3.79	3.22×3.44	
Lemudong'o 45934			2.00×1.70						
<i>T. swinderianus</i>									
Omo J		6.15×4.56							5.60×6.50
<i>T. gregorius</i>									
Omo B							3.70×4.28		
<i>T. gregorius</i>									
OM6435 Kenya	18.48	5.32×3.73	4.23×4.29	4.31×4.62	4.35×3.79	15.55		4.12×4.84	4.36×4.22
OM7595 Kenya		5.65×3.64	4.45×4.46	4.45×4.31				4.14×4.90	
BM 30.3.4.4 Kenya		5.84×4.70	4.50×4.94	4.94×4.72				4.64×5.00	4.90×5.00
BM 32.8.6.4 Kenya		5.40×4.10	4.60×4.92	4.94×5.36				4.16×5.4	4.20×5.8
<i>T. swinderianus</i>									
1892-1607									
Central African Republic	20.27		4.56× –	4.62×5.76	5.23×5.70	17.20	4.87×6.56	5.66×6.4	5.59×6.49
1974-35 Gabon	20.85	6.42×4.18	4.66×5.45	4.76×5.49	4.75×5.16	18.03	4.62×5.95	4.58×6.25	5.83×6.05
1991-200 Congo	20.62	6.30×4.22	4.75×5.47	4.77×5.14	4.59×5.54	18.19	3.97×5.53	4.46×5.44	4.52×5.17

Data sources: Manonga, *Thryonomys* sp. (Winkler 1997); *T. asakomae* (Wesselman et al. 2009), Lemudong'o (Manthi 2007), Omo Shungura, *T. swinderianus* and *T. gregorius* (Wesselman 1984), modern representatives from museum collections. LTR: Upper tooth row length (DP/4-M/3); UTR: Upper tooth row length (DP4-M/3/)

Table 2.11 Buccolingual width of the upper (UI) and lower (LI) incisors of modern *Thryonomys swinderianus* from MNHN collections and of fossil *T. wesselmani* sp. nov

Species	UI width	LI width
<i>T. swinderianus</i> 1892-1607	5.79	5.72
<i>T. swinderianus</i> 1947-35	5.42	5.17
<i>T. swinderianus</i> 1991-200	5.82	5.61
<i>T. wesselmani</i> sp. nov.		
EP1252/00	4.77	
EP 464/05		5.31
EP 814/01		5.65
Omo J		3.67
Omo C		4.88
Omo F	4.40	

inflexion of the loph at the place where the anteroloph starts on P4/ and is reminiscent of this crest (Fig. 2.22). This is not visible on the modern *Thryonomys swinderianus*, which have very rectilinear lophs (Fig. 2.23). The M1/ or M2/ was described in Denys (1987a: fig. 2, plate 6.8), and we summarize here the main features. It bears three lophs. The anteroloph is long and convex and joins a small crestiform protocone at the anterolingual corner of the tooth. The metaloph is oblique and is prolonged by the paracone, which is situated in the anterolingual part of the tooth. The posteroloph is also long and reaches the posterolingual corner of the molar to a crestiform metacone, which is also nearly longitudinal in its disposition. The protocone is nearly longitudinal, while the hypocone is oblique; both are joined by a longitudinal ectoloph. The crown is low and the cusps are bunodont.

The DP/4 is broken in all the new specimens, but LAET 17E-32 displays four lophs as in modern *Thryonomys* species (Fig. 2.25). Denys (1987a) mentioned that the M/1 protoconid and hypoconid are more transverse than in modern *Thryonomys* (where they are very oblique and crestiform) and the lophs are convex distally, which is also visible in EP 814/01 (Fig. 2.25), while in the modern species they are much more rectilinear and transverse. There is a short anterolophid running obliquely from the protoconid, which is visible as a separate cusp/crest on the M/1-2; a feature not seen on modern *Thryonomys* spp. or only present as a small inflated zone incorporated into the anterolophid. Lophid III is shorter in *T. wesselmani* than in modern species, where it occupies the whole breadth of the molar. The M/3 is preserved in EP 814/01 and displays three lophs and a short anteroconid incorporated into the base of the protoconid and protolophid. The molar is as long as M/2, but narrower distally, with a very reduced hypoconid and a very small posterolophid (loph III). Compared with modern *Thryonomys*, it is smaller, less convex and crestiform, and the distal half of the M/3 is proportionally wider, with the same proportions and width as the M/2. This loph is narrower on modern *Thryonomys*

only when the molars are slightly worn and there is no link between the two lobes of the molar. In EP 814/01, which is intermediate in wear, the link is made between the two distal lobes of the molars, and it has low crowns (Fig. 2.25).

The oldest *Thryonomys* comes from late Miocene deposits of the Middle Awash of Asakoma, Biki Mali Koma, and Gigiba Dora localities, all dated at 5.7 Ma (Wesselman et al. 2009). On the figured molars of *T. asakomae* one can see that the lophs are much longer and more transverse, and the cusps are much more crestiform than in the new Laetoli species. The crowns appear higher, and this gives the Middle Awash fossils a very modern aspect. All the molars of *T. asakomae* are larger than the Lothagam and Manonga specimens, and smaller than Laetoli *T. wesselmani* and the modern *Thryonomys* species (Table 2.10). In addition, *Thryonomys* cf. *gregorianus* was described from the Nachukui Formation at Lothagam (Winkler 2003), and specimens attributed to *Thryonomys* sp. occur in the Manonga Valley at Ibole (Winkler 1997). They are represented by two upper molars of much smaller size and moderate hypsodonty compared to *Thryonomys* from the Upper Ndolanya Beds. They could belong to a different species from the Laetoli material, and may represent an ancestral form. According to Wesselman et al. (2009) they are related to modern *T. gregorianus*. The discovery of new specimens of a bunodont *Thryonomys* at Laetoli confirms that the divergence between the two modern lineages of *Thryonomys* had already occurred by the mid-Pliocene.

The only other record of the genus from East Africa is from the Omo Shungura Formation, where Wesselman (1984) recorded both *T. swinderianus* in Member J and *T. gregorianus* in Members B, C and F. Examination of these specimens shows that the Omo L1-174 (from Member B, Fig. 2.24) assigned by Wesselman (1984) to *T. gregorianus* belongs to a young animal. It displays a small anteroloph, not reaching the labial corner of the molar, and it is smaller in size than modern *T. gregorianus* (Table 2.10). It could belong to a species distinct from the modern one, and close to *T. wesselmani*. As for the specimens referred to *T. swinderianus* from Omo Member J, they are clearly larger than *T. wesselmani*. Manthi (2007) figured and describe a thryonomyid indet. of small size from Lemudong'o that displays three transverse lophs on the M/1-2. It is difficult to assign this specimen to any previously described species, but it could be the earliest known representative of the genus at 6 Ma (Table 2.10). No *Thryonomys* specimens have been described from the South African Pliocene sites.

T. wesselmani sp. nov. retains some primitive characters, such as the anteroloph/anterolophid trace and its intermediate size, and it could represent the ancestor of the two species living in tropical Africa today. Compared to *Thryonomys* sp. from Ibole (Manonga Valley) described by Winkler

(1997), *T. wesselmani* has a smaller upper M1-2, even smaller than those we have measured for *T. gregorianus*, the smallest of the modern species. However, the paucity of the Ibole and Laetoli material does not allow refinement of species attributions, but they probably constitute two valid species.

Family Petromuridae Wood, 1955

Petromus sp. A. Smith, 1831

(Figs. 2.26–2.27)

Three very damaged mandibles from the Lower Laetolil Beds (EP 014/98, mandible with M/1, Kakesio; EP 014/99, left mandible with M/2 (Fig. 2.26), Kakesio; and EP 2076/03, right mandible with P/4-M/3, Emboremony 1) (Fig. 2.27), can be attributed to *Petromus* because the molars display only two wide lophs and traces of a small posteroloph (Fig. 2.26). The distal parts of the mandibles are broken, but there are signs of less of a hystricognath disposition than in *Thryonomys*, which characterizes the modern *Petromus*. The M/3 displays two distinct anterior cusps (or a cusp consisting of two fused ones) as in modern *P. typicus* from South Africa (Fig. 2.27). The presence of a very small posteroloph differentiates it also from *Paraulacodus* and *Paraphiomys*, which have three and four lophs on M/1-2. The DP/4 is clearly distinct from that of *Thryonomys* in displaying only three lophs and in being very simplified, with no mesolophid (Fig. 2.27). In some regards, the DP/4 resembles *P. shipmani* from Fort Ternan (Denys and Jaeger 1992) and *P. roessneri* from Harasib (Mein et al. 2000b). The Lower Laetolil specimens have a strong metaconid linked to the hypoconid by a slightly oblique crest, and there is still a trace of a posteroloph that is not present on specimens of *P. antiquus* from the early Pliocene of South Africa (Sénégas 2004). *Petromus antiquus* has an ectolophid situated in the middle of the molars and arranged longitudinally, and the cusps are much more transversely fused and aligned than in the Lower Laetolil specimens. Mein and Pickford (2006) briefly described a single left mandible with damaged M/1-2 from Kapsomin, Lukeino Formation, which they identified as *P. cf. antiquus*. The published photograph does not allow identification of the main characters, except for the fused and transverse labial and lingual cusps.

On modern *P. typicus* the two lophs are oblique, the distal cusps are well fused and poorly individualized, the teeth have higher crowns and the presence of cement, and they are of comparable size or slightly smaller than the Lower Laetolil specimens (Table 2.12). The Lower Laetolil *Petromus* sp. clearly represents a very early evolutionary stage, and it could represent an extinct genus intermediate between *Phiomys* spp. and modern *Petromus*. However, pending further material, notably of upper molars, we attribute these fossils to *Petromus* sp. for the moment. If this attribution is



Fig. 2.26 *Petromus* sp. Detail of the M/2, EP 014/99, Emboremony 1 (Lower Laetolil Beds). Scale bar in mm

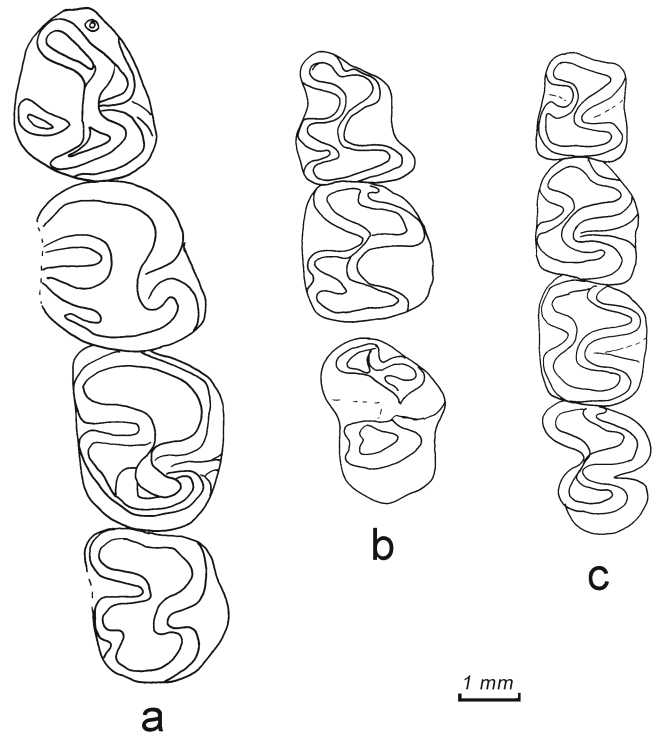


Fig. 2.27 Comparisons of lower dentition of *Petromus*. (a) EP 2076/03, right mandible with DP/4-M/3 of *Petromus* sp.; (b) juvenile mandible with DP/4-M/2 of modern *P. typicus* from southwest Africa (Cape museum collections, ZM119111A); (c) modern adult right mandible of *P. typicus* from the NHM collections. Drawings to the same scale

Table 2.12 Dimensions (mm) of *Petromus* spp. from Lower Laetoli Beds compared with *P. antiquus* from Waypoint 160 (Sénégas, unpublished) and modern *P. typicus*

	P/4-M/3	P/4	M/1	M/2	M/3
EP 014/98				3.10×2.71	
EP 2076/03	11.46	2.91×2.33	2.72×2.72	3.00×2.48	2.52×2.24
<i>P. antiquus</i>		1.90×1.74	2.82×2.65	2.65×2.88	2.89×2.53
<i>P. typicus</i> BM25.1.2.219		1.73×1.58	2.19×1.77	2.12×1.89	2.23×1.92
<i>P. typicus</i> ZM119.111A		2.08×2.00	2.40×2.24	2.72×2.12	

confirmed, it would be the second record of fossil *Petromus* for the Pliocene of East Africa. The first record being the poorly known *P. cf. antiquus* from Lukeino (Mein and Pickford 2006). Other fossil *Petromus* are known from South African sites, and recently Sénégas (2004) described *P. antiquus* from the Gauteng Province, South Africa at Waypoint 160 (close to Bolt's Farm) of early Pliocene age. A single specimen was previously recorded from Taung: *P. minor* Broom, 1939 and a *Petromus* sp. is recorded from Namibian sites in the Otavi mountains and Kaokoland (Pickford et al. 1994). According to Sénégas (2004), *P. minor* is similar to *P. antiquus*, but there are some differences in molar proportions. *Petromus typicus* is found today only in western South Africa, Namibia and southwest Angola (Woods and Kilpatrick 2005).

Family Bathyergidae Waterhouse, 1841

Genus *Heterocephalus* Rüppell, 1842

Heterocephalus manthii sp. nov.

(Figs. 2.28–2.31)

Holotype: Half cranium, KK 82-28 (currently on loan to the National Museum of Kenya, Nairobi, but part of the permanent collections of the National Museum of Tanzania, Dar es Salaam) (Fig. 2.28)

Paratypes: (currently on loan to National Museum of Kenya, Nairobi, but part of the permanent collections of the National Museum of Tanzania, Dar es Salaam): KK 82-1, maxilla with left M13/ and right M2/ (Fig. 2.29). KK 82-43, maxillary fragment. All from Kakesio.

Type locality: Kakesio, Lower Laetolil Beds, Tanzania.

Age and horizon: Mid-Pliocene, Lower Laetolil Beds.

Diagnosis: Small hypsodont *Heterocephalus* species with a long, bilobed M3/, well marked anterior and posterior depressions on M1/, presence of elongated distolingual angle on M1/.

Differs from modern *H. glaber* in the proportions of the molars, smaller size, and greater hypsodonty. It is distinguished from *H. quenstedti* by the bilobed, longer M3/. It has smaller molars than *H. atikoi* from Omo Members F and G,

and *H. jaegeri* from Olduvai Bed I. It is less hypsodont than *H. quenstedti* and *H. jaegeri*, but it is much more hypsodont than modern *H. glaber*.

Measurements: Tables 2.13 and 2.14

Description: One cranium with the lower jaw in articulation (KK 82-28) and two fragments of maxilla (KK 82-43 and KK 82-1) with three upper molars can be attributed to the genus *Heterocephalus*. These were all collected in 1982 by Mary Leakey's expedition working in the Lower Laetolil Beds at Kakesio. To our knowledge this is the oldest representative of the genus in Africa. The anterior part of the cranium (nasal and upper incisors) is broken and the dorsal view does not show any significant differences from modern or other fossil *Heterocephalus* species (Fig. 2.28). The width of the interorbital constriction measures 6.4 mm, which is wider than in modern *H. glaber* (5.2–6.2 mm) and similar to *H. quenstedti* from the Upper Laetolil Beds (the holotype measures 6.2 mm) and narrower than *H. jaegeri* from Olduvai Bed I (6.6 mm). Neither the tympanic bullae nor the distal part of the cranium are visible, which prevents further comparison with other species. The Kakesio molar dimensions (except M3/ length) are smaller than or equivalent in size to *H. quenstedti* specimens from the Upper Laetolil Beds (Tables 2.13 and 2.14). The very long, but narrow M3/ of *H. manthii* allows it to be distinguished from *H. quenstedti*, as well as from other species of *Heterocephalus*. The M1/ is square and it presents a small anterior median depression, a very shallow labial sinus, barely extended along the labial wall of the crown (Fig. 2.29). The distolingual angle is elongated. There is a small posterior median depression. The M2/ is only slightly larger than M1/. The labial sinus is as deep as one half of the width of the tooth (Fig. 2.29). The distolingual angle is not as well marked as on M1/. There is no anterior median depression. The M3/ is the largest tooth of the molar row, but is narrower. It displays two separate lobes (Fig. 2.29). The anterior lobe is twice as wide as the posterior one, and it presents an anterior depression that is slightly lingually displaced. The second lobe is rounded.

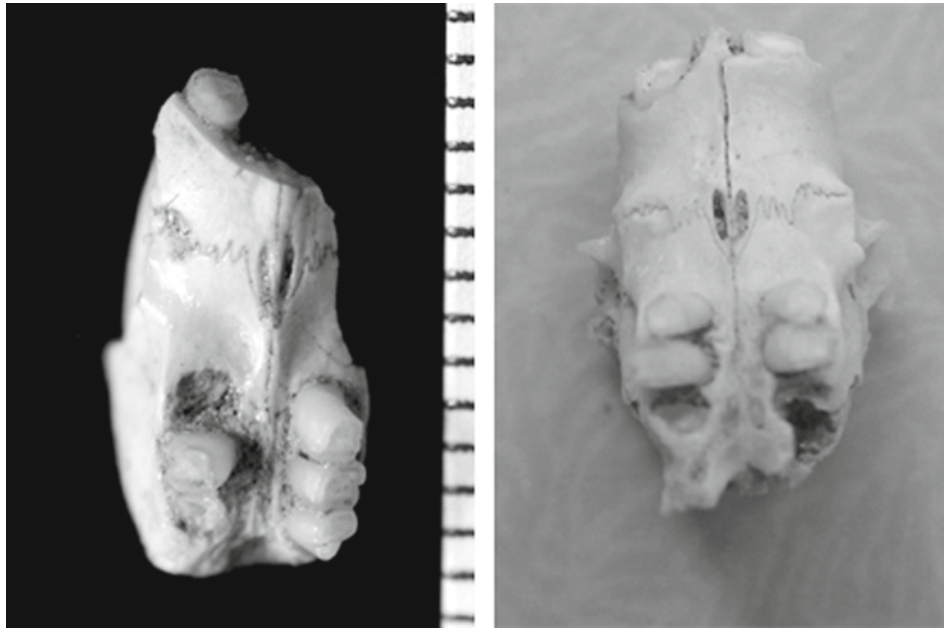


Fig. 2.28 *Heterocephalus manthii* sp. nov. KK 82-1 (right) from Kakesio. EP 2205/03 (left), *H. quenstedti* from Loc. 7, Upper Laetolil Beds

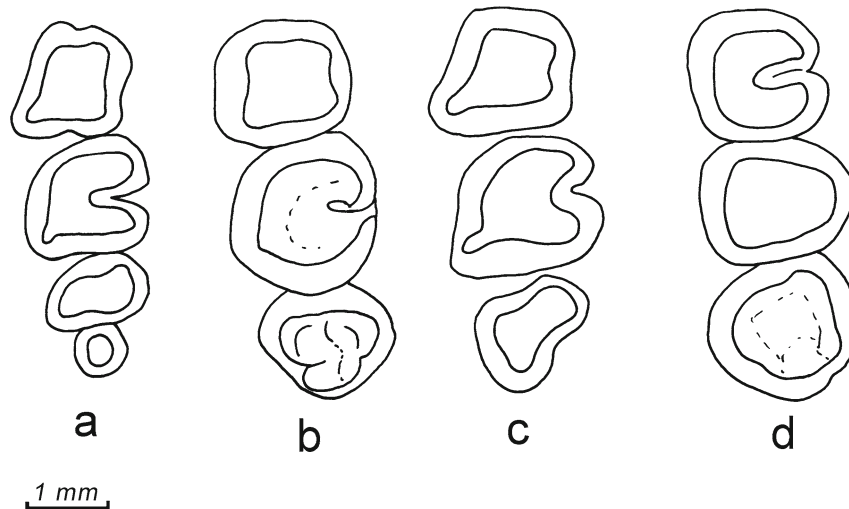


Fig. 2.29 Comparison of the upper left molar rows of *Heterocephalus* spp. (a) *H. manthii*, holotype, KK 82-1; (b) *H. quenstedti*, LAET 75-2808; (c) *H. jaegeri*, Olduvai Bed I, FLK N1 M3; (d) *H. glaber* (MNHN 1901-72)

This molar is as long as one of the specimens from Olduvai and the Upper Laetolil Beds, but much narrower (Table 2.14). *Heterocephalus manthii* displays greater hypsodonty than modern *H. glaber*, but a lower degree of hypsodonty than the Upper Laetolil *H. quenstedti*.

Compared with the material from Upper Laetolil and Olduvai, the Kakesio specimens exhibit several distinctive characteristics, including the longer, bilobed M3/, and the

well-marked anterior and posterior depressions on M1/. Like *H. jaegeri* and *H. quenstedti*, one sees the elongated distolingual angle, and the absence of labial sinus on M1/ related with increased hypsodonty. This indicates that they belong to the same extinct lineage of naked mole rats. *Heterocephalus manthii* from Kakesio has small molars compared to *H. quenstedti*, but the range of variability of this species is not yet known (Table 2.14).

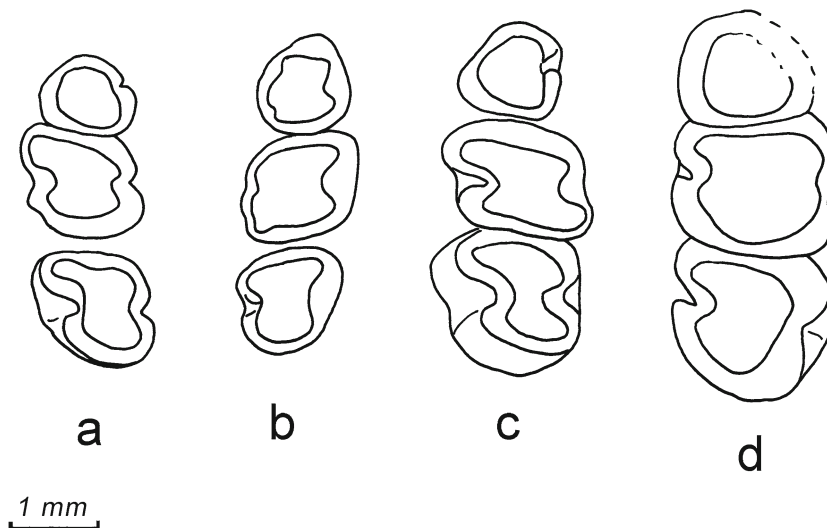


Fig. 2.30 Lower molar rows of fossil and modern *Heterocephalus* spp. (a) left mandible with M/1-3, EP 1059/98 from Loc. 9S, *H. quenstedti*; (b) right mandible with M/1-3, EP 2921/00 *H. quenstedti* from Loc.

10E, *H. quenstedti*; (c) right mandible with M/1-3 of *H. jaegeri*, FLKN1 M4 Olduvai Bed I; (d) right mandible with M/1-3 of modern *H. glaber* (MNHN-1978-268) from Somalia. Drawings to the same scale

Heterocephalus quenstedti Dietrich, 1942
(Figs. 2.28–2.32)

Naked mole rats were relatively common in the Upper Laetolil Beds and are well represented by cranial fragments (Denys 1987a). The new collections have led to the recovery of additional specimens of this species from various horizons and localities. The specimens exhibit the same dental pattern as previously described. The new material is listed in Appendix 2.4. The following three specimens have been illustrated using SEM: EP 4151/00, left mandible with M/1-3 (Fig. 2.32), Loc. 8; EP 1082/03, right mandible with M/1-3, (Fig. 2.32) Loc. 10W; EP 1990/00, half cranium with M1-2/ (Fig. 2.32), Loc. 5.

Additional specimens (32 new specimens) have been recovered from Locs. 1NW, 2, 5, 7, 8, 9S, 10, 10W, 10E, 22 and 22E from levels throughout the Upper Laetolil Beds. This extends the distribution of the species at Laetoli and also increases the number of available specimens. Previously it was described from Garusi by Dietrich (1942) and from Locs. 2, 5, 6, 8, 10, 11, 13 and 21 by Denys (1987a). The length of the complete lower molar row of the three new specimens has an average of 3.95 mm (Table 2.13), which fits with the Garusi, Deturi 160, LAET 75-608 and LAET 75-3512 specimens of *H. quenstedti*. One new specimen displays an M1-3/ length of 4.05, which is larger than in the type specimen (LAET 75-2808, M1-3/ = 3.6 mm), but identical to LAET 76-4166, which has a length of about 4.0 mm (Table 2.13).

A scatterplot of molar size for the two most common molars of *Heterocephalus* spp. is presented in Fig. 2.31. The M/2 of *H. quenstedti* from the Upper Laetolil Beds is smaller

than that of the Olduvai Bed I *H. jaegeri* and modern *H. glaber*. *Heterocephalus atikoi* (Omo Shungura F, G) is intermediate between the largest individuals in the *H. quenstedti* range and the smallest ones of *H. jaegeri*. The M1/ of *H. manthii* (Lower Laetolil Beds) falls in the middle of the *H. quenstedti* range, while the Olduvai *H. jaegeri* and *H. glaber* have longer, but not wider molars.

Family Hystricidae G. Fischer, 1817

This family is quite well represented at Laetoli, with three different species of porcupines. The new collections confirm the remarkable diversity of this group in East Africa during the Pliocene.

Hystrix leakeyi Denys, 1987
(Fig. 2.33)

New specimens: EP 392/98, germ of P/4, Loc. 10E. EP 1037/05, germ of M/1-2, Loc. 2. EP 655/05, mandible with P/4-M/2, Loc. 6 (Fig. 2.33). EP 1377/00, left mandible with M/1, Loc. 6. EP 3068/00, maxilla with DP4-M3/, Loc. 5. EP 142/05, isolated left DP/4, Loc. 8.

Referred material: Hadar and Laetoli type series in Denys (1987a).

Measurements: Table 2.15.

Denys (1987a) indicated that *H. leakeyi* occurred in Locs. 3, 5, 7, 9, 11, 12S, 15 and 20 of the Upper Laetolil Beds. The new material from Laetoli adds Locs. 6, 8, and 10E to the distribution of this species. Some new specimens display the same size and shape (i.e., small, wide, very rounded and low-crowned molars) as in *Hystrix leakeyi* from the Upper

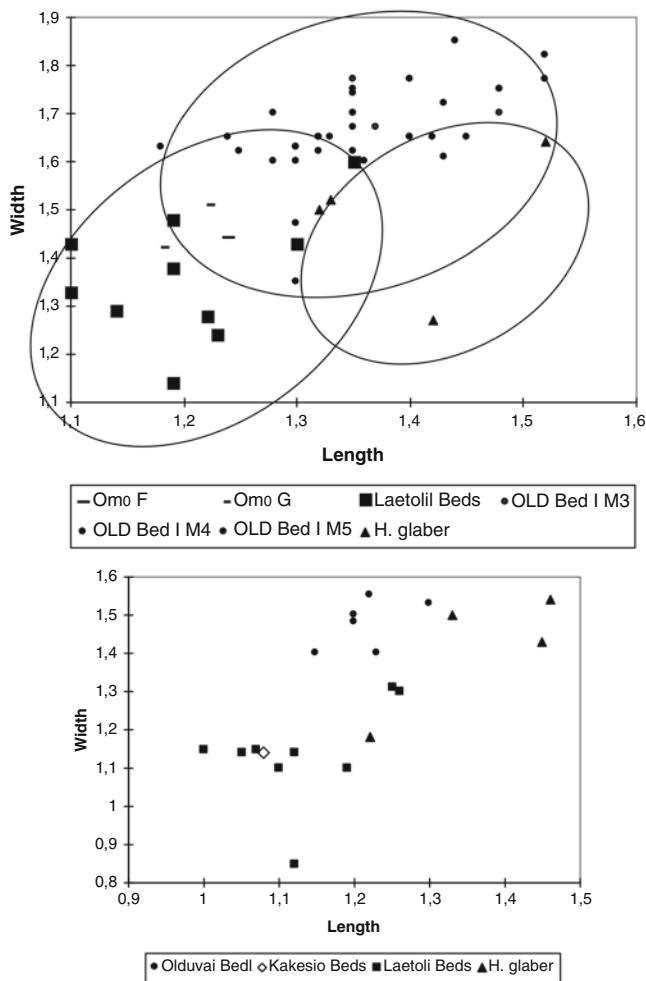


Fig. 2.31 Scatterplots of length×width (mm) of M/2 (top) and M1/ (bottom) of fossil and modern *Heterocephalus* spp. Measurements for Kakesio and Upper Laetolil Beds (this work, Denys 1987a), Omo F and G (Wesselman 1984), Olduvai Bed FLKN M3, M4, M5, after (Denys 1989b), modern *H. glaber* from Kenya and Ethiopia measured from NHM and MNHN specimens

Laetolil Beds and Hadar. Hlusko (2007) described a small *Hystrix* sp., based upon a very worn isolated molar from Lemudong'o, which displays the brachyodont pattern of *H. leakeyi*. The length of M/1 or M/2 is smaller (6.7 mm) than in *H. leakeyi* specimens from Laetoli. *Hystrix* sp. has been recorded at Lothagam and Lukeino. Both are of small size (Table 2.15), with visible roots and brachyodont molars that could be attributed to *H. leakeyi* (Winkler 2003; Mein and Pickford 2006). A third Kenyan *Hystrix* sp. of unknown age is recorded by Manthi (2006), and is also characterized by small molar size (Table 2.15). However, the variability of these late Miocene/early Pliocene fossils is poorly known.

Hystrix makapanensis Greenwood, 1958

This larger species of *Hystrix* appears to be very common in East and South Africa during Plio-Pleistocene time, and it

Table 2.13 Upper and lower molar row lengths of modern and fossil *Heterocephalus* spp.

Specimen	Species	M/13	M13/
KK 1	<i>H. manthii</i>		3.41
EP 043/01	<i>H. quenstedti</i>		3.79
EP 1082/03	<i>H. quenstedti</i>		4.05
EP 2921/00	<i>H. quenstedti</i>	3.94	
EP 4151/00	<i>H. quenstedti</i>	3.86	
LAET 75-608	<i>H. quenstedti</i>	3.57	
LAET 76-4166	<i>H. quenstedti</i>		4.00
LAET 75-2808	<i>H. quenstedti</i>	3.60	3.60
DET 160	<i>H. quenstedti</i>	3.97	
M3BED1	<i>H. jaegeri</i>	3.92	
M4BED1	<i>H. jaegeri</i>	4.05	
M4BED1	<i>H. jaegeri</i>	3.65	
M5BED1	<i>H. jaegeri</i>	3.82	
M5BED1	<i>H. jaegeri</i>	3.95	
M5BED1	<i>H. jaegeri</i>	3.78	
1884-1572	<i>H. glaber</i>	3.65	3.85
BM51-703	<i>H. glaber</i>	3.84	3.56

has recently been suggested that *Hystrix* sp. from the Middle Awash is related to this Pliocene species (Wesselman et al. 2009). It has high crowned and rather large molars (larger than modern *H. cristata* and *H. africae australis*).

Referred material: EP 1996/00, isolated right M/1 or M/2, Loc. 5, Upper Laetolil Beds. EP 329/00, six associated molars, Loc. 8, Upper Laetolil Beds. EP 988/00, left mandible with DP/4-M/2, Loc. 18, Upper Ndolanya Beds. EP 086/03, isolated M1/or M2/, Loc. 18, Upper Ndolanya Beds. EP 3354/00, left lower DP/4, Loc. 15, Upper Laetolil Beds. EP2015/00 isolated right M1-2, Loc. 5, Upper Laetolil Beds. EP 376/05, broken molar, Loc. 15, Upper Ndolanya Beds.

Measurements: Table 2.15.

Denys (1987a) indicated that *H. makapanensis* occurred in Locs. 3 and 10 of the Upper Laetolil Beds. The new material from Laetoli adds Locs. 5, 8 and 15 to the distribution of this species. The Upper Ndolanya Beds did not yield any hystricids from the Mary Leakey collections, but Dietrich recorded several specimens that were attributed to *Hystrix* sp. by Denys (1987a). These are from Garusi and were attributed to the Upper Ndolanya Beds. New specimens collected since 1998 come from the Upper Ndolanya beds (Locs. 15 and 18). These new findings are the first testimony of *Hystrix makapanensis* discovered *in situ* in the Upper Ndolanya Beds since 1939.

Xenohystrix crassidens Greenwood, 1955

An isolated DP/4 with a very wide crown (11.88×8.69 mm) (Table 2.15) and displaying the same root pattern as specimens of the extinct species *X. crassidens*. This tooth (EP 1786/00) comes from Loc. 2 in the Upper Laetolil beds. Two other large indeterminate molars, which are very corroded,

Table 2.14 Molar dimensions of fossil and modern *Heterocephalus* spp.

Species	Level	Molars	Length			Width				
			N	Mean	SD	Range	N	Mean	SD	Range
<i>H. manthii</i> sp. nov.	Kakesio (Lower Laetolil Beds)	M1/	1	1.08			1	1.02		
		M2/		1.14				1.17		
		M3/		1.19				0.91		
<i>H. quenstedti</i>	Upper Laetolil Beds Denys (1987a)	M1/	2	1.18	0.13	1.07–1.26	3	1.28	0.04	1.15–1.3
		M2/	3	1.4	0.17	1.23–1.56	3	1.34	0.03	1.33–1.38
		M3/	1	1.03			1	1.13		
<i>H. quenstedti</i>	Upper Laetolil Beds this work	M1/	4	1.12	0.06	1.05–1.19	4	1.12	0.02	1.1–1.14
		M2/	1	1.24			1	1.19		
		M3/	1	0.95			1	1.05		
<i>H. atikoi</i>	Omo F	M3/	1	1.1			1	1.47		1.39–1.52
	Omo G	M2/	2			1.34–1.47	2			
<i>H. jaegeri</i>	Olduvai Bed I	M1/	8	1.21	0.05	1.15–1.3	8	1.47	0.06	1.4–1.55
		M2/	6	1.32	0.11	1.17–1.4	6	1.63	0.08	1.52–1.75
			1	1.18			1	1.2		
<i>H. quenstedti</i>	Upper Laetolil Beds Denys (1987a)	M1/	5	1.04	0.13	0.87–1.13	5	1.03	0.08	0.95–1.07
		M2/	4	1.22	0.09	1.1–1.35	4	1.4	0.08	1.28–1.6
		M3/	3	1.43	0.18	1.4–1.6	3	1.28	0.1	1.25–1.4
<i>H. quenstedti</i>	Upper Laetolil Beds this work	M1/	4	1.02	0.04	0.95–1.13	4	1.08	0.06	0.95–1.25
		M2/	6	1.17	0.02	1.1–1.23	6	1.31	0.05	1.14–1.48
		M3/	5	1.31	0.04	1.19–1.43	5	1.29	0.06	1.12–1.48
<i>H. atikoi</i>	Omo F	M2/	1	1.24			1	1.44		
	Omo G	M2/	2			1.18–1.22	2			1.42–1.51
<i>H. jaegeri</i>	Olduvai Bed I	M1/	30	1.21	0.06	1.15–1.44	30	1.18	0.08	1.0–1.45
		M2/	45	1.36	0.09	1.18–1.62	45	1.66	0.08	1.5–1.85
		M3/	17	1.52	0.07	1.4–1.62	17	1.61	0.07	1.5–1.75

N number of molars, *SD* standard deviationData sources: *H. atikoi* Omo Shungura (Wesselman 1984), *H. jaegeri* (Denys 1989b)



Fig. 2.32 SEM images of *Heterocephalus quenstedti* molars. Left, EP 4151/00, left mandible with M1-3 from Loc. 8; right, EP 1082/03, right mandible with M1-3 from Loc. 10W; bottom, EP 1990/00, left maxillary fragment with M1-2/ from Loc. 5. Scale bar in mm

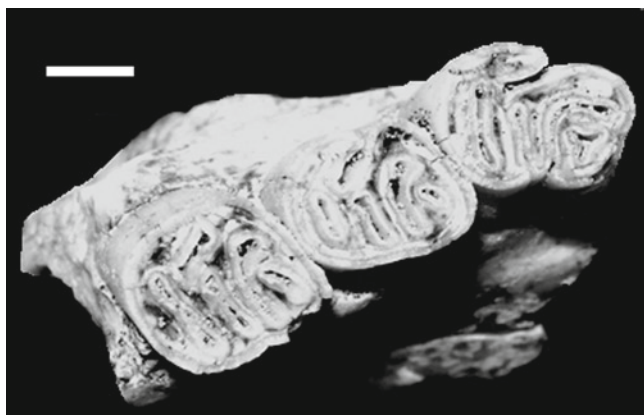


Fig. 2.33 *Hystrix leakeyi*. EP 655/05, left mandible with DP/4-M2. Scale bar indicates 5 mm

also belong to *Xenohystrix* (EP 3624/00 and EP 3623/00, Loc. 21, Upper Laetolil Beds). Denys (1987a) recorded *Xenohystrix* in the Upper Laetolil Beds at Locs. 1, 2, 10 and 15, and we add here Loc. 21 to that list.

Hlusko (2007) described *Xenohystrix* sp. from Lemudong'o. The low crown and occlusal pattern fits well with *X. crassidens* from the Upper Laetolil Beds and suggests conspecificity, as suggested by Hlusko (2007). Wesselman et al. (2009) also described *Xenohystrix* sp. from the late Miocene Adu Dora sites and mentioned its presence at Aramis at around 3.4 Ma (Wesselman and Black, unpublished). *Xenohystrix crassidens* is also known from Makapansgat and Hadar, but it has never been recorded from Pleistocene sites.

Hystrix sp. 1

A single specimen (EP 2352/03), comprising two associated mandibles from the late Pleistocene Upper Ngaloba Beds (Loc. 13), exhibits a wide tooth row, with a length greater than modern *H. cristata* from Kenya (even old adults) (Table 2.15). The indication in the literature that *H. africae-australis* has larger teeth than *H. cristata* can be found in Denys (1987a: fig. 6.20). However, museum specimens are in general not well identified taxonomically, and there is great variability depending on age, with quite late replacement of DP/4 by P/4 and emergence of M3/3. Although our reference sample is too small to reach a taxonomic conclusion, this specimen does seem close in morphology to modern *Hystrix* species.

Discussion and Conclusion

The new collections from Laetoli have allowed a more refined assessment of the status of the rodent taxa previously unattributed to species, as well as the description of several new species, including *Gerbilliscus satimani*, *G. winkleri*, *Thryonomys wesselmani*, *Paraxerus meini* and *Heterocephalus manthii*. It has also allowed a better appreciation of the intraspecific variability among *S. major*, *X. janenschii*, *H. quenstedti* and *P. laetoliensis* populations. Moreover, thanks to the newly recovered material, we have been able to assign Laetoli specimens for the first time to *Petromys* sp and *Aethomys* sp.

Muridae are quite rare at Laetoli and only a few new remains can be attributed to this family. The new material provides additional *T. laetoliensis* molars and a few attributable to *M. cinereus* from the Upper Laetolil Beds. Unfortunately, we do not have any supplementary specimens of *T. cf. laetoliensis* and *M. cf. cinereus* from the Upper Ndolanya Beds. Since very few species are found in both the

Table 2.15 Molar row length and lower tooth dimensions (length×width, mm) of *Hystrix* spp., including data from Denys (1987a), Greenwood (1955), Mein and Pickford (2006), Winkler (2003) and Manthi (2006). Measurements on modern *H. cristata* specimens from collections of the Kenya National Museum

Number	LM/1-3	DP/4	M/1	M/2	M/3	Species
EP 2352/03	37.33	9.14×6.65		11.44×9.16		<i>H. sp.</i> Ngaloba Beds
					6.12×5.90	<i>Hystrix</i> sp. Lothagam
			6.00×5.90	7.05×6.20	6.6×5.00	<i>Hystrix</i> sp. Lukeino
						<i>Hystrix</i> sp. Kanapoi
EP 392/98		6.87×5.13				<i>H. leakeyi</i>
EP 655/05		10.41×8.24	9.05×7.87	10.13×9.18		<i>H. leakeyi</i>
EP 142/05		8.09×7.02				<i>H. leakeyi</i>
EP 1037/05			7.31×6.06			<i>H. leakeyi</i>
LAET 75-1368		8.64×7.34	7.28×7.64	7.96×6.70	7.34×6.00	<i>H. leakeyi</i>
LAET 75-2594		9.70×7.80				<i>H. leakeyi</i>
LAET 74-398			8.20×7.10	8.7×7.00	7.2×6.10	Type <i>H. leakeyi</i>
Makapan		13×9.05				<i>H. makapanensis</i>
1996			9.64×8.69			<i>H. makapanensis</i>
2015				10.35×7.10		<i>H. makapanensis</i>
3354		8.99×7.38				<i>H. makapanensis</i>
329				10.86×9.51		<i>H. makapanensis</i>
988			12.13×9.11			<i>H. makapanensis</i>
Olduvai		11.5×9.6	11.5×8.9	11.6×9.5	10.8×8.4	<i>H. makapanensis</i>
LAET 75-1971		12.6×9.5				<i>H. makapanensis</i>
1786		11.88×8.69				<i>X. crassidens</i>
LAET 75-3411		14.6×10.4				<i>X. crassidens</i>
OM5329		8.69×5.87	7.43×6.5	8.68×6.06		<i>H. cristata</i>
OM5324	34.95	8.14×6.91	8.39×7.26	8.92×7.25	7.32×5.45	<i>H. cristata</i>
OM5322	33.44	8.65×5.26	8.35×5.62	9.05×5.58	7.62×4.55	<i>H. cristata</i>
OM7190	33.62	10.2×7.54	7.93×7.02	8.87×7.40	8.28×7.15	<i>H. cristata</i>
OM7114	34.40					<i>H. cristata</i>

Upper Laetoli Beds and Upper Ndolanya Beds it would have been interesting to examine the relationships between samples from these two stratigraphic units.

We did not find any additional specimen of the unattributed murid indet. from the Laetoli Beds (Denys 1987a), which may be close to *Acomys*. The absence of Deomyinae at Laetoli is surprising, because representatives of this taxon are quite abundant in the late Miocene and early Pliocene of Ethiopia, Kenya (Winkler 1997; Geraads 2001; Manthi 2006; Mein and Pickford 2006; Wesselman, personal communication) and Harasib, Namibia (Mein et al. 2004).

A recent molecular phylogeny has demonstrated the monophyly of the African Murinae and the existence of four major clades in tropical Africa (Lecompte et al. 2008), which differentiated as early as 7–8 Ma. The first Arvicanthini clade includes *Thallomys*, as well as *Aethomys*. The second one is composed of the tribe Praomyini, which comprises *Mastomys*. The two remaining major murine lineages, containing the

Mus (*Nannomys*) and *Malacomys* clades respectively, are not yet recorded at Laetoli, despite relatively good fossil samples. The Laetoli Beds still represent the first occurrence of *Thallomys*.

In the present study, a new murid belonging to the genus *Aethomys* is described for the first time from Laetoli. This taxon has already been identified at Kanapoi (Manthi 2006), Lemudong'o (Manthi 2007), Langebaanweg, Makapansgat and Bolt's Farm (Denys 1999). Some Dendromurinae, such as *Dendromus* sp. and *Steatomys* sp. described by Denys (1987a), were not recovered again, but this may be due to sampling methods (only surface collection rather than screening) considering their very small size. Such a bias in sampling may also explain the absence of *Mus* (*Nannomys*). Manthi (2006) has recorded the presence of *Steatomys* sp. and *Mus* sp. in Nzube's mandible site at Kanapoi (~4.1 Ma), which confirms the early Pliocene occurrence of these taxa in East Africa.

The new material from Laetoli allows confirmation of the absence of *Heterocephalus* and *Aethomys* in the Upper Ndolanya Beds. We do, however, confirm the presence of *Hystrix makapanensis* in the Upper Ndolanya Beds. The Laetolil Beds only lack *Thryonomys* compared with the Upper Ndolanya Beds. One should note that two Gerbillinae and *Hystrix* coexist in the Upper Laetolil Beds. Because *Heterocephalus* is a mole-rat living exclusively underground one can assume that the absence of this genus in the Upper Ndolanya Beds may result from the lack of suitable soils for tunneling. It could also result from taphonomic causes, including absence of a predator that specializes in such rodents. The absence of *Thryonomys*, the cane rat, in the Upper Laetolil Beds may indicate the lack of availability of leaves, stems and shoots of grasses, reeds and sedges that are an important part of the diet of these rodents, which mostly live in the high grass zones close to rivers. The Upper Ndolanya Beds would have, at least in some places, a different landscape relative to the Laetolil Beds, as previously indicated by Denys (1987a).

The rodent diversity of the Upper Ndolanya Beds still remains very low. There are only nine species represented, compared with 17 species from the Upper Laetolil Beds. However, only three species are recorded from the Lower Laetolil Beds (Table 2.16). The present work has added three species and one genus to the general faunal list of the Upper Laetolil Beds and two species to the Upper Ndolanya Beds. By plotting the diversity against the number of identifiable specimens (NISP) it can be shown that there is a direct link between the high NISP and the highest diversity in the Laetolil Beds (Table 2.17). However, the diversity is much lower in the Upper Ndolanya Beds compared to the Upper Laetolil Beds. Some taphonomic considerations may allow a better understanding of these differences between the Upper Laetolil and Upper Ndolanya accumulations. This will allow an appreciation of whether there are paleoecological differences between the two rodent communities, as highlighted previously by Denys (1987a) and Gentry (1987), or whether the relatively low diversity in the Upper Ndolanya Beds results from a different mode of accumulations of fossil remains compared to the Laetolil Beds. We also observe the increased temporal range of some species, such as *Pedetes*, which is now known to occur in the Upper Ndolanya Beds, and *X. janenschii*, which now occurs in Upper Laetolil Beds. The only rodent present in the three main stratigraphic units, and displaying the same size and morphology, is *Saccostomus major*. This species occurs first at Ibole in the Manonga Valley at around 5–4 Ma (Winkler 1997). Since the same species is found in both the Manonga and the Lower Laetolil Beds it confirms that the two sites are close in age and belong to the same biogeographical province. *Saccostomus major* occurs in sites between 5–2.7 Ma and 1.7 Ma in Tanzania. Its

Table 2.16 List of rodent taxa from the Laetolil and Upper Ndolanya Beds (based upon this work and Denys 1987a)

Species	Lower Laetolil Beds	Upper Laetolil Beds	Upper Ndolanya Beds
<i>Pedetes laetoliensis</i>		x	
<i>Pedetes</i> sp.			x
<i>Xerus janenschii</i>		x	x
<i>Xerus</i> sp.		x	
<i>Paraxerus meini</i>		x	x
<i>Gerbilliscus satimani</i>		x	
<i>Gerbilliscus winkleri</i>			x
<i>Gerbilliscus</i> cf. <i>inclusus</i>		x	
<i>Dendromys</i> sp.		x	
<i>Steatomys</i> sp.		x	
<i>Saccostomus major</i>	x	x	x
<i>Aethomys</i> sp.		x	
Murid indet.		x	
<i>Thallomys laetolilensis</i>		x	cf.
<i>Mastomys cinereus</i>		x	cf.
<i>Heterocephalus quenstedti</i>		x	
<i>Heterocephalus manthii</i>	x		
<i>Thryonomys wesselmani</i>			x
<i>Petromus</i> sp.	x		
<i>Hystrix leakeyi</i>		x	
<i>Hystrix makapanensis</i>		x	x
<i>Xenohystrix crassidens</i>		x	
Species richness	3	17	9

Table 2.17 NISP (number of identifiable specimens) of rodent genera and species recorded from the Upper Laetolil Beds and Upper Ndolanya Beds in 1987, in this work, and combined

	NISP	Genera	Species
1987			
ULB	243	13	15
UNB	55	8	8
This work			
ULB	227	10	17
UNB	45	9	9
Total			
ULB	470	15	17
UNB	100	9	9

local disappearance, not yet documented in any intervening site after the Upper Ndolanya Beds (2.66 Ma) and before the FLKNN1 Olduvai site (1.7 Ma), may be due to the strong

climatic event that occurred around 2.4 Ma (see references in Maslin and Christensen 2007). Concerning the Upper Laetoli Beds, we do not see any real differences between the different localities or different stratigraphic levels in relation to *Saccostomus*. Along with *Pedetes*, *Saccostomus* is the dominant rodent in the assemblage (75 and 78 individuals respectively based on the new material), followed by *Heterocephalus* (Minimum number of individuals or MNI=32) and *Thallomys* (MNI=16). In the Upper Ndolanya Beds, *Xerus* (MNI=30) dominates the assemblage, followed by *G. winkleri* (MNI=11) and *T. wesselmani* (MNI=5).

The presence of *Petromus* at Kakesio (Lower Laetoli Beds) could indicate the close proximity of a rocky area or relatively dry conditions. Today, the dassie rat is a southwest African endemic, but during the Pliocene they were present at Taung, Bolt's Farm and Lukeino (Sénégas 2004; Mein and Pickford 2006). This suggests the existence of a common southern savanna biogeographic province (or southwest arid region) extending from southwest-central Africa to Kenya-Tanzania. This is corroborated by the common presence of *Saccostomus* at Harasib, Lukeino, Ibole and Laetoli, which is unique to these sites, and is not found in early Pliocene sites in the Transvaal region. Alternative hypotheses to the presence of *Petromus* in Laetoli are that there was an extension of the Namib desert to the northeast of Africa, allowing Petromuridae to colonize Kenya and Tanzania, or that these

rodents were abundant throughout East Africa in the Pliocene, followed by a marked reduction in their geographic distribution for unknown reasons. *Petromus* is rare in East and South African sites, but this may also be due to taphonomic causes. In the absence of geographically intermediate sites of Miocene age we cannot give preference to any particular hypothesis.

Figure 2.34 presents an F1×F2 graph of the correspondence analysis based on the presence-absence of rodent genera from Mio-Pleistocene sites. Axis 1 shows a clear separation of the late Miocene localities (i.e., Chorora, Harasib 3, Lukeino, Ibole), which have a high diversity of extinct thryonomyids and a low count of modern genera (Fig. 2.34). Along axis 2 there is a continuous distribution of the Lower Pliocene to Pleistocene sites, which are dominated by modern genera. On the positive part of axis 2 one sees all the southern African localities grouped together (i.e., Langebaanweg, Makapansgat, Sterkfontein, Humpata, Taung, Kromdraai, Ngamiland) and on the negative part of axis 2 one finds a grouping of East African sites, including Lemudong'o and Kanapoi. At the extremes of axis 2, one finds Langebaanweg and the Ethiopian localities of Adu Asa and Hadar. The two Laetoli faunas (Upper Laetoli and Upper Ndolanya Beds) are positioned close together and are associated with Lemudong'o, Kanapoi, Omo Shungura Members B, C, F and G, Olduvai Beds I and II, and Natron. There is

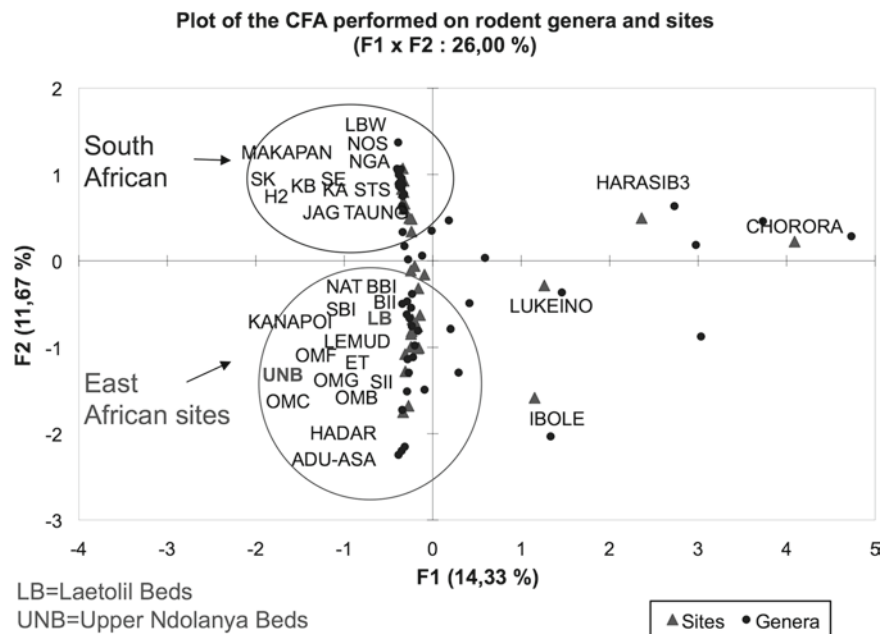


Fig. 2.34 Correspondence analysis diagram on presence-absence of the rodent genera (except hystricids) for late Miocene to late Pleistocene East African and South African sites (after Winkler et al. 2010; data taken from the literature). Site abbreviations: LBW Langebaanweg; NOS Nosib; SK Swartkrans; KB, KA Kromdraai A, B; H2 Humpata 2; JAG Jägerquelle;

STS Sterkfontein; SE Sterkfontein extension; NG Ngamiland; NAT Natron (Pening); BBI Olduvai Base Bed I; SBI Olduvai Upper Bed I; SII Olduvai Upper Bed II; BII Olduvai Base Bed II; OMF, OMC, OMB Omo members F, G, M, C, B; LEMUD Lemudong'o; UNB Upper Ndolanya Beds; LB Laetoli Beds; ET East Turkana

some distance between the Upper Laetoli Beds and Upper Ndolanya Beds indicating the two faunas are not very similar. These results confirm the hypothesis of a regional differentiation of the rodent faunas during the Plio-Pleistocene times, and a strong link between rodent taxa and vegetation, at least as early as 6 Ma (Denys 1985, 1999).

Due to its peculiar faunal composition and its close affinities with Ibole, Olduvai Bed I, Omo, Lemudong'o and Kanapoi, the Laetoli faunas represent a distinct type of rodent community in comparison to the Ethiopian Hadar and Adu Asa sites. With a distance of 3,000 km, the Rift Valley and the Equator separating the two sites, Laetoli and Hadar may have had quite different vegetation and climates. Rodents are very restricted in terms of their habitats, while hominins and other large mammals often have a better capacity for dispersal. This study highlights the importance of rodents as a tool for paleoenvironmental and paleogeographical reconstructions.

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Appendix 2.1 List of new material attributed to *Pedetes laetoliensis* from the Upper Laetoli Beds (ULB)

EP number	Locality	Level	Anatomical element				
1161/01	1	ULB	Right mandible + P/4-M/2	2916/00	10E	ULB	Right maxilla + M2/
1089/05	1	ULB	Maxilla with P/4-M/3	2920/00	10E	ULB	Vertebrae + metapodials + bone fragments
1090/05	1	ULB	Anterior cranium + molars				
1091/05	1	ULB	Two isolated molars	794/00	10E	ULB	Three isolated molars
1783/00	2	ULB	Astragalus	572/01	10E	ULB	Six isolated molars
1867/00	2	ULB	Right mandible + P/4-M/3	573/01	10E	ULB	Premaxilla + incisors
1868/00	2	ULB	Left mandible + M/1-2	885/03	10E	ULB	Left + right mandibles + P/4-M/2 + left and right M/1-2
3067/00	2	ULB	Astragalus				
714/00	2	ULB	Left mandible + P/4-M/3				
640/03	2	ULB	Postcrania	887/03	10E	ULB	Right mandible + P/4-M/2
1036/05	2	ULB	Two isolated molars	1264/04	10E	ULB	Four isolated molars
994/05	2	ULB	Isolated molar	046/04	10E	ULB	Five isolated molars
220/00	1	ULB	Isolated molar	048/04	10E	ULB	Cranium + molars + mandible + postcranial
1993/00	5	ULB	Left + right mandibles + P/4-M/2	878/05	10E	ULB	Ten isolated molars
398/03	5	ULB	Left mandible + M/2-3	881/05	10E	ULB	Partial skeleton
399/03	5	ULB	Six isolated molars	068/05	11	ULB	Right mandible + P/4-M/2
1334/04	5	ULB	Right mandible + P/4-M/2	536/05	12E	ULB	Two isolated molars
1335/04	5	ULB	Four isolated molars	2367/03	13	ULB	Partial skeleton

(continued)

784/05	5	ULB	Six associated molars
785/05	5	ULB	Isolated molar
1392/00	6	ULB	Left mandible + M/1-2
1444/04	6	ULB	Right mandible + P/4-M/2
1445/04	6	ULB	Eight isolated molars
3905/00	7	ULB	Left mandible fragment + P/4
616/05	7	ULB	Two isolated molars
327/00	8	ULB	Right mandible + P/4-M/1
1572/01	8	ULB	Right mandible + M/2-3
1420/03	8	ULB	Left maxilla + P/4-M/1/
1421/03	8	ULB	Six isolated molars
1422/03	8	ULB	Premaxilla + 2 incisors + postcrania
1423/03	8	ULB	Distal femur + tibia + proximal femur + pelvis
1088/98	9	ULB	Three isolated molars
1509/98	9	ULB	Right mandible + P/4-M/3
239/99	9	ULB	Left mandible + M/1-3
2435/03	9S	ULB	Mandible + M/1-3 aggregated together by tuff
783/03	9	ULB	Twelve isolated molars
784/03	9	ULB	Associated postcranial fragments
992/04	9	ULB	Seven isolated molars
1263/05	9	ULB	Isolated molar
240/05	9	ULB	Five isolated molars
1562/98	10E	ULB	Two left mandibles + M/1-2 + M/1
234/98	10E	ULB	Left maxilla + P/4-M/2/
255/98	10E	ULB	Five isolated molars
257/98	10E	ULB	Right mandible + M/1-3
383/98	10E	ULB	Right mandible + M/2-3
745/98	10W	ULB	Two associated molars M/1-2
078/99	10E	ULB	Right mandible + P/4-M/2
079/99	10E	ULB	Eight isolated molars
2914/00	10E	ULB	Cranium + incisor + P/4-M/3/ left + right mandibles + right P/4-M/3

Appendix 2.1 (continued)

EP number	Locality	Level	Anatomical element
1441/98	15	ULB	Four isolated molars
603/01	16	ULB	Right mandible + P/4-M/2
604/01	16	ULB	Left mandible + M/1-3
289/03	16	ULB	Complete femur, premaxilla, germ P4/ other fragments
290/03	16	ULB	Left mandible + P/4-M/2
190/05	16	ULB	Isolated molar
3625/00	21	ULB	Right maxilla + P4/
529/00	21	ULB	Right mandible + P/4
1235/98	22	ULB	Left toothrow P/4-M/3
3741/00	22	ULB	Anterior cranial fragment + right maxilla + P4-M1/+left maxilla + P4-M2/
573/00	22	ULB	Left maxilla + M1-3/
144/04	22	ULB	Three isolated molars
1220/05	22E	ULB	Isolated molar

Appendix 2.2 List of specimens attributed to *Xerus janenschi* from the Upper Laetoli Beds (ULB) and the Upper Ndolanya Beds (UNB)

EP number	Locality	Level	Anatomical element
1534/01	Silal Artum	UNB	Neurocranium
1561/01	Silal Artum	UNB	Mandible + P/4-M/1
2512/03	Silal Artum	UNB	Cranium
033/03	Silal Artum	UNB	Skull
034/03	Silal Artum	UNB	Left mandible + M/1-M/3
1134/05	Silal Artum	UNB	Anterior cranium
1135/05	Silal Artum	UNB	Left mandible + P/4-M/3
1136/05	Silal Artum	UNB	Left mandible + P/4-M/3
3648/00	9S	ULB	Left mandible + M/1-M/3 + partial skeleton
3496/00	15	UNB	Maxilla fragment + M/1 + postcranial
3497/00	15	UNB	Partial skull
3498/00	15	UNB	Anterior cranial fragment (edentulous)
3499/00	15	UNB	Left mandible M/1-M/2
4055/00	15	UNB	Right mandible + P/4-M/2
1690/03	15	UNB	Cranium
1691/03	15	UNB	Left mandible + P/4-M/3
1692/03	15	UNB	Right mandible
1699/03	15	UNB	Molar
219/04	15	UNB	Cranium
383/05	15	UNB	Cranium
1000/00	18	UNB	Right mandible + P/4-M/3
2356/00	18	UNB	Maxilla + P4-M3
813/01	18	UNB	Right mandible + P/4-M/3
816/01	18	UNB	Left mandible + M/1 broken + M/2
087/03	18	UNB	Right maxilla + M1-2/
292/04	18	UNB	Mandible + P/4-M/3
293/04	18	UNB	Mandible + P/4-M/3

Appendix 2.3 List of specimens attributed to *Saccostomus major* from the Upper Laetoli Beds (ULB) and *S.cf. major* from the Upper Ndolanya Beds (UNB)

EP number	Locality	Level	Anatomical element
218/00	1	ULB	Left mandible + M/2-3
1162/01	1	ULB	Right mandible + M/1-2
1890/03	1	ULB	Left maxilla + M1-2/
1878/00	2	ULB	Left mandible + M/1-3
1879/00	2	ULB	Right mandible + M/1-3
4255/00	2	ULB	Right mandible with M/1-2
4256/00	2	ULB	Left mandible + M/2
732/00	2	ULB	Left mandible + M/1-2
584/03	2	ULB	Left maxilla + M1/
651/03	2	ULB	Right mandible + M/1
652/03	2	ULB	Right maxilla + M1-2/
1738/04	2	ULB	Left mandible + M/1-3
1038/05	2	ULB	Left mandible + M/1-2
997/05	2	ULB	Right maxilla + M1/
998/05	2	ULB	Left maxilla + M1-2/
2745/00	3	ULB	Right mandible + M/1-2
2746/00	3	ULB	Right mandible + M/2-3
226/01	3	ULB	Right mandible + M/1
508/03	3	ULB	Right maxilla + M1-2/
659/04	3	ULB	Cranial fragment + right M/1-3
185/03	4	ULB	Left mandible + M/1-2
186/03	4	ULB	Left maxilla + M1-2/
1987/00	5	ULB	Left mandible + M/3 and right mandible + M/1-3
1988/00	5	ULB	Right mandible + M/1-3
1989/00	5	ULB	Right mandible + M/2-3
3071/00	5	ULB	2M1/+2M/1 + postcranials
3072/00	5	ULB	2 incisors
392/03	5	ULB	Right M1/
393/03	5	ULB	Right maxilla + M1-3/
394/03	5	ULB	Left mandible + M/2
395/03	5	ULB	Right mandible + M/2
395/03	5	ULB	Right mandible + M/2-3
1331/04	5	ULB	Left mandible + M/1-2
782/05	5	ULB	Right mandible + M/1-3
783/05	5	ULB	Left maxilla + M1-2/
1375/00	6	ULB	Associated left maxilla + M1/ and right maxilla + M1-2/ and right mandible + M/1-3
1455/04	6	ULB	Right mandible + M/1-2
3904/00	7	ULB	Right maxilla + M1-3/
1247/03	7E	UNB	Isolated right M/1
1248/03	7E	UNB	Left mandible with M/1-3 in connection with left maxilla with M1-3/
1249/03	7E	UNB	Left mandible + M/1-2
1958/03	7	ULB	Left mandible + M/1
2138/03	7	ULB	Left mandible + M/1-3
2211/03	7	ULB	Left maxilla + M/1-2
1424/03	8	ULB	Left mandible + M/1-2
1425/03	8	ULB	Left mandible + M/2-3
1426/03	8	ULB	Right mandible + M/1-2
361/04	8	ULB	Right edentulous mandible, right maxilla + M1/

(continued)

Appendix 2.3 (continued)

EP number	Locality	Level	Anatomical element
1251/01	9S	ULB	Left mandible+M/2-3
2433/03	9S	ULB	Right mandible+M/1-2
2434/03	9S	ULB	Right mandible+M/1-3
2922/00	10E	ULB	Left mandible+M/1-2
2923/00	10E	ULB	Right maxilla+M1/
549/01	10E	ULB	Right mandible+M/1-M/3
550/01	10E	ULB	Right mandible+M/2
552/01	10E	ULB	Right mandible+M/2
641/01	10	ULB	Right mandible+M/1
1066/03	10W	ULB	Right mandible+M/1-3
882/03	10E	ULB	Right M1/
883/03	10E	ULB	Right mandible+M/1
990/03	10	ULB	Right mandible+M/1-2
296/05	10	ULB	Right maxilla+M1-2/
699/05	10W	ULB	Left mandible+M/1-2
700/05	10W	ULB	Left maxilla+M1-2/
4329/00	11	ULB	Broken M1/
1326/03	11	ULB	Maxilla+M1/
1327/03	11	ULB	Left mandible+M/1-2
1612/03	15	ULB	Right mandible+M/1-2
191/05	16	ULB	Cranium
160/03	17	ULB	Right maxilla+M1-3/ + edentulous mandible maxilla fragment
1344/05	22E	ULB	Left mandible+M/1-3

Appendix 2.4 List of specimens attributed to *Heterocephalus quenstedti* from the Upper Laetoli Beds (ULB)

EP number	Locality	Level	Anatomical element
1782/00	2	ULB	Right+left edentulous maxillae
1990/00	5	ULB	Half cranium with upper molars
396/03	5	ULB	Right mandible+M/1-2
781/05	5	ULB	Right mandible+M/2
2205/03	7	ULB	Anterior cranial frag- ment+left M/1-2+right mandible+M/2
1171/00	8	ULB	Mandible fragments+incisors
326/00	8	ULB	Anterior skull fragment+left M/1-2
4151/00	8	ULB	Left mandible+M/1-3
043/01	8	ULB	Right mandible+M/2-3 & anterior cranium with left M1-3/
1427/03	8	ULB	Left mandible+M/1-2
140/05	8	ULB	Right+left mandible+M/1-3
1059/98	9S	ULB	Left mandible+M/1-3
2436/03	9S	ULB	Left mandible+M/1-3
258/98	10E	ULB	Edentulous left mandible
2921/00	10E	ULB	Right mandible+M/1-3
3119/00	10	ULB	Left mandible+M/2-3
638/01	10	ULB	Maxilla fragment+M/1-2
639/01	10	ULB	Left mandible+M/1-3
640/01	10	ULB	Left mandible+M/1
1067/03	10W	ULB	Right mandible+M/2
1068/03	10W	ULB	Right mandible+M/2-3

1069/03	10W	ULB	Mandible+M/2
1082/03	10W	ULB	Right mandible with M/1-3
1083/03	10W	ULB	Anterior cranial fragment+ edentulous left and right maxilla
1084/03	10W	ULB	Anterior cranial fragment+ left M1/
989/03	10	ULB	Associated mandibles left+right+M/1-3
701/05	10W	ULB	Edentulous left mandible
883/05	10E	ULB	Maxilla fragment
884/05	10E	ULB	Left mandible+M/2-3
1784/03	22	ULB	Left mandible+M/2-3
1222/05	22E	ULB	Left mandible+M/1

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