

# **Paleontology and Geology of Laetoli: Human Evolution in Context**

# Vertebrate Paleobiology and Paleoanthropology Series

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# **Paleontology and Geology of Laetoli: Human Evolution in Context**

## **Volume 2: Fossil Hominins and the Associated Fauna**

Edited by

**Terry Harrison**

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ISBN 978-90-481-9961-7      e-ISBN 978-90-481-9962-4  
DOI 10.1007/978-90-481-9962-4  
Springer Dordrecht Heidelberg London New York

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*Cover illustration:* Photograph of the L.H. 4 (lectotype) mandible of *Australopithecus afarensis* superimposed on a view of Laetoli Locality 10 (© and courtesy of Terry Harrison).

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*To Australopithecus afarensis for being there when it mattered*



## Preface

Laetoli in northern Tanzania is one of the most important paleontological and paleoanthropological sites in Africa. It is renowned for the recovery of early hominin fossils belonging to *A. afarensis* and for the discovery of remarkably well-preserved trails of footprints of hominins. Given the significance of Laetoli for understanding and interpreting the evolutionary history of early hominins the author initiated long-term geological and paleontological investigations at Laetoli and at other fossil localities on the Eyasi Plateau. The overall objectives of the project were to recover additional fossil hominin specimens and to obtain more detailed contextual information on the paleontology, geology, dating, and paleoecology.

The field campaigns (1998–2005) have produced important original data on the fossil hominins, their associated fauna, and the paleoecological and paleoenvironmental context. The work presented here is the culmination of that research. It represents the combined effort of a dedicated and experienced field crew who were responsible for collecting the fossils and samples described and analyzed here, and subsequent research by a multidisciplinary team of international specialists.

The present volume focuses on the morphology, systematics and paleobiology of the fossil hominins and the associated invertebrate and vertebrate fauna. The companion volume provides an interdisciplinary perspective on the geology, geochronology, paleoecology, taphonomy, paleobotany, and modern-day Serengeti ecosystem. Together, these two volumes present a comprehensive account of the geology, paleontology and paleoecology of Laetoli. It is hoped that the research presented here will provide an important building block in a broader understanding of early hominin evolution, faunal diversity and ecological change in East Africa during the Pliocene, and provide the basis for analyzing early hominin adaptation within the context of broader macroevolutionary models of speciation, diversification and extinction.

A special thanks goes to all of the dedicated team members who participated in the expeditions to Laetoli that contributed to the recovery of the material discussed and analyzed here (they are identified individually in the introductory chapter in Volume 1). I am especially grateful to the graduate students (current and former) who participated in the project, often under difficult conditions, and I fully acknowledge their significant contributions to the success of the project. The students who accompanied me into the field were as follows: E. Baker, S. Cooke, C. Fellmann, K. Kovarovic, A. Malyango, L. McHenry, K. McNulty, G. Mollé, C.P. Msuya, T. Rein, C. Robinson, L. Rossouw, M. Seselj, D. Su, M. Tallman and S. Worthington. Of my former graduate students, Denise Su deserves special recognition for taking on the primary role of curating and cataloguing the Leakey and Harrison Laetoli collections at the National Museum of Tanzania in Dar es Salaam, as well as for her valuable assistance with logistics at Laetoli and in Dar es Salaam.

I thank the Tanzania Commission for Science and Technology and the Unit of Antiquities in Dar es Salaam for permission to conduct research in Tanzania. Special thanks go to the late Norbert Kayombo (Director General), Paul Msemwa (Director), Amandus Kweka and all of the curators and staff at the National Museum of Tanzania in Dar es Salaam for their support and assistance. I thank the regional, district and ward officers in Arusha Region for their support and hospitality. I am grateful to the Ngorongoro Conservation Area Authority for permission

to conduct research in the conservation area. Emin Korcelik and Naphisa Jahazi of Hertz International in Dar es Salaam arranged the field transportation, and H. Meghji and A. Esmail helped with logistical support in Dar es Salaam.

Research at Laetoli benefited from the advice, discussion, help and support from numerous individuals, especially the following: P. Andrews, R. Blumenschine, E. Delson, A. Deino, P. Ditchfield, C. Feibel, S. Frost, C. Harrison, T.S. Harrison, D. M. K. Kamamba, O. Kileo, J. Kingston, A. Kweka, J. LeClair, M. G. Leakey, S. Mataro, G. Ole Moita, E. Mbua, L. McHenry, C. P. Msuya, C. S. Msuya, G. Mollel, M. Muungu, O. Mwebi, J. Pareso, C. Peters, M. Pickford, K. Reed, C. Saanane, W. Sanders, C. Swisher, and S. Waane. Bill Sanders deserves special mention for applying his exceptional talents to preparing and casting some of the Laetoli specimens, as does Jen LeClair for her tireless efforts in helping to organize the collections and entering data in the catalogue.

I thank the curators and staff at the various museums and repositories for allowing me access to archival materials, fossils and comparative specimens in their care. These include: National Museums of Tanzania, Kenya National Museum, American Museum of Natural History, Natural History Museum in London, Humboldt-Universität Museum für Naturkunde in Berlin, Eberhard-Karls Universität Tübingen Institut für Ur- und Frühgeschichte und Archäologie des Mittelalters and Institut und Museum für Geologie and Paläontologie.

The following individuals provided critical comments and advice about the research presented in this volume and its companion: A. Alexandre, P. Andrews, M. Anton, M. Avery, M. Bamford, F. Bibi, L. Bishop, R. Bobe, R. Bonnefille, F. Brown, P. Butler, C. Crumly, A. Deino, P. Ditchfield, P. Düringer, M. Erbajeva, R. Evander, C. Feibel, Y. Fernandez-Jalvo, B. Fine-Jacobs, L. Flynn, S. Frost, T. Furman, J. Genise, A. Gentry, D. Geraads, H. Gilbert, U. Goehlich, J.H. Harris, K. Heissig, A. Hill, P. Holroyd, D. Iwan, N. Jablonski, J. Kappelman, T. Kaiser, R. Kay, J. Kingdon, J. Kingston, W. Kimbel, J. Knott, K. Kovarovic, N. Kristensen, O. Kullmer, F. de Lapparent de Broin, M. Lewis, N. Lopez-Martinez, S. Manchester, I. MacDougall, L. McHenry, S. McNaughton, K. Metzger, P. Meylan, C. Mourer-Chauviré, R. Oberprieler, E. O'Brien, D. Parmley, M. Pavia, C. Peters, M. Pickford, I. Poole, B. Ratcliffe, D. Reed, K. Reed, W.J. Sanders, M. Sponheimer, D. Su, Z. Szyndlar, R. Tabuce, P. Tassy, B. Tiffney, J. van der Made, A. Vincens, C. Ward, H. Wesselman, E. Wheeler, and A. Winkler. Special thanks go to Terri Harrison, Chris Harrison and Leahanne Sarlo for their assistance with many aspects of the editorial process. I thank Eric Delson, Eric Sargis and the Editorial and Production team at Springer, especially Tamara Welschot and Judith Terpos. Fieldwork at Laetoli and subsequent research was supported by grants from the National Geographic Society, the Leakey Foundation, and the National Science Foundation (Grants BCS-0216683 and BCS-0309513).

New York

Terry Harrison



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# Chapter 1

## Introduction: The Laetoli Hominins and Associated Fauna

Terry Harrison

**Abstract** Laetoli in northern Tanzania is one of the most important paleontological and paleoanthropological localities in Africa. In addition to fossil hominins, there is a diverse associated fauna. The Laetoli fauna is important because it serves as a key comparative reference for other Plio-Pleistocene sites in Africa, it samples several time periods that are generally poorly represented at other paleontological sites in East Africa, and it provides key insights into the faunal and floral diversity during the Pliocene. As a result of renewed fieldwork at Laetoli (1998–2005) more than 25,000 fossils have been collected, of which more than half are fossil mammals. Most of the fossils were recovered from the Upper Laetolil Beds (3.6–3.85 Ma), but smaller samples came from the Lower Laetolil Beds (3.85–4.4 Ma) and Upper Ndolanya Beds (2.66 Ma). These include new specimens of *Australopithecus afarensis* from the Upper Laetolil Beds and the first finds of fossil hominins from the Upper Ndolanya Beds, attributable to *Paranthropus aethiopicus*. Inferences about the paleoecology at Laetoli are important for understanding the possible range of hominin habitat preferences and ecological change in East Africa during the Pliocene. The evidence from a wide range of analyses indicates that a mosaic of closed woodland, open woodland, shrubland and grassland dominated the paleoecology of the Upper Laetolil Beds. The region would have been dry for most of the year, except for the possible occurrence of permanent springs along the margin of the Eyasi Plateau and ephemeral pools and rivers during the rainy season. The paleoecological reconstruction of the Upper Ndolanya Beds is more problematic because of conflicting lines of evidence, but it is very likely that conditions were drier than in the Upper Laetolil Beds with a greater proportion of grassland, but that closed and open woodlands were still a major part of the ecosystem.

**Keywords** Pliocene • Laetolil Beds • Ndolanya Beds • Fauna • Paleontology • Paleoecology

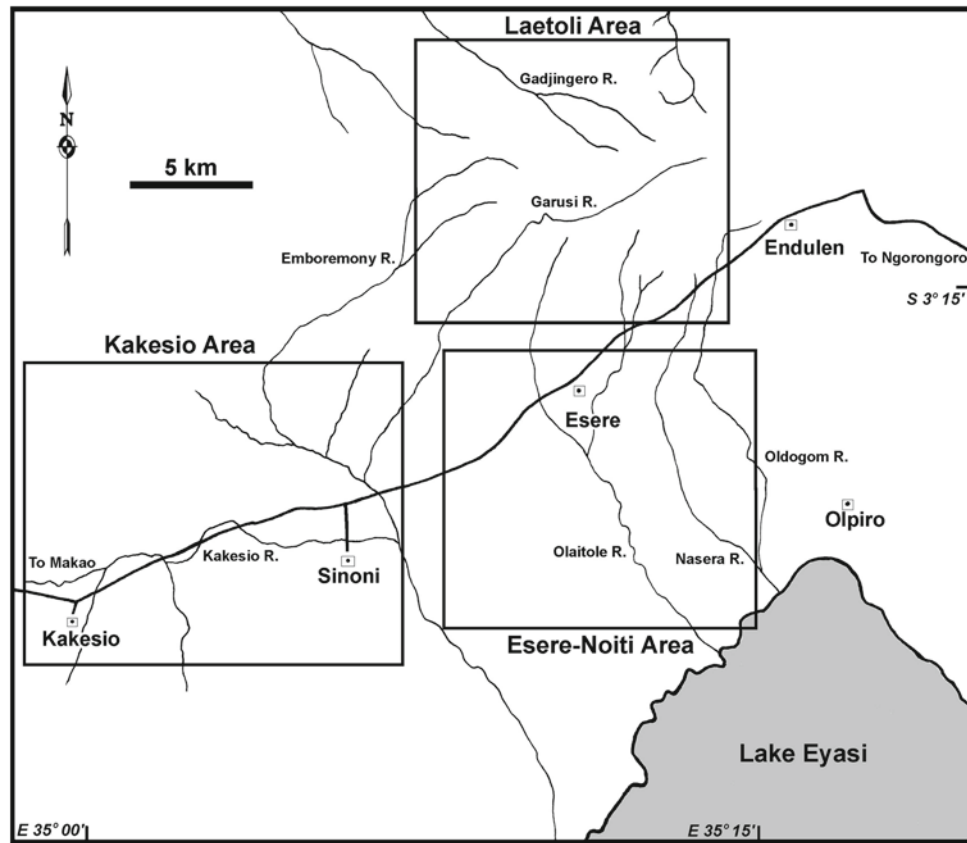
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### Introduction

Laetoli in northern Tanzania is one of the most important paleontological and paleoanthropological localities in Africa. The site is well known for the recovery of fossils of the early hominin *Australopithecus afarensis*, as well as trails of hominin footprints. The associated fauna from Laetoli is very diverse (Leakey and Harris 1987), with over 100 species of mammals identified, along with the remains or traces of fossil amphibians, reptiles, birds, insects, gastropods and plants. As such, it serves as a key reference fauna, one that is reliably dated, for comparisons with other Plio-Pleistocene sites in Africa. Equally importantly, the Upper Laetolil Beds (3.6–3.85 Ma) and Upper Ndolanya Beds (2.66 Ma) sample time periods that are generally poorly represented at other paleontological sites in East Africa, and the fossils from these stratigraphic units provides key insights into the faunal and floral diversity during the Pliocene. Detailed information on the paleontological localities and geology at Laetoli is presented in the companion volume (Harrison 2011a), but the essential information is summarized in Figs. 1.1–1.5.

Laetoli is unusual among sites in East Africa in the absence of sedimentological or paleontological evidence for extensive and/or permanent bodies of water, and in having an inferred paleoecological setting that is less extensively wooded than its penecontemporaneous sites. Given these distinctive characteristics of the paleoecology at Laetoli, the site provide an important building block for inferring the possible range of hominin habitat preferences and for understanding ecological change in East Africa during the Pliocene and its impact on early human evolution. As a consequence, the ecological context at Laetoli has been extensively investigated in the past (Leakey and Harris 1987; Andrews 1989, 2006; Cerling 1992; Andrews and Humphrey 1999; Musiba 1999; Kovarovic et al. 2002; Kovarovic 2004; Su 2005; Harrison 2005; Kovarovic and Andrews 2007; Kingston and Harrison 2007; Musiba et al. 2007; Su and Harrison 2007, 2008; Andrews and Bamford 2008; Peters et al. 2008), and is a special focus of renewed investigations since 1998.



**Fig. 1.1** A sketch map of the Eyasi Plateau showing the major rivers and villages, as well as the three main paleontological research areas: Laetoli, Kakesio and Esere-Noiti (see Figs. 1.2–1.4 for detail of insets) (From Harrison and Kweka 2011)

## The Laetoli Fauna

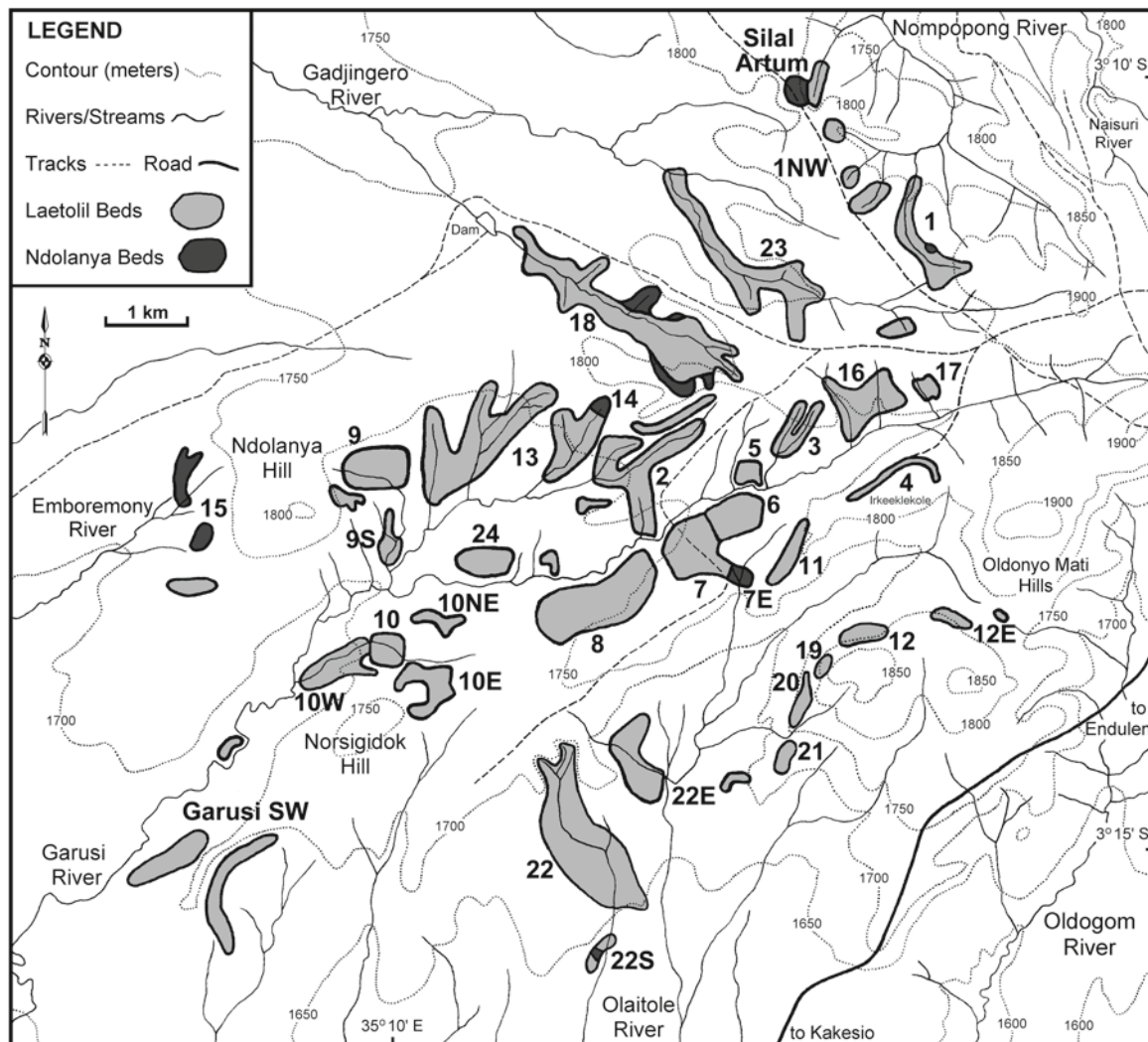
During the course of renewed fieldwork at Laetoli, between 1998 and 2005, more than 25,000 fossils have been collected (Table 1.1). These consist mainly of fossil mammals (58.1%), but also include the remains of birds (4.9%), reptiles and amphibians (1.9%), invertebrates (33.3%) and plants (1.8%) (Table 1.2). Most of the fossil mammals were recovered from the Upper Laetolil Beds, but smaller samples came from the Lower Laetolil Beds and Upper Ndolanya Beds. Representative fossil vertebrates were also recovered from the Olpiro and Ngaloba Beds, but no systematic collections were made from these stratigraphic units.

Renewed investigations at Laetoli have led to the recovery of additional fossil hominins (Harrison 2011b). These include further specimens attributable to *A. afarensis* from the Upper Laetolil Beds, and provide the basis, along with other previously undescribed specimens, for a reassessment of the morphology and evolutionary status of the *A. afarensis* sample from Laetoli. In addition, two hominins were recovered from the Upper Ndolanya Beds, and these represent the first homi-

nins from this stratigraphic unit. A maxilla from the Upper Ndolanya Beds at Silal Artum (EP 1500/01) is important because it represents the only specimen of *Paranthropus aethiopicus* recovered from outside the Turkana basin, and it is among the oldest securely dated specimens definitively attributable to this taxon (Harrison 2011b).

The contributions in Leakey and Harris (1987) provided the last comprehensive account of the systematics of the Laetoli fauna. Since that time, however, there have been major advances in our understanding of the systematics and paleobiology of late Miocene and Plio-Pleistocene faunas of Africa, as well as many reports of new localities and faunas. Renewed investigations at Laetoli have allowed a thorough revision of the systematics of the Laetoli fauna, along with a greater emphasis on understanding the paleobiology of the fauna and its paleoecological implications. All of the mammalian taxa have been restudied, with the exception of the Camelidae and Chalicotheriidae (their analysis is still ongoing). The faunal list now includes nine new species of mammals and six new species of invertebrates, all of which are described in this volume. In addition, one new species of



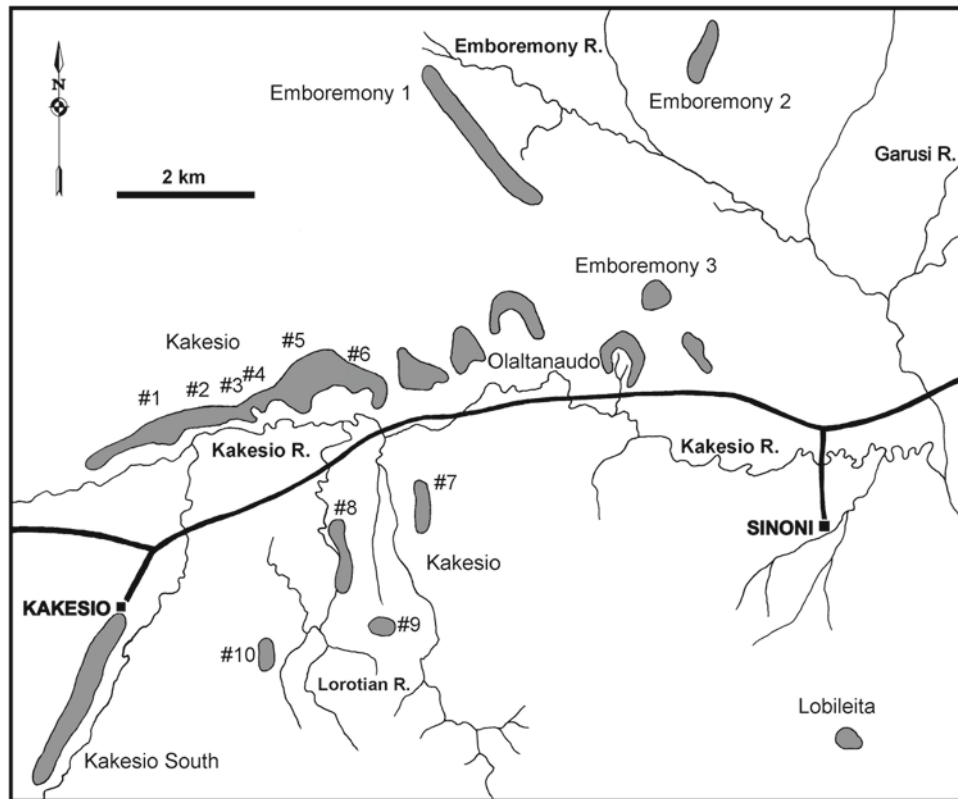


**Fig. 1.2** Map of the Laetoli area showing the main outcrops of the Upper Laetolil and Upper Ndolanya Beds and the paleontological collecting localities (From Harrison and Kweka 2011)

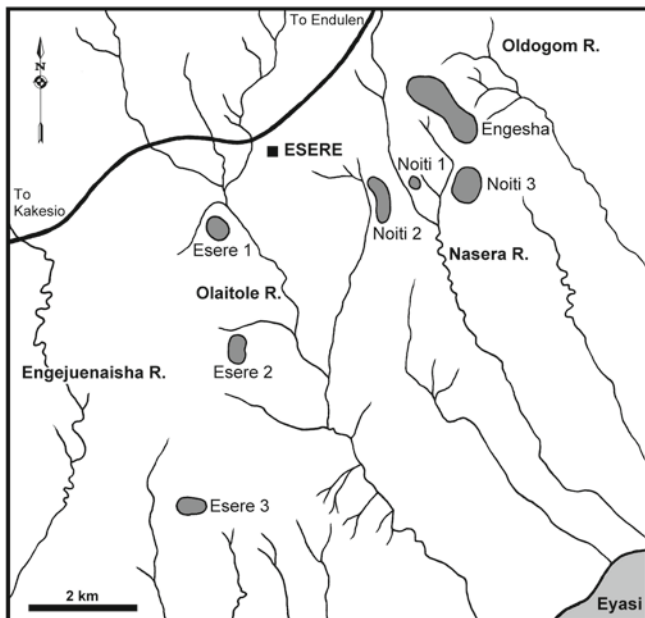
ostrich, *Struthio kakesiensis*, has been named previously (Harrison and Msuya 2005), based on new collections from the Lower and Upper Laetolil Beds.

Mary Leakey's team did recover a small sample of fossil vertebrates from the Lower Laetolil Beds at Kakesio early in their campaign, but the most intensive phase of research at the site took place in 1982, and as a result most of the fossil material and geological information obtained were not included in the Laetoli monograph (Leakey and Harris 1987). Harris (1987) published a brief summary of the fauna from the Lower Laetolil Beds, but most of the specimens remained undescribed. The specimens have been incorporated in the current studies of the fauna. The new collection of fossil mammals from the Lower Laetolil Beds is small ( $n=251$  specimens), but with more intensive prospecting, especially in the areas of Kakesio and Noiti, it would

be possible to recover a much larger sample. Given the age of the Lower Laetolil Beds (3.85–4.4 Ma), the fauna from these beds could be extremely important in the study of human evolution, because it samples the time period between the last occurrence of *Ardipithecus* and the first appearance of *Australopithecus*. The Lower Laetolil fauna now includes 27 species of mammals (up from 18 in 1987) (Table 1.3). It is dominated by bovids, equids and proboscideans. Small mammals are rare, and there is a strong taphonomic bias in favor of large mammals. Most of the mammalian taxa (78%) in the Lower Laetolil Beds also occur in the Upper Laetolil Beds, implying a strong biogeographic provinciality, despite the time difference (Table 1.3). However, several species occur in the Lower Laetolil Beds that are not present in the Upper Laetolil Beds. These include: *Anancus kenyensis*, *Petromus* sp., *Heterocephalus manthii*, aff.



**Fig. 1.3** Map of the Kakesio area showing the main outcrops of the Lower Laetolil Beds and the paleontological collecting localities (grey shaded areas) (From Harrison and Kweka 2011)



**Fig. 1.4** Map of the Esere-Noiti area showing the main outcrops of the Lower Laetolil Beds and the paleontological collecting localities (grey shaded areas) (From Harrison and Kweka 2011)

*Proteles*, *Aonyxini* gen. et sp. nov., and possibly *Gazella granti* (Sanders 2011; Denys 2011; Werdelin and Dehghani 2011; Gentry 2011). Most of these are very rare taxa (just one or a few specimens), with the exception of *Anancus kenyensis*.

There are now 85 species of mammals recorded from the Upper Laetolil Beds (compared with 71 in 1987) (Table 1.3). Including the Harrison and Leakey collections combined there are now over 18,000 mammal specimens known from the Upper Laetolil Beds (Table 1.3). The large mammal fauna is dominated by bovids (34% of all mammal specimens), with *Madoqua aviflumina*, *Parmularius pandatus* and *Gazella janenschi* being especially common (Gentry 2011). At most East African localities Neotragini are rare, whereas at Laetoli *Madoqua* is the by far the most common bovid taxon. Giraffids, with three species of different sizes represented, are also quite common (6.3% of all mammal specimens). Micromammals are well-represented in the Upper Laetolil Beds, especially the lagomorph *Serengetilagus praecapensis*, which is the commonest species, occurring ubiquitously throughout the unit (Denys 2011; Winkler and Tomida 2011). However, there is a high likelihood that small species of

<b>Ngaloba Beds</b>	>0.2 Ma
<b>Olpiro Beds</b>	2.0 Ma
<b>Naibadad Beds</b>	2.06-2.16 Ma
<b>Ogol Lavas</b>	2.3 Ma
<b>Ndolanya Beds</b>	2.66 Ma
<b>Laetolil Beds, Upper Unit</b>	3.6 Ma
<b>Laetolil Beds, Lower Unit</b>	3.85 Ma
	4.36 Ma

50 m

**Fig. 1.5** Simplified stratigraphic scheme of Laetoli sediments showing the main stratigraphic units (*left*) and the chronology (*right*, Ma = megannum) (After Hay 1987; Ndessokia 1990; Manega 1993; Ditchfield and Harrison 2011; Deino 2011)

**Table 1.1** Number of fossils collected 1998–2005

Taxon	LLB	ULB	UNB	Total	% of total
Mammals <sup>a</sup>	258	12,383	2,378	15,019	58.1
Birds <sup>b</sup>	3	185	9	197	0.8
<i>Struthio</i> <sup>c</sup>	427	343	289	1,059	4.1
Reptiles and amphibians <sup>d</sup>	103	352	34	489	1.9
Mollusks <sup>e</sup>	290	4,612	282	5,184	20.1
Insects <sup>f</sup>	460	1,857	1,103	3,420	13.2
Plants <sup>g</sup>	7	457	4	468	1.8
Total	1,548	20,189	4,095	25,832	100.0

Specimen counts do not include fossils from the Olpiro or Ngaloba Beds  
 LLB Lower Laetolil Beds, ULB Upper Laetolil Beds, UNB Upper Ndolanya Beds

<sup>a</sup>For more detailed information on fossil mammals see Table 1.2

<sup>b</sup>Includes bones and eggs, except for those assigned to *Struthio*

<sup>c</sup>Egg shell fragments of *Struthio*

<sup>d</sup>Mostly the remains of tortoises, but the count does include snakes, lizards and amphibians

<sup>e</sup>Terrestrial gastropods (For more detailed data on specimen counts see Tattersfield 2011)

<sup>f</sup>Mainly consists of cocoons and brood cells of solitary bees, but also includes casts of insects, termitaries, and brood cells of dung beetles

<sup>g</sup>Includes wood, twigs, leaves, and seeds (see Bamford 2011a, b)

**Table 1.2** Number of specimens and the frequency of fossil mammals collected at Laetoli and other localities on the Eyasi Plateau from 1998 to 2005

Taxon	Lower Laetolil Beds		Upper Laetolil Beds		Upper Ndolanya Beds	
	N	%	N	%	N	%
Macroscelididae	0	0	4	0.03	0	0
Galagidae	0	0	1	0.01	0	0
Cercopithecidae	1	0.40	111	0.91	1	0.04
Hominidae	0	0	2	0.02	2	0.09
Rodentia	10	3.97	855	7.00	104	4.55
Leporidae	15	5.95	4,640	38.00	398	17.41
Carnivora	13	5.16	424	3.47	54	2.36
Proboscidea	37	14.68	158	1.29	24	1.05
Orycteropodidae	1	0.40	26	0.21	2	0.09
Equidae	55	21.83	330	2.70	110	4.81
Rhinocerotidae	21	8.33	473	3.87	29	1.27
Chalicotheriidae	0	0	3	0.02	0	0
Suidae	12	4.76	244	2.00	27	1.18
Camelidae	0	0	26	0.21	6	0.26
Giraffidae	8	3.17	772	6.32	70	3.06
Bovidae	79	31.35	4,145	33.95	1,459	63.82
Total	252	100.0	12,214	100.01	2,286	99.99

rodents are under-represented in the collections due to taphonomic and collecting biases (Denys 2011; Reed and Denys 2011). Primates, including hominins, are rare, and comprise less than 1% of the mammalian fauna (Harrison 2011b, c, d; Table 1.2).

Fossil mammals are also abundant in the Upper Ndolanya Beds, which are separated in time from the Upper Laetolil Beds by a hiatus of about one million years. Forty-nine species of mammals are currently recognized (up from 38 species in 1987) (Table 1.3). Of these, just over half of the species (53%) are shared with the Upper Laetolil Beds. However, there is apparently a significant faunal turnover between these two units (between 3.6 and 2.66 Ma). Among the large mammals, *Eurygnathohippus* aff. *cornelianus* replaces *Eurygnathohippus* aff. *hasumense*, and *Ceratotherium simum*, *Metridiochoerus andrewsi*, *Giraffa pygmaea*, and *Camelus* sp. make their first appearance in the Laetoli fauna (Armour-Chelu and Bernor 2011; Hernesniemi et al. 2011; Bishop 2011; Robinson 2011). Several bovids also appear for the first time, including *Parmularius altidens*, *Parmularius parvicornis*, *Megalotragus* sp., *Tragelaphus* sp. cf. *T. buxtoni* and *Antidorcus recki* (Gentry 2011). Among the micromammals *Gerbilliscus winkleri* replaces *G. satimani*, and *Thryonomys wesselmani* appears for the first time (Denys 2011). There is also an important difference in the hominins, with *Australopithecus afarensis* being replaced by *Paranthropus aethiopicus* (Harrison 2011b). A better understanding of the ecological differences and changes in the community structure between the Upper Laetolil Beds and the Upper Ndolanya Beds should provide important clues to

**Table 1.3** List of the fauna from the main stratigraphic units at Laetoli

Class	Order	Family	Genus and species	LLB	ULB	UNB	
Insecta	Hymenoptera	Indeterminate			X	X	
		Coleoptera	Tenebrionidae	Tentyriini sp. A (?Tentyria)		X	
				Tentyriini sp. B		X	
				?Tentyriini sp. C		X	
				Molurini sp. A (?Arturium)		X	
		Scarabaeidae		<i>Calcitoryctes magnificus</i>		X	
				Melolonthinae: Schizonychini, sp. A		X	
				<i>Coprinisphaera ndolanyanus</i>			X
				<i>Coprinisphaera laetoliensis</i>			X
				<i>Lazaichnus amplus</i>			X
		Diptera	Indeterminate			X	
		Lepidoptera	Saturniidae	Bunaeini indet.		X	
		Isoptera	Termitidae	<i>Macrotermes</i> spp.		X	
	Apicotermitinae indet.				X		
	Gastropoda	Pulmonata	Indeterminate		X		
			Succineidae	“ <i>Succinea</i> ” sp. A	X		
			Cerastidae	<i>Gittenouardia laetoliensis</i>	X	X	
<i>Cerastus</i> sp. A				X			
Subulinidae			<i>Subulona pseudinvoluta</i>		X		
			<i>Pseudoglessula (Kempioconcha) aff. gibbonsi</i>		X		
			<i>Kenyaella leakeyi</i>	?	X		
			<i>Kenyaella harrisoni</i>			X	
			<i>Subuliniscus</i> sp. A			X	
Vertiginidae			<i>Pupoides coenopictus</i>	X			
Streptaxidae			<i>Streptostele (Raffraya) aff. horei</i>			X	X
			<i>Streptostele</i> sp. A			X	
			<i>Gulella</i> sp. A			X	
Achatinidae			<i>Burtoa nilotica</i>	X	X		
			<i>Limicolaria martensiana</i>	X	X		
			<i>Achatina (Lissachatina) indet.</i>	X	X		
			Urocyclidae	<i>Trochonanina</i> sp. B	X	X	X
			Urocyclinae sp. A		X	X	
			Urocyclinae sp. B		X	X	
	Urocyclinae sp. C		X	X			
	Urocyclinae sp. D		X	X			
	Urocyclinae sp. E		X	X			
	Urocyclinae sp. F		X	X			
Bradybaenidae	<i>Halolimnohelix rowsoni</i>		X				

(continued)

**Table 1.3** (continued)

Class	Order	Family	Genus and species	LLB	ULB	UNB		
Amphibia	Anura	Indeterminate			X			
Reptilia	Chelonii	Testudinidae	<i>Stigmochelys brachygularis</i>	X	X	X		
			" <i>Geochelone</i> " <i>laetoliensis</i>	X	X			
	Crocodylia Squamata	Crocodylidae	Acrodonta indet.	<i>Crocodylus</i> sp.	X	X		
				Scincomorpha indet.			X	
		Boidae		<i>Python sebae</i> or <i>P. natalensis</i>		X		
				Colubridae	cf. <i>Thelotornis</i> sp.		X	
					cf. <i>Rhamphiophis</i> sp.		X	
		Elapidae		Indeterminate sp. A		X		
				Indeterminate sp. B		X		
				<i>Naja robusta</i>		X		
				?indeterminate sp.		X		
				Viperidae	<i>Bitis</i> sp. nov. or <i>Bitis olduvaiensis</i>	X	X	X
		Aves	Struthioniformes	Struthionidae	<i>Struthio kakesiensis</i>	X	X	
<i>Struthio camelus</i>					X	X		
Galliformes	Phasianidae		<i>Francolinus</i> sp. A aff. <i>F. (Peliperdix) sephaena</i>		X	X		
			<i>Francolinus (Pternistis)</i> sp. B		X	X		
			cf. <i>Francolinus</i> sp. indet.		X			
			Numididae	cf. <i>Agelastes</i> sp.		X		
				<i>Numida/Guttera</i> sp.	X	X	X	
			Ciconiiformes	Ardeidae	<i>Acryllium vulturinum</i>		X	
					cf. <i>Ardea</i> sp.			X
			Charadriiformes	Scolopacidae	<i>Aegyptus</i> sp.		X	
					Calidrinae indet.		X	
			Accipitriformes	Accipitridae	cf. <i>Buteo</i> sp.		X	
Aquilini indet. sp. A					X			
Falconiformes	Falconidae		cf. Aquilini indet. sp. B		X			
			<i>Falco</i> cf. <i>eleonora</i>			X		
Columbiformes	Columbidae		Falconiformes indet.		X			
			<i>Columba</i> sp. (sp. A)		X			
Strigiformes	Tytonidae	<i>Streptopelia</i> sp. (sp. B)		X	X			
		Columbidae indet. (sp. C)			X			
		<i>Tyto</i> sp.		X				
	Strigidae	<i>Bubo</i> cf. <i>lacteus</i> (sp. A)			X			
		<i>Asio</i> sp. (sp. B)			X			
		cf. Strigidae (sp. C)			X			
		Coliiformes	Collidae	<i>Colius</i> sp.		X		
Passeriformes	Indeterminate	cf. Passerida indet.		X				

(continued)

**Table 1.3** (continued)

Class	Order	Family	Genus and species	LLB	ULB	UNB			
Mammalia	Macroscelidea	Macroscelididae	<i>Rhynchocyon pliocaenicus</i>		X				
	Tubulidentata	Orycteropodidae	<i>Orycteropus</i> sp.	X	X				
	Proboscidea	Deinotheriidae	<i>Deinotherium bozasi</i>			X	?		
		Gomphotheriidae	<i>Anancus kenyensis</i> <i>Anancus ultimus</i>	X X		X			
		Stegodontidae	<i>Stegodon</i> sp. cf. <i>Stegodon kaisensis</i>			X			
		Elephantidae	<i>Loxodonta</i> sp. cf. <i>Loxodonta cookei</i>	X					
			<i>Loxodonta exoptata</i>	X	X		X		
			Primates	Galagidae	<i>Laetolia sadimanensis</i>		X		
		Cercopithecidae	<i>Parapapio ado</i> Papionini indet. cf. <i>Rhinocolobus</i> sp. <i>Cercopithecoides</i> sp.			X X X X	X  X		
			Hominidae	<i>Australopithecus afarensis</i> <i>Paranthropus aethiopicus</i>			X		
								X	
			Rodentia	Sciuridae	<i>Paraxerus meini</i> <i>Xerus</i> sp. <i>Xerus janenschi</i>		X X X	X  X	
		Cricetidae			<i>Gerbilliscus satimani</i> <i>Gerbilliscus winkleri</i> <i>Gerbilliscus</i> cf. <i>inclusus</i> <i>Dendromus</i> sp. <i>Steatomys</i> sp. <i>Saccostomus major</i> <i>Saccostomus</i> sp.			X  X  X X X	
							cf.		cf.
								X	
								X	
								X	
								X	
		Muridae		<i>Aethomys</i> sp. <i>Thallomys laetolilensis</i> <i>Mastomys cinereus</i> <i>Mus</i> sp.			X X X	X  X	
				Thryonomyidae	<i>Thryonomys wesselmani</i>				X
		Petromuridae		<i>Petromus</i> sp.	X				
		Bathyergidae		<i>Heterocephalus quenstedti</i> <i>Heterocephalus manthii</i>			X		
						X			
		Hystricidae	<i>Hystrix leakeyi</i> <i>Hystrix makapanensis</i> <i>Xenohystrix crassidens</i>			X X X	X  X		
			Pedetidae	<i>Pedetes laetoliensis</i> <i>Pedetes</i> sp.			X		
								X	
		Lagomorpha	Leporidae	<i>Serengetilagus praecapensis</i>	X	X	X		
		Soricomorpha	Soricidae	? <i>Crociodura</i> sp.			X		

(continued)

**Table 1.3** (continued)

Class	Order	Family	Genus and species	LLB	ULB	UNB
	Carnivora	Canidae	? <i>Nyctereutes barryi</i> cf. <i>Canis</i> sp. A cf. <i>Canis</i> sp. B aff. <i>Otocyon</i> sp.		X X X X	
		Mustelidae	<i>Prepoecilogale bolti</i> <i>Mellivora</i> sp. Aonyxini gen. et sp. nov.	X	X X	X
		Viverridae	Mustelidae indet. <i>Viverra leakeyi</i> <i>Genetta</i> sp. aff. Viverridae		X X X X	
		Herpestidae	<i>Herpestes palaeo-serengetensis</i> <i>Herpestes ichneumon</i> <i>Galerella</i> sp. <i>Helogale palaeogracilis</i> <i>Mungos dietrichi</i> <i>Mungos</i> sp. nov.		X X X X X	
		Hyaenidae	<i>Crocuta dietrichi</i> <i>Parahyaena howelli</i> <i>Ikelohyaena</i> cf. <i>I. abronia</i> <i>Lycyaenops</i> cf. <i>L. silberbergi</i> ? <i>Pachycrocuta</i> sp. aff. <i>Proteles</i> sp.	X X	X X X X X	X X ?
		Felidae	<i>Dinofelis petteri</i> <i>Homotherium</i> sp. <i>Panthera</i> sp. aff. <i>P. leo</i> <i>Panthera</i> sp. cf. <i>P. pardus</i> <i>Acinonyx</i> sp. <i>Caracal</i> sp. or <i>Leptailurus</i> sp. <i>Felis</i> sp.	X	X X X X X X X	X X X X
	Perissodactyla	Equidae	<i>Eurygnathohippus</i> aff. <i>hasumense</i> <i>Eurgnathohippus</i> aff. <i>cornelianus</i>	X	X	X
		Chalicotheriidae	<i>Ancylotherium hennigi</i>		X	
		Rhinocerotidae	<i>Ceratotherium efficax</i> <i>Ceratotherium</i> cf. <i>simum</i> <i>Ceratotherium</i> sp. <i>Diceros</i> sp.	X	X	X X X
	Artiodactyla	Suidae	<i>Notochoerus euilus</i> <i>Notochoerus jaegeri</i> <i>Nyanzachoerus kanamensis</i> <i>Potamochoerus afarensis</i>	X X	X X X X	

(continued)

**Table 1.3** (continued)

Class	Order	Family	Genus and species	LLB	ULB	UNB
			<i>Kolpochoerus heseloni</i>		X	X
			<i>Metridiochoerus andrewsi</i>			X
		Giraffidae	<i>Giraffa stillei</i>	aff.	X	aff.
			<i>Giraffa jumae</i>		aff.	
			<i>Giraffa pygmaea</i>			aff.
			<i>Sivatherium maurusium</i>	X	X	aff.
		Camelidae	<i>Camelus</i> sp.			X
		Bovidae	<i>Tragelaphus</i> sp.		X	
			<i>Tragelaphus</i> sp. cf. <i>T. buxtoni</i>			X
			<i>Simatherium kohllarseni</i>		X	
			<i>Brabovus nanincisus</i>		X	
			Bovini sp. indet.	X	X	X
			Cephalophini sp.		X	?
			<i>Hippotragus</i> sp.	X	X	
			<i>Hippotragus</i> sp. aff. <i>cookei</i> ?			X
			<i>Oryx deturi</i>		X	
			<i>Oryx</i> sp.			X
			<i>Parmularius pandatus</i>	X	X	
			<i>Parmularius ?altidens</i>			X
			<i>Parmularius parvicornis</i>			X
			Alcelaphini, larger sp. indet.	X	X	
			Alcelaphini, small sp.		?	
			<i>Megalotragus kattwinkeli</i> or <i>M. isaaci</i>			X
			? <i>Connochaetes</i> sp.			X
			Reduncini sp. indet.		X	X
			<i>Madoqua avifluminis</i>	X	X	X
			? <i>Raphicerus</i> sp.	X	X	X
			<i>Aepyceros dietrichi</i>	X	X	
			<i>Aepyceros</i> sp.			X
			" <i>Gazella</i> " <i>kohllarseni</i>		X	
			<i>Gazella janenschi</i>	X	X	X
			<i>Gazella granti</i>	X	?	?
			<i>Gazella</i> sp.			X
			<i>Antidorcas recki</i>			X

understanding the differentiation of the *Paranthropus* lineage. The mammalian fauna from the Upper Ndolanya Beds is heavily skewed towards bovids (63.8% of all specimens), especially medium- and large-sized alcelaphines, probably as a consequence of an unusual combination of taphonomic

factors (Table 1.2). The other common species in the Upper Ndolanya fauna is *Serengetilagus praecipensis* (17.4% of all mammal specimens) (Table 1.2).

In addition to fossil mammals, study of the non-mammalian fauna and paleobotanical remains are essential for a complete



understanding and appreciation of the biotic diversity and paleoecology at Laetoli during the Pliocene. These investigations include the first detailed studies to be undertaken of the fossil insects, gastropods, birds, lizards and snakes from Laetoli (Krell and Schawaller 2011; Kitching and Sadler 2011; Tattersfield 2011; Louchart 2011; Rage and Bailon 2011). Research on the fossil ostriches and birds' eggs has already been published (Harrison 2005; Harrison and Msuya 2005). The contributions presented in this volume provide the basis for a major systematic revision of the Laetoli fauna, as well as a much better appreciation of the paleobiology and paleoecology. The fossil wood and other paleobotanical remains, which provide important insights into the paleoecology of Laetoli, are described in the companion volume (Bamford 2011a, b; Rossouw and Scott 2011).

## Paleoecology

A major focus of renewed investigations at Laetoli has been on reconstructing the paleoecology (Harrison 2011e). Study of the paleoecology provides critical evidence for understanding the context of early hominin evolution. It also allows researchers to pose important questions about hominin habitat preferences, ecology and paleobiology, and to include these data in larger-scale macroevolutionary models of speciation, biogeography, diversification and extinction. With these questions in mind, renewed work at Laetoli has attempted to reconstruct the paleoecology using information from a wide diversity of sources (i.e., modern-day ecosystems, paleobotany, phytoliths, palynology, invertebrate and invertebrate paleontology, stable isotopes, mesowear, ecomorphology, and community structure analyses) (Andrews et al. 2011; Bamford 2011a, b; Rossouw and Scott 2011; Kingston 2011; Kaiser 2011; Hernesniemi et al. 2011; Harrison 2011f; Bishop et al. 2011; Kovarovic and Andrews 2011; Su 2011; Reed 2011; Reed and Denys 2011).

The geological and sedimentological evidence indicates that the Laetoli area had a relatively low topography during the Pliocene, with a gently undulating terrain. There is evidence of rivers and streams in the Upper Laetolil Beds, probably with a greater extent and capacity than the present-day hydrological system, but these rivers only flowed during the wet season, and were dry for most of the year (Ditchfield and Harrison 2011). The watercourses originated in the volcanic highlands about 20 km to the east, and flowed southwest across the Laetoli area, and it is likely that they drained into the developing Eyasi basin. This network of watercourses would have supported a complex vegetational mosaic, including dense stands of riverine woodland and bushland (Ditchfield and Harrison 2011). Ephemeral ponds and small lakes would have dotted the landscape during the rainy sea-

son, but these would have dried up during the dry season. There is no evidence of large permanent bodies of water in the Upper Laetolil Beds or Upper Ndolanya Beds, and this is consistent with the absence of aquatic and hydrophilic vertebrates (i.e., hippopotamids, crocodiles, turtles and fishes), with the exception of rare finds of anurans (Rage and Bailon 2011; Ditchfield and Harrison 2011). The paleoenvironment of the Lower Laetolil Beds appears to have been similar to that of the Upper Laetolil Beds and Upper Ndolanya Beds, but there is better evidence of shallow pools and lakes. Aquatic vertebrates are extremely rare in the Lower Laetolil Beds, but the fauna does include an otter and there is also single confirmed specimen of *Crocodylus*. Harris (1987) reported the presence of fish from the Lower Laetolil Beds, but this has not been confirmed, and their record has been removed from the revised faunal list (Table 1.3).

The very common traces of termite bioturbation, burrows of solitary hymenoptera, and the occurrence of aestivating gastropods throughout the Laetoli sequence, all point to widespread paleosols that were well drained and free from inundation for much of the year. It is very likely that run-off from the volcanic highlands would have continued year-round, with water flowing below the surface even during the dry season, just as it does today. Presently, springs occur along the edge of the Eyasi escarpment where the Laetolil Beds interface with the underlying impervious Precambrian basement rocks, and these provide a permanent source of water for wildlife and the local inhabitants. Given that similar geomorphological and topographic features were in place during the Pliocene, it is likely that springs were present in the Laetoli area, and that these offered an important source of water during the long dry season in what would otherwise have been a relatively dry and waterless terrain.

Ash fall deposits periodically blanketed the Laetoli area, forming distinctive marker tuffs in the Upper Laetolil Beds. These heavy inundations of carbonatite volcanic ash would have had an adverse effect on the local ecosystem, including burial of the ground vegetation and making standing bodies of water toxic (Peters et al. 2008). The subsequent formation of calcretes and hardpans would have led to a landscape dominated by grasslands and open woodlands. However, these periods of disruption were apparent relatively short-lived, and the climax vegetation would have quickly re-established itself. The ash falls in the Lower Laetolil Beds were thicker and more frequent than in the Upper Laetolil Beds, and undoubtedly would have caused more dramatic short-term disruptions to the local ecosystem. However, the greater degree of fluvial reworking and bioturbation of the Lower Laetolil Beds indicates that the sediments quickly formed weakly developed paleosols that could have supported rapid re-establishment of the climax vegetation.

The paleobotanical evidence provides important clues to reconstructing the paleoecology at Laetoli. The fossil wood

from the Lower Laetolil Beds at Noiti suggests that woodlands and forest covered the lower slopes of the volcanic highlands to the east of Laetoli, and that a mosaic of woodland, bushland and wooded grasslands occurred more distally (Bamford 2011a). Plant macrofossils from the Upper Laetolil Beds suggest a diverse flora, with vegetation that included forest and woodland elements (Bamford 2011b). The study of the phytoliths indicates that grasses were common at Laetoli during the Pliocene, but they were probably not the dominant vegetation type (Rossouw and Scott 2011). The Lower Laetolil Beds appear to have been deposited in a relatively mesic habitat dominated by  $C_3$  grasses. Conditions became drier during the lower part of the Upper Laetolil Beds and more mesic conditions prevailed again during the upper part, with a shift from  $C_3$  dominated grasses to  $C_4$  dominated grasses. The phytolith evidence indicates that the paleoecology of Upper Ndolanya Beds was one of relatively arid grasslands, dominated by  $C_4$  grasses.

Studies of the stable isotopes, mesowear, bovid postcranial ecomorphology, small and large mammal community structure, and the bird fauna provide a picture of the Laetoli paleoecology that is largely consistent with that of the paleobotanical evidence (Kingston 2011; Kaiser 2011; Bishop et al. 2011; Su 2011; Denys 2011; Hernesniemi et al. 2011; Louchart 2011; Kovarovic and Andrews 2011). The ecology during deposition of the Upper Laetolil Beds was a vegetational mosaic with woodland, bushland and grassland-savanna. The ungulate fauna was dominated by browsers and mixed feeders. Such a fauna, especially that with a large proportion of very large browsers (i.e., three species of giraffids, several large bovids and suids, chalicotheres, *Ceratotherium*, deinotheres), has no modern analogs, because there are no present-day ecosystems, beyond tropical forests, that have such a diverse guild of browsing herbivores. There is some evidence to suggest that conditions became slightly drier, with a greater proportion of grassland and open woodland, in the upper part of the Upper Laetolil Beds above Tuff 7. The evidence from the fossil mammals consistently points to a major shift in the Upper Ndolanya Beds to an ecosystem dominated by grassland.

Further important evidence about the paleoecology is provided by the fossil gastropods (Tattersfield 2011). These indicate an abundance of woodland habitats throughout the Upper Laetolil Beds, but again they suggest that conditions became somewhat drier above Tuff 7. The gastropods from the Upper Ndolanya Beds, in contrast to the evidence from the fossil mammals, indicate that more mesic conditions prevailed, with extensive woodlands, similar to the paleoecology from the lower part of the Upper Laetolil Beds, which were the most mesic part of the sequence. A similar conclusion can be inferred from the oxygen isotope data from ostrich eggshell, which suggests that more mesic conditions were present in the Upper Ndolanya Beds. In addition, one of

the main differences distinguishing the rodent community from the Upper Ndolanya Beds in comparison with the Upper Laetolil Beds, is the occurrence of *Thryonomys* (cane rat) (Denys 2011). The extant species of *Thryonomys* live in waterlogged valley bottoms and moist areas with reliable rainfall, where they specialize in feeding on coarse grasses and reeds (Kingdon 1997). Given that gastropods are highly sensitive indicators of the local ecology compared to most mammals, I am inclined to accept that the paleoecology of the Upper Ndolanya Beds was characterized by a greater extent of woodland than is indicated by the large mammal fauna. It is possible that the paleoecological signal derived from the large mammals is influenced by taphonomic factors (i.e., a bias towards larger-bodied ungulates) or that a significant part of the large mammal community may be transitory or migratory in nature, and therefore not reflective of the local ecology.

The balance of the evidence would suggest that the paleoecology of the Upper Laetolil Beds was dominated by a mosaic of closed woodland, open woodland, shrubland and grassland. It was certainly more densely wooded than the modern-day Laetoli ecosystem, which is dominated by grassland and open woodland (Andrews et al. 2011). Water was probably more abundant during the rainy season, judging from the size and frequency of watercourses and small-scale fluvial deposits, but the region would have been dry for most of the year, except for the possible occurrence of permanent springs along the margin of the Eyasi Plateau. The paleoecology of the Lower Laetolil Beds was probably quite similar to that of the Upper Laetolil Beds. There is evidence, however, of semi-permanent bodies of water, but generally the inferred ecology is one of a dry woodland and bushland, possibly representative of an ecosystem that was disturbed by heavy inundations of volcanic ashes. The paleoecological reconstruction of the Upper Ndolanya Beds is more problematic because of the conflicting evidence derived from different proxies. However, it is very likely that conditions became drier than in the Upper Laetolil Beds, with a greater proportion of grassland, but that closed and open woodlands were still a significant part of the ecosystem.

**Acknowledgements** A special thanks to all of the dedicated and resourceful team members who participated in the expeditions to Laetoli that contributed to the recovery of the material discussed and analyzed here. This volume and its companion would not have been possible without them. I would especially like to single out the following individuals who were critical to the success of the field project: Amandus Kweka, Michael L. Mbago, Charles P. Msuya, Simon Odunga, Al Deino, Carl Swisher, Peter Ditchfield, Godwin Mollel, Lindsay McHenry, Craig Feibel, Moses Lilombero, Simon Mataro, Denise Su, Peter Andrews, Terri Harrison and Bill Sanders. I thank all of the authors for their excellent contributions to this volume. For those who got their chapters in on time I am especially grateful; to those who were late with their submission, I hope that I am forgiven for the persistent nagging. To the senior physical anthropologist that accused me of doing stamp collecting rather

than science, I will let the content of this volume speak for itself. I thank the Tanzania Commission for Science and Technology and the Unit of Antiquities in Dar es Salaam for permission to conduct research in Tanzania. Special thanks go to Paul Msemwa (Director), Amandus Kweka and all of the curators and staff at the National Museum of Tanzania in Dar es Salaam for their support and assistance. Fieldwork at Laetoli was supported by grants from the National Geographic Society, the Leakey Foundation, and the National Science Foundation (Grants BCS-0216683 and BCS-0309513). This chapter is dedicated to the memory of the late Norbert Kayombo (former Director General of the National Museums of Tanzania) for his unwavering support.

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## Chapter 2 Rodents

Christiane Denys

**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 *Petromys* 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-M/2 (EP 2196/00, Loc. 7E, Upper Ndolanya Beds). Scale bar in mm