Paleontology and Geology of Laetoli: Human Evolution in Context

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Paleontology and Geology of Laetoli: Human Evolution in Context

Volume 2: Fossil Hominins and the Associated Fauna

Edited by

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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. Mollel, 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 Universitat Tübingen Institut für Ur- und Frühgeschichte und Archäologie des Mittelalters and Institut und Museum für Geologie and Paläontologie.

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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.

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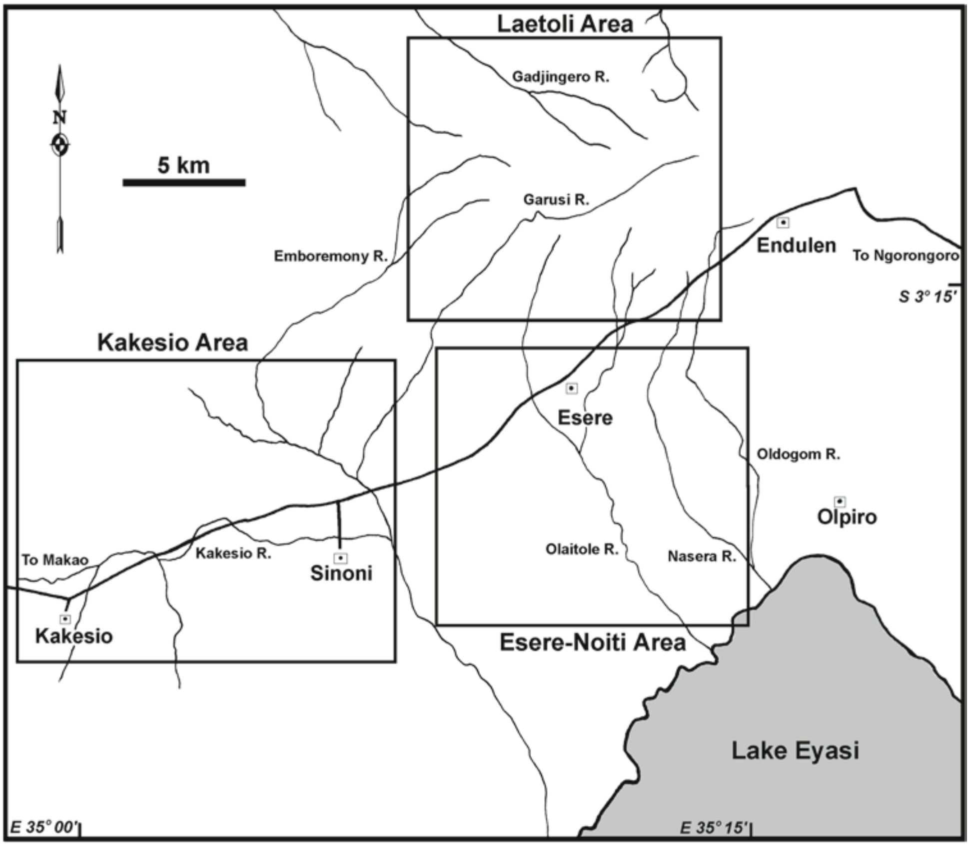

Fig. 1.1 A sketch map of the Eyasi Plateau showing the major rivers and villages, as well as the three main paleontological research areas: Laetoli, Kakesio and Esere-Noiti (see Figs. 1.2–1.4 for detail of insets) (From Harrison and Kweka 2011)

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 hominins 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

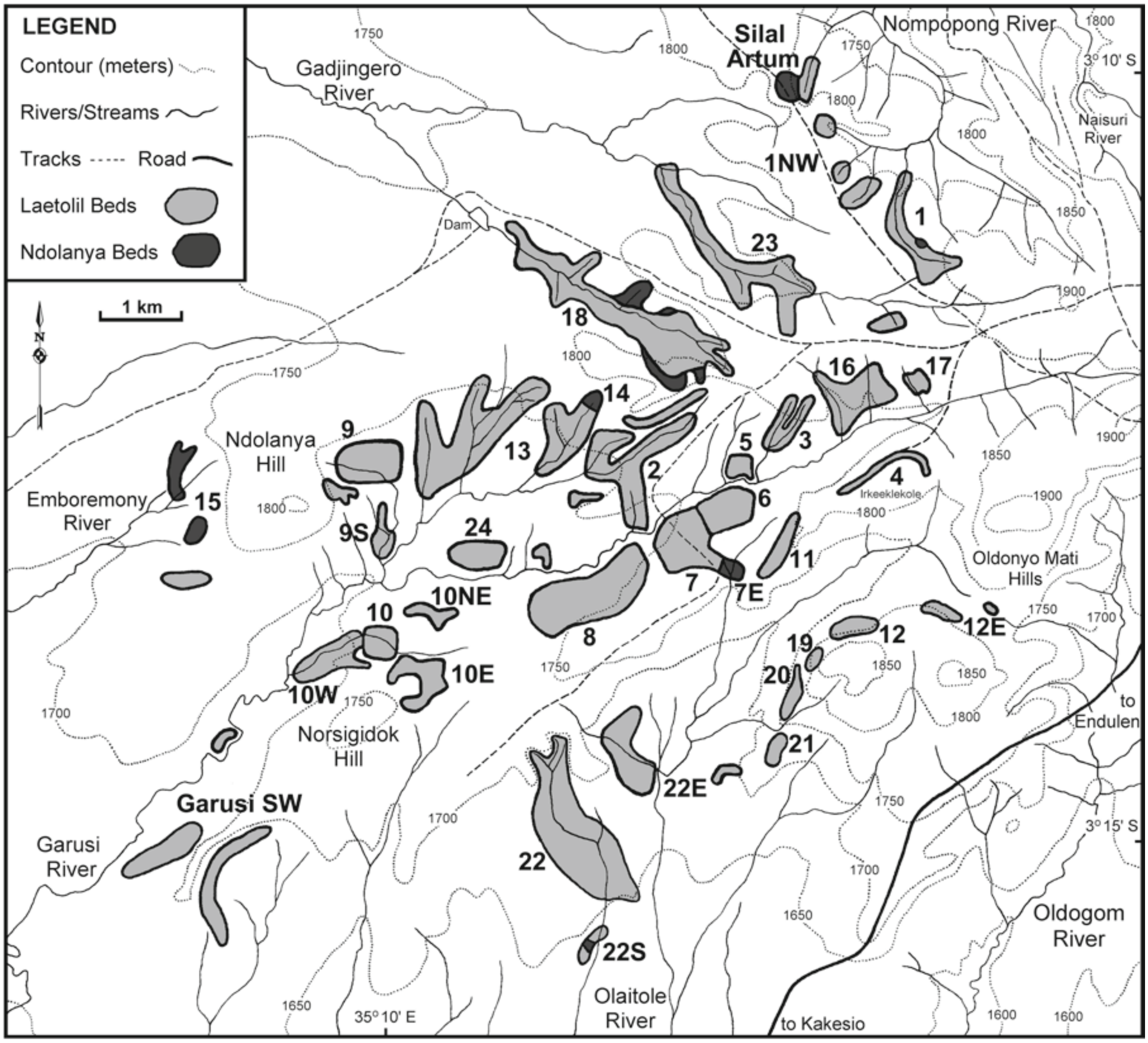

Fig. 1.2 Map of the Laetoli area showing the main outcrops of the Upper Laetolil and Upper Ndolanya Beds and the paleontological collecting localities (From Harrison and Kweka 2011)

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.

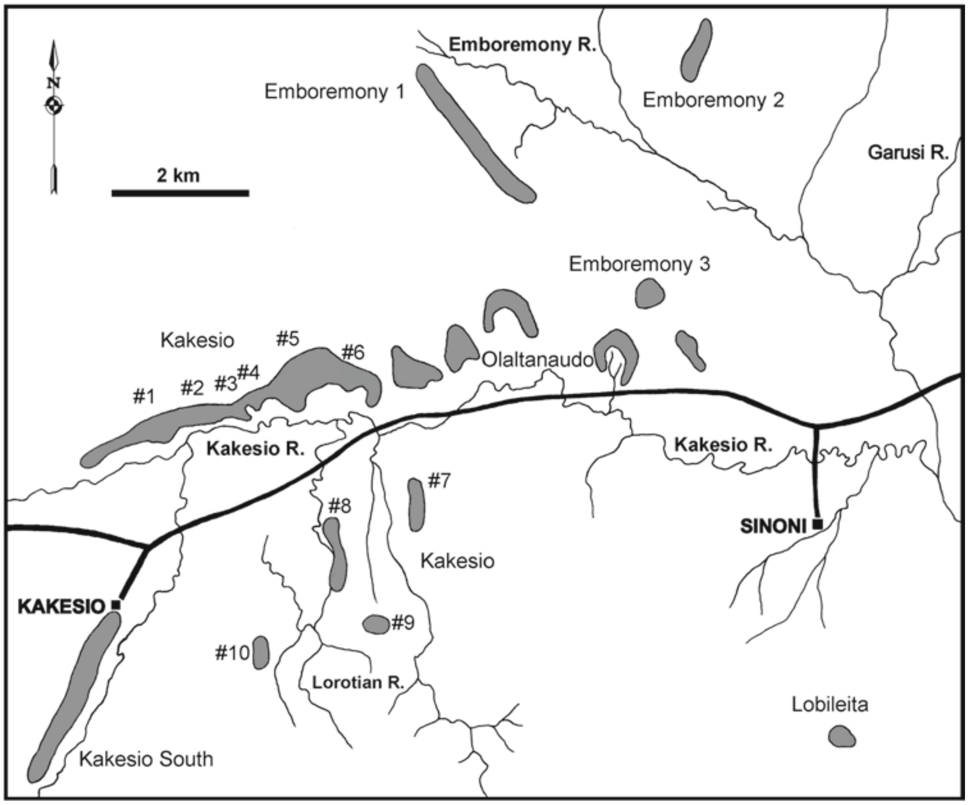

Fig. 1.3 Map of the Kakesio area showing the main outcrops of the Lower Laetolil Beds and the paleontological collecting localities (grey shaded areas) (From Harrison and Kweka 2011)

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 avifluminis*, *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

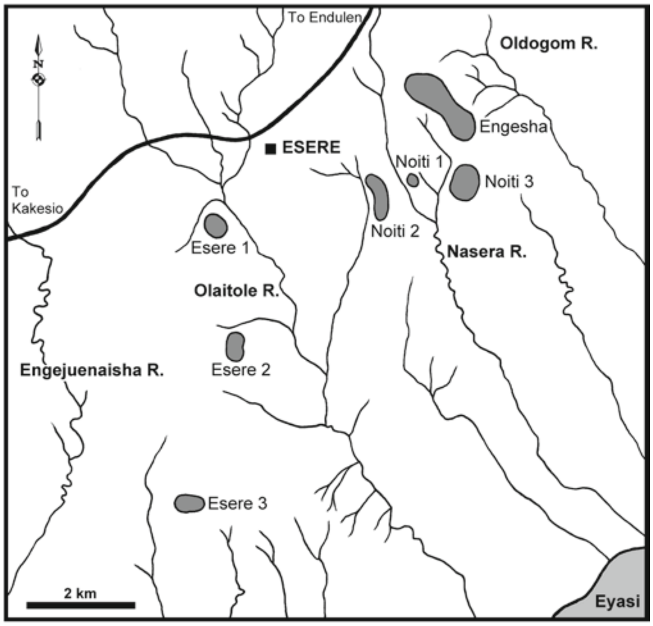

Fig. 1.4 Map of the Esere-Noiti area showing the main outcrops of the Lower Laetolil Beds and the paleontological collecting localities (grey shaded areas) (From Harrison and Kweka 2011)

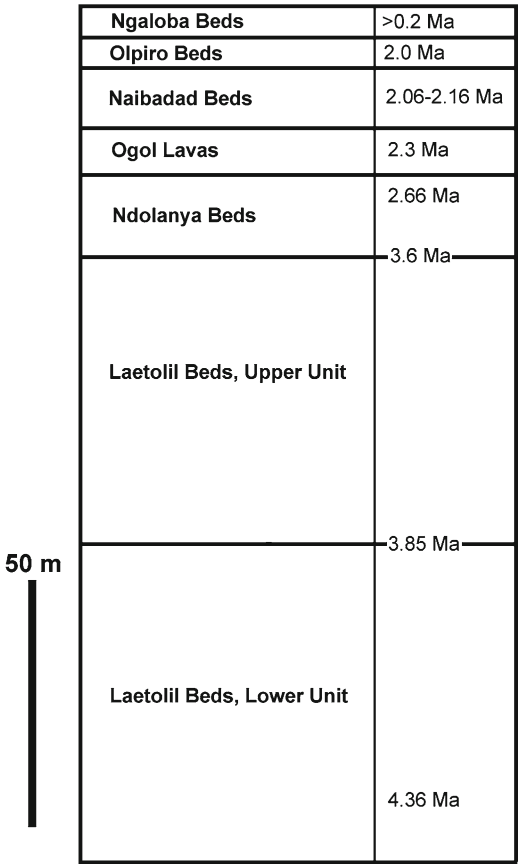

Fig. 1.5 Simplified stratigraphic scheme of Laetoli sediments showing the main stratigraphic units (*left*) and the chronology (*right*, Ma = mega-annum) (After Hay 1987; Ndessokia 1990; Manega 1993; Ditchfield and Harrison 2011; Deino 2011)

Table 1.1 Number of fossils collected 1998–2005

Taxon	LLB	ULB	UNB	Total	% of total
Mammals[a]	258	12,383	2,378	15,019	58.1
Birds[b]	3	185	9	197	0.8
Struthio[c]	427	343	289	1,059	4.1
Reptiles and amphibians[d]	103	352	34	489	1.9
Mollusks[e]	290	4,612	282	5,184	20.1
Insects[f]	460	1,857	1,103	3,420	13.2
Plants[g]	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

[a] For more detailed information on fossil mammals see Table 1.2

[b] Includes bones and eggs, except for those assigned to *Struthio*

[c] Egg shell fragments of *Struthio*

[d] Mostly the remains of tortoises, but the count does include snakes, lizards and amphibians

[e] Terrestrial gastropods (For more detailed data on specimen counts see Tattersfield 2011)

[f] Mainly consists of cocoons and brood cells of solitary bees, but also includes casts of insects, termitaries, and brood cells of dung beetles

[g] 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

	Lower Laetolil Beds		Upper Laetolil Beds		Upper Ndolanya Beds	
Taxon	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	*Calcitoryctes magnificus*		X	
			Melolonthinae: Schizonychini, sp. A		X	
			Coprinisphaera ndolanyanus			X
			Coprinisphaera laetoliensis			X
			Lazaichnus amplus			X
	Diptera	Indeterminate			X	
	Lepidoptera	Saturniidae	Bunaeini indet.		X	
	Isoptera	Termitidae	*Macrotermes* spp.		X	
			Apicotermitinae indet.		X	
		Indeterminate		X		
Gastropoda	Pulmonata	Succineidae	"*Succinea*" sp. A	X		
		Cerastidae	*Gittenedouardia laetoliensis*	X	X	
			Cerastus sp. A	X		
		Subulinidae	*Subulona pseudinvoluta*		X	
			Pseudoglessula (Kempioconcha) aff. *gibbonsi*		X	
			Kenyaella leakeyi	?	X	
			Kenyaella harrisoni			X
			Subuliniscus sp. A			X
		Vertiginidae	*Pupoides coenopictus*	X		
		Streptaxidae	*Streptostele (Raffraya)* aff. *horei*		X	X
			Streptostele sp. A		X	
			Gulella sp. A		X	
		Achatinidae	*Burtoa nilotica*	X	X	
			Limicolaria martensiana	X	X	
			Achatina (Lissachatina) indet.	X	X	
		Urocyclidae	*Trochonanina* 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	*Halolimnohelix rowsoni*		X	

(continued)

Table 1.3 (continued)

Class	Order	Family	Genus and species	LLB	ULB	UNB
Amphibia	Anura	Indeterminate			X	
Reptila	Chelonii	Testudinidae	*Stigmochelys brachygularis*	X	X	X
			"Geochelone" laetoliensis	X	X	
	Crocodilia	Crocodylidae	*Crocodylus* sp.	X		
	Squamata	Acrodonta indet.			X	
		Scincomorpha indet.				X
		Boidae	*Python sebae* or *P. natalensis*		X	
		Colubridae	cf. *Thelotornis* sp.		X	
			cf. *Rhamphiophis* sp.		X	
			Indeterminate sp. A		X	
			Indeterminate sp. B		X	
		Elapidae	*Naja robusta*		X	
			?indeterminate sp.		X	
		Viperidae	*Bitis* sp. nov. or *Bitis olduvaiensis*	X	X	X
Aves	Struthioniformes	Struthionidae	*Struthio kakesiensis*	X	X	
			Struthio camelus		X	X
	Galliformes	Phasianidae	*Francolinus* sp. A aff. *F. (Peliperdix) sephaena*		X	X
			Francolinus (Pternistis) sp. B		X	X
			cf. *Francolinus* sp. indet.		X	
		Numididae	cf. *Agelastes* sp.		X	
			Numida/Guttera sp.	X	X	X
			Acryllium vulturinum		X	
	Ciconiiformes	Ardeidae	cf. *Ardea* sp.			X
			Aegypius sp.		X	
	Charadriiformes	Scolopacidae	Calidrinae indet.		X	
	Accipitriformes	Accipitridae	cf. *Buteo* sp.		X	
			Aquilini indet. sp. A		X	
			cf. Aquilini indet sp. B		X	
	Falconiformes	Falconidae	*Falco* cf. *eleonorae*			X
			Falconiformes indet.		X	
	Columbiformes	Columbidae	*Columba* sp. (sp. A)		X	
			Streptopelia sp. (sp. B)		X	X
			Columbidae indet. (sp. C)			X
	Strigiformes	Tytonidae	*Tyto* sp.		X	
		Strigidae	*Bubo* cf. *lacteus* (sp. A)		X	
			Asio sp. (sp. B)		X	
			cf. Strigidae (sp. C)		X	
	Coliiformes	Collidae	*Colius* 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	*Rhynchocyon pliocaenicus*		X	
	Tubulidentata	Orycteropodidae	*Orycteropus* sp.	X	X	
	Proboscidea	Deinotheriidae	*Deinotherium bozasi*		X	?
		Gomphotheriidae	*Anancus kenyensis*	X		
			Anancus ultimus	X	X	
		Stegodontidae	*Stegodon* sp. cf. *Stegodon kaisensis*		X	
		Elephantidae	*Loxodonta* sp. cf. *Loxodonta cookei*	X		
			Loxodonta exoptata	X	X	X
	Primates	Galagidae	*Laetolia sadimanensis*		X	
		Cercopithecidae	*Parapapio ado*		X	X
			Papionini indet.		X	
			cf. *Rhinocolobus* sp.		X	X
			Cercopithecoides sp.		X	
		Hominidae	*Australopithecus afarensis*		X	
			Paranthropus aethiopicus			X
	Rodentia	Sciuridae	*Paraxerus meini*		X	X
			Xerus sp.		X	
			Xerus janenschi		X	X
		Cricetidae	*Gerbilliscus satimani*		X	
			Gerbilliscus winkleri			X
			Gerbilliscus cf. *inclusus*		X	
			Dendromus sp.		X	
			Steatomys sp.		X	
			Saccostomus major	cf.	X	cf.
			Saccostomus sp.			X
		Muridae	*Aethomys* sp.		X	
			Thallomys laetolilensis		X	X
			Mastomys cinereus		X	
			Mus sp.		X	
		Thryonomyidae	*Thryonomys wesselmani*			X
		Petromuridae	*Petromus* sp.	X		
		Bathyergidae	*Heterocephalus quenstedti*		X	
			Heterocephalus manthii	X		
		Hystricidae	*Hystrix leakeyi*		X	
			Hystrix makapanensis		X	X
			Xenohystrix crassidens		X	
		Pedetidae	*Pedetes laetoliensis*		X	
			Pedetes sp.			X
	Lagomorpha	Leporidae	*Serengetilagus praecapensis*	X	X	X
	Soricimorpha	Soricidae	?*Crocidura* sp.			X

(continued)

Table 1.3 (continued)

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

(continued)

Table 1.3 (continued)

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

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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 *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 janenschi* 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); Zoologishe 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 toothrow length (mm) for the new Laetolil 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
P. capensis	17.9	19.1
P. surdaster	18.5	18.0
P. capensis	Mean 17.26	Mean 17.42
N=4	Range 16.67–17.38	Range 16.60–18.94

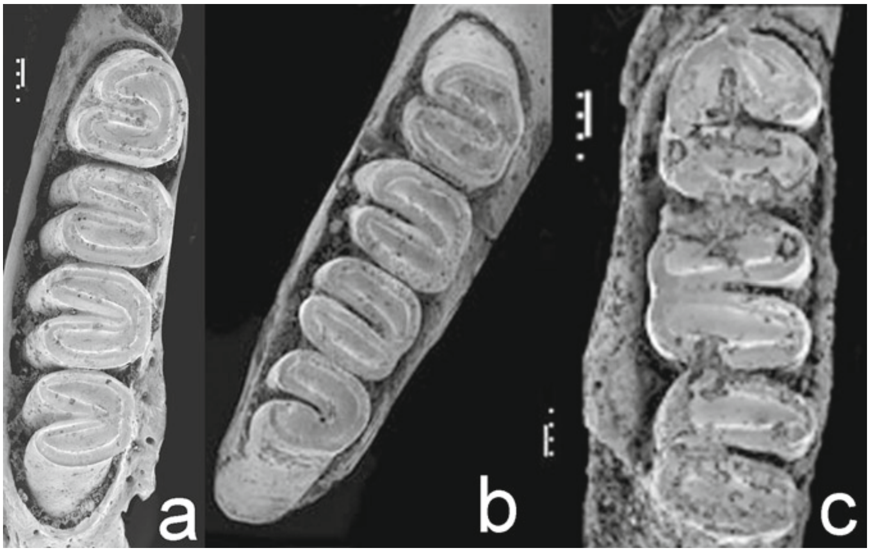

Fig. 2.1 New specimens of *Pedetes* from Laetoli. (**a**) right maxilla with DP4-M3/ of *P. laetoliensis* (EP 1994/00, Loc. 5, Upper Laetolil Beds); (**b**) right mandible with DP/4-M/3 of *P. laetoliensis* (EP 1867/00, Loc. 2, Upper Laetolil Beds); (**c**) mandible of *Pedetes* sp. with DP/4-M/2 (EP 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. *janenschi* (Loc. 2). The Upper Ndolanya Beds at Locs. 7E and 18 have yielded well-preserved remains of *Xerus janenschi*. 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.

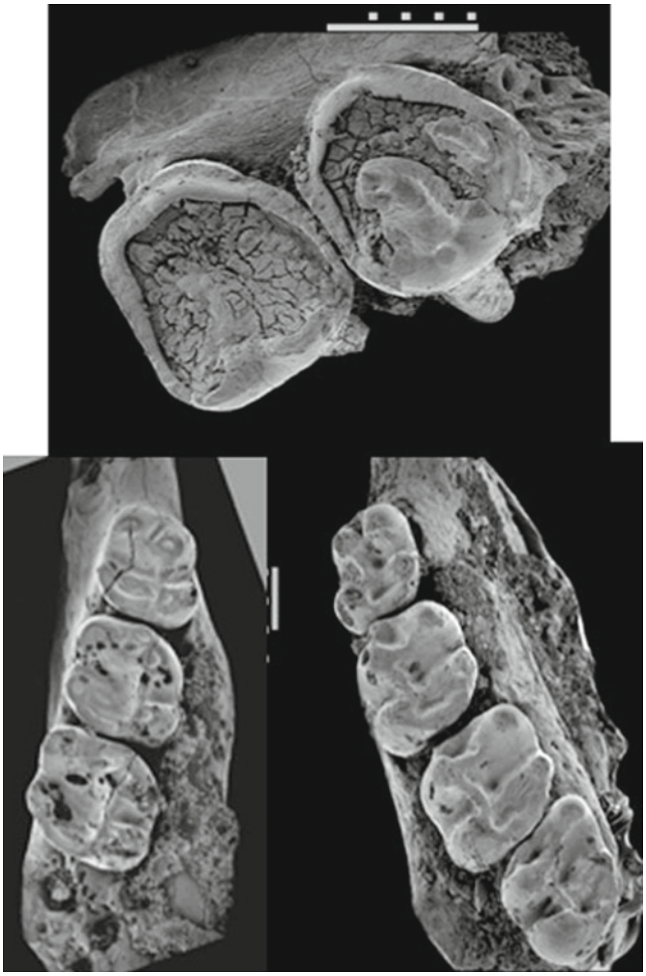

Fig. 2.2 *Paraxerus meini* sp. nov. upper and lower molars. *Top*, EP 881/03 (paratype) (Loc. 10E, Upper Laetolil Beds), left maxillary fragment with P4/M1; *below*, EP 1250/03 (Loc.7E, Upper Ndolanya Beds), right mandible with P/4-M/2 and EP 2816/00 (holotype) (Loc. 5, Upper Laetolil Beds)

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 P/4-M/2. EP 1000/01 (Loc. 11), mandible with P/4-M/3. EP 4152/00 (Loc. 8), right and left hemi-mandibles with M/1-3. EP 1250/03 (Loc. 7E), right mandible with P/4-M/2.

Referred material from Laetolil Beds (previously identified as *Paraxerus* sp. indet. by Denys 1987a): LAET 76-4121A, lower P/4; LAET 74-304, upper P4-M3/ (figured in Denys 1987a, plate 6.2-1 p. 123); LAET 76-4178, lower P/4-M/1; LAET 76-4170, right mandible fragment with P/4- 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 P/4 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 P/4. 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) toothrow 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
P. meini	Laetoli (this work; Denys 1987a)	2	6.63	0.53	6.25–7.00	4	6.88	0.69	5.96–7.58
P. flavovittis	Tanzania	12	7.60	0.316	7.03–8.18	14	7.41	0.213	7.02–7.76
P. cepapi	Tanzania Zimbabwe South Africa	10	7.93	0.52	7.08–8.43	10	7.66	0.55	6.8 – 8.29
P. boehmi	Uganda DR Congo	2	6.13		5.48–6.79	2	5.60		5.57–5.64
P. ochraceus	Kenya Somalia Tanzania	4	7.09	0.57	6.32–7.72	4	6.88	0.49	6.25–6.97

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
P. meini								
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**
P. ochraceus								
26.5.12.50	1.57	1.29	1.62	1.48	1.62	1.66	1.86	1.48
P. flavovittis								
2007-1236	1.52	1.52	1.57	1.62	1.72	1.86	2.05	1.62
***Paraxerus* sp.**								
KNM-NK 44920	2.08	2.0						
KNM-KP 46313			2.0	2.2	2.0	2.6	3.0	2.5
P. cepapi								
DM521	1.81	1.76	1.91	1.91	1.95	2.05	1.91	1.86
P. ochraceus 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
H. karsticus								
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 protoloph 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 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.

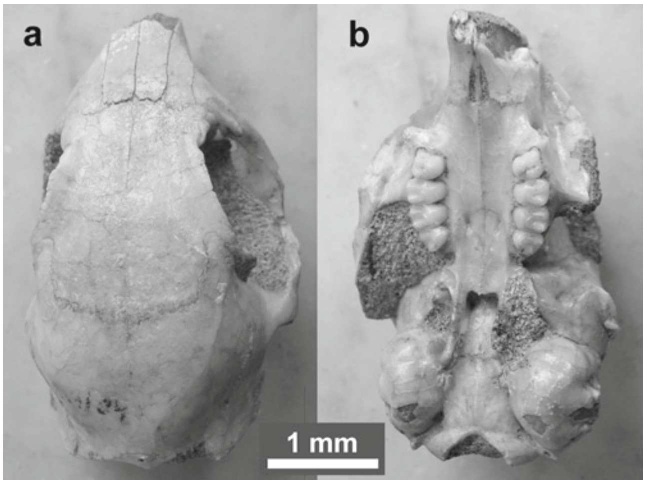

Fig. 2.3 Dorsal and ventral views of *Xerus janenschi* cranium, EP 219/04 from Loc. 15 (Upper Ndolanya Beds)

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 Laetolil 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.

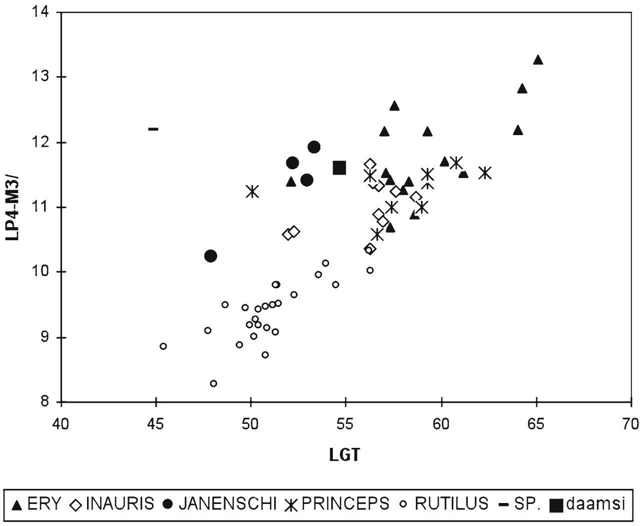

Fig. 2.4 Scatter plot of modern and fossil *Xerus* specimens. LP4-M3/: upper tooth row length. *LGT*: total length of the cranium (axis scales in mm). *ERY*: modern *Xerus erythropus* from East and Central Africa. *INAURIS*: modern *X. inauris* from South Africa. *JANENSCHI*: Laetoli fossils, *X. janenschi*.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

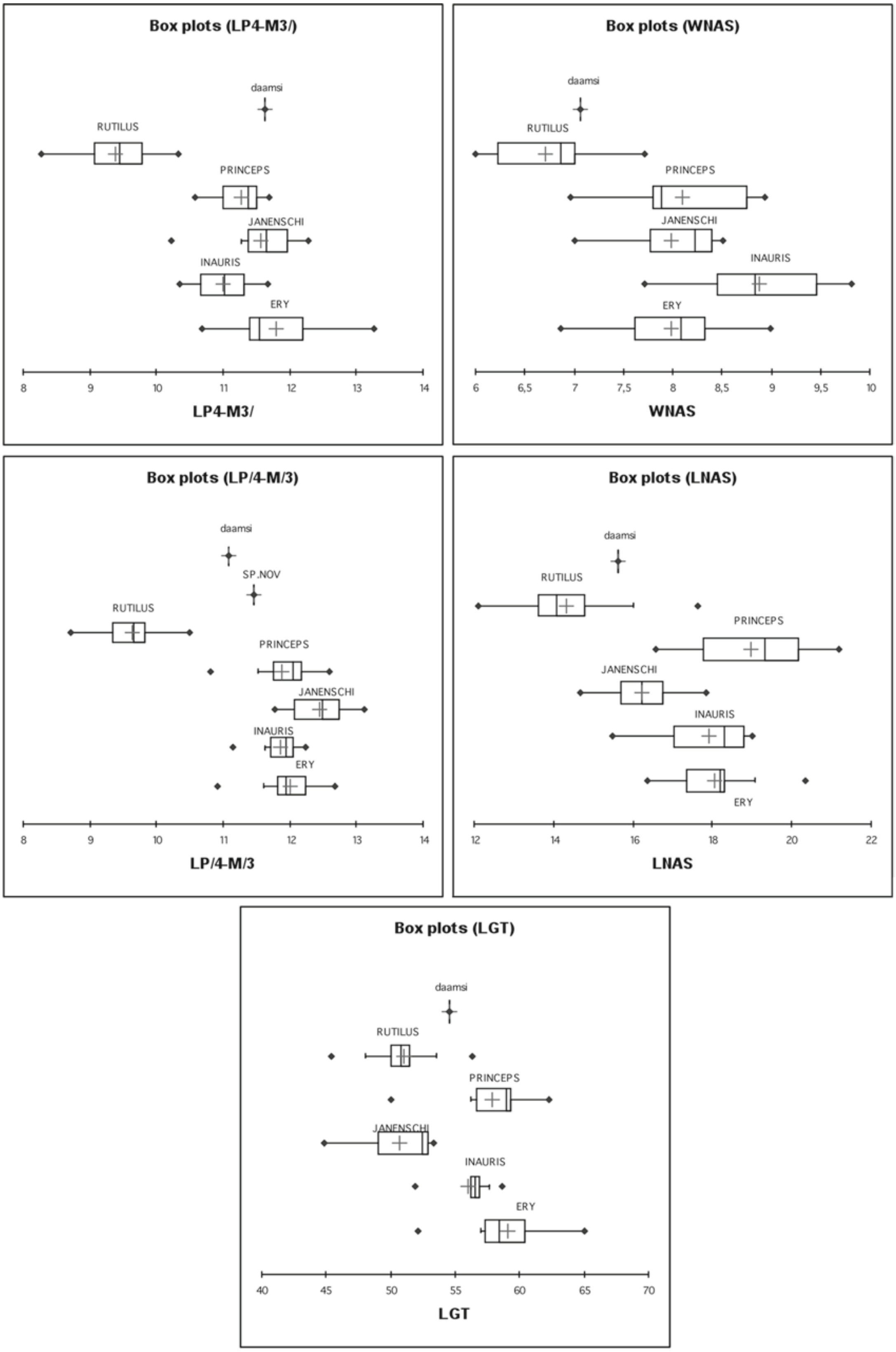

Fig. 2.5 Box plots for the different modern and fossil *Xerus* spp. for different cranial measurements (*LP4-M3/*: Upper tooth row length. *WNAS*: Nasal width. *LP/4-M/3*: Lower tooth row length. *LNAS*: Nasal length. *LGT*: Total cranium length) in mm. *ERY*: modern *Xerus erythropus* from East and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

Fig. 2.6 Lower (*left*) and upper (*right*) toothrows of *Xerus janenschi*. EP 292/04 (mandible with P/4-M/2) 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

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

Species	LGT	LNAS	WNAS	LP4/-M3/	LP/4-M/3
Xerus daamsi					
Chad (KB)	54.59	15.64	7.06	11.62	11.08
X. erythropus					
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
X. rutilus					
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
X. inauris					
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
X. princeps					
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
X. janenschi					
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
***Xerus* sp.**					
Berlin Gadj. 100, Laetoli	44.8			12.2	

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, P/4-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)

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 Laetolil Beds at Loc. 9S. The new specimens display the same skull characteristics previously described for *X. janenschi*, including a short nasal, trace of three transbullae 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 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. janenschi*

		Length				Width			
Tooth	Locality	N	Mean	SD	Range	N	Mean	SD	Range
P4/	Laetoli UNB 1987	4	3.13	0.4	2.49–3.77	4	2.65	0.62	1.66–3.63
or	Laetoli UNB this work	4	2.63	0.12	2.29–2.86	4	2.9	0.23	2.24–3.29
DP4/	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	Laetoli UNB 1987	6	2.76	0.36	2.38–3.14	6	2.68	0.36	2.30–3.06
or	Laetoli UNB this work	7	2.43	0.15	1.86–3.10	7	2.27	0.18	1.71–3.10
DP/4	LB *Xerus* 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 *Xerus* 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 *Xerus* 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 UNB1987	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%).

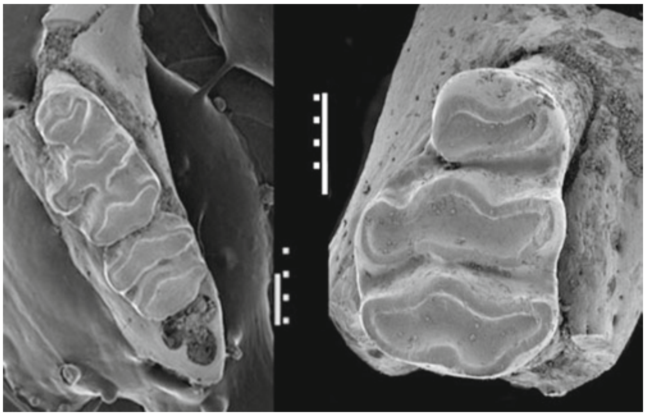

Fig. 2.7 Left maxillary toothrow of *Saccostomus major* from the Upper Laetolil Beds. EP 1738/04 from Loc. 2 (*left*) and EP 1326/03 (right M1/) from Loc. 11 (*right*). Scale bar indicates 1 mm

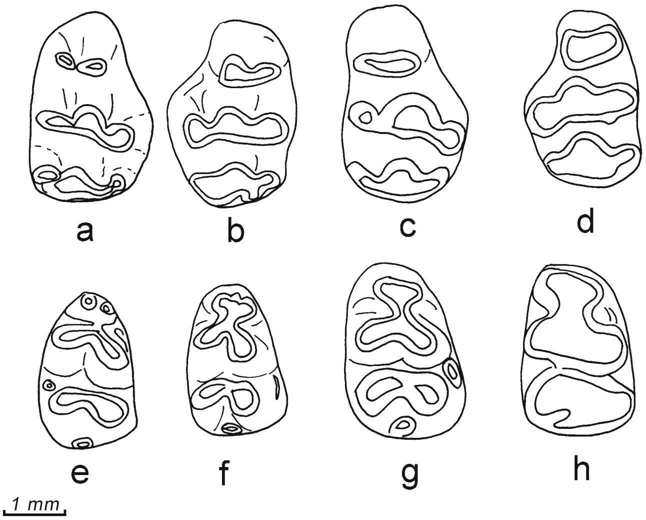

Fig. 2.8 Wear stages of the M1/ and M/1 *Saccostomus major* from the Upper Laetolil Beds. *Top row*, M1/. (**a**) stage 1, EP 1375/00; (**b**) stage 2, EP 160/03; (**c**) stage 3, EP 3904/00; (**d**) stage 4, EP 998/05. *Bottom row*, M/1. (**e**) stage 1, EP 162/03; (**f**) stage 2, EP 1424/03; (**g**)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

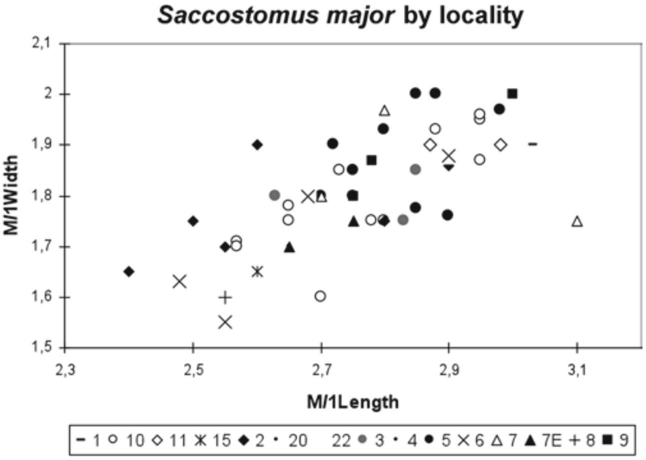

Fig. 2.9 Scatterplot of the M/1 dimensions (mm) of *Saccostomus major* by locality. The specimens from Loc. 7E (black *triangles*) come from the Upper Ndolanya Beds

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.

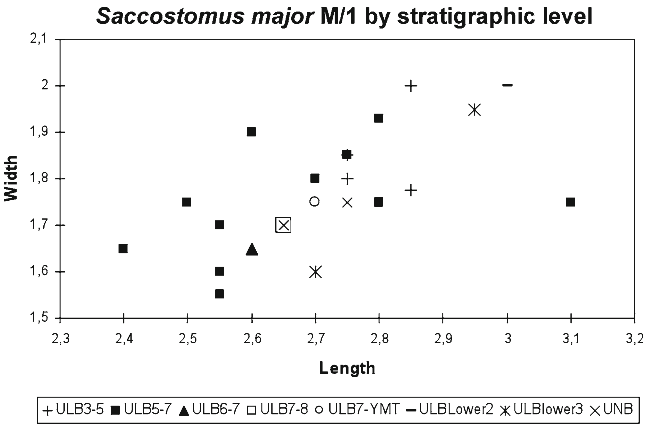

Fig. 2.10 Scatter plot of *Saccostomus major* M/1 grouped by stratigraphic level: *ULB*, Upper Laetolil Beds; 3-5 = between Tuffs 3 and 5; 6-7 = between Tuffs 6 and 7; 7-8 = between Tuffs 7 and 8; 7-YMT = between Tuff 7 and Yellow Marker Tuff; Lower 2 = below marker tuff 2; Lower 3 = below Tuff 3, *UNB*,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

		Length				Breadth			
Tooth	Locality	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
	Lukeino	3			2.24–2.40	3			1.57–1.65
M2/	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
	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
M3/	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
	Harasib 3	20	1.11	0.02	0.93–1.29	20	1.16	0.02	0.93–1.28
M/1	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
	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
M/2	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
	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
M/3	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)

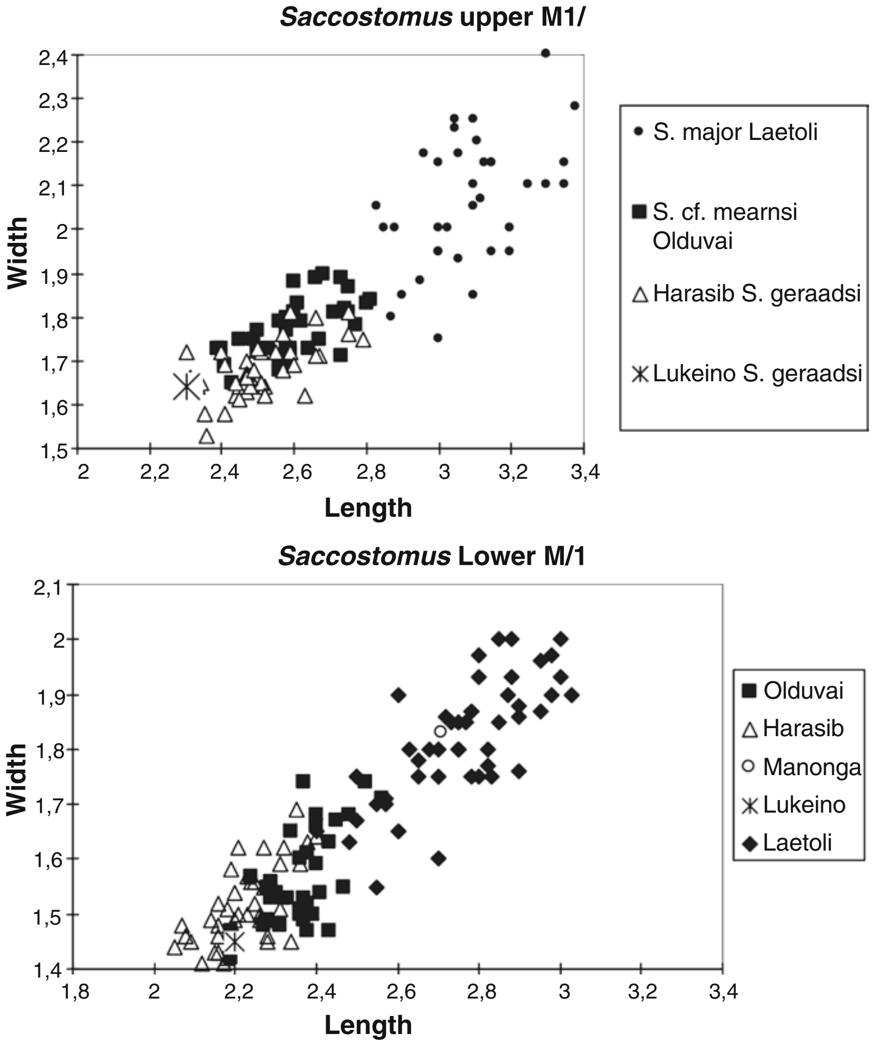

Fig. 2.11 Comparison of fossil *Saccostomus* spp. M1/ and M/1 from different localities. Length and width in mm. After Winkler (1997), *S. major* Ibole, Manonga Valley; Mein et al. (2004), *S. geraadsi*, Harasib; Mein and Pickford (2006), *S. geraadsi*, Lukeino; Denys (1987a, this study) *S. major,* Laetoli; Denys (1992), *S.* cf. *mearnsi,* Olduvai Bed I

Type series: EP 782/03, left mandible with M/1-2, 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 M/1 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 toothrows 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 M/1 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 M/1. 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

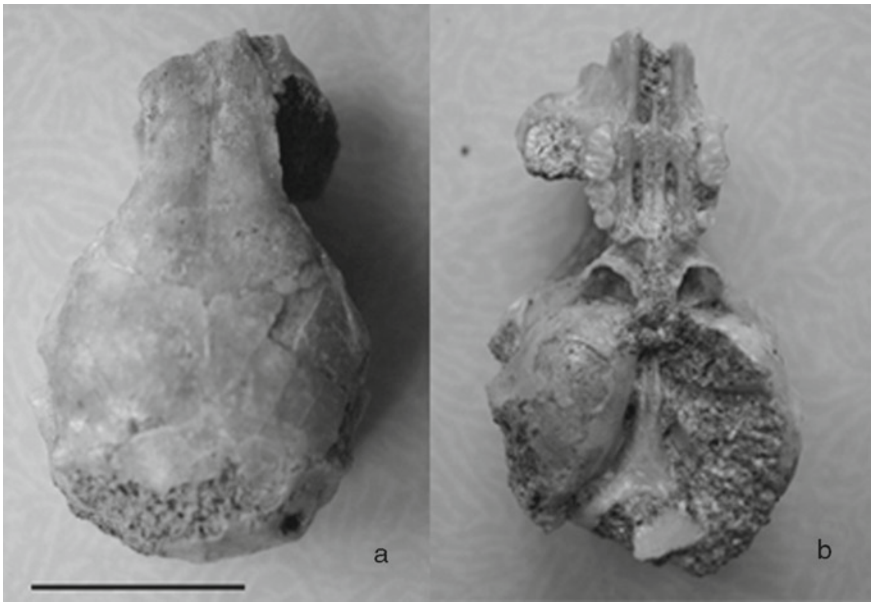

Fig. 2.13 Dorsal (**a**) and ventral (**b**) view of the holotype of *G. satimani* nov. sp. Cranium EP 147/01 from Loc. 6, Laetolil Beds. Scale bar 1cm

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 M/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 Laetolil 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 M/1, 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 M/1, 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 M/1 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 M/2, 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 M/1 (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 M/1 (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
G. satimani					
EP 147/01		5.11	5.28	6.33	11.7
EP 1889/03		5.51			
G. cf. inclusus					
EP 1372/98		7.2			
LAET 75-3588		7.2			
G. gentryi	N	13	1		
Olduvai Bed I	Min	5.30			
	Max	5.91			
	Mean	5.61	5.4		
	SD	0.21			
G. leucogaster	N	48	46	48	48
Tanzania &	Min	4.94	5.28	5.64	9.07
South Africa	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
G. vallinus					
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
G. afra					
Angola					
NHM29-10-1-19		5.2	6.1		10.5
G. paeba					
South Africa					
NHM3-1-4-27		4.04	4.05		8.32
NHM49-345		3.97	4.22		9.39
G. swalius					
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.

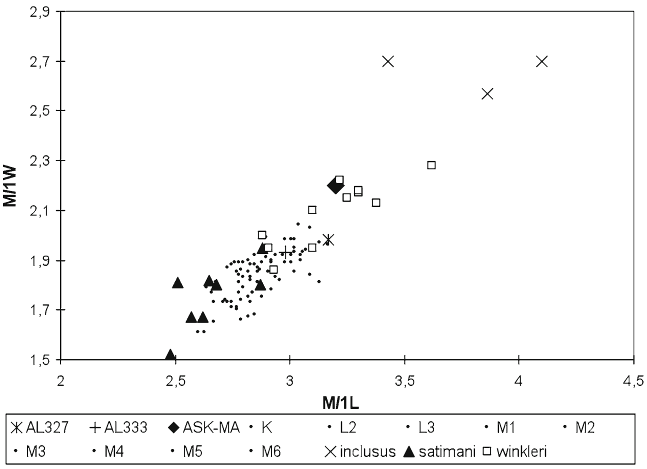

Fig. 2.15 Size comparisons of M/1 between Olduvai Bed I *Gerbilliscus gentryi* (Levels K, L2, L3, M1, M2, M3, M4, M5, M6 after Denys 1989a), *Gerbilliscus* spp. from Hadar (A.L. 333 and A.L. 327, mean value after Sabatier 1982) and Asakoma (ASK-MA after Wesselman et al. 2009), with *G.* cf. *inclusus,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

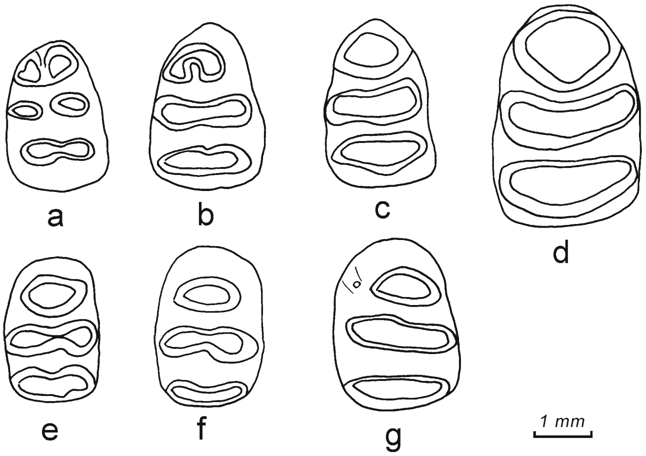

Fig. 2.16 Comparison of the upper and lower M1 of the different species of *Gerbilliscus* from Laetoli. *Upper row*, M/1. (**a**) *G. satimani*, EP 1075/04; (**b**) *G. winkleri*, EP 3319/00; (**c**) *G. winkleri*, EP 3500/00, (**d**) *G.* cf. *inclusus*, EP 1372/98. *Lower row*, M1/. (**e** and **f**) *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 Molar dimensions of fossil *Gerbilliscus* spp.

		Length				Breadth			
Tooth	Locality	N	Mean	SD	Range	N	Mean	SD	Range
M1/	G. *satimani* this work	2			2.76–2.81	2			1.67–1.86
	G. *satimani* Denys, 1987a	3	2.62	0.06	2.55–2.62	3	1.98	0.03	1.95–2.00
	G. *winkleri* this work	1	2.95			1	2.15		
	G. *winkleri* Denys, 1987a	2			3.12–3.18	2			2.33–2.45
	G. *gentryi* Denys, 1989a	23	2.94	0.14	2.62–3.18	23	2.15	0.08	1.96–2.28
	G. sp. Lemudong'o	1	1.90			1	1		
	G. sp. Hadar	19	3.20	0.09	3.01–3.40	19	2.16	0.06	2.03–2.25
	G. sp. Omo B	4	2.60		2.32–2.77	4	1.88		2.79–1.98
	G. sp. Omo F	3	2.73		2.52–2.95	1	2.07		
	G. sp. ASK-VP3	1	2.95			1	2.17		
	G. sp. Kanapoi	4	2.23		2.10–2.52	4	1.65		1.6–1.81
M2/	G. *satimani* this work	1	1.52			1	1.67		
	G. *winkleri* this work	1	1.86			1	2.05		
	G. *winkleri* Denys, 1987a	1	1.85			1	2.05		
	G. *gentryi* Denys, 1989a	7	1.69	0.09	1.57–1.81	7	1.90	0.11	1.74–2.03
	G. sp. Lemudong'o	1	1.00			1	1.20		
	G. sp. Hadar	16	1.85	0.09	1.66–1.98	16	1.98	0.06	1.89–2.08
	G. sp. Omo F	1	1.82			1	1.90		
M3/	G. *satimani* this work	1	0.86			1	1.10		
	G. *gentryi* Denys, 1989a	1	0.85			1	1.29		
	G. sp. Hadar	1	1.08			1	1.40		
	G. sp. Omo F	1	1.06			1	1.27		
M/1	G. *satimani* this work	5	2.54	0.11	2.43–2.72	5	1.64	0.11	1.52–1.81
	G. *santimani* Denys, 1987a	4	2.77	0.12	2.65–2.88	4	1.84	0.07	1.80–1.95
	G. *winkleri* this work	3	2.95	0.08	2.88–3.05	3	1.92	0.07	1.86–2.00
	G. *winkleri* Denys, 1987a	8	3.29	0.16	3.1–3.62	9	2.16	0.07	2.02–2.28
	G. cf. *inclusus* this work	1	3.86			1	2.57		
	G. cf. *inclusus* Denys, 1987a	2	3.77	0.47	3.43–4.1	1	2.70		
	G. sp. Lemudong'o	7	1.79	0.06	1.6–2.00	7	1.30	0.03	1.20–1.40
	G. *gentryi* Denys, 1989a	28	2.90	0.1	2.76–3.11	28	1.87	0.09	1.69–2.05
	G. sp. Hadar	19	3.17	0.09	3.01–3.38	19	1.98	0.06	1.89–2.06
	G. sp. Omo B	1	2.72			1	1.64		
	G. sp. Omo F	2	2.79		2.67–2.90	4	1.72		1.68–1.80
	G. sp. AMW-VP1	1	3.20			1	2.12		
	G. sp. Kanapoi	6	2.05		1.9–2.20	6	1.48		1.40–1.50

(continued)

Table 2.8 (continued)

Tooth	Locality	Length N	Length Mean	Length SD	Length Range	Breadth N	Breadth Mean	Breadth SD	Breadth Range
M/2	G. *satimani* this work	4	1.50	0.06	1.43–1.57	4	1.61	0.11	1.52–1.76
	G. *satimani* Denys, 1987a	1	1.55			1	1.70		
	G. *winkleri* this work	1	1.71			1	1.95		
	G. *winkleri* 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. *inclusus*	1	2.12			1	2.52		
	G. *gentryi* 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. *satimani* this work	3	0.56	0.4	0.57–0.91	3	1.11	0.12	1.00–1.24
	G. *gentryi* 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. *inclusus*	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 M1/1. 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.

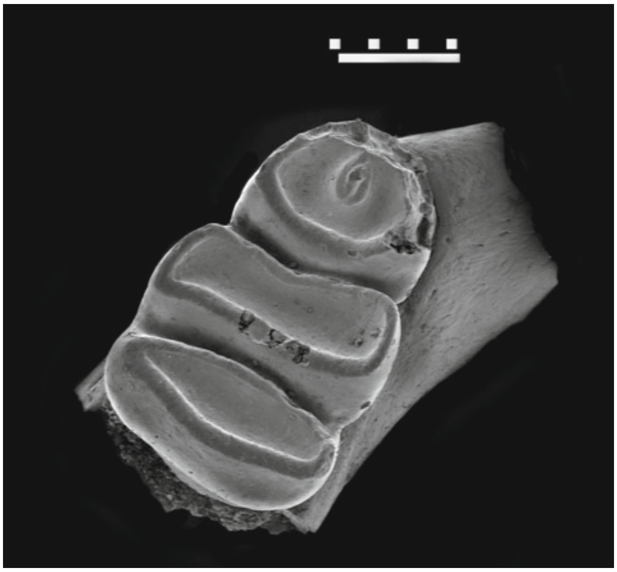

Fig. 2.17 *Gerbilliscus. winkleri* sp. nov. EP 817/01 (paratype) from Loc.18 (Upper Ndolanya Beds), left mandibular fragment with M/1. Scale bar indicates 1 mm

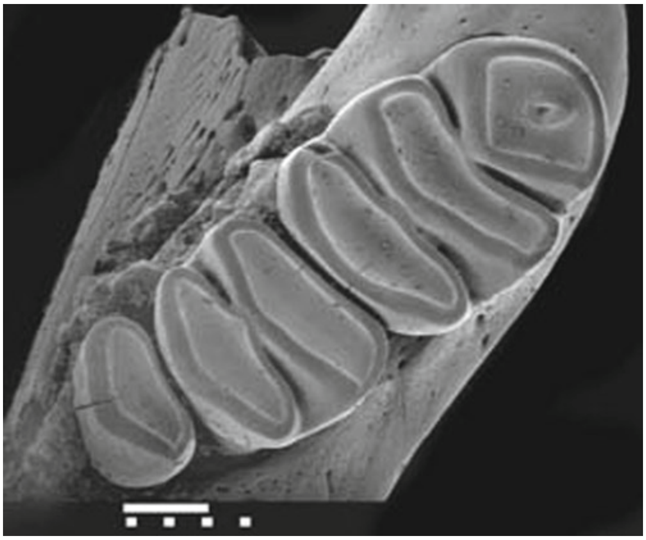

Fig. 2.18 *Gerbilliscus* cf. *inclusus* (EP 1372/98) from Loc. 13. Mandible fragment with M/1-3. Scale bar indicates 1 mm

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 Laetolil 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 Laetolil *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 Laetolil 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

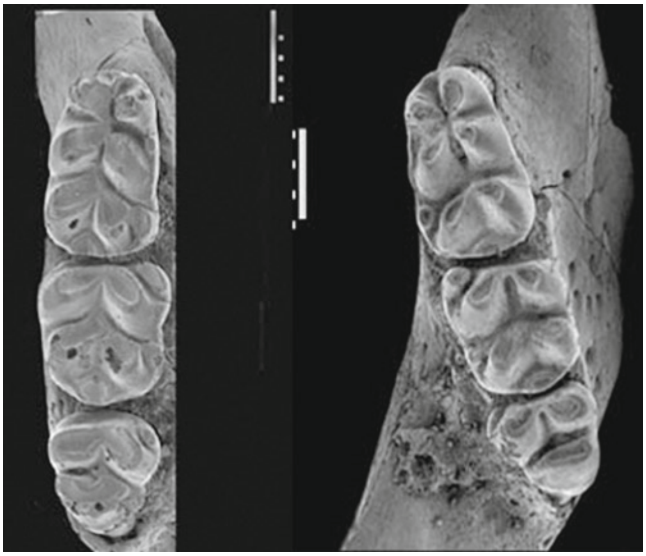

Fig. 2.19 *Thallomys laetolilensis*. *Left*, EP 397/03 from Loc. 5; *right*, EP 2033/03 from Loc. 6. Scale bars indicates 1 mm

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. deheinzelini* 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. deheinzelini* 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.

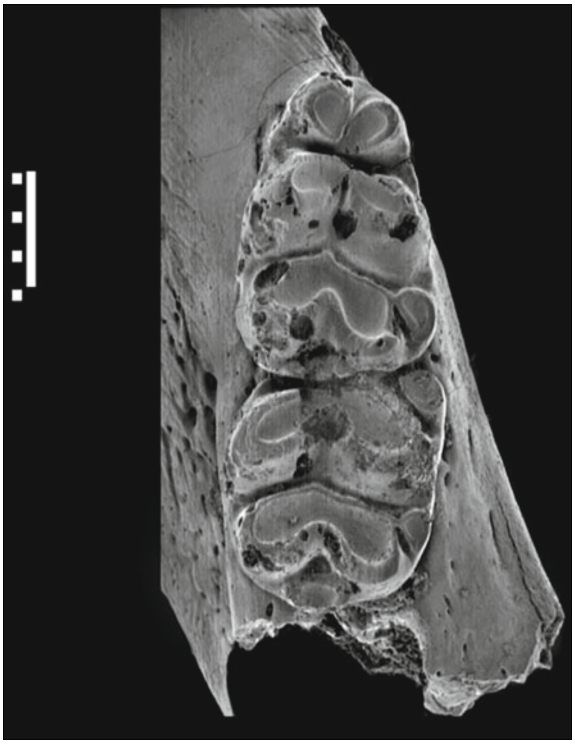

Fig. 2.20 SEM images of *Aethomys* sp. EP 1648/00 from Loc. 3, Upper Laetolil Beds. Scale bar indicates 1 mm

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

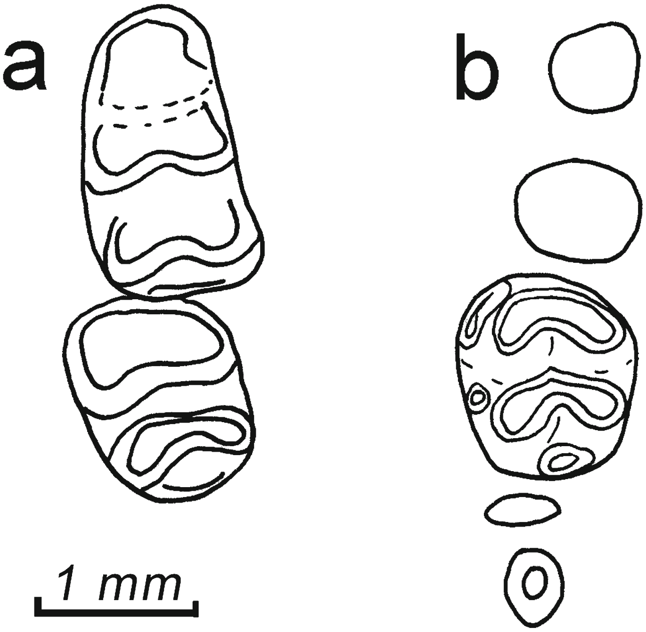

Fig. 2.21 *Mastomys cinereus* from the Upper Laetolil Beds. (**a**) EP 1485/03 (Loc. 8), left mandible with M/1-2; (**b**) EP 2592/00 (Loc. 11), left mandible with M/2 and roots of M/1 and M/3

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 *Thryonomys* Fitzinger, 1867

Some hystricognathous mandibles and four-lophed isolated molars were attributed by Denys (1987a) to *Thryonomys* 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.

Thryonomys 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-M1/ (Plate 6.8 in Denys 1987a).

Diagnosis: Intermediate-sized *Thryonomys,* 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 extinct Miocene *Paraphiomys* in lacking a mesoloph (*Thryonomys* has only three lophs on the upper molars) and relatively similar to fossil *Paraulacodus* and modern *Thryonomys* species.

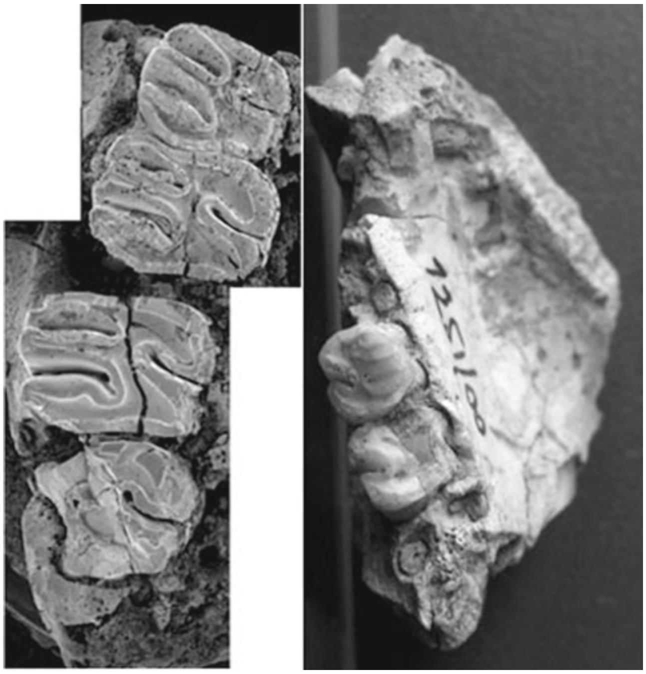

Fig. 2.22 SEM images of *Thryonomys wesselmani* sp. nov. from the Upper Ndolanya Beds. *Left*, EP 1324/05 (holotype) from Loc. 22S (P4/-M3/). *Right*, EP 1251/00 from Loc. 22S (left mandible with M/1-2)

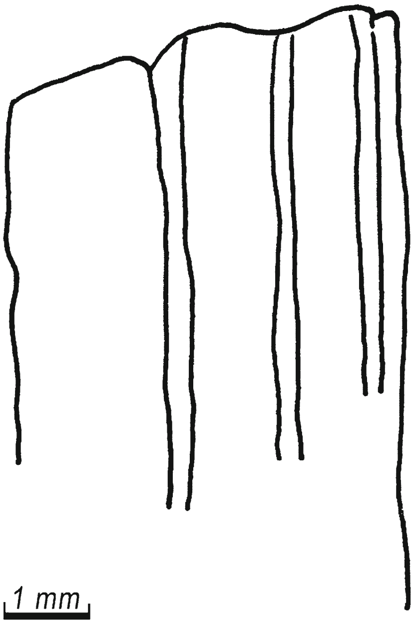

Fig. 2.23 Buccal side of the upper incisor of *Thryonomys wesselmani* sp. nov. (EP 1251/00). Scale bar indicates 1 mm

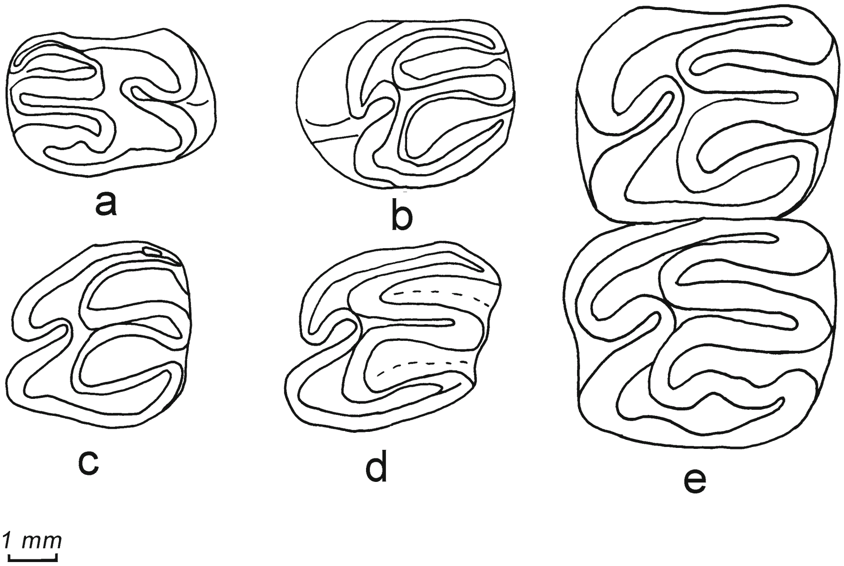

Fig. 2.24 Drawings of upper molars of *T. wesselmani* sp. nov. compared with other fossil and modern *Thryonomys* spp. (**a**) holotype, M1/, *T. wesselmani* sp. nov.; (**b**) LAET 73A, M1/, *T. wesselmani* sp. nov.; (**c**) right M1/ *Thryonomys gregorianus* Omo L1-374, Member B; (**d**) left M1/ of a young modern *T. gregorianus*, BM(NH) 32.864, Kenya; (**e**) M1-2/ of modern *T. swinderianus*, MNHN 1892-1608 from the Congo

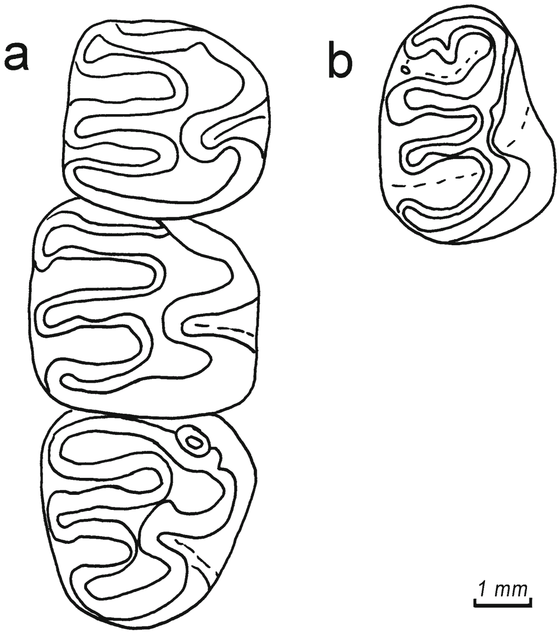

Fig. 2.25 Lower molar row of *T. wesselmani* sp. nov. (**a**) EP 814/01, right mandible with M/1-3; (**b**) LAET 7E-32, right DP/4

Differs from the modern *T. swinderianus* by the lower hypsodonty (lower crowns with visible roots), and smaller size. Differs from *T. gregorianus* 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 M/1, 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 wesselmani* includes material from this work and Denys (1987a)

Specimen	LTR	DP/4	M/1	M/2	M/3	UTR	M1/	M2/	M3/
T. wesselmani									
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			4.7×4.8						
LAET 75-117		(4.8)×3.1	4.2×4.8	4.4×5.2					
LAET 74-31		4.8×3.6							
Mean		**4.83×3.27**	**4.61×4.53**	**4.85×4.57**	**4.62×4.37**				
T. asakomae			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
Thryonomys sp. Manonga							3.07×3.79	3.22×3.44	
Lemudong'o 45945			1.50×1.20	1.50×1.40					
Lemudong'o 45934			2.00×1.70						
T. *swinderianus*									
Omo J		6.15×4.56							5.60×6.50
T. gregorianus									
Omo B							3.70×4.28		
T. gregorianus									
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
T. swinderianus									
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. gregorianus* (Wesselman 1984), modern representatives from museum collections. LTR: Upper tooth row length (DP/4-M/3); UTR: Upper tooth row length (DP4/-M3/)

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
T. swinderianus 1892-1607	5.79	5.72
T. swinderianus 1947-35	5.42	5.17
T. swinderianus 1991-200	5.82	5.61
T. wesselmani 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 bundont *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

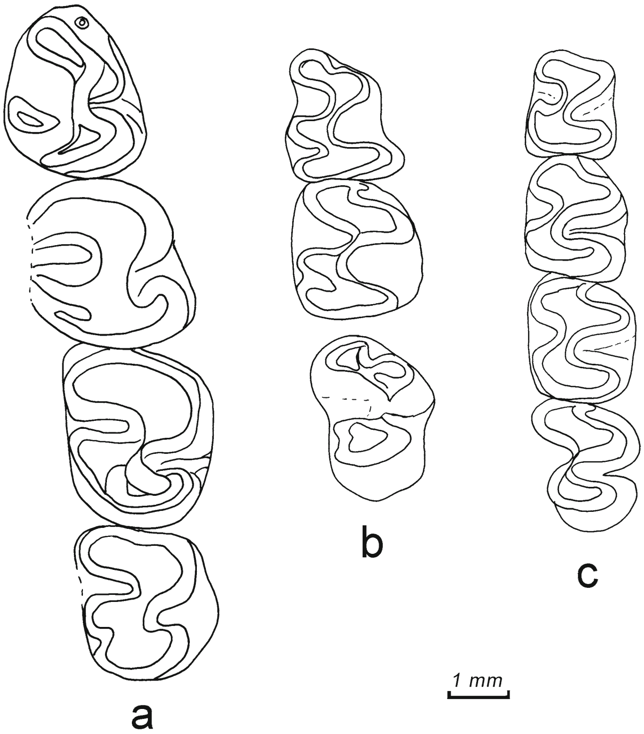

Fig. 2.27 Comparisons of lower dentition of *Petromus*. (**a**) EP 2076/03, right mandible with DP/4-M/3 of *Petromus* sp.; (**b**) juvenile mandible with DP/4-M/2 of modern *P. typicus* from southwest Africa (Cape museum collections, ZM119111A); (**c**) modern adult right mandible of *P. typicus* from 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
P. antiquus		1.90×1.74	2.82×2.65	2.65×2.88	2.89×2.53
P. typicus BM25.1.2.219		1.73×1.58	2.19×1.77	2.12×1.89	2.23×1.92
P. typicus 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.

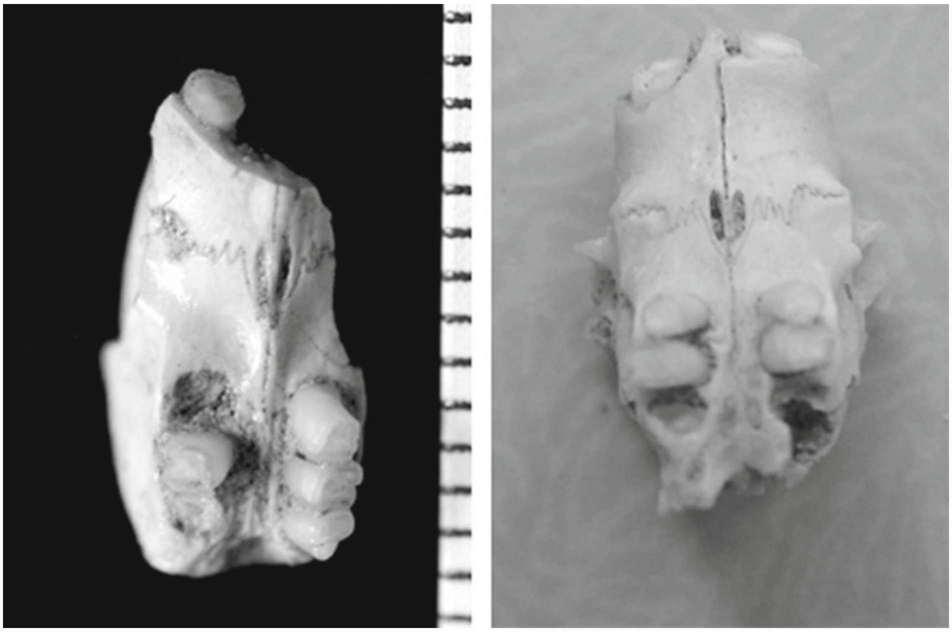

Fig. 2.28 *Heterocephalus manthii* sp. nov KK 82-1 (*right*) from Kakesio. EP 2205/03 (*left*), *H. quenstedti* from Loc. 7, Upper Laetolil Beds

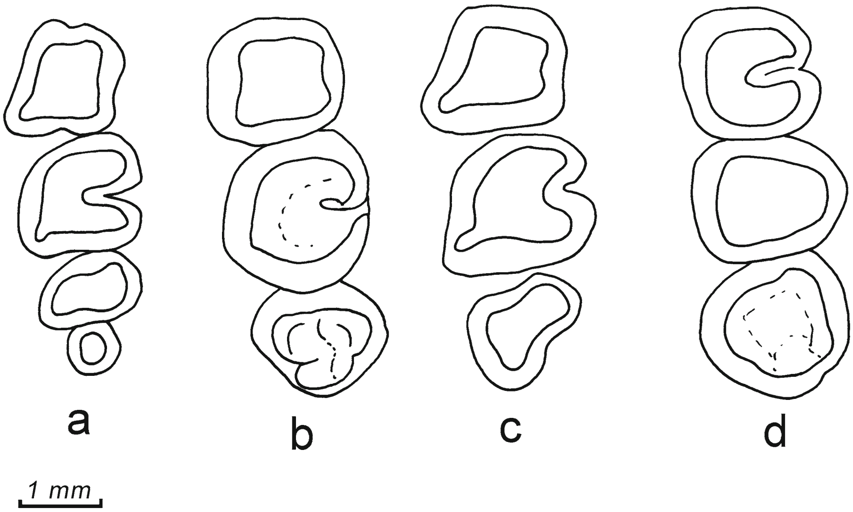

Fig. 2.29 Comparison of the upper left molar rows of *Heterocephalus* spp. (**a**) *H. manthii*, holotype, KK 82-1; (**b**) *H. quenstedti*, LAET 75-2808; (**c**) *H. jaegeri*, Olduvai Bed I, FLK N1 M3; (**d**) *H. glaber* (MNHN 1901-72)

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).

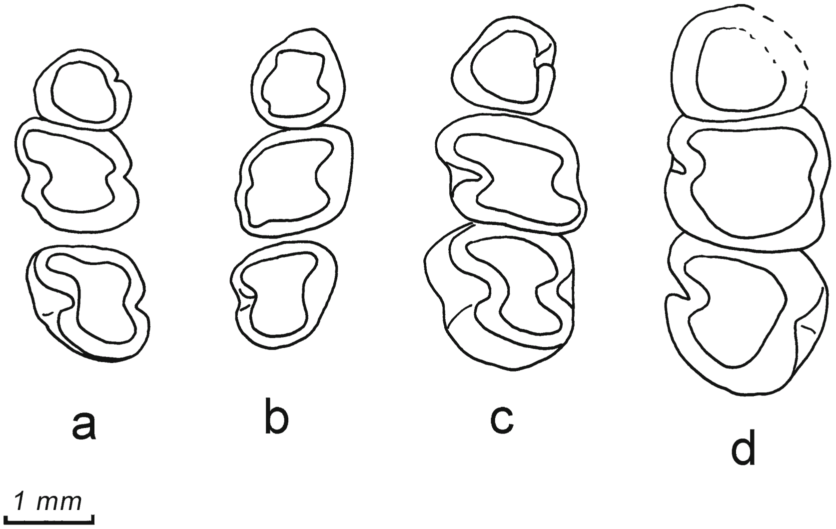

Fig. 2.30 Lower molar rows of fossil and modern *Heterocephalus* spp. (**a**) left mandible with M/1-3, EP 1059/98 from Loc. 9S, *H. quenstedti*; (**b**) right mandible with M/1-3, EP 2921/00 *H. quenstedti* from Loc. 10E *H. quenstedti*; (**c**) right mandible with M/1-3 of *H. jaegeri*, FLKN1 M4 Olduvai 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

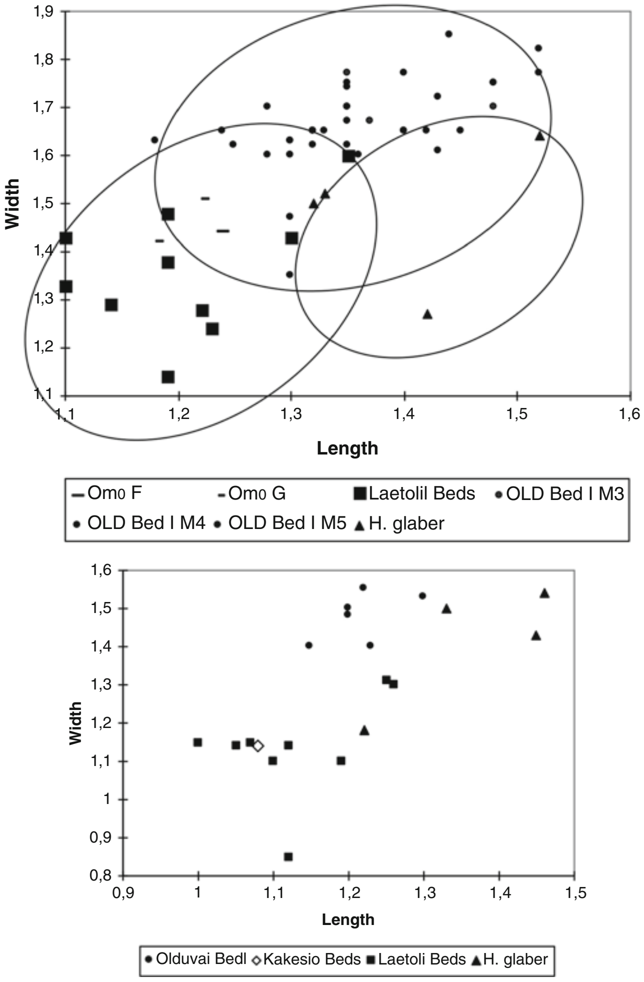

Fig. 2.31 Scatterplots of length × width (mm) of M/2 (*top*) and M1/ (*bottom*) of fossil and modern *Heterocephalus* spp. Measurements for Kakesio and Upper Laetolil Beds (this work, Denys 1987a), Omo F and G (Wesselman 1984), Olduvai Bed FLKN M3, M4, M5, after (Denys 1989b), modern *H. glaber* from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

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

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

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

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 M/1-2, 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.

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

N number of molars, *SD* standard deviation
Data 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 M/1-3 from Loc. 8; *right*, EP 1082/03, right mandible with M/1-3 from Loc. 10W; *bottom*, EP 1990/00, left maxillary fragment with M1-2/ from Loc. 5. Scale bar in mm

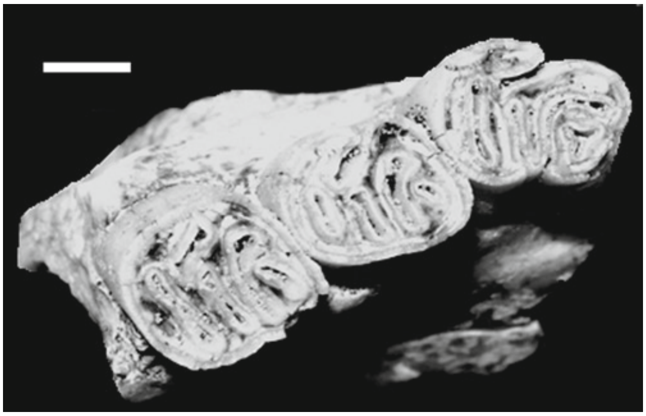

Fig. 2.33 *Hystrix leakeyi.* EP 655/05, left mandible with DP/4-M/2. Scale bar indicates 5 mm

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. africaeaustralis* 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. janenschi, 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 *Petromus* 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. laetolilensis* molars and a few attributable to *M. cinereus* from the Upper Laetolil Beds. Unfortunately, we do not have any supplementary specimens of *T.* cf. *laetolilensis* 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					*H.* sp. Ngaloba Beds
		9.14×6.65		11.44×9.16		*Hystrix* sp. Lothagam
					6.12×5.90	*Hystrix* sp. Lukeino
			6.00×5.90	7.05×6.20	6.6×5.00	*Hystrix* sp. Kanapoi
EP 392/98		6.87×5.13				*H. leakeyi*
EP 655/05		10.41×8.24	9.05×7.87	10.13×9.18		*H. leakeyi*
EP 142/05		8.09×7.02				*H. leakeyi*
EP 1037/05			7.31×6.06			*H. leakeyi*
LAET 75-1368		8.64×7.34	7.28×7.64	7.96×6.70	7.34×6.00	*H. leakeyi*
LAET 75-2594		9.70×7.80				*H. leakeyi*
LAET 74-398			8.20×7.10	8.7×7.00	7.2×6.10	Type *H. leakeyi*
Makapan		13×9.05				*H. makapanensis*
1996			9.64×8.69			*H. makapanensis*
2015				10.35×7.10		*H. makapanensis*
3354		8.99×7.38				*H. makapanensis*
329				10.86×9.51		*H. makapanensis*
988			12.13×9.11			*H. makapanensis*
Olduvai		11.5×9.6	11.5×8.9	11.6×9.5	10.8×8.4	*H. makapanensis*
LAET 75-1971		12.6×9.5				*H. makapanensis*
1786		11.88×8.69				*X. crassidens*
LAET 75-3411		14.6×10.4				*X. crassidens*
OM5329		8.69×5.87	7.43×6.5	8.68×6.06		*H. cristata*
OM5324	34.95	8.14×6.91	8.39×7.26	8.92×7.25	7.32×5.45	*H. cristata*
OM5322	33.44	8.65×5.26	8.35×5.62	9.05×5.58	7.62×4.55	*H. cristata*
OM7190	33.62	10.2×7.54	7.93×7.02	8.87×7.40	8.28×7.15	*H. cristata*
OM7114	34.40					*H. cristata*

Upper Laetolil 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 Laetolil 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 Praomyni, 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 Laetolil 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.

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
Pedetes laetoliensis		x	
Pedetes sp.			x
Xerus janenschi		x	x
Xerus sp.		x	
Paraxerus meini		x	x
Gerbilliscus satimani		x	
Gerbilliscus winkleri			x
Gerbilliscus cf. *inclusus*		x	
Dendromus sp.		x	
Steatomys sp.		x	
Saccostomus major	x	x	x
Aethomys sp.		x	
Murid indet.		x	
Thallomys laetolilensis		x	cf.
Mastomys cinereus		x	cf.
Heterocephalus quenstedti		x	
Heterocephalus manthii	x		
Thryonomys wesselmani			x
Petromus sp.	x		
Hystrix leakeyi		x	
Hystrix makapanensis		x	x
Xenohystrix crassidens		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

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. janenschi*, 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 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 Laetolil 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 Laetolil 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 Laetolil 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

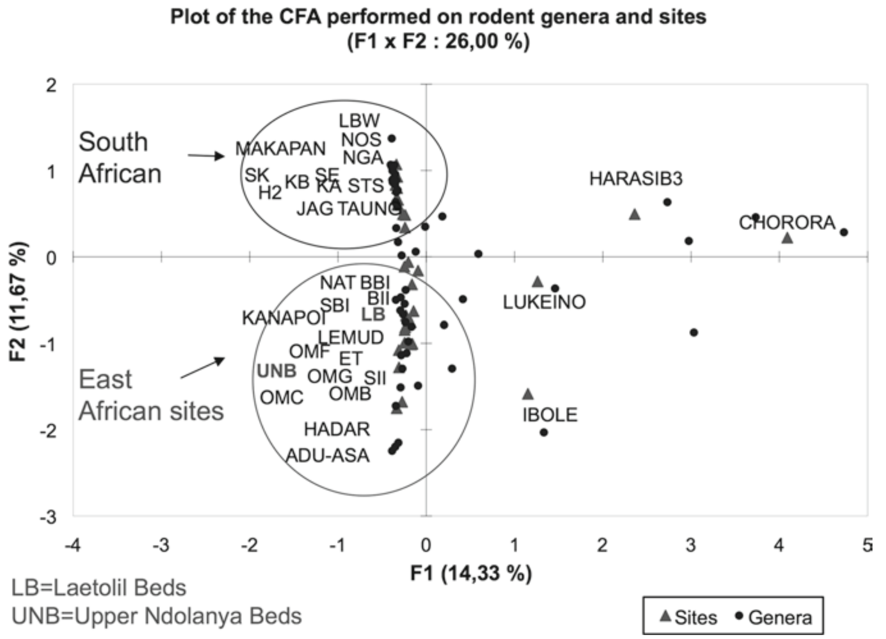

Fig. 2.34 Correspondence analysis diagram on presence-absence of the rodent genera (except hystricids) for late Miocene to late Pleistocene East African and South African sites (after Winkler et al. 2010; data taken from the literature). Site abbreviations: *LBW* Langebaanweg; *NOS* Nosib; *SK* Swartkrans; *KB*, *KA* Kromdraai A, B; *H2* Humpata 2; *JAG* Jägerquelle; *STS* Sterkfontein; *SE* Sterkfontein extension; *NGA* Ngamiland; *NAT* Natron (Peninj); *BBI* Olduvai Base Bed I; *SBI* Olduvai Upper Bed I; *SII* Olduvai Upper Bed II; *BII* Olduvai Base Bed II; *OMF, OMG, OMM, OMC, OMB* Omo members F, G, M, C, B; *LEMUD* Lemudong'o; *UNB* Upper Ndolanya Beds; *LB* Laetolil Beds; *ET* East Turkana

some distance between the Upper Laetolil 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 Laetolil Beds (ULB)

EP number	Locality	Level	Anatomical element
1161/01	1	ULB	Right mandible + P/4-M/2
1089/05	1	ULB	Maxilla with P/4-M/3
1090/05	1	ULB	Anterior cranium + molars
1091/05	1	ULB	Two isolated molars
1783/00	2	ULB	Astragalus
1867/00	2	ULB	Right mandible + P/4-M/3
1868/00	2	ULB	Left mandible + M/1-2
3067/00	2	ULB	Astragalus
714/00	2	ULB	Left mandible + P/4-M/3
640/03	2	ULB	Postcrania
1036/05	2	ULB	Two isolated molars
994/05	2	ULB	Isolated molar
220/00	1	ULB	Isolated molar
1993/00	5	ULB	Left + right mandibles + P/4-M/2
398/03	5	ULB	Left mandible + M/2-3
399/03	5	ULB	Six isolated molars
1334/04	5	ULB	Right mandible + P/4-M/2
1335/04	5	ULB	Four isolated molars
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 + P4/-M1/
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 + P4-M2/
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 + P4-M3/ left + right mandibles + right P/4-M/3
2916/00	10E	ULB	Right maxilla + M2/
2920/00	10E	ULB	Vertebrae + metapodials + bone fragments
794/00	10E	ULB	Three isolated molars
572/01	10E	ULB	Six isolated molars
573/01	10E	ULB	Premaxilla + incisors
885/03	10E	ULB	Left + right mandibles + P/4-M/2 + left and right M/1-2
887/03	10E	ULB	Right mandible + P/4-M/2
1264/04	10E	ULB	Four isolated molars
046/04	10E	ULB	Five isolated molars
048/04	10E	ULB	Cranium + molars + mandible + postcranial
878/05	10E	ULB	Ten isolated molars
881/05	10E	ULB	Partial skeleton
068/05	11	ULB	Right mandible + P/4-M/2
536/05	12E	ULB	Two isolated molars
2367/03	13	ULB	Partial skeleton

(continued)

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 Laetolil 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 Laetolil 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+/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 Laetolil 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 fragment + 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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Chapter 3
The Lower Third Premolar of *Serengetilagus praecapensis* (Mammalia: Lagomorpha: Leporidae) from Laetoli, Tanzania

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Abstract The present study suggests evolutionary changes in the morphology and size of the lower third premolar of the leporid *Serengetilagus praecapensis* from the Upper Ndolanya and Upper Laetolil Beds, Laetoli, Tanzania (ca. 3.85–2.66 Ma). Mandibular depth at p3 was compared also as a proxy indicator of size. The occlusal morphology of p3s from Laetoli is variable, but most commonly the tooth is crescentic with a posteroexternal reentrant (PER) extending about half way across the width of the tooth, plus distinct anteroexternal (AER) and anterior (AR) reentrants. An anterointernal reentrant (AIR) is weak to distinct. A proportionally higher percentage of p3s from the Upper Ndolanya Beds (50%) and the uppermost Upper Laetolil Beds (ULB, between Tuff 7 and the Yellow Marker Tuff, 49%) had a weak AIR compared to only 29% of specimens from between Tuffs 5–7, ULB. The higher frequency of a weak AIR in the geologically younger population is interpreted as the character state being newly reversed to the plesiomorphic condition (AIR weak to absent). There are only two poorly preserved p3s from the Lower Laetolil Beds: on both specimens the AIR and AR are weak to absent (plesiomorphic condition). AR is almost always present on p3s from the Upper Ndolanya and Upper Laetolil Beds. On average, p3s from the Upper Ndolanya Beds are slightly shorter and narrower, and the mandibles slightly less deep at the level of p3 than those from the Upper Laetolil Beds. However, the range of variation of measurements is quite similar between samples from the Upper Ndolanya and Upper Laetolil Beds. A specimen from the Upper Ndolanya Beds (EP 1223/03.1) has a p3 proportionally wider than mean values for other specimens from both the Upper Ndolanya and Upper Laetolil Beds. In conjunction with p3 occlusal morphology, this specimen may represent a new, as yet unnamed, species. Although interesting, the differences observed between samples from the Upper Ndolanya Beds and subunits of the Upper Laetolil Beds are not considered adequate for separation into a distinct species or subspecies.

Keywords Pliocene • Rabbit • Phylogeny • Taxonomy

Introduction

Laetoli is located on the Eyasi Plateau, in the southern part of the East African Rift, in northern Tanzania. It is one of the most important and prolific paleontological and paleoanthropological localities in Africa, having yielded one of the largest collections of specimens attributable to the early hominin *Australopithecus afarensis*, as well as a spectacular collection of plants, ichnofossils, invertebrates, reptiles, birds, and other mammals. Laetoli was first collected in the 1930s and was more extensively investigated from 1974–1982 by Mary Leakey and colleagues (Leakey and Harris 1987). Renewed collecting from the area by the Eyasi Plateau Paleontological Expedition under the direction of Terry Harrison from 1998–2005 has yielded 15,019 mammalian specimens from 60 localities and sub-localities, of which about 34% are lagomorphs (Harrison 2011; Harrison and Kweka 2011). Leakey et al. (1976) noted that lagomorphs were one of the most common taxa from Laetoli, and Leakey (1987: table 1.5) reported that they constituted about 31% of the better-represented taxa from the (Upper) Laetolil Beds and about 5% of the fauna from the Upper Ndolanya Beds. Among the recent collections, lagomorphs represent 38.0% of mammals from the Upper Laetolil Beds, 6.0% from the Lower Laetolil Beds, and 17.4% from the Upper Ndolanya Beds (Harrison 2011). Lagomorph remains from Laetoli (all attributed to *Serengetilagus*) are primarily isolated incomplete dentitions. Incomplete postcrania are also relatively common and partial skeletons (sometimes articulated) are known, but less common.

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Overall, the fossil record of African lagomorphs is relatively sparse. It includes ochotonids (minimum of two genera) from the early to middle Miocene of northern, eastern, and southern Africa. Prolagids (one genus) are known only from the late Miocene to early Pleistocene of northern Africa. Fossil leporids (five genera total) are first reported from the late Miocene of eastern Africa. The specimens of *Serengetilagus* from Laetoli are the most numerous and complete of any known fossil lagomorph from Africa.

Serengetilagus praecapensis was described originally by Dietrich (1941, 1942) based on approximately 76 specimens (cranial and postcranial remains: some of this material likely associated with particular individuals) collected by Kohl-Larsen in 1938–1939 (housed at the Museum für Naturkunde in Berlin). Unfortunately, Dietrich did not designate a holotype. MacInnes (1953) described 21 specimens of *Serengetilagus* collected by Louis and Mary Leakey in 1935 and housed in the Natural History Museum, London. Although this material is described as coming from Laetoli, Davies (1987: 190) considered it unlikely. Erbaeva and Angermann (1983) provided additional descriptions of Dietrich's cranial material and designated a lectotype. They noted that the p3 of this species showed great morphologic variability and recognized nine morphotypes (Erbaeva and Angermann 1983: figs. 3, 4).

Davies (1987) did a preliminary study of the cranial and postcranial remains (number of examined specimens not indicated) of *S. praecapensis* collected from Laetoli (Upper Ndolanya and [Upper] Laetolil Beds) by Mary Leakey and now housed at the National Museum of Tanzania, Dar es Salaam, Tanzania. Although remains of *Serengetilagus* from Laetoli had traditionally been considered to represent a single species, *S. praecapensis*, Davies (1987) suggested two (unnamed) subspecies were present: one in the Upper Ndolanya Beds and a second in the Upper Laetolil Beds. These subspecies were distinguished primarily on three characters of the auditory region of the cranium. In specimens from the Upper Ndolanya Beds: (1) the auditory bulla is slightly smaller; (2) there is a better developed mastoid flange; and, in particular, (3) the squamosal process above the bulla extends farther posteriorly.

Serengetilagus praecapensis has been reported from a few other localities in eastern and central Africa. Four specimens of *S. praecapensis* are illustrated and briefly described from the Adu-Asa Formation (5.8–5.2 Ma), Middle Awash, Ethiopia (Wesselman et al. 2008). Winkler (2003) described a mandible of *S. praecapensis* from the early Pliocene (4.22–4.20 Ma) at Lothagam, Kenya. *Serengetilagus* aff. *S. praecapensis* is reported from Kossom Bougoudi, northern Chad (ca. 5 Ma; Brunet et al. 2000). The latter material is noted (without description or illustration) to be primitive with respect to *S. praecapensis* from Laetoli (Brunet et al. 2000).

The only other species of *Serengetilagus* is *S. tchadensis* from Toros Menalla, Chad (late Miocene; López-Martínez et al. 2007). This species is known from 18 numbered specimens, some including associated elements, and some probably referable to particular individuals. Cranial and limited postcranial remains are present. *Serengetilagus tchadensis* is considered to have some of the more primitive character states of the genus, such as a simpler p3 with only two main external reentrants and upper cheek teeth strongly widened transversely with wear (López-Martínez et al. 2007).

Serengetilagus sp. has been noted from several other African localities. It is reported from a minimum of 17 specimens from the late Miocene Lukeino Formation, Tugen Hills, Kenya (Mein and Pickford 2006). Assignment of all this material to *Serengetilagus*, however, is not considered definitive based on the descriptions given (there are no illustrations) (see discussion in Winkler and Avery 2010). Flynn and Bernor (1987) suggested that an isolated leporid p3 (KNM-KW 138) from the Pliocene Kanam West locality, Kenya, was likely referable to *Serengetilagus*. Leakey (1965) listed, and very briefly discussed (only a distal tibia was illustrated), lagomorphs from the 1951–1961 excavations at Olduvai Gorge, Tanzania (early Pleistocene). Lagomorphs are reported only from Bed I, and are described as uncommon. They include a large taxon, considered to pertain to *Lepus*, plus another taxon similar to *Serengetilagus* (Leakey 1965). Leakey (1971) listed *Serengetilagus* sp. from the 1960–1963 excavations in Bed I, but there was no discussion or illustration of the material.

Lagomorphs of the "*Serengetilagus*-*Trischizolagus* group" are reported from Ahl al Oughlam, Morocco (ca. 2.5 Ma; Geraads 2006). *Serengetilagus raynali* from Grotte des Rhinocéros, Oulad Hamida I, Morocco (Geraads 1994) pertains to *Trischizolagus* according to several authors (see discussion in Winkler and Avery 2010). In southern Africa, *Serengetilagus* is listed as occurring in the Plio-Pleistocene of southern Angola (Pickford et al. 1992), although these authors cast some doubt on the identification (Pickford et al. 1992: 20).

As noted above, Davies (1987) suggested that more than one taxon of leporid might be present at Laetoli. Erbaeva (personal communication) has also made this suggestion based on p3 morphology. Harrison (personal communication) observed that some remains from the Upper Ndolanya Beds and Upper Laetolil Beds above Tuff 7 were much larger than others from the Upper Ndolanya and Upper Laetolil Beds. Davies (1987) thought that specimens from the Upper Ndolanya Beds were different enough in cranial morphology from those of the Upper Laetolil Beds to warrant subspecies recognition, but he did not mention any differences in p3 morphology or size of the specimens from the two units.

The specimens studied by Dietrich (1941, 1942) and MacInnes (1953) were not collected with specific stratigraphic provenance. Davies (1987) even questioned if the material studied by MacInnes (1953) was from Laetoli. Thus, individual specimens from these collections could potentially date from ca. 2.66 to >4.4 Ma (see Stratigraphic Context). Erbaeva and Angermann (1983) noted tremendous variability in p3 morphology in the Dietrich collection, but without stratigraphic control, they could not evaluate if the variability may have been from differences in geologic age. The collection made by Harrison is extensive and has excellent stratigraphic control. Thus, the main goal of the present study is to compare attributes of the p3 (the most significant tooth for morphological comparisons) among the three main stratigraphic horizons (and sub-horizons of the Upper Laetolil Beds) to determine if there is significant variability among the units. The ultimate goals are to better understand the evolutionary history of *S. praecapensis* and determine if more than one taxon was present at Laetoli.

Stratigraphic Context

The Laetoli fossils are derived from several localities within the 'main Laetoli area' and from other localities on the Eyasi Plateau. Pliocene deposits from Laetoli are divided into two main units, the Laetolil Beds (≥4.4–3.63 Ma) and the Upper Ndolanya Beds (~2.66 Ma). Together, these units crop out over more than 1,600 km^2. Leporids are known from the Lower (>4.4–3.85 Ma) and Upper (3.85–3.63 Ma) Laetolil Beds, and the Upper Ndolanya Beds (2.66 Ma). Leporids have not been reported (Leakey or Harrison collections) from younger units in the area, the Olpiro and Ngaloba Beds. All specimens were surface collected, but in most cases derived from known stratigraphic horizons.

A stratigraphic profile for Laetoli is illustrated in Fig. 3.1. The Laetoli sediments include aeolian, airfall, and waterlain tuffs that are interbedded with mafic lavas and medium- to fine-grained epiclastics (Deino 2011). In stratigraphic thickness, the Upper Ndolanya Beds are from about 8–16 m thick (Ditchfield and Harrison 2011) and consist primarily of clayey aeolian tuffs (Hay 1987). The Upper Laetolil Beds are about 44–59 m in thickness: the Lower Laetolil Beds, where well developed, may be 64 m in thickness (Hay 1987). The Upper Laetolil Beds are primarily composed of aeolian tuff, but contain some airfall tuffs (Hay 1987). The Lower Laetolil Beds are composed largely of aeolian tuff interbedded with airfall and waterlain tuffs (Hay 1987). Lagomorphs examined

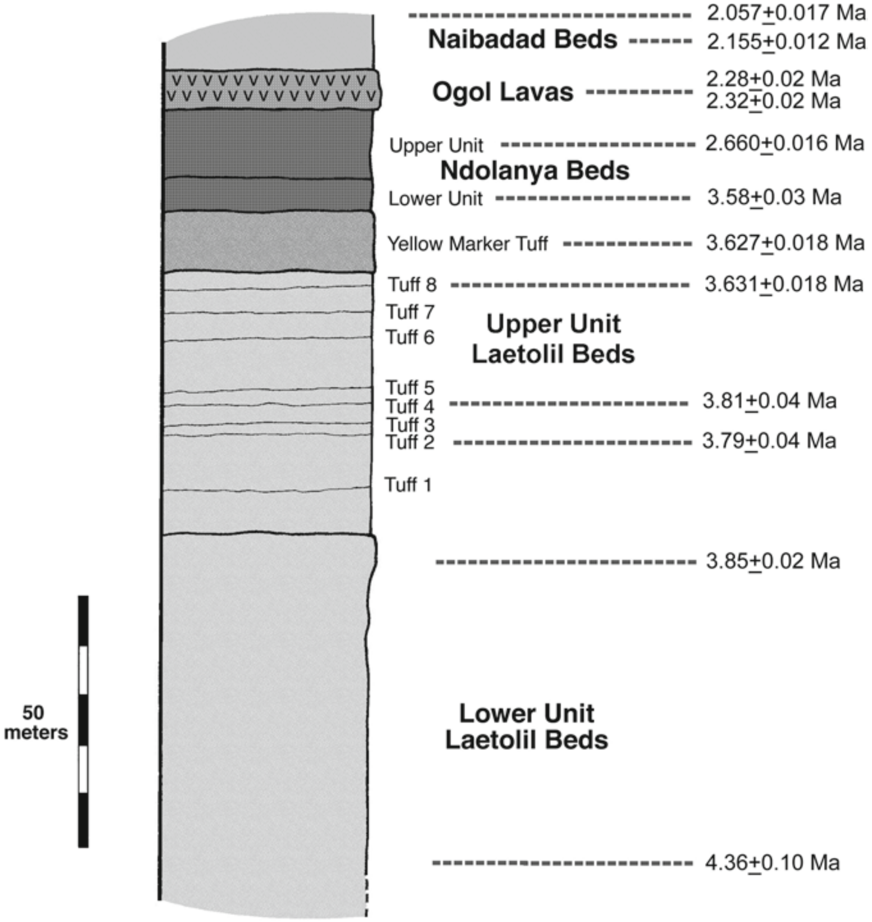

Fig. 3.1 Stratigraphic profile for Laetoli, Tanzania (From Harrison and Kweka (2011); based on Drake and Curtis (1987); Hay (1987); Ndessokia (1990); Manega (1993); Ditchfield and Harrison (2011); Deino (2011))

for this study from the Upper Laetolil Beds had been collected with reference to eight marker tuffs, with Tuff 1 the oldest and Tuff 8 the youngest (Fig. 3.1).

The Upper Ndolanya Beds are well sampled and have yielded an extensive fauna, of which about 17% of all specimens of mammals are lagomorphs (Harrison collection; Leakey 1987: table 1.5 reported about 5%). However, there is a strong taphonomic bias against small mammals in this unit, which may be reflected in the lower proportion of lagomorphs compared to the Upper Laetolil Beds (Harrison, personal communication). The Lower Laetolil Beds have not yet been sampled adequately (i.e., the collection from these beds is about 1% of the size of that from the upper unit): of the 258 specimens collected, about 6% are lagomorphs (Harrison 2011).

Small mammals comprise a large proportion of the well-sampled fauna from the Upper Laetolil Beds. In the Harrison collection, about 37% of all specimens of mammals from the Upper Laetolil Beds are lagomorphs (Harrison 2011). In the Leakey collection, lagomorphs represent about 31% of the mammals from the Upper Laetolil Beds (Leakey 1987: table 1.5).

Materials and Methods

Lagomorph crania constitute the most useful element for identification. However, even relatively complete crania are extremely rare from Laetoli, and most cranial remains are incomplete mandibles and maxillae. Of this material, the most diagnostic tooth is the p3. Hence, the present study focuses on p3 morphology and occlusal size (i.e., length, width, length/width, depth of posteroexternal reentrant, depth of posteroexternal reentrant/width of tooth). When possible, the height of the mandible at p3 was also measured as an additional indicator of size of the specimen. Measurements of occlusal and alveolar toothrow length would also have been useful adjunct indicators of size of the specimens, but too few toothrows were preserved for these measurements to be helpful.

All p3s from the Upper Ndolanya Beds (*N*=40) and Lower Laetolil Beds (*N*=2) were examined. About half (*N*=168) of the p3s from the Upper Laetolil Beds were included. Specimens from the Upper Ndolanya Beds are from five localities (7E, 15, 18, 22S, and Silal Artum). Specimens from the Lower Laetolil Beds are from Kakesio 8. Specimens from the Upper Laetolil Beds include: 64 from between Tuffs 7 and the Yellow Marker Tuff (Locs. 1, 3, 7, 8, 11, 15–17), 76 from between Tuffs 5 and 7 (Locs. 2, 8, and 10E), 13 from between Tuffs 3 and 5 (Loc. 5), and 15 from below Tuff 3 (Locs. 9S, 10, and 10W). Specimens studied (210 total from all units) are listed in the Appendix 3.1.

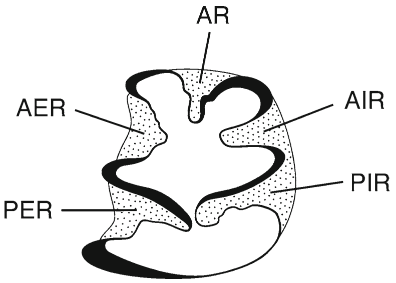

Fig. 3.2 Tooth terminology for leporid p3. AER, anteroexternal reentrant (= protoflexid); AIR, anterointernal reentrant (= paraflexid); AR, anterior reentrant (= anteroflexid); PER, posteroexternal reentrant (= hypoflexid); PIR, posterointernal reentrant (= mesoflexid) (Tooth terminology modified from White 1991)

Tooth terminology for a leporid p3 (from White 1991) is illustrated in Fig. 3.2. Measurements of the occlusal surface of the teeth were made using a reticule in a Wild Heerbrugg dissecting stereomicroscope. In addition to measurements of the p3, the depth of the mandible was measured at the level of p3 using Mitutoyo digital calipers. Measurements were taken only on specimens believed to be adults. Specimens were considered juveniles (and excluded) if they had any of the following characteristics: cone-shaped p3, dp3 or dp4 present, or they were of proportionally smaller size (often including a more gracile mandible and more porous appearing, less calcified bone) than other specimens. Morphology of juvenile p3s was, however, noted.

The pattern of enamel reentrants on p3 is of taxonomic significance for leporids, and is the most widely used criterion for classification. Studies of modern and fossil populations have demonstrated, however, that although the vast majority of individuals within a population possess the diagnostic p3 pattern (or slight variants of it), there are often individuals with patterns that might be considered diagnostic of other taxa (Hibbard 1963). Sometimes these aberrant patterns are observed more commonly in younger individuals: certain reentrants may not persist along the full length of the crown, so may be “present” or “not present” depending upon occlusal wear. For this reason, one needs to look carefully at morphological variation in a fossil sample to decide if one or multiple taxa are represented.

Erbaeva and Angermann (1983) classified 143 p3s of *S. praecapensis* from the Dietrich collection into nine morphotypes based on the presence or absence of particular reentrants plus the development of some of these reentrants (I–IX; Fig. 3.3). Their classification scheme included: I, only PER and AER present; II, PER, AER, and AR present; III, PER, AER, and AR (doubled or branched) present; IV, PER, AER, AR, and AIR present; V, PER, AER, AR (doubled or branched), and AIR present; VI, PER, AER, AR, AIR, and large PIR present; VII, PER, AER, AR, AIR, and small PIR present; VIII, PER, AER, and AIR present, but AR absent;

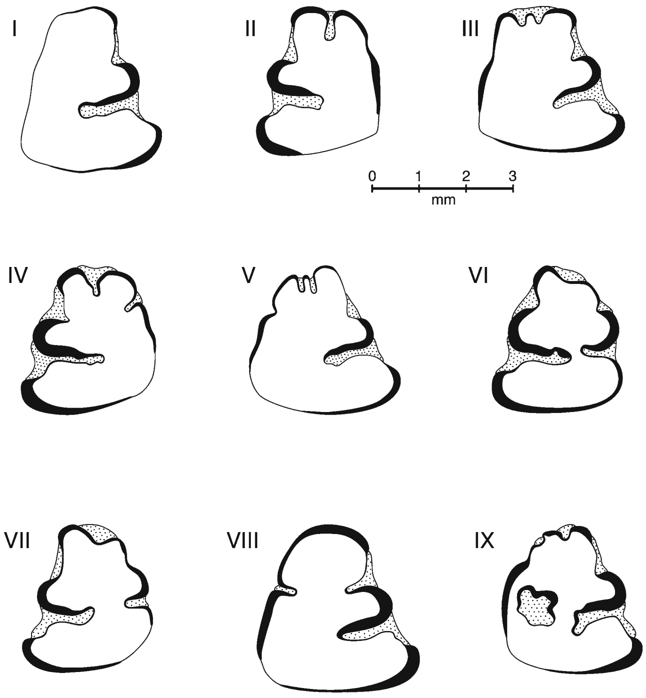

Fig. 3.3 Camera lucida drawings of *Serengetilagus praecapensis* p3s illustrating the nine occlusal morphotypes of Erbaeva and Angermann (1983: I–IX). Illustrations are the same teeth figured by Erbaeva and Angermann (1983: fig. 3), but the original teeth were redrawn to show enhanced detail of the enamel pattern and thickness. **(I)** (Winkler and Tomida, morphotype A), MB.Ma 1449/4 (only PER and AER present); **(II)** (type B), MB.Ma 1451/46 (PER, AER, AR); **(III)** (type B), MB.Ma 1450/2 (PER, AER, AR with double or multiple crenulations); **(IV)** (type B+), Mb.Ma 1447/6 (PER, AER, AR, AIR); **(V)** (type B+), MB.Ma 1449/3 (PER, AER, AIR, AR with double or multiple crenulations); **(VI)** (type C), MB.Ma 1448/3 (PER, AER, AR, AIR, PIR large); **(VII)** (type C), MB.Ma 1450/15 (PER, AER, AR, AIR, PIR small); **(VIII)** (no corresponding type), MB.Ma 1447/17 (PER, AER, AIR present, AR absent); **(IX)** (type C), MB.Ma 1451/44 (PER, AER, AR, AIR, enamel lake)

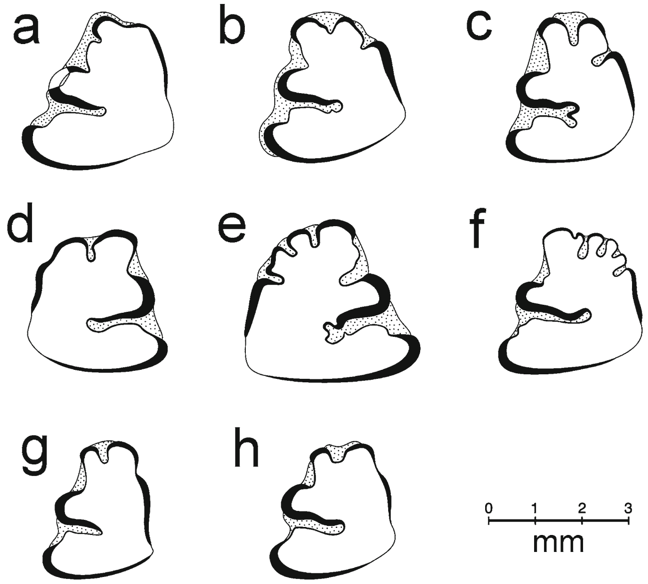

Fig. 3.4 Camera lucida drawings of representative examples of *Serengetilagus praecapensis* p3 occlusal morphology from the Harrison collections. The specimens are from (**a**) the Lower Laetolil Beds, (**b**–**d**) Upper Laetolil Beds, and (**e–h**) Upper Ndolanya Beds. (**a**) EP 208/03, morphotype B; (**b**) EP 902/03.1, type B+; (**c**) EP 554/01.2, type B+; (**d**) EP 1565/98.1, type B−; (**e**) EP 1223/03.1, type B+; (**f**) EP 810/01.1, type B+; (**g**) EP 3475/00.1, type B−; (**h**) EP 810/01.2, type A

IX, PER, AER, AR, AIR, and enamel lake present. The most common morphotype seen in their sample was IV (PER, AER, AR, and AIR present; 57% of the sample).

For the present study, we noted a wide range of variation in the size of AIR and found it was often difficult to classify objectively extremely small AIRs as present or absent. Often the AIR would be present as a slight indentation on the occlusal surface (e.g., Fig. 3.3 II; which would have been classified as absent by Erbaeva and Angermann 1983), but it was observed still as a distinct groove on the side of the tooth. Thus, we used a modified classification scheme to more precisely incorporate the variability of AIR. We used five morphotypes: A, only PER and AER present (= morphotype I of Erbaeva and Angermann 1983); B, AER, PER, AR (single or multiple crenulations) present, and AIR completely absent (= morphotypes II and III); B−, AER, PER, AR (single or multiple crenulations) present, and AIR very weak (may be observed only as a weak indentation on the occlusal surface, but present as a groove on the side of the tooth; Erbaeva and Angermann 1983, did not classify this morphotype); B+, AER, PER, AR (single or multiple crenulations), and distinct AIR present (= morphotypes IV and V); C, AER, PER, AR, AIR, and PIR (relatively large or small or as an enamel lake) present (= morphotypes VI, VII, IX). No specimens had a distinct AIR, but lacked AR and PIR (morphotype VIII). A very weak groove in the area where PIR would be located was sometimes observed along the side of the tooth: sometimes this groove was expressed as a slight indentation on the occlusal surface. These very weak grooves or indentations were not considered distinct enough to count PIR as present.

Specimens illustrated in Fig. 3.3 and representative specimens of *Serengetilagus* from the Harrison collection (Fig. 3.4) were made by YT using a camera lucida. Final illustrations were made by tracing these pencil drawings using Adobe Illustrator CS4. Statistical analyses were made using SPSS 13.0.

Institutional abbreviations. KNM-KW, National Museums of Kenya, Kanam West locality; KNM-LT, National Museums of Kenya, Lothagam locality; M, Natural History Museum, London; MB.Ma, Museum für Naturkunde, Berlin.

Anatomical abbreviations for p3. AER, anteroexternal reentrant (= protoflexid); AIR, anterointernal reentrant (= paraflexid); AR, anterior reentrant (= anteroflexid); PER, posteroexternal reentrant (= hypoflexid); PIR, posterointernal reentrant (= mesoflexid). Tooth terminology modified from White (1991).

Results

Dietrich (1941, 1942: 58); translation from López-Martínez et al. 2007) diagnosed *S. praecapensis*, stating that on p3 the PIR was either extremely reduced, or, in most cases, absent, and the other reentrants were as usually seen in Palaeolaginae (i.e., presence of PER, AER, AR, AIR). López-Martínez et al. (2007: 4) provided a generic diagnosis and reiterated the "Extended Diagnosis" of *S. praecapensis* by Erbaeva and Angermann (1983: 59). López-Martínez et al. (2007) noted that *Serengetilagus* belongs in Archaeolaginae, not Palaeolaginae, because the former subfamily includes taxa with the PIR usually absent. For p3, the generic diagnosis (López-Martínez et al. 2007: 4) includes "p3 crescentic in shape with two main, constant external folds [PER (hypoflexid) extending about half-way across the crown and shallow AER (protoflexid)] and up to three additional folds variably present [AR (anteroflexid) variably developed, weak AIR (paraflexid) and exceptionally a PIR-enamel lake (mesoflexid-mesofossetid), mainly in young individuals]; when an AR (anteroflexid) is present, lingual anteroconid is weaker than the labial one." The diagnosis for *S. praecapensis* by Erbaeva and Angermann (1983: 59) includes (for p3): the most common morphotype has a short PER extending about half-way across the occlusal surface, plus an AR, AER, and an AIR; rudimentary PIR extremely rare; mean p3 length is 3.3 mm and mean width is 3.1 mm; occlusal shape of p3 variable, but mostly anteroposteriorly elongated.

Occlusal Morphology

Table 3.1 presents the frequency of each p3 morphotype (A, B, B−, B+, C) in the Harrison collection based on stratigraphic position. Figure 3.4 illustrates representative specimens from the Upper Ndolanya Beds and the Upper and Lower Laetolil Beds. The two most common morphotypes are B − and B+: PER, AER, AR, and AIR are present. Morphotype B − (Fig. 3.4d, g) has a weak AIR and B + (Fig. 3.4b, c, e, f) has a distinct AIR. Although the sample sizes from all units are relatively low, it is noteworthy that *S. praecapensis* from the younger part of the section (Upper Ndolanya Beds, [UNB], and between Tuffs 7 and YMT [Yellow Marker Tuff], Upper Laetolil Beds [ULB]) more commonly exhibits a weak AIR (B−, about 49–50% of specimens) than one that is distinct (B+, 26%). This pattern is reversed in the next geologically older sample, from between ULB Tuffs 5 and 7, where a distinct AIR is more commonly observed (B+, 51%; B−, 29%). Specimens collected below Tuff 5 also more commonly have a distinct AIR, however, sample sizes are very low. The distribution of the frequency of morphotype B, complete absence of AIR, does not show a meaningful pattern: this is likely because there are so few teeth overall with that morphotype. Abundances of all other morphotypes are low. White's (1991) diagnosis of the most primitive leporid,

Table 3.1 Lower third premolar morphotypes of *Serengetilagus praecapensis* (adults and juveniles) from Laetoli, Tanzania

	Stratigraphic unit (Harrison collection; total *N* = 191)					
		Upper Laetolil Beds				
Morphotypes	Upper Ndolanya Beds	Between T7 and YMT	Between T5 and T7	Between T3 and T5	Below Tuff 3	Dietrich collection
A	1 (2.9%)	0	0	0	0	5 (3.5%)
B	3 (8.8%)	6 (10.5%)	2 (2.8%)	2 (15.4%)	1 (6.7%)	31 (21.7%)
B−	17 (50.0%)	28 (49.1%)	21 (29.2%)	3 (23.1%)	4 (26.7%)	Not applicable
B+	9 (26.5%)	15 (26.3%)	37 (51.4%)	7 (53.8%)	10 (66.7%)	97 (67.8%)
C	4 (11.8%)	8 (14.0%)	12 (16.7%)	1 (7.7%)	0	6 (4.2%)
VIII	0	0	0	0	0	4 (2.8%)
Total number of specimens (100%)	34	57	72	13	15	143

Morphotype designations: A, only PER and AER present (= morphotype I of Erbaeva and Angermann (1983)); B, AER, PER, AR (single or multiple crenulations) present, and AIR absent (= morphotypes II and III); B−, AER, PER, AR (single or multiple crenulations) present, and AIR very weak (may be observed only as a weak indentation on the occlusal surface, but present as a groove on the side of the tooth); B+, AER, PER, AR (single or multiple crenulations), and distinct AIR present (= morphotypes IV and V); C, AER, PER, AR, AIR, and PIR (large or small or as an enamel lake) present (= morphotypes VI, VII, IX). No specimen from the Harrison collection has a distinct AIR, but lacks AR and PIR (morphotype VIII). Values for Dietrich collection from Erbaeva and Angermann (1983)

T Tuff, *YMT* Yellow Marker Tuff

Alilepus (here considered the outgroup), stated that AIR is usually absent: thus, absence (or, by implication, weakness) of AIR could be considered the plesiomorphic condition for the Leporidae. Averianov (1999) had also considered the lack of AIR to be the plesiomorphic condition. The lower frequency of p3s with a distinct AIR in the Upper Ndolanya Beds and uppermost part of the Upper Laetolil Beds is interpreted as this character newly reverting to the plesiomorphic condition.

The vast majority of the p3s in the Harrison collection (from all stratigraphic units) are from adult individuals: 33 are classified as juveniles, using the criteria in Materials and Methods. The distribution of morphotypes of the juveniles includes A (0%), B (*N*=2, 9.1%), B− (*N*=9, 27.3%), B+ (*N*=9, 27.3%), and C (*N*=12, 36.4%; characterized by presence of a PIR or enamel lake in the area PIR would be located). One specimen (EP 1629/04) is very young (unworn) and is close to morphotype C, but it lacks AR at the occlusal surface and on the side of the tooth. The total sample of juveniles is too small to analyze by stratigraphic unit. In the younger specimens, PER, AER, AIR and PIR are present at the occlusal surface: PER and PIR are comparable in size. Slightly older specimens have a cement-filled groove for AR further down the crown, which would be exposed with occlusal wear (e.g., EP 810/01.5). Some very young specimens with a large cement-filled PIR at the occlusal surface (e.g., EP 3296/00.1) show this reentrant greatly reduced (and lacking cement) at the base of the crown. Of the total sample of specimens (adults and juveniles from the UNB and Laetolil Beds) with a PIR or enamel lake (morphotype C, *N*=25), 48% are juveniles and about 7% are adults. Although our sample of very young individuals is extremely small, it appears that developmentally the distinct PIR observed in the youngest p3s is lost eventually through occlusal wear. The PIRs (or enamel lakes) seen in some adult *S. praecapensis* represent retention (in part) of the juvenile pattern.

The frequencies of morphotypes of specimens examined by Erbaeva and Angermann (1983) from the Dietrich collection are also listed in Table 3.1, with the morphotype designations adjusted to the system used in the present paper. The most common morphotype (B+) is characterized by the presence of a PER, AER, AR, and AIR (weak or distinct). Morphotype B (AIR absent) is observed more commonly in the Dietrich than in the Harrison collection, because some specimens with a weak AIR may have been classified as having AIR absent. Because different classification systems were used, one cannot use the distribution of morphotypes to decipher where the Dietrich material was most likely collected from within the Laetoli stratigraphic section.

Only two p3s are known currently from the Lower Laetolil Beds (EP 208/03 and EP 1508/03). Neither of these specimens is preserved sufficiently to measure, but a drawing from the cross-section of EP 208/03 (Fig. 3.4a) illustrates a tooth with morphotype B and comparable in size to other specimens of *S. praecapensis*. Compared to most other specimens of *S. praecapensis*, however, the AR of EP 208/03 is shallow and does not appear to extend to the base of the crown. The AER has a distinctive additional crenulation observed uncommonly in *S. praecapensis*. EP 1508/03 appears to lack AR and PIR, and the AIR is very small (close to morphotype A). As for AIR, an AR that is extremely weak to absent is the plesiomorphic condition (with *Alilepus* as the outgroup; White 1991; Averianov 1999).

Measurements

Occlusal measurements of p3 and measurement of the depth of the mandible at p3 are given in Table 3.2. Unlike morphology of the p3, where the distribution of morphotypes is most similar between the Upper Ndolanya Beds and between Tuff 7-YMT, mean values are most similar between Tuff 7-YMT and Tuff 5–7 (sample sizes from below T5 are very low: all measurements from these units are within the ranges seen for other units). This is observed for p3 length and width, and mandibular depth at p3. For these measurements, the mean values of specimens from the Upper Ndolanya Beds are slightly lower. However, the ranges of values from all three units are comparable, although a couple of exceptions from the Upper Ndolanya Beds should be noted. For p3 width, one specimen (EP 3296/00.1) has a p3 that is narrower (2.58 mm) than any other p3 measured. This specimen is broken, and the measurement was made on the cross-section of the tooth, so this may have introduced some error to the reading. The next narrowest p3 (from any unit) is 2.75 mm. The narrow width of EP 3296/00.1 affects the length to width ratio resulting in the high value of 1.32 for the Upper Ndolanya Beds. The next upper value for p3 length to width (L:W) ratio for the UNB is 1.21, which is closer to the upper values for the other units. The very wide p3 from the Upper Ndolanya Beds (EP 1223/03.1, width=3.92 mm; the next widest tooth is 3.50 mm) is discussed in more detail below. The p3 length to width ratio, depth of the PER, and depth of the PER to tooth width ratio are comparable among specimens from all units, including the mean values and the observed ranges. Unfortunately, sample sizes from the Upper Ndolanya and Upper Laetolil Beds are relatively small, so statistical comparisons among the units for the different parameters may not be meaningful. Larger sample sizes may confirm that *S. praecapensis* from the Upper Ndolanya Beds is smaller on average in some measurements, but the observed difference may also be an artifact of sample size.

Erbaeva and Angermann (1983) provided measurements of specimens in the Dietrich collection (Table 3.2). The

Table 3.2 Measurements (mm) of the p3 and mandibular depth at p3 of adult *Serengetilagus praecapensis* from Laetoli, Tanzania

	Stratigraphic unit (Harrison collection)						
		Upper Laetolil Beds					
Measurements	Upper Ndolanya Beds	Between Tuff 7 and YMT	Between Tuffs 5 and 7	Between Tuffs 3 and 5	Below Tuff 3	Lower Laetolil Beds	Dietrich collection
p3 length							
X	3.26	3.35	3.36	3.33	3.22	–	3.27
SD	0.18	0.21	0.16	0.08	0.14	–	0.02
OR	3.00–3.67	2.92–3.75	3.08–3.75	3.25–3.42	3.08–3.42	–	2.9–3.7
N	24	24	29	5	6	–	54
p3 width							
X	3.05	3.26	3.26	3.19	3.25	–	3.08
SD	0.31	0.20	0.22	0.18	0.16	–	0.03
OR	2.58–3.92	2.75–3.50	2.75–3.58	2.92–3.33	3.00–3.42	–	2.7–3.5
N	23	23	28	4	5	–	52
p3 length/width							
X	1.07	1.03	1.03	1.04	0.98	–	1.07
SD	0.10	0.07	0.07	0.05	0.06	–	–
OR	0.88–1.32	0.90–1.16	0.93–1.13	1.00–1.11	0.93–1.06	–	0.91–1.21
N	22	22	29	4	5	–	52
Depth of PER							
X	1.44	1.42	1.47	1.23	1.28	–	1.38
SD	0.18	0.19	0.17	0.04	0.27	–	0.02
OR	1.08–1.83	1.08–1.75	1.17–1.75	1.17–1.25	1.00–1.67	–	1.0–1.8
N	23	17	25	4	5	–	52
Depth PER/width p3							
X	0.48	0.43	0.44	0.38	0.38	–	0.45
SD	0.05	0.06	0.06	0.03	0.06	–	–
OR	0.38–0.56	0.32–0.54	0.32–0.59	0.36–0.43	0.31–0.43	–	0.34–0.56
N	22	16	25	4	4	–	51
Mandibular depth at p3							
X	10.49	11.36	11.16	10.68	11.05	–	11.11
SD	0.55	0.73	0.64	0.67	0.61	–	0.15
OR	9.65–11.82	9.47–12.50	9.71–12.27	10.11–11.98	10.17–11.82	11.72–12.02	9.7–13.0
N	21	14	23	6	6	2	33

Measurements of Dietrich collection from Erbaeva and Angermann (1983)
X mean, *SD* standard deviation, *OR* observed range, *N* number of specimens

ranges of values for this larger sample are quite similar to those for specimens in the Harrison collection from all stratigraphic units in all measurements and ratios (except for the two teeth discussed above). In mean values, however, the measurements for p3 length and width for specimens from the Dietrich collection are closer to those from the Upper Ndolanya Beds than the Upper Laetolil Beds. Mean mandibular depth at p3 for the Dietrich collection is more similar to values from the Upper Laetolil Beds than the smaller value for the Upper Ndolanya Beds. As mentioned earlier regarding differences in mean size in the Harrison collection, comparisons between the Dietrich and Harrison collections are plagued by issues of sample size. It is premature, at this point, to speculate on whether the Dietrich collection samples primarily the Upper Ndolanya or Upper Laetolil Beds (or a subunit within the ULB), or a combination of the two.

As also noted earlier, some dental and postcranial remains of specimens from the Upper Ndolanya Beds appear to be extremely large compared to other specimens from the Upper Ndolanya and Upper Laetolil Beds. Only one specimen from the Upper Ndolanya Beds had a p3 that caught our attention as being unusually large, EP 1223/03.1, an incomplete mandible. On a scatter plot of p3 length versus width (Fig. 3.5), the p3 of EP 1223/03.1 (circle) is distinctly wider than other p3s from the Upper Ndolanya and Upper Laetolil Beds. This tooth is at the upper end of the range of variation for p3 length. The p3 of EP 1223/03.1 is statistically significantly wider than the p3s from both the Upper Ndolanya and the Upper Laetolil Beds at $p<0.01$ (using a one sample *t*-test). The mandible of EP 1223/03.1 is deeper at p3 (11.82 mm) than other specimens from the Upper Ndolanya Beds, but is not the deepest mandible compared to specimens from the Upper and Lower Laetolil Beds.

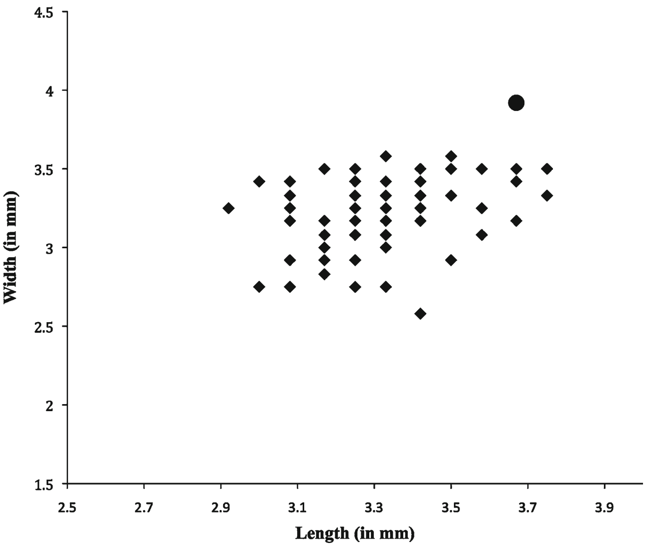

Fig. 3.5 Scatter plot of p3 length versus width measurements for specimens from the Upper Ndolanya Beds and Upper Laetolil Beds. Specimen indicated by a circle is EP 1223/03.1, an unusually large individual from the Upper Ndolanya Beds

The p3 of EP 1223/03.1 (Fig. 3.4e) has type B+ occlusal morphology: PER, AER, AR, and a distinct AIR are present. This tooth is unusual in having an additional crenulation between the AR and AIR and a lingually bifid PER. Additional crenulations or a lingually bifid PER are rare variations in *S. praecapensis*: (e.g., EP 810/01.1, Fig. 3.3f, and EP 554/01.2, Fig. 3.3c; Erbaeva and Angermann 1983: fig. 5.5).

The larger size and more complicated enamel pattern of EP 1223/03.1 are likely derived characters, suggesting EP 1223/03.1 might belong to a different species of *Serengetilagus*. The specimen is not referable to *S. tchadensis*, which has a p3 with plesiomorphic characters, such as absence of AIR and AR weak to absent. EP 1223/03.1 is conservatively not assigned to a new species pending analysis of other dental, cranial and postcranial elements.

Comparisons with *Serengetilagus* from Other Localities

In addition to its occurrence at Laetoli, *Serengetilagus praecapensis* has been reported from the Adu-Asa Formation, Middle Awash, Ethiopia (5.8–5.2 Ma; Wesselman et al. 2008) and Lothagam, Kenya (Winkler 2003). Wesselman et al. (2008) briefly described the small sample from the Middle Awash, and included measurements of three p3s, plus photographs of two specimens. The observed range for p3 length was 3.27–3.86 mm and width 2.97–3.25 mm (compare with Table 3.2). Size of the Middle Awash specimens is within the range of variation recorded for the Laetoli specimens, although the length of 3.86 mm for a Middle Awash specimen is slightly larger than specimens from the Dietrich or Harrison collections (as currently described) from Laetoli. As judged from the illustrations (Wesselman et al. 2008: fig. 5.6 C [STD-VP-2/911], D [ALA-VP-2/176]), both specimens pertain to *Serengetilagus* based on development of the PER and AER. Development of the AR and AIR (as described by Wesselman et al. 2008) of STD-VP-2/911 suggests assignment to *S. praecapensis*. Development of the trigonid of ALA-VP-2/176, however, is quite different: the more anterior reentrant was described as an AR by Wesselman et al. (2008), but it could be an AIR. Lack of an AR is a rare variant of adult *S. praecapensis*.

Winkler (2003) described a single mandible with p3-m3 (KNM-LT 24963) from the Apak Member, Nachukui Formation, Kenya (4.22–4.20 Ma). Length of the p3 (3.14 mm; both measurements made on a cast) is within the range for *S. praecapensis* (compare to Table 3.2), but the width (2.57 mm) is at the lowest end of the range of specimens from Tanzania (2.58 mm, Upper Ndolanya Beds, Table 3.2). The tooth is smaller than the values given for the small sample of *S. tchadensis* (mean length=3.41 mm, mean width=3.28 mm; López-Martínez et al. 2007, Table 3.2). The AR and AIR of KNM-LT 24963 are diminutive, more like the condition in *S. tchadensis*. A small PIR may be present, but the tooth is broken in this area, and the position on the tooth for this reentrant would be unusual (Winkler 2003: fig. 5.2C). This specimen cannot be referred confidently to *Serengetilagus praecapensis*.

As noted earlier, Flynn and Bernor (1987) suggested that an isolated leporid p3 (KNM-KW 138) from the Pliocene Kanam West locality, Kenya, was likely referable to *Serengetilagus*. This specimen, and a dentary from Kanam West in collections of the Natural History Museum, London (M 15889), are illustrated in Fig. 3.6. The occlusal morphology of both these specimens is well within the range of variation seen for *S. praecapensis*. Measurements of KNM-KW 138 (made on a cast) are L=3.17 mm, W=3.25, L:W ratio=0.98, depth PER=1.75, depth PER:width of p3 ratio=0.54. All of these measurements are within the range seen for *S. praecapensis* (Table 3.2). The measurements for the p3 of M 15889 (made on the camera lucida drawing) are L=3.20 mm, W=2.90, L:W ratio=1.10, depth PER=1.60, depth PER:width of p3 ratio=0.55. These measurements are also within the range seen for *S. praecapensis* (Table 3.2). Based on p3 morphology and size, these two specimens are both assigned to *S. praecapensis*.

The only other well-studied species of *Serengetilagus* is *S. tchadensis* from Toros Menalla, Chad (late Miocene; López-Martínez et al. 2007). Average measurements of the p3 of *S. tchadensis* are length (3.41 mm), width (3.28 mm), and length:width ratio (1.02): these measurements are within the range of variation for *S. praecapensis*. Measurements of depth of the PER of the Chad specimens were not published. The single

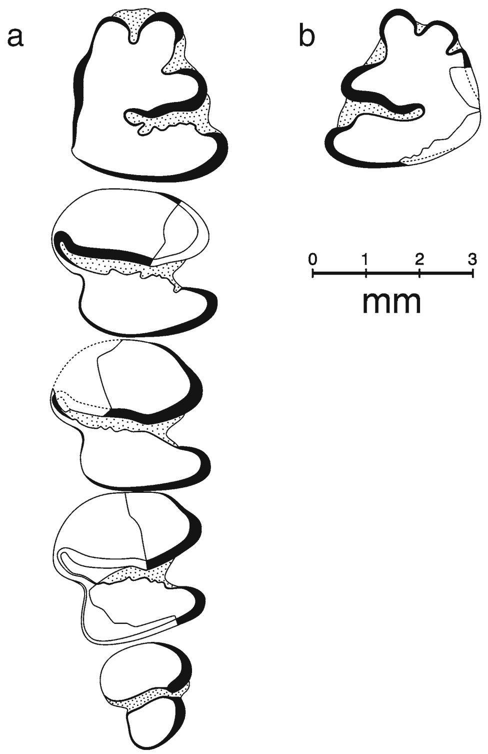

Fig. 3.6 Camera lucida drawings of the occlusal morphology of *Serengetilagus praecapensis* from Kanam West, Kenya. (**a**) *right* p3-m3, M 15889; (**b**) *left* p3, KNM-KW 138

measurement for *S. tchadensis* of the mandibular height at p3 (12.55 mm) is at the upper end of the size range for *S. praecapensis*. Known specimens of *S. tchadensis* lack AIR, and AR is weak to absent (both primitive characters). AR is almost always present in *S. praecapensis* and AIR is also usually present.

Conclusions

It has been suggested that the lagomorph remains from Laetoli may include more than one taxon: for example, one from the Upper Ndolanya Beds and one from the Upper Laetolil Beds (differing cranially). Another suggestion was that there are two taxa that differ significantly in size: a rare large form found in the Upper Ndolanya Beds and Upper Laetolil Beds above Tuff 7, and a common smaller form found in both units. Considering the wide geographic area sampled (>1,600 km^2), amount of geologic time represented (from older than 4.3 to ~2.66 Ma), and tremendous sample size (>4,000 specimens) from Laetoli, evidence of evolutionary change and even the presence of multiple taxa would not be unexpected.

Comparing p3 morphology of the samples from the Upper Ndolanya Beds and sediments between Tuff 7 and YMT, ULB, to specimens from between Tuffs 5 and 7, ULB, a weak AIR (49–50%) is more commonly observed in the upper younger units than in the older units (weak AIR 29%). A weak to absent AIR is likely the plesiomorphic condition in leporids: its lower frequency in the upper units is interpreted as this character newly reversing to the plesiomorphic condition.

Only two poorly preserved p3s are currently known from the Lower Laetolil Beds: on both specimens the AIR and AR are weak to absent. AR is almost always present (derived condition) on p3s from the younger horizons.

Although sample sizes are small and the observed ranges of values overlap, p3s from the Upper Ndolanya Beds are on average slightly shorter and narrower than those from the Upper Laetolil Beds. The length to width ratio, depth of the PER, and depth of the PER relative to the width of the tooth, are similar in both samples. The mandibles from the Upper Ndolanya Beds tend also to be less deep at the level of p3 compared to those from the Upper Laetolil Beds.

A single mandible from the Upper Ndolanya Beds (EP 1223/03.1) has a p3 larger and proportionally wider, and a mandible deeper at the level of p3 than mean values for other specimens from the Upper Ndolanya. In conjunction with its unusual p3 occlusal morphology, this specimen may represent a new, as yet unnamed, species.

The results of this study suggest some differences between the p3s of *S. praecapensis* from the Upper Ndolanya Beds and the subunits of the Upper Laetolil Beds. However, sample sizes are relatively small, and these differences are not considered significant enough to warrant specific (or subspecific) separation. The ranges of measurements and morphology overlap, and specimens, if collected individually, could not be identified confidently as belonging to one population or the other.

Laetoli has also produced abundant fragmentary maxillary and postcranial remains: nearly complete crania and associated skeletons are present but rare (crania with mandibles extremely rare). It will be interesting to see if differences in size and morphology suggested by this study are also present in other skeletal elements. Davies (1987) had observed morphological differences in the crania of some specimens from the Upper Ndolanya Beds compared to those from the Upper Laetolil Beds. It will be important to see if his observations can be confirmed, and if differences in cranial morphology are associated with any differences in p3 size or morphology. This should provide a more in depth picture of the evolution of this interesting animal.

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Appendix 3.1 Specimens of *Serengetilagus praecapensis* from Laetoli, Tanzania, included in this study

Horizon	Locality	Field numbers
Upper Ndolanya Beds		
–	7E	1480/00.1–.2; 1223/03.1–.4
–	15	208/04.1–.2; 1064/01.1–.2; 3296/00.1–.3; 3475/00.1; 3488/00; 4049/00
–	18	092/03.1–.3; 282/04.1–.3; 810/01.1–.5; 992/00.1–.7; 2355/00.1–.2
–	22S	1824/03.1–.2
–	Silal Artum	560/04; 1540/01.1
Upper Laetolil Beds		
Between T7 and YMT	1	221/00.1–.3; 1429/00
	17	1629/04; 1633/04; 2326/00
Between T7 and 2 m above T8	16	1480/00.1–.2; 1223/03.1–.4
Between T7 to just above T8	11	1081/04.1–.2
	16	276/03; 599/00.1–.2
Between T7 and T8	1	512/04; 1897/03.1–.2
	3	478/03.1–.3; 1627/00.1–.7; 2760/00.1–.2
	7	2213/03.1–.3; 2289/01.1
	8	258/00.1–.3; 1492/03; 1493/03A (2 specimens)
	11	1319/03.1–.3; 2586/00.1–.5; 4309/00.1–.2
	15	1448/98.1–.6
Above T7	7	932/01.1–.4
	11	996/01.1–.4
Between T6 and T7	10E	070/99.1–.5; 234/98.1–.22; 380/98.1–.6; 1565/98.1
Between T5 and T7	2	337/01.1–.3; 503/01; 609/03.1–.2
	8	373/04
	10E	049/04.1–.3; 080/04.1–.4; 554/01.1–.7; 798/00.1–.2; 902/03.1–.14; 1267/04.1–.3; 2893/00.1–.2
Between T3 and T5	5	261/01; 425/03.1–.3; 1388/04.1–.2; 1976/00.1–.5; 2806/00.1–.2
Below T3	10W	629/01
Below T2	9S	1050/98.1–.2; 1266/01.1–.2; 2444/03.1–.2
	10	521/98.1–.3; 882/98; 182/99.1–.2
	10W	739/98.1–.2
Lower Laetolil Beds		
	Kakesio 8	208/03
	Kakesio 2–4	1508/03

All field numbers begin with prefix EP. Format for field numbers is specimen/year collected. Numbers to right of year (e.g., 1452/00.1) indicate individual specimens grouped under one field number. *T* Tuff; *YMT* Yellow Marker Tuff

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Chapter 4
Macroscelidea

Alisa J. Winkler

Abstract Two incomplete mandibles (plus a third tentatively referred) and an isolated P4 of *Rhynchocyon pliocaenicus* are reported from Localities 2, 3, and 10E, Upper Laetolil Beds, Laetoli, Tanzania, East Africa. The specimens are dated at ca. 3.7–3.6 Ma. Morphology of this newly recovered material confirms and enhances a diagnosis based previously on only the holotype and paratype. Mean jaw depth and almost all dental measurements of *R. pliocaenicus* are on average about 21% smaller than those of the extant species *R. cirnei*, *R. petersi*, and *R. chrysopygus*. *Rhynchocyon pliocaenicus* is diagnosed also by a p2 with a strong posterior heel with a prominent posterior basal cusp, consistent presence of an anterobuccal cingulum on p4-m2, and a posterior cingulum on p4-m1. The protoloph of P4 and M1 of *R. pliocaenicus* connects to the tip of the paracone. If the habitat preferences of *R. pliocaenicus* were similar to extant *Rhynchocyon*, then the presence of this fossil species suggests that closed canopy habitats were present at Laetoli ca 3.7–3.6 Ma, but probably relatively rare.

Keywords *Rhynchocyon* • Pliocene • Laetoli • Sengis • Elephant shrews • Paleoecology

Introduction

Paleontological collections from the Upper Laetolil and Upper Ndolanya Beds, Laetoli, Tanzania, by Mary Leakey and associates primarily from 1974 to 1982 yielded only two specimens of sengis (elephant shrews) (Butler 1987). This material was assigned to a new species of *Rhynchocyon*, *R. pliocaenicus*, which has been reported only from Laetoli. More extensive collecting in these units and in the Lower Laetolil, Upper Ndolanya and Ngaloba Beds by Terry Harrison and associates (1998–2005) supports the rarity of sengis at Laetoli: only four new specimens were recovered out of a total sample of 15,019 specimens of all mammalian taxa from Laetoli (Harrison 2011). The new specimens of *Rhynchocyon* support Butler's (1987) assignment of the Laetoli material to an extinct species, and necessitate only slight changes to the original diagnosis.

Holroyd and Mussell (2005) have provided the most current classification and summary of the fossil record of the Macroscelidea. Sengis are known since the early Eocene. As fossils, and at present, the group is exclusively African. Paleogene reports (early or middle Eocene to early Oligocene) are only from North Africa and include representatives of two extinct subfamilies, the Herodotiinae (Hartenberger 1986; Simons et al. 1991; Tabuce et al. 2001) and Metoldobotinae (Schlosser 1910). The Miocene records are from Kenya, Uganda, and Namibia and include members of the Macroscelidinae (Stromer 1932; Butler 1984), Myohyracinae (extinct; Andrews 1914; Stromer 1922; Butler 1984; Senut 2003), and Rhynchocyoninae (Butler and Hopwood 1957; Butler 1969; Senut 2003). In the Plio-Pleistocene, the Macroscelidinae are reported from Tanzania (Butler and Greenwood 1976) and South Africa (Butler and Greenwood 1976), the Mylomygalinae (extinct) from South Africa (Broom 1948), and the Rhynchocyoninae from Tanzania (Butler 1987). At present, sengis are represented by the Macroscelidinae and the Rhynchocyoninae.

Comparisons of the Laetoli sengi are made only within the Rhynchocyoninae, which include *Rhynchocyon* and the extinct genus *Miorhynchocyon*. *Miorhynchocyon* is known from the early Miocene of Kenya at Meswa Bridge, Koru, Legetet, Chamtwara, Songhor, Rusinga, Karungu, and Mfangano (Butler 1984). An isolated P3 and P4 are described from the middle Miocene at Fort Ternan, Kenya (Butler 1984). *Miorhynchocyon* is also present in the early Miocene at Napak, Uganda (personal observation) and in the middle Miocene at Arrisdrift, Namibia (Senut 2003). Four species of *Miorhynchocyon* have been described: *M. clarki* Butler and Hopwood, 1957, and *M. rusingae* Butler, 1969, are relatively well represented; *M. meswae* Butler, 1984, is known from a

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single mandibular fragment with p3-p4, and *M. gariepensis* Senut, 2003, is represented by a mandible with p4-m2, a right m2, and an incomplete M1 (a skull and three isolated incisors are referred provisionally). The only fossil record of the genus *Rhynchocyon* is from Laetoli (Butler 1987).

Schlitter (2005) lists three extant species of *Rhynchocyon*: *R. chrysopygus* from eastern Kenya; *R. cirnei* from Mozambique, Malawi, Tanzania, Zambia, Democratic Republic of the Congo, and Uganda; and *R. petersi* from Tanzania and Kenya. A fourth species of *Rhynchocyon*, *R. udzungwensis* was described recently (Rovero et al. 2008) from the northern Udzungwa Mountains of Tanzania. At present, *Rhynchocyon* is "confined mainly to forest (lowland and montane) and thick riverine bush, although they have been taken in clearings amid grass and cane growth" (Nowak 1999: 1741). Kingdon (1974) notes that they occupy a wide range of elevation, from sea level to 2,300 m, and that they are dependent on shaded leaf litter.

Methods

Comparisons of the new material and casts of the holotype (rami and maxillary fragment with P4-M1) and paratype were made with dental remains of three extant species of *Rhynchocyon*, *R. cirnei*, *R. petersi*, and *R. chrysopygus* in collections of the Museum für Naturkunde der Humboldt-Universität, Berlin (ZMB), and the American Museum of Natural History, New York (AMNH) (Appendix). It is noteworthy that these three species were defined based on pelage and geographic distribution: cranial-dental characters were not used (Corbet and Hanks 1968; also see Kingdon 1974, who recognized only one species). Comparisons were not made with the four skulls of *R. udzungwensis* currently reported to be in museum collections (Rovero et al. 2008). Among fossil sengis, comparisons were made with all four species of *Miorhynchocyon* using published descriptions (descriptions only for *M. gariepensis*) and casts. A cast of the single specimen of *M. meswae* was unavailable; this specimen is a mandibular fragment with p3, p4, and the roots of p2. Casts are in collections of the Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas.

Tooth terminology in this paper follows Butler (1987). Classification follows Holroyd and Mussell (2005) and Schlitter (2005).

Systematic Paleontology

ORDER Macroscelidea Butler, 1956
FAMILY Macroscelididae Bonaparte, 1838
SUBFAMILY Rhynchocyoninae Gill, 1872

Rhynchocyon Peters, 1947
Rhynchocyon pliocaenicus Butler, 1987
(Figs. 4.1 and 4.2)

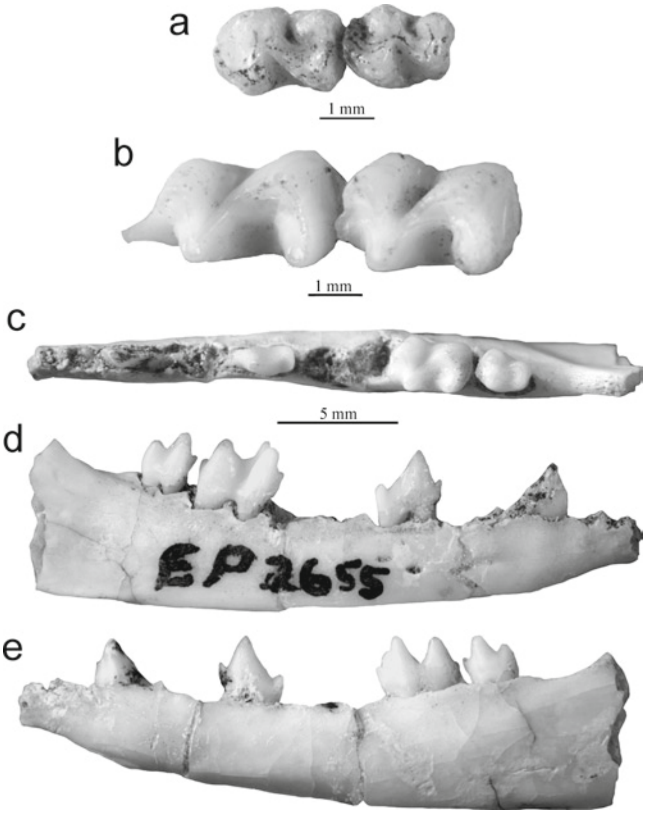

Fig. 4.1 *Rhynchocyon pliocaenicus* from the Upper Laetolil Beds, Laetoli, Tanzania. (**a**) occlusal view of EP 552/01, left mandible with m1 and m2, tentatively referred. (**b**) EP 2743/00, right mandible with p4 (incomplete) and m1. (**c–e**) EP 2655/00, right mandible with p1, p3, m1, and m2; (**c**) occlusal view; (**d**) labial view; (**e**) lingual view. Anterior is to the left for all illustrations except (**d**). Lower scale applies to (**c–e**)

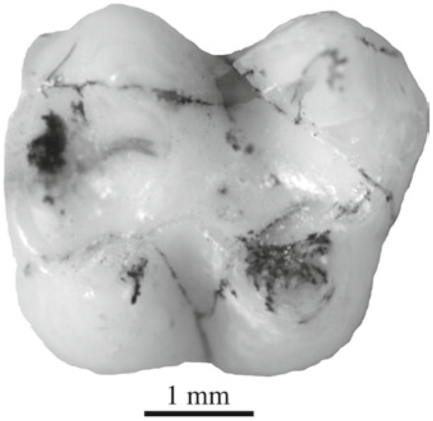

Fig. 4.2 *Rhynchocyon pliocaenicus* from the Upper Laetolil Beds, Laetoli, Tanzania. Occlusal view of EP 637/03, isolated right P4. Anterior is to the *right*

Revised diagnosis: Mean jaw depth and dental measurements on average 21% less than Recent species of the genus. Second lower premolar with distinct posterior heel bearing a prominent posterior basal cusp; anterobuccal cingulum present on p4-m2; posterior cingulum present on p4-m1. Protoloph of P4 and M1 connects to tip of paracone versus continuing to the anterior cingulum.

Holotype: LAET 75-2527, left mandible with base of p1, m1; right mandible with base p1, p2, p4-m2; five maxillae fragments, one with part of the left P4 (*contra* Butler 1987: fig. 4.1E) and also the M1. Considered one individual (Butler 1987).

Paratype: LAET 79-5470, left mandible with p1-m1 (p4 missing talonid).

Newly referred specimens: EP 2655/00, right mandible with p1, p3, m1, m2, and six associated bone fragments (two long bones, two vertebrae, one a caudal). EP 2743/00, right mandible with p4 (missing most of the paraconid), m1. EP 637/03, isolated right P4. EP 552/01, left mandible with m1 and m2 is tentatively referred.

Stratigraphic horizon: The holotype and paratype were collected by M. Leakey and associates from the Upper Laetolil Beds: the holotype is from Loc. 2, and the paratype is from Loc. 5 (Butler 1987). Additional specimens were collected by T. Harrison and colleagues. These specimens are also from the Upper Laetolil Beds. EP 2655/00 and EP 637/03 are from Loc. 2, between Tuffs 5 and 7. EP 2743/00 is from Loc. 3, between Tuffs 7 and 8. EP 552/01 is from Loc. 10E, between Tuffs 5 and 7. All specimens were surface finds.

Geologic age: ca. 3.7–3.6 Ma (Drake and Curtis 1987; Deino 2011).

Description: The horizontal ramus of EP 2655, the most complete new specimen, is long and slender. The specimen is broken proximally where the ramus begins its gentle ascent. Mental foramina are present below p2 and p3, as noted by Butler (1987) for the hypodigm. A mental foramen was not observed below the talonid of m1, as on the holotype (Butler 1987).

Morphology of the hypodigm is as described by Butler (1987) except as noted. In the original description of the species, Butler (1987) observed that p2 had a posterior heel. Comparison of the p2 (preserved only on the paratype and the right ramus of the holotype) to that of 16 extant specimens showed that *R. pliocaenicus* was distinctive in its strong development of the posterior heel on this tooth. Although some extant specimens were similar to the paratype in development, most were not. In particular, none of the extant material had a posterior basal cusp as tall as that on the right ramus of the holotype of *R. pliocaenicus*. Butler (1987) described his single p3 as having a protostylid. The single p3 in the new collections (EP 2655/00; Fig. 4.1c–e) lacks a protostylid: presence or absence of this cusp was variable in the extant specimens examined. Butler (1987) also noted that the talonid of p3 was composed of two small cusps. This area appears to include a single cusp on EP 2655/00. Development of this area was variable in seven extant specimens.

Butler (1987) did not have a complete P4 to describe. The newly recovered P4, EP 637/03 (Fig. 4.2), is roughly trapezoidal in outline. The anterior and posterior widths of the tooth are similar (3.44 and 3.60 mm), suggesting the tooth is a P4. This is in comparison to the greater discrepancy in anterior (3.15 mm) to posterior (2.35) width of the M1 (LAET 75-2527). As on the M1, the trigon is roughly "V" shaped with the base of the "V" pointing anteriorly. The protoloph connects laterally to the tip of the paracone. A paraconule is either lacking or might be considered minute and located at about the middle of the paraloph. There is a low cingulum anterior to the paracone. The protocone-paracone and metacone-hypocone pairs are essentially parallel and transverse, with the labial cusps slightly anterior. The major labial cusps are about two times the height of the lingual cusps. A curved crest connecting the metacone and hypocone closes the talon. There is a low posterolabial cingulum on the metacone. The trigon and talon basins are deep. The tooth has three roots: two labial and a single large lingual root.

The teeth of EP 552/01 (only m1 and m2 are preserved and they are broken and heavily etched; Fig. 4.1a) are a maximum of about 28% (M1) to 8% (M2) smaller than the mean size for the species. Approximate measurements (in millimeters) of EP 552/01 (not included in the compiled measurements in Table 4.1) are: m1L = 2.42, m1Wtrigonid = 1.58, m1wtalonid = 1.50, m2L = 2.08, m2Wtrigonid = 1.58, and m2Wtalonid = 1.17. EP 552/01 also differs from others of the species in having a less distinct groove between the protoconid and paraconid, on m1 lacking a posterior cingulum behind the hypoconid, and on m2 having a narrower connection between the trigonid and talonid. However, the m1 and m2 both have distinct long and low anterobuccal cingula. Due to these differences, EP 552/01 is referred tentatively to *R. pliocaenicus*.

Discussion

The new specimens of *R. pliocaenicus* and more extensive comparisons with extant species confirm Butler's (1987) observations and provide additional information about *R. pliocaenicus*. Butler (1987) noted that *R. pliocaenicus* was smaller than Recent species of *Rhynchocyon*, but provided comparative measurements for only one specimen of *R. cirnei* (Butler 1987: Table 4.1). Comparative measurements for three extant species are provided here (Table 4.1), using a larger data set for *R. cirnei* (ten specimens), and an

Table 4.1 Measurement statistics for *Rhynchocyon pliocaenicus* and samples of extant *R. cirnei*, *R. petersi*, and *R. chrysopygus*. Measurements in mm

	Taxon			
Measurement	*R. pliocaenicus*[a]	*R. cirnei*[b, c]	*R. petersi*[c]	*R. chrysopygus*[d]
p1L N	3	10	4	3
X	2.94	3.20	3.17	3.42
SD	0.37	0.19	0.12	0.14
OR	2.56–3.30	2.97–3.59	3.00–3.24	3.28–3.55
p1W N	3	10	4	3
X	0.95	1.08	1.20	1.24
SD	0.13	0.09	0.61	0.10
OR	0.80–1.05	0.98–1.25	1.14–1.26	1.15–1.34
p2L N	2	10	4	3
X	–	3.24	3.26	3.22
SD	–	0.24	0.25	0.10
OR	2.60–2.80	2.88–3.70	2.96–3.56	3.11–3.30
p2W N	2	10	4	3
X	–	1.43	1.54	1.41
SD	–	0.12	0.12	0.07
OR	1.10–1.20	1.29–1.58	1.43–1.69	1.35–1.48
p3L N	2	10	4	3
X	–	4.08	4.37	4.33
SD	–	0.27	0.38	0.42
OR	2.84–3.35	3.74–4.60	4.00–4.86	4.08–4.82
p3W N	2	10	4	3
X	–	1.94	1.95	1.94
SD	–	0.11	0.15	0.08
OR	1.36–1.45	1.74–2.10	1.73–2.05	1.84–1.98
p4L N	2	10	4	3
X	–	4.98	5.25	5.10
SD	–	0.57	0.24	0.20
OR	3.95–4.08	4.35–6.00	5.03–5.59	4.88–5.26
p4Wtrigonid N	3	10	4	3
X	2.04	2.60	2.66	2.69
SD	0.04	0.20	0.11	0.12
OR	2.00–2.08	2.40–2.98	2.60–2.83	2.56–2.79
p4Wtalonid N	2	10	4	3
X	–	2.79	2.95	2.97
SD	–	0.19	0.17	0.02
OR	2.20–2.24	2.54–3.10	2.80–3.14	2.94–2.98
m1L N	4	10	4	3
X	3.44	3.97	4.06	4.27
SD	0.08	0.20	0.14	0.14
OR	3.35–3.55	3.69–4.27	3.91–4.24	4.10–4.36
m1Wtrigonid N	4	10	4	3
X	2.13	2.72	2.74	2.86
SD	0.14	0.14	0.08	0.09
OR	1.92–2.24	2.43–2.85	2.66–2.83	2.75–2.92
m1Wtalonid N	4	9	4	3
X	2.11	2.59	2.66	2.87
SD	0.05	0.17	0.12	0.12
OR	2.05–2.16	2.23–2.78	2.54–2.78	2.75–2.98
m2L N	2	10	4	2
X	–	2.72	2.71	–
SD	–	0.27	0.21	–
OR	2.24–2.25	2.40–3.20	2.57–3.01	2.99–3.02

(continued)

Table 4.1 (continued)

	Taxon			
Measurement	*R. pliocaenicus*[a]	*R. cirnei*[b, c]	*R. petersi*[c]	*R. chrysopygus*[d]
m2Wtrigonid N	2	10	4	2
X	–	2.09	2.14	–
SD	–	0.13	0.11	–
OR	1.75–1.76	1.89–2.26	2.02–2.24	2.17
m2Wtalonid N	1	9	4	2
X	–	1.58	1.65	–
SD	–	0.11	0.10	–
OR	1.25	1.41–1.79	1.58–1.79	1.72–1.73
Jaw depth[e] N	3	10	4	3
X	4.41	5.74	5.69	6.45
SD	0.25	0.35	0.26	0.27
OR	4.15–4.65	5.13–6.10	5.40–6.0	6.22–6.75
p1-m2L N	2	4	–	2
X	–	22.79	–	–
SD	–	0.32	–	–
OR	17.98–18.08	22.47–23.20	–	24.61–25.53
p4-m2L N	1	10	4	2
X	–	11.77	12.48	–
SD	–	0.96	0.45	–
OR	9.70	10.80–13.37	12.22–13.16	12.85–13.14
P4L N	1	9	4	3
X	–	4.30	4.77	4.18
SD	–	0.33	0.59	0.13
OR	4.32	3.92–4.86	4.10–5.30	4.03–4.21
P4Wanterior N	1	9	4	3
X	–	4.02	4.43	4.41
SD	–	0.33	0.31	0.04
OR	3.44	3.70–4.63	4.15–4.87	4.37–4.44
P4Wposterior N	2	10	4	3
X	–	3.96	4.19	4.18
SD	–	0.44	0.21	0.13
OR	2.90–3.60	3.29–4.70	4.04–4.50	4.03–4.29
M1L N	1	10	4	3
X	–	3.82	3.88	4.02
SD	–	0.24	0.44	0.07
OR	3.15	3.42–4.20	3.55–4.53	3.95–4.08
M1Wanterior N	1	10	4	3
X	–	4.04	4.28	4.44
SD	–	0.29	0.21	0.13
OR	3.15	3.58–4.50	4.03–4.49	4.39–4.59
M1Wposterior N	1	10	4	3
X	–	3.28	3.36	3.56
SD	–	0.23	0.18	0.14
OR	2.35	2.96–3.52	3.26–3.63	3.40–3.67

L length, *OR* observed range, *N* number of specimens, *SD* standard deviation, *W* width, *X* mean

[a] Combined measurements from Butler (1987) and the author's measurements (maximum) on specimens from the Harrison collection. The latter were measured with an ocular on a Wild dissecting scope with measurement error of ± 0.08 mm

[b] Measurements (maximum) of all extant specimens made with a Mitutoyo digital calipers with measurement error of ± 0.01 mm

[c] Specimens of *R. cirnei* and *R. petersi* are from multiple localities

[d] Specimens of *R. chrysopygus* are from the same locality

[e] Lingual jaw depth at anterior end m1. Measured on the labial side when jaws were articulated

admittedly small data set for *R. petersi* (four specimens) and *R. chrysopygus* (three specimens). *Rhynchocyon udzungwensis* is larger than the other three extant species, for example, its mean weight is 25–50% greater than that of other species and its mean total body length is 10–20% longer (Rovero et al. 2008).

In almost all dental measurements, *R. pliocaenicus* is smaller than Recent species: mean measurements for *R. pliocaenicus* are on average 21% smaller (range 3% larger to 34% smaller) than mean measurements for the extant species. Only the length of P4 (one specimen of *R. pliocaenicus*) is comparable (*R. cirnei*) or slightly larger (by 3% to *R. chrysopygus*) than the mean length of extant species. P4 length of *R. pliocaenicus* is 9% shorter than the mean length for *R. petersi*. The P4 of *R. pliocaenicus* is narrower than the mean values for extant species, but the posterior width of the larger Laetoli P4 is within the range of variation for *R. cirnei*. Although the mean length and width of the p1 of *R. pliocaenicus* are less than the mean values for the three extant species, the length of the p1 of *R. pliocaenicus* is within the range of variation seen in the other species, and the width is within the range of variation for *R. cirnei* (but not the other extant species).

As noted by Butler (1987), an anterobuccal cingulum is present on the paraconid of p4-m2 of *R. pliocaenicus*. Butler observed this on only a few specimens of Recent species. In the present study, this structure was seen distinctly on the m1 and only faintly on the m2 (and not at all on p4) on only 2 out of 16 extant specimens of *Rhynchocyon*. A posterior cingulum is present consistently on the p4-m1 of *R. pliocaenicus*. Butler did not observe this structure on extant material. In the present study, a posterior cingulum was observed on 1 of 16 recent specimens.

Butler (1987) noted that on the one known M1 of *R. pliocaenicus* (LAET 75-2527) the protoloph was a strong crest connecting to the tip of the paracone. In the present study, Butler's (1987) observation that the protoloph of M1 of Recent *Rhynchocyon* usually does not connect to the tip of the paracone was confirmed. In nine of ten Recent specimens, the protoloph of M1 extends anterior to the paracone. On one of those specimens (*R. petersi*, ZMB 20025, on one maxilla, but not the other), the protoloph did turn toward and contact the paracone, but the bend was not as abrupt as seen on the fossil. On the P4 of *R. pliocaenicus* (EP 637/03), the protoloph connects to the tip of the paracone. This condition is variable on the five Recent specimens examined: On two specimens the protoloph extended anterior to the paracone and on three specimens the protoloph contacted the paracone on one side of the skull but not on the other.

Butler (1987) also made comparisons of *R. pliocaenicus* with the early and middle Miocene genus *Miorhynchocyon* (*M. clarki* and *M. rusingae*). Comparisons are extended here to *M. meswae* and *M. gariepensis*. Butler's (1987: 86) observations are augmented here by comparisons with the larger sample of *R. pliocaenicus*. *Miorhynchocyon* was diagnosed (for the dentition) as differing from *Rhynchocyon* in the following (Butler 1984): (1) the oblique crest on the lower molariform teeth (anterior hypoconid crest) ends midway between the protoconid and hypoconid (in extant *Rhynchocyon* it joins the metaconid), (2) a metastylid is absent on dp4 and m1, (3) on p4 and m1 the paraconid is higher and located more lingually, and (4) the cheek teeth are more brachydont.

Butler noted that in size, measurements of *R. pliocaenicus* fell within the range of values for *M. clarki* (Butler 1984: table 2). The additional specimens of *R. pliocaenicus* demonstrate that it is comparable in size or slightly larger than *M. clarki*. *Rhynchocyon pliocaenicus* is smaller than *M. rusingae*, comparable to slightly smaller than the single specimen of *M. meswae*, and comparable (p4, m1) to smaller (m2) than *M. gariepensis* (Senut 2003).

Butler (1987) observed that on the p4-m2 of *R. pliocaenicus* the anterior hypoconid crest connected the hypoconid to the metaconid: it did not end midway between the hypoconid and metaconid as in *Miorhynchocyon*. Connection of this crest to the metaconid was observed on the additional specimens of *R. pliocaenicus*, although it was less clear on the m2 of EP 2655/00. The dp4 is not known for *R. pliocaenicus*, but the m1 lacks a metastylid, comparable to *Miorhynchocyon*. The paraconids of p4 and m1 are usually low, but the teeth of *R. pliocaenicus* are generally less brachydont compared to *Miorhynchocyon*.

As noted by Butler (1987), *R. pliocaenicus* resembles *Miorhynchocyon* in development of the anterobuccal and posterior cingula (also described as present on m1 of *M. gariepensis*, but not described or illustrated for p4 [Senut 2003]), and in the M1 having the protoloph connecting to the tip of the paracone (although *Miorhynchocyon* usually lacks a paraconule). The incomplete M1 of *M. gariepensis* is not illustrated and the most anterior portion of the tooth is not discussed. The new P4 of *R. pliocaenicus* is also similar to the P4 of *Miorhynchocyon* in having the protoloph connecting to the tip of the paracone (on *R. pliocaenicus* the paraconule is either lacking or minute; *Miorhynchocyon* usually lacks a paraconule). Butler (1987) also commented on differences in the presence or absence of a protostylid on p2 and p3. In all species of *Rhynchocyon* and *M. clarki*, p2 lacks a protostylid. A protostylid is present on the p2 of *M. rusingae* (condition of *M. meswae* unknown). A protostylid is absent on the p3 of *M. clarki*, present on *M. rusingae* and *M. meswae* (Butler 1984), present on *R. pliocaenicus*, and generally present in recent species (Butler 1987). Presence or absence of protostylids on p2 and p3 thus does not appear to be a useful character for differentiating between the two genera.

In summary, *R. pliocaenicus* differs from *Miorhynchocyon* primarily in characters that differentiate the two genera, but *R. pliocaenicus* still shares some characters with *Miorhynchocyon* that differentiate both of these taxa from extant species of *Rhynchocyon*.

Conclusions

Sengis remain an extremely rare component of the Laetoli fauna in spite of eight seasons (and over 15,000 specimens) of additional collecting. From both the Leakey and Harrison collections, *Rhynchocyon pliocaenicus* is known from only the Upper Laetolil Beds, and not the Upper Ndolanya or Lower Laetolil Beds. It should be noted that for the Harrison collections, all specimens were collected as surface finds and collectors recovered all specimens they considered anatomically identifiable (Su and Harrison 2008). Specimens from the Leakey collections, Upper Laetolil Beds, were collected primarily as surface finds (except most rodents were recovered from screen washing at Localities 5 and 6), but excavations yielded many of the fossils from the Upper Ndolanya Beds (Leakey 1987). The Upper Ndolanya Beds are well sampled and have yielded an extensive fauna. However, there is a strong taphonomic bias against small mammals in this unit, which may be reflected in the lack of sengis (Harrison, personal communication). The Lower Laetolil Beds have not yet been sampled adequately (i.e., the collection from these beds is about 50× smaller than that from the upper unit) and this sampling bias may account for the lack of sengis (Harrison, personal communication).

Small mammals do comprise a large proportion of the fauna from the Upper Laetolil Beds. For example, in the Harrison collection 37.5% of all specimens of mammals are lagomorphs (Harrison, personal communication): lagomorphs represent about 31% of the Leakey collection (Leakey 1987: Fig. 1.3). Although not as common as lagomorphs, rodents are well represented in both the Leakey (about 6%; Leakey 1987: Fig. 1.3; Denys 1987) and Harrison collections (6.9%; Harrison, personal communication). Although smaller in size than the Laetoli lagomorph, *Serengetilagus*, *Rhynchocyon pliocaenicus* is larger than many of the rodent taxa reported from the Upper Laetolil Beds (however, 70% of all rodents were spring hares, *Pedetes*, which are larger than *Rhynchocyon*; Su and Harrison 2008). Thus, it is unlikely that the rarity of sengis in the Upper Laetolil Beds is from either a preservational or collecting bias against small mammals in general. However, relatively little screen washing was done by both the Leakey and Harrison teams, and that may account for the small proportion of the smallest small mammals.

The paucity of sengis from the Upper Laetolil Beds likely reflects the scarcity of suitable paleohabitats. It is, admittedly, a tenuous assumption assuming that the habitat preferences of a fossil species were similar to those of its extant relatives. However, the dental remains (the only part of the animal preserved) of *R. pliocaenicus* are very similar to those of extant species, so it is likely that their diets, and perhaps their preferred habitat, were similar.

Leakey (1987) suggested that the Laetolil Beds represented a dry savanna habitat. Andrews' (2006: 572) interpretation was that of a "heavily wooded environment with local patches of forest and few open grassland areas." Su and Harrison's (2008) interpretation was more similar to that of Andrews', but they considered the Upper Laetolil Beds to be derived from a predominately open woodland, which also included extensive open bushland, shrubland, and grassland habitats. Recent species of *Rhynchocyon* prefer areas of closed canopy and are dependent on shaded leaf-litter. This suggests that closed canopy habitats were present, but rare, at Laetoli ca. 3.7–3.6 Ma. It is noteworthy that the only published fossil record of *Rhynchocyon* is from Laetoli, and the only other published records of the Rhynchocyoninae are 84 specimens from nine early Miocene faunas (plus two isolated teeth from the middle Miocene; Butler 1984) from Kenya and three (possibly seven) specimens from the middle Miocene of Namibia (Senut 2003). East African early Miocene sites are considered to sample a larger percentage of closed canopy habitat than Laetoli, and this is likely reflected in the relatively greater abundance of Rhynchocyoninae in the earlier samples.

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Appendix 4.1 Species and provenance of comparative specimens of extant *Rhynchocyon*

Taxon	Specimen number	Provenance
R. cirnei	ZMB 19987, 19992, 19995	Nynga, Bez Songea, Tanzania
R. cirnei	ZMB 20014	Mitononi am Mbemkuru, Tanzania
R. cirnei	ZMB 31798	Mikindani, Tanzania
R. cirnei macrurus	BMNH 63.1854	Not given (Butler 1987: table 4.1)
R. cirnei hendersoni	AMNH 81332–81335	Rungwe, Tanzania
R. petersi	ZMB 11428	Majoni, Tanzania

(continued)

Appendix 4.1 (continued)

Taxon	Specimen number	Provenance
R. petersi	ZMB 20023, 20025	Mitononi am Mbemkuru, Tanzania
R. petersi	ZMB 84895	Kimbuguru, Pangani Bez, Tanzania
R. chrysopygus	AMNH 187231, 187232, 187234	Kilifi District, Kenya

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Chapter 5
Galagidae (Lorisoidea, Primates)

Terry Harrison

Abstract An additional specimen of a fossil galagid was recently recovered from the Upper Laetolil Beds at Laetoli in northern Tanzania. This new find represents the most complete specimen of a galagid known from Laetoli, and comprises associated partial right and left mandibular corpora. The galagid material from Laetoli can all be attributed to a single species, previously referred to as *Galago sadimanensis*. However, the taxon is sufficiently distinct from all extant galagids, as well as stem galagids from the Miocene of East Africa, to be placed in its own genus, *Laetolia*. The fossil record of galagids from the Pliocene of Africa is exceedingly poor, and *Laetolia sadimanensis* represents the best-known form. *Laetolia* can be distinguished from other galagids by its unique suite of morphological features. The stout and vertical implantation of P_2, the steeply inclined and robust symphysis, and the relatively deep corpus are all specialized features that are probably functionally linked. However, *Laetolia* has a less molariform P_4 than extant galagids, and it can be inferred to represents their primitive sister taxon. Based on molecular clock estimates, extant galagids shared a last common ancestor during the late Oligocene. It is interesting, therefore, to discover a sister taxon of extant galagids surviving in East Africa until at least the Pliocene, contemporary with more advanced crown members of the clade. From a paleoecological perspective, the occurrence of fossil galagids at Laetoli implies the presence of habitats with at least a sparse coverage of trees and/or thorn bush.

Keywords Galagids • Laetoli • Mabaget Formation • Pliocene • Phylogeny

Introduction

A single species of galagid, *Galago sadimanensis*, is represented by a number of partial mandibles from the Upper Laetolil Beds (3.63–3.85 Ma) at Laetoli (Walker 1987; Harrison 2010). A mandibular fragment from the Mabaget Formation (~5 Ma), in the Tugen Hills of Kenya, collected earlier, has been referred to the same species (Walker 1987). Renewed investigations at Laetoli have yielded an additional galagid specimen (EP 1064/03). The specimen was discovered by Chris Robinson in 2003 at Loc. 10W in the Upper Laetolil Beds between Tuffs 1 and 3 (~3.8 Ma). It consists of associated right and left mandibular fragments with P_2-M_3 and P_2, P_4-M_1 respectively, and it represents the most complete specimen of *Galago sadimanensis* known. The aim of this chapter is to describe briefly the new specimen, to present an updated account of the morphology of *G. sadimanensis* to highlight its distinctive features, and to clarify its taxonomic and phylogenetic relationships. As discussed below, the species is considered to be sufficiently distinct from extant galagids and from other fossil genera to be placed in its own genus.

The fossil record of galagids from the Plio-Pleistocene is exceedingly poor (Harrison 2010). Apart from *Galago sadimanensis*, the only other extinct species formally described is *Otolemur howelli*, based on a fragmentary maxilla, an isolated M_2, and an edentulous mandible from the lower part of the Shungura Formation (~3.0–3.2 Ma) in the Omo Valley, Ethiopia (Wesselman 1984). Fragmentary finds of other fossil galagids are known from localities in East Africa, some of which probably belong to extant taxa. Several mandibular fragments, isolated teeth, and postcranial elements from Bed I (~1.8 Ma), Olduvai Gorge, northern Tanzania, can be referred to the extant species, *Galago senegalensis* (Simpson 1965; Szalay and Delson 1979; Gebo 1986; Harrison 2010). Wesselman (1984) described a fragmentary M_2 from lower Member G (~2.0 Ma) of the Shungura Formation, Omo, Ethiopia, which he referred to *Galago senegalensis*, but the tooth is smaller than those of the modern taxon and it is best considered an indeterminate species (Harrison 2010). Wesselman (1984) also described an isolated M_2 from upper Member B of the Shungura Formation (~3.0 Ma), which is very similar to *Galagoides zanzibaricus*, except that the crown is slightly narrower. Denys (1987) reported an isolated upper canine of a galagid from the Humbu Formation (~1.3–1.7 Ma) at Peninj, Tanzania, which is consistent in

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morphology and only slightly smaller than that of extant *Galago senegalensis*. Finally, Harris et al. (2003) described a mandibular fragment with M_2 of a diminutive galagid from Kanapoi in Kenya (~4.1–4.2 Ma).

Fossil galagids are also known from the late Miocene of Africa. These include an isolated upper molar from Harasib 3a (~9–10 Ma) in Namibia (Conroy et al. 1993, 1996; Rasmussen and Nekaris 1998), several isolated teeth and postcranials of a small galagid, *Galago farafraensis*, from Sheikh Abdallah (~10–11 Ma) in Egypt (Pickford et al. 2006), and an undescribed mandible of a galagid from Kapsomin, in the Lukeino Formation (~6 Ma) in Kenya (Mein and Pickford 2006).

Extant galagos are included together in a single family, the Galagidae, which is restricted to sub-Saharan Africa. There are at least 24 species currently recognized, belonging to five genera - *Galago*, *Galagoides*, *Otolemur*, *Euoticus*, and *Sciurocheirus* (Kingdon 1997; Bearder 1999; Masters and Bragg 2000; Groves 2001; Grubb et al. 2003). A further genus name might be required to accommodate the *Galagoides orinus* group (sensu Grubb et al. 2003) if the *Galagoides demidovii* group proves not to be its sister taxon (see Fabre et al. 2009). The extant members of the family are characterized by the following cranio-dental features: molariform upper and lower P4; upper molars with large hypocone on an expanded distolingual lobe, well-developed prehypocone crista, deeply notched distal margin, long and distobuccally directed postmetacrista; lower molars with, elongated subtriangular trigonid with beak-like mesial margin; relatively lightly constructed cranium; orbits lacking strong frontation and raised margins; shallow mandible and lower face; very inflated auditory bulla with pneumatization extending into the mastoid region (Harrison 2010).

Systematics

Order Primates Linnaeus, 1758
Suborder Strepsirrhini Geoffroy, 1812
Infraorder Lorisiformes Gregory, 1915
Superfamily Lorisoidea Gray, 1821
Family Galagidae Gray, 1825
Subfamily Galaginae Gray, 1825
Genus *Laetolia* gen. nov.

Diagnosis: A galagid similar in overall dental dimensions to the extant *Galago senegalensis*. It differs from extant genera of galagids (i.e., *Galago*, *Euoticus*, *Galagoides*, *Sciurocheirus* and *Otolemur*) in the following features: relatively deeper and more robust mandibular corpus; mandibular symphysis more vertical, with a relatively greater cross-sectional area, and an inverted tear-drop (rather than oval) sagittal section; P_2 stouter, lower-crowned, and more vertically implanted; P_2 larger in occlusal area than P_4; P_3 and P_4 relatively small in relation to M_1; P_4 less molarized with shorter and more ovoid crown, rounded mesial margin, less well-developed metaconid, shorter and narrower talonid basin, and weakly developed entoconid and hypoconid; lower molars relatively narrower (Emended from Walker 1987; Harrison 2010). It differs from *Komba* (early and middle Miocene of East Africa) in the following respects: relatively thicker mandibular corpus; mandibular symphysis more vertical, with a relatively greater cross-sectional area, and an inverted tear-drop sagittal section; P_2 relatively larger; P_4 relatively shorter, with a less pronounced mesial beak, a less well-developed metaconid, relatively smaller distal cuspules, a shorter, broader and shallower talonid basin; P_4 slightly larger in occlusal area relative to M_1. Differs from *Progalago* (early Miocene of East Africa) in having a relatively shallower mandibular corpus that does not increase in depth posteriorly, and lacks a flange-like inferior margin; mandibular symphysis steeper and more robust; P_2 relatively larger; P_4 relatively shorter, with more pronounced distal cuspules, and a smaller talonid basin; P_4 slightly larger in occlusal area relative to M_1; lower molars narrower, with less-pronounced buccal flare, longer and more triangular trigonid, more pronounced mesial beak, greater height differential between the trigonid and talonid, narrower and shallower talonid basin, more voluminous cusps, weaker occlusal crests, and more obliquely oriented distal margin (Walker 1987; Phillips and Walker 2002; Harrison 2010).

Type species: *Laetolia sadimanensis* (Walker 1987).
Included species: *L. sadimanensis* (Walker 1987).
Holotype: LAET 74-294, right mandibular fragment with P_2-M_2. Laetoli, Tanzania.
Hypodigm: Specimens listed in Table 5.1, plus KNM-BC 1646 from the Mabaget Formation, Kenya.

Table 5.1 List of galagid specimens from the Upper Laetolil Beds, Laetoli

Specimen	Locality	Element
LAET 74-294	Loc. 5	Left mandibular fragment with P_2-M_2
LAET 75-2433	Loc. 10W	Right mandibular corpus and much of the ramus with P_2-M_2
LAET 75-2880	Loc. 10W	Left mandibular fragment with P_2-P_3
LAET 76-4144	Loc. 11	Left mandibular fragment with base of P_2
LAET 78-4702	Loc. 7	Right mandibular fragment with M_2-M_3
EP 1064/03	Loc. 10W	Right mandibular corpus with P_2-M_3 and left mandibular corpus with P_2, P_4-M_1

Distribution: Pliocene, ~3.6–5.0 Ma. Upper Laetolil Beds, Laetoli, Tanzania and Mabaget Formation, Kapchebrit, Baringo Basin, Kenya.
Diagnosis: Same as genus.

Description of EP 1064/03

The specimen consists of two associated mandibular fragments comprising the right mandibular corpus with P_2-M_3 and the left mandibular corpus with P_2 and P_4-M_1 (Fig. 5.1). The right mandibular fragment comprises the entire corpus and the anterior and inferior aspects of the ramus. The corpus is preserved anteriorly as far as the symphysis, but the alveoli for the canine and incisors are poorly preserved, and the symphysis is incomplete superiorly. The rest of the corpus is entire and well-preserved, except for some faint pitting caused by weathering. On the lateral side of the corpus below P_4 there is single large elliptical mental foramen. A tiny accessory foramen is located vertically below P_3. The ramus is broken obliquely and abraded, preserving only the root of the anterior margin of the ramus and the inferior border, extending posteriorly 8.3 mm beyond M_3. The dentition is lightly worn and generally well-preserved, except for some minor weathering and abrasion. P_2 is missing the tip of the crown.

The left mandibular fragment consists of the symphyseal region and the corpus as far posteriorly as the alveolus for the anterior root of M_2. The symphysis and alveoli for the canine and incisors are better preserved than on the right side and are almost complete. A large mental foramen is located below P_3/$P_{4,}$ and a minute accessory foramen is positioned below P_2. There is a fresh break through the corpus behind M_1, indicating that the posterior portion of the corpus was detached after the specimen eroded out onto the surface. The preserved teeth are complete, but their enamel surfaces are slightly weathered. P_3 is represented by the roots only.

Morphology of *Laetolia sadimanensis*

Only the lower dentition and mandibles of *Laetolia sadimanensis* are known (see Table 5.1). The mandibular corpus is relatively deep and more robust than in modern galagids. It maintains a constant depth below the cheek teeth or shallows slightly posteriorly. There is a single mental foramen positioned vertically below P_3 or P_4 (Table 5.2), and located just below mid-height (40–45% up from the inferior margin). A tiny accessory foramen is commonly located just anterior to the main foramen. The symphysis is stout, with an anteroposterior thickness of 65–75% of its height, compared with

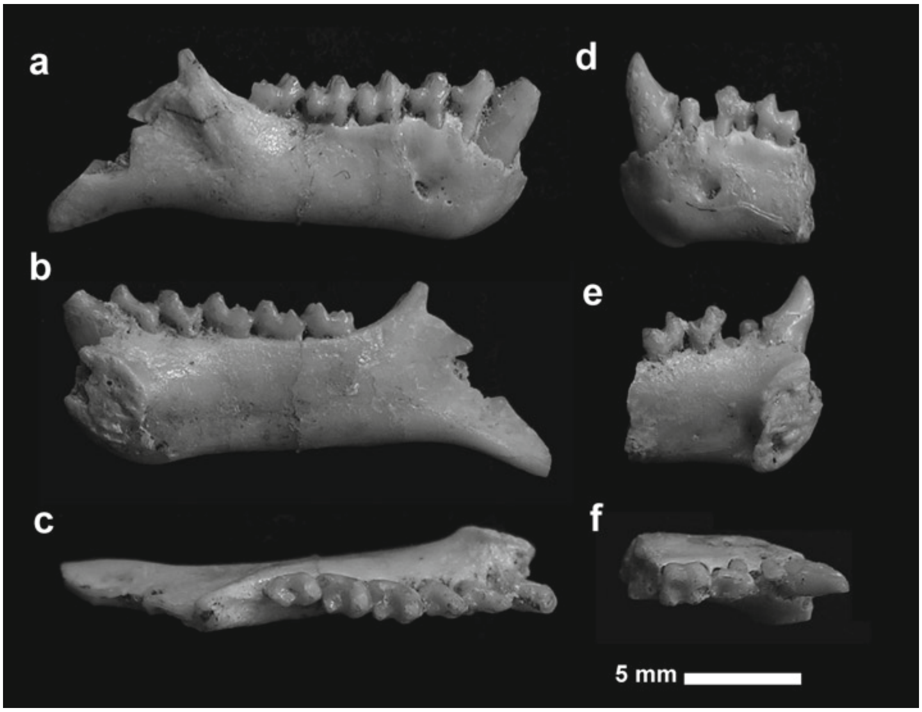

Fig. 5.1 EP 1064/03, right and left mandibular fragments of *Laetolia sadimanensis*. (**a**) right mandibular fragment with P_2-M_3, lateral view; (**b**) right mandibular fragment with P_2-M_3, medial view; (**c**) right mandibular fragment with P_2-M_3, occlusal view; (**d**) left mandibular fragment with P_2, P_4-M_1, lateral view; (**e**) left mandibular fragment with P_2, P_4-M_1, medial view; (**f**) left mandibular fragment with P_2, P_4-M_1, occlusal view. All to the same scale

55–65% in extant galagids. The symphysis was unfused with no indication of synostosis. In section, the symphysis forms the shape of an apostrophe, with an almost circular superior portion and a smaller inferior torus that projects posteriorly. In modern galagids, the symphysis forms a flat ellipse, with no development of an inferior torus. The symphysis is more steeply inclined than in modern galagids, as well as in Miocene taxa, with a mean angle of the long-axis at 66° to the alveolar plane. The incisors and canines are not preserved in any of the specimens, so it is not possible to determine the degree of procumbency of the toothcomb. The average minimum width between the P_2s can be estimated to be 3.2 mm (range 3.0–3.6 mm). This is comparable in breadth to the similar-sized *Galago senegalensis*, and implies that the Laetoli galagid had a narrow toothcomb as in extant taxa.

Parts of the ramus are preserved in LAET 75-2433, LAET 78-4702 and EP 1064/03. The anterior margin of the ramus is set far back from M_3 and inclined posteriorly at angle of about 125° relative to the alveolar plane as in extant galagids. The coronoid process is not preserved. The base of the condyle is preserved in LAET 75-2433, and appears to have been slightly lower than in extant galagids, being situated just above the level of the occlusal plane of the molars. The ramus is antero-posteriorly quite long, being 185% the length of the molar row. This exceeds the relative length in extant galagids, and more closely approximates the condition seen in some lorisids, such as *Perodicticus*. The posterior angle of the mandible is not preserved, but judging from the strongly downturned inferior margin behind M_3 it was quite expanded. A similar pattern is seen in *Otolemur*, but is less pronounced in the smaller extant galagids.

Dimensions of the lower cheek teeth of *Laetolia sadimanensis* are presented in Table 5.3. P_2 is a robust caniniform tooth, relatively vertically implanted, with a single stout root. It has a convex mesial face and a longer concave distal face, with a short distal heel. The lingual face is bordered basally by a narrow cingulum. The P_2 is more robust than the similar-sized tooth in *Galago senegalensis*, and contrasts with the more procumbent sectorial tooth seen in all extant galagids. Even accounting for the variability in the form of P_2 in modern galagids, in which the larger species tend to have the most vertical and caniniform teeth, the degree of procumbency in the Laetoli galagid is much less marked even than in *Otolemur*. In the robusticity and orientation of the P_2 *Laetolia sadimanensis* approaches the specialized condition in extant lorisids. P_2 is larger than P_4, with the average occlusal area 117% of that of P_4. In Miocene and extant galagids, the occlusal area of P_2 is typically smaller than P_4 (e.g., *Progalago dorae*, 97%; *Komba robustus*, 88%; *Komba winamensis*, 67%; *Galago senegalensis*,

Table 5.2 Mandibular dimensions (mm) of *Laetolia sadimanensis*

	LAET 294	LAET 2433	LAET 2880	LAET 4144	LAET 4702	KNM-BC 1646	EP 1064/03 (right)	EP 1064/03 (left)
Angle of symphysis[a]	64°	64°	71°	63°		70°		62°
Depth at symphysis[b]	5.2	5.7		5.5		5.2		
Thickness at symphysis[c]	3.4	4.2	3.6	3.6		3.3		
Depth at M1[d]	5.1	5.2		5.1		4.0	4.9	4.7
Depth at M2[d]	4.9	4.9			5.0		4.4	
Depth at M3[d]		5.4			5.2		4.5	
Position of foramen[e]	mid P4	mes P4	dist P3	mid P4		mes P4	mes P4	P3/P4

[a] Angle of the symphysis midline axis relative to the alveolar plane of the mandibular corpus

[b] Maximum length of the symphyseal face measured along the midline of its long-axis

[c] Maximum breadth of the symphyseal face measured perpendicular to the midline long-axis

[d] Infero-superior depth of the mandibular corpus below the lower molars

[e] Vertical position of the main mental foramen below the cheek teeth: dist P3, below the distal moiety of P_3; P3/P4, below the contact between P_3 and P_4; mes P4, below the mesial moiety of P_4; mid P4, below the transverse midline of P_4

Table 5.3 Dental dimensions (mm) of *Laetolia sadimanensis*

	P_2		P_3		P_4		M_1		M_2		M_3	
Specimen	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
LAET 74-294	2.1	1.4	1.8	0.9	2.0	1.3	2.0	1.8				
LAET 75-2433	2.4	1.6	2.0	1.0	2.0	1.5	2.0	1.9		2.0		
LAET 75-2880	2.2	1.4	1.9	1.0								
LAET 76-4144	2.2	1.3										
LAET 78-4702									2.3	2.0	2.8	1.8
KNM-BC 1646	2.4	1.3	1.8	1.1			1.8	1.5				
EP 1064/03 (right)	2.0	1.3	1.8	1.0	1.7	1.4	2.2	1.8	2.1	1.7	2.2	1.4
EP 1064/03 (left)	2.3	1.4			1.7		2.1	1.8				
Mean	2.2	1.4	1.9	1.0	1.9	1.4	2.0	1.8	2.2	1.8	2.5	1.6

68%; *Otolemur crassicaudatus*, 96%; *Galagoides zanzibaricus*, 68%). In this respect, *Laetolia sadimanensis* begins to approach the more specialized condition in extant lorisids (e.g., *Loris tardigradus*, 137%; *Perodicticus potto*, 136%; *Nycticebus coucang*, 181%).

P_3 is a long, slender sectorial tooth with a single main cusp, the protoconid, situated in the midline one-third back from the mesial margin of the crown. The mesial and distal crests are sharp. The distolingual crest is more rounded. There is a weakly developed lingual cingulum. There are two roots. The tooth is similar in overall morphology to that of *G. senegalensis*, but differs in being relatively smaller in relation to M_1. The average occlusal area of P_3 is 53% of that of M_1 (compared with 63% in *Galago senegalensis*).

P_4 is a short, ovoid tooth with an elevated protoconid and a poorly developed metaconid. The talonid basin is short, and bordered distally by a pair of low, rounded tubercles, the entoconid and hypoconid. There are two roots. P_4 is relatively small in relation to M_1. The occlusal area averages 70% of that of M_1, slightly greater than in early Miocene galagids (e.g., *Progalago dorae*, 64%; *Komba robustus*, 63%), but smaller than in extant taxa (e.g., *Otolemur crassicaudatus*, 74%; *Galago senegalensis*, 77%). In sum, the P_4 is less molarized than in extant galagids, with a shorter, more ovoid crown, less well-developed metaconid, shorter and narrower talonid basin, and weakly developed entoconid and hypoconid. *Laetolia* also differs from extant galagids in having a less pronounced prow-like mesial beak at the front of the tooth. The P_4 of *Laetolia* is more derived than *Komba* from the Miocene of East Africa, in having a broader talonid basin and in being relatively larger in comparison to the occlusal area of M_1. Both of these features presage the greater degree of molarization seen in extant galagids. The P_4 of *Progalago*, a possible stem galagid from the early Miocene of East Africa, differs in having a longer crown, with a more voluminous talonid basin, and weaker distal cuspules.

M_1 has four main cusps. The protoconid and metaconid are subequal in height, relatively low, and positioned quite close together. The protoconid is situated slightly more mesially than the metaconid, so that the transverse crest connecting them is slightly oblique. There is a slight trace of a buccal cingulum around the protoconid. The mesial fovea is quite short, with a convex mesial margin. The hypoconid and entoconid are less elevated than the trigonid cusps and are spaced further apart than the protoconid and metaconid. The cristid obliqua, passing mesially from the hypoconid, is long and obliquely directed. The metaconid and entoconid are separated by a shallow lingual notch. The talonid basin is quite broad, but shallow. The distal margin of the tooth is obliquely oriented to the transverse axis of the crown. M_2 is subequal in size to M_1 and morphologically very similar. It differs in being broader mesially, with the mesial cusps set further apart, and having a more oblique distal margin. M_3 is relatively narrower than M_2, but variable in overall relative size (see Table 5.3). In LAET 78-4702 its occlusal area is slightly larger than that of M_2 (110%), whereas in EP 1064/03 it is smaller (86%). The crown narrows distally. It has five cusps, with a variably developed hypoconulid. The hypoconulid heel is well-developed in LAET 78-4702 and relatively weak in LAET 1064/03. The hypoconid and entoconid are reduced in size relative to the trigonid cusps.

Taxonomic and Phylogenetic Relationships

Laetolia sadimanensis can be distinguished from all extant galagids by its unique combination of morphological features. These include a relatively deeper and more robust mandibular corpus, a more vertical mandibular symphysis with a greater cross-sectional area and an inverted tear-drop sagittal section, a more robust, lower-crowned, relatively larger and more vertically implanted P_2, posterior premolars relatively small in relation to the molars, P_4 less molarized, with a shorter and more ovoid crown, a rounded mesial margin, a less prominent metaconid, a shorter and narrower talonid basin, and more weakly developed entoconid and hypoconid, and relatively narrower lower molars. The extent of these difference necessitate including the Laetoli galagid in a separate genus. The distinctive features of the mandible and P_2 are best interpreted as autapomorphies (see Walker 1987; Harrison 2010). The hypertrophy and vertical implantation of the P_2, the steep inclined and robust symphysis, and the relatively deep corpus are probably functionally linked, and exhibit some degree of convergence on the morphology seen in extant lorisids. However, as noted above, *Laetolia sadimanensis* appears to be more primitive than all extant galagids in having a less molariform P_4. This condition is most closely approximated by *Galago* spp. among extant galagids, although the latter do have a relatively larger P_4 with a more expanded talonid basin. Compared to Miocene galagids, such as *Progalago* and *Komba*, *Laetolia* is more derived in having a greater degree of P_4 molarization, with a relatively larger crown, more expansive talonid (compared with *Komba*) and better-developed distal cuspules (compared with *Progalago*). Thus, based on this evidence, *Laetolia* can be inferred to be the sister taxon of all extant galagids (see Fig. 5.2).

Conclusions

An additional specimen of a fossil galagid, comprising associated partial right and left mandibular corpora (EP 1064/03), was recovered from the Upper Laetolil Beds at Loc. 10W in 2003.

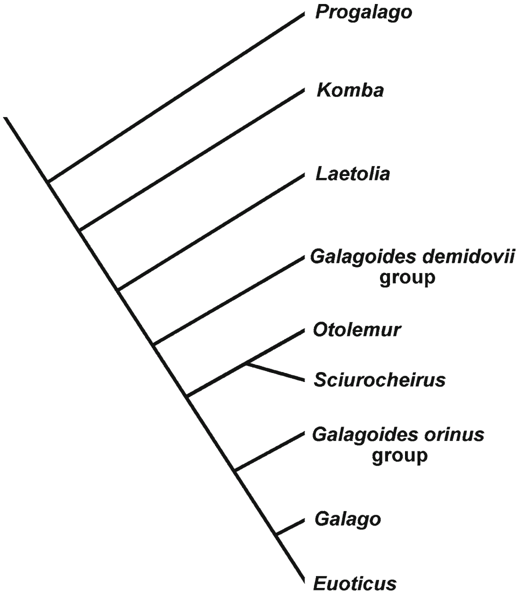

Fig. 5.2 Cladogram showing the inferred phylogenetic relationships of *Laetolia* with Miocene galagids (i.e., *Komba* and *Progalago*) and extant galagids (i.e., *Galagoides*, *Otolemur*, *Sciurocheirus*, *Galago*, *Euoticus*). Relationships between extant galagids are based on data from Fabre et al. (2009). Morphological features used to place *Laetolia* as the sister taxon to extant galagids are described in the text

This specimen now represents the most complete specimen of a Pliocene galagid. The material from Laetoli can all be attributed to a single species, previously known as *Galago sadimanensis*. However, the taxon is considered to be sufficiently distinct from extant and Miocene galagids to be placed in its own genus, *Laetolia* nov. gen. The fossil record of galagids from the late Miocene and Pliocene is relatively poor, and *Laetolia sadimanensis* represents the best-known form.

Laetolia sadimanensis is distinguished from all extant galagids by its unique combination of features. The stout and vertical implantation of the P_2, the steeply inclined and robust symphysis, and the relatively deep corpus are all specialized features and probably functionally linked. However, *Laetolia sadimanensis* has a less molariform P_4 than extant galagids, and it probably represents the primitive sister taxon to crown galagids (see Fig. 5.2). Given that crown galagids are estimated to have shared a last common ancestor during the late Oligocene (Fabre et al. 2009), based on molecular evidence, it is interesting to discover that a rather specialized sister taxon of extant galagids survived in East Africa until at least the mid-Pliocene contemporary with more advanced crown members.

Not much can be deduced about the paleoecology at Laetoli based on the rare occurrence of fossil galagids. Modern-day species have a wide distribution throughout sub-Saharan Africa, ranging from tropical forests and dry forests, to acacia woodland, savanna and thorn scrub (Kingdon 1997). *Galago senegalensis* is found today at Laetoli, occurring in riverine and open acacia woodland. Given that all extant galagids are arboreal, and need trees or thorn bushes for feeding and as sleeping sites, we can infer that the vegetation at Laetoli during the Pliocene included at least open woodland or thorn scrub.

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Chapter 6
Cercopithecids (Cercopithecidae, Primates)

Terry Harrison

Abstract New finds from Laetoli have allowed a more detailed assessment of the taxonomy and paleobiology of the fossil cercopithecids. Most of the specimens consist of isolated teeth, jaw fragments and postcranial bones from the Upper Laetolil Beds (~3.5–3.8 Ma), but four specimens are known from the Upper Ndolanya Beds (~2.66 Ma) and a proximal humerus has been recovered from the Lower Laetolil Beds (~3.8–4.3 Ma). Four species are represented: *Parapapio ado*, Papionini gen. et sp. indet., cf. *Rhinocolobus* sp., and *Cercopithecoides* sp. *Parapapio ado* is the most common species. Based on dental size and proportions and facial morphology, *Pp. ado* can be distinguished from all other species of *Parapapio*. The postcranial specimens attributed to *Pp. ado* indicate that it was a slender and agile semi-terrestrial monkey. A few isolated teeth represent a second species of papionin, larger in dental size than *Pp. ado*. Due to the paucity of the material, the taxon is left unassigned at the genus and species level. A distal humerus attributed to this taxon indicates that it was large terrestrial cercopithecid. The most common species of colobine is referred to cf. *Rhinocolobus* sp., based on its overall similarities to *Rhinocolobus turkanaensis*. The material can be distinguished from all fossil colobine species previously recognized from Africa, but without more complete cranial specimens it is not possible to diagnose a new taxon. From the postcranial material it can be inferred that it was generally adapted for arboreal quadrupedalism. The somewhat smaller species of colobine represents a previously undescribed species of *Cercopithecoides*. The postcranial specimens attributed to this taxon indicate that it was fully arboreal. Analysis of the distribution of the Laetoli cercopithecids provides provisional evidence of spatial patterning and temporal trends. For example, the dentition of *Parapapio* exhibits a trend to increase in size during the course of the Upper Laetolil Beds. As at other late Miocene and early Pliocene localities older than 3.5 Ma, the Laetoli cercopithecid community is characterized by the absence of *Theropithecus* and the relatively large proportion of colobines. After 3.5 Ma *Theropithecus* becomes the dominant cercopithecid at all East African localities, and the proportion of colobines declines accordingly.

Keywords *Parapapio* • *Paracolobus* • *Rhinocolobus* • *Cercopithecoides* • Papionin • Colobines • Monkey • Pliocene • East Africa

Introduction

Fossil cercopithecids were first discovered at Laetoli by L.S.B. Leakey in 1935. These included two mandibular fragments of a small to medium-sized species of papionin that were forwarded to the Natural History Museum in London. Hopwood (1936) described the right mandibular corpus of a female individual (NHM M14940) from the 1935 collection, and made it the holotype of a new species, *Cercocebus ado*. In 1938–1939 Kohl-Larsen made extensive collections of fossil vertebrates in the Laetoli region, and these included 38 cercopithecids, now housed in the Humboldt-Universität Museum für Naturkunde in Berlin. Although precise locality information is lacking, most of the specimens were recorded as coming from the Garussi and Vogelfluss (= Garusi), Deturi Ost (= Olaitoli) and Marambu (= Locality 1) valleys (see Harrison and Kweka 2011), and presumably all of them derive from the Upper Laetolil Beds. The preservation of the fossils and lithology of the adhering matrix support such a provenience. Two additional cercopithecid specimens from the Kohl-Larsen collection, attributable to *Papio* sp., were recovered from a Pleistocene locality called Lemagrut Korongo on the northwestern slope of Lemagurut.

Dietrich (1942) published a brief account of the cercopithecids from the Kohl-Larsen collection. He erected a new species *Papio* (*Simopithecus*) *serengetensis* for the medium-sized papionin, assuming that the assigned material was distinct from *Cercocebus ado* Hopwood, 1936. Leakey and Delson (1987) presumed that Dietrich's "kurzschnauzigen Catarrhinen" related to short-faced colobines from Laetoli,

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although Dietrich was evidently referring to *Cercocebus ado* (Dietrich 1942: 53). They also mistakenly indicated that Reck and Kohl-Larsen (1936) reported cercopithecids from Laetoli (*Cercocebus* sp. and *Papio* sp.), when, in fact, this material was from the Pleistocene locality of Eyasi.

L. S. B. Leakey and M. D. Leakey briefly revisited Laetoli in 1959 and 1964, and recovered additional fossil cercopithecids. According to M. D. Leakey (1987a), these finds and the 1935 collections were mainly from the Locality 10 complex (Locs. 10, 10W and 10E). Leakey and Leakey (1976) assigned the specimens to *Cercocebus ado*. Delson (1978; Szalay and Delson 1979), based on his study of the specimens in Berlin, recognized? *Parapapio ado* and Colobinae gen. et sp. indet. in the Laetoli collections.

Mary Leakey's expeditions recovered 81 cranio-dental specimens of fossil cercopithecids at Laetoli from 1974 to 1979. Locality information is recorded for most of these specimens, but precise stratigraphic information is largely unknown. All of the specimens come from the Upper Laetolil Beds, with the exception of two isolated teeth from the Upper Ndolanya Beds (Loc. 7E). A detailed systematic account of the entire Laetoli collection was presented by Leakey and Delson (1987). They recognized four species of cercopithecids – *Parapapio ado*, cf. *Papio* sp., cf. *Paracolobus* sp., and Colobinae gen. et sp. indet. The fragmentary nature of the material prevented more precise taxonomic assignments. They designated a lectotype (MB Ma 42441 = MB 1938.1) for *Papio* (*Simopithecus*) *serengetensis* Dietrich, 1942, and recognized the nomen as a junior synonym of *Parapapio ado* (Hopwood 1936).

The present author has recovered an additional 83 cranio-dental specimens of cercopithecids in the course of his 1998–2005 fieldwork at Laetoli (Table 6.1). These are all from the Upper Laetolil Beds, except for a deciduous upper central incisor of *Parapapio* from the Upper Ndolanya Beds at Loc. 7E. In addition, a proximal humerus from Emboremony 1 represents the first cercopithecid recovered from the Lower Laetolil Beds. The new material from Laetoli consists primarily of isolated teeth and jaw fragments, so several of the long-standing taxonomic issues remain unresolved. However, the larger sample of specimens now available (more than 200 cranio-dental specimens; see Table 6.1), the discovery of several key finds, and a detailed reassessment of the morphology has helped to clarify the taxonomic relationships of the Laetoli cercopithecids, as well as improving our understanding of their paleobiology.

Following Leakey and Delson (1987), four cercopithecid species are recognized – two papionins and two colobines. These are recognized here as *Parapapio ado*, Papionini gen. et sp. indet., cf. *Rhinocolobus* sp., and *Cercopithecoides* sp. Few of the postcranial remains are directly associated with cranio-dental specimens, but most can be assigned, at least provisionally, to a specific taxon on their basis of size and morphology. The aim of this chapter is to present a detailed description and comparison of the cranio-dental morphology of each species, and a preliminary account of the postcranial material. This provides the basis for a reassessment of the taxonomy of the Laetoli cercopithecids, as well as some initial observations on their paleobiology and ecology.

Table 6.1 Distribution by locality of cercopithecid cranio-dental specimens from Laetoli

Main locality	*Parapapio ado*	cf. *Rhinocolobus* sp.	*Cercopithecoides* sp.	Papionini gen. et sp. indet.
Laetolil Beds				
1	4	2	0	0
2	12	4	0	0
3	5	4	0	0
4	0	0	0	0
5	1	0	0	0
6	8	3	1	0
7	11	2	1	0
8	12	2	0	0
9	6	7	0	0
9S	0	1	0	0
10	3	1	0	0
10W	1	0	0	0
10E	17	1	2	0
11	9	5	1	1
12 + 12E	0	2	0	0
13	2	1	0	1
15	0	0	0	0
16	6	1	0	0
17	1	2	0	0
19	0	0	0	0
20	1	0	0	0
21	5	4	1	0
22	4	0	0	0
22E	0	0	0	0
Ndolanya Beds				
7E	2	1	0	0
14	0	0	0	0
15	0	0	0	0
18	0	0	0	0
Silal Artum	0	0	0	0
Unknown	29	18	3	1
Total	139	61	9	3

Material and Methods

The sample of cercopithecids from Laetoli comprises 212 cranio-dental specimens and 25 postcranial specimens (Table 6.1). This includes 93 specimens recovered from 1998 to 2005 and described here for the first time. Almost all of the cercopithecids from Laetoli have been recovered from the Upper Laetolil Beds. The exceptions are three isolated teeth from the Upper Ndolanya Beds at 7E and a proximal humerus from the Lower Laetolil Beds at Emboremony 1. A catalog of fossil cercopithecids from Laetoli is presented in Tables 6.2, 6.5, 6.6, 6.9 and 6.11.

The cranio-dental specimens consist primarily of isolated teeth (62%). Although a number of cranial and mandibular specimens are represented, these are rather fragmentary and there are no partial or complete crania and mandibles, which hampers comparisons and taxonomic assessments. The relative paucity of postcranial remains is not due to a collecting bias, but rather is a consequence of the taphonomic impact that carnivore predation and scavenging had on the composition of the fossil assemblage (Su and Harrison 2008). Cercopithecids, like the hominins, show a markedly disproportionate representation of cranio-dental specimens over postcranial specimens. Disarticulation of the skeleton and much of the damage to individual bones occurred prior to burial and fossilization, but additional damage was caused after the specimens eroded out of the sediments by weathering and transportation, and especially by trampling (Su and Harrison 2008). Although none of the cranial remains (and few of the postcranials) shows evidence of carnivore bite marks, 11 (6.7%) of the teeth collected by Leakey and Harrison show signs of having been digested (Carter-Menn unpublished data), confirming that carnivores had an important taphonomic impact on the cercopithecid assemblage.

The Laetoli specimens described here are housed in the Natural History Museum in London (NHM.M; 1935 Leakey collection), Humboldt-Universität Museum für Naturkunde in Berlin (MB Ma.; 1938–1939 Kohl-Larsen collection), Kenya National Museum in Nairobi (LIT and LAET; 1959, 1964 and 1974–1979 Leakey collections on loan from Tanzania), and National Museum of Tanzania (EP, Eyasi Plateau expedition; 1998–2005 Harrison collection). Comparison with extant and fossil cercopithecids were carried out at the American Museum of Natural History (AMNH), Natural History Museum in London (NHM), and Kenya National Museum (KNM).

Molar terminology follows Jolly (1972) and Delson (1975), with additional crest terminology following Szalay and Delson (1979). Metrical data on extant primates were collected by the author, and supplemented by dental metrics from Swindler (2002).

Systematics and Description

Order Primates Linnaeus, 1758
Infraorder Catarrhini Geoffroy, 1812
Superfamily Cercopithecoidea Gray, 1821
Family Cercopithecidae Gray, 1821
Subfamily Cercopithecinae Gray, 1821
Tribe Papionini Burnett, 1828

Parapapio Jones, 1937

Diagnosis: Cranium characterized by lack of an anteorbital drop (i.e., line from glabella to nasion straight or gently concave). Supraorbital tori relatively thin, and do not project anteriorly. Supraorbital sulcus (= ophryonic groove) weakly developed or absent. Suborbital fossae and well-developed maxillary ridges are generally absent, although a shallow depression may be present in some individuals. Fossae on lateral side of mandibular corpus weakly excavated or absent. Postcranial morphology indicates more arboreal positional behaviors than *Papio* and *Theropithecus* (Adapted from Freedman 1957; Szalay and Delson 1979; Leakey and Delson 1987; Frost and Delson 2002; Heaton 2006).

Distribution and Taxonomy

Five species of *Parapapio* are currently recognized (Jablonski 2002; Gilbert 2007; Frost 2007): *Pp. ado* Hopwood, 1936; *Pp. broomi* Jones, 1937; *Pp. jonesi* Broom, 1940; *Pp. whitei* Broom, 1940; *Pp. lothagamensis* Leakey et al., 2003. The alpha-taxonomy and assignment of specimens to *Parapapio* species from Plio-Pleistocene localities in South Africa have proved problematic (Eisenhart 1974; Freedman 1957, 1976; Szalay and Delson 1979; Frost and Delson 2002; Jablonski 2002; Heaton 2006; Williams et al. 2007; Gilbert 2007, 2008). Most researchers currently recognize three species from South Africa, distinguished primarily on the basis of size, as well as aspects of the facial morphology (Jablonski 2002; Frost and Delson 2002; El-Zaatari et al. 2005; Frost 2007). *Parapapio jonesi* is the smallest species, followed in size progression by *Pp. broomi* and *Pp. whitei*. All three species occur contemporaneously at Sterkfontein and Makapansgat (~3.3–2.3 Ma), while *Pp. broomi* (Taung and Bolt's Farm) and possibly *Pp. jonesi* (Taung and Kromdaai A) extend their temporal range to ~2.3–2.0 Ma and ~1.5–1.0 Ma respectively (Jablonski 2002; El-Zaatari et al. 2005).

Similar material has been recovered from Plio-Pleistocene cave sites on the Humpata Plateau in Angola and in the Koanaka Hills in Botswana, but they have not yet been attributed to species (Pickford et al. 1992; Jablonski 1994, 2002; Senut 1996). Fragmentary remains of *Parapapio* sp. of mid- to late Pliocene age have also been recovered from the Chiwondo Beds of Malawi (Bromage and Schrenk 1986; Bromage et al. 1995; Frost and Kullmer 2008). Two isolated teeth from the Quartzose Sand Member of the Varswater Formation (Fm.) at Langebaanweg, South Africa (~5.0 Ma), also have their closest affinities with teeth of *Parapapio* (Grine and Hendey 1981).

Two of the South African species have been recorded provisionally from localities in East Africa. *Parapapio* cf. *jonesi* is identified in the Hadar Fm. (~3.4–2.9 Ma) in Ethiopia

(Frost and Delson 2002), and *Parapapio* cf. *Pp. whitei* is recorded from the Lomekwi Mb., Nachukui Fm., West Turkana (~2.5–3.3 Ma) in northern Kenya (Harris et al. 1988). *Parapapio ado*, which is slightly larger in mean dental size than *P. jonesi*, is known definitively only from Laetoli, the type locality (~3.5–3.8 Ma). A few isolated teeth of this species are recorded from the younger Upper Ndolanya Beds at Laetoli (Leakey and Delson 1987; see below), and these extend the temporal range of the taxon to ~2.6–2.7 Ma. Patterson (1968) referred a partial mandible from Kanapoi (~4.1–4.2 Ma) to *Pp. jonesi*, but with the recovery of a relatively large sample of cercopithecid specimens from this site in the 1990s (Leakey et al. 1995, 2003), the mandible fragment and other *Parapapio* specimens were attributed to *Pp. ado*. *Parapapio ado* has also been provisionally identified from the lower Lomekwi Mb. of the Nachukui Fm. (~3.4 Ma) in West Turkana (Area 106) and in the Koobi Fora Fm. (~4.0–3.4 Ma) in East Turkana, Kenya (Harris et al. 1988; Leakey et al. 1995; Jablonski et al. 2008a).

A new species of *Parapapio*, *Pp. lothagamensis*, was described by Leakey et al. (2003) from the Upper and Lower Nawata Fm. of Lothagam, Kenya (~5.0–7.4 Ma). It can be distinguished from other species of *Parapapio* by its smaller size and by a suite of distinctive features of its dentition and mandible.

Unidentified species of *Parapapio* or other small papionins are recorded from the Omo Shungura Mb. B-lower G and the lower part of the Nachukui and Koobi Fora Fms. in the Lake Turkana Basin of Ethiopia and Kenya (Leakey and Leakey 1976; Eck 1976, 1977; Delson 1984; Jablonski et al. 2008a), the Nkondo Fm. in Uganda (~3.6 Ma) (Senut 1994), Unit 2 of the Chiwondo Beds (~4 Ma or older) in Malawi (Frost and Kullmer 2008), and the late Miocene (~6–7 Ma) of As Sahabi in Libya (Benefit et al. 2008). Jablonski et al. (2008a) have recently recognized three additional unnamed morphs of *Parapapio* from the Koobi Fora Fm. – sp. indet. A (2.0–1.4 Ma), sp. indet. B (4.0–1.6 Ma), and sp. indet. C (3.6–1.4 Ma).

In addition to *Parapapio*, two genera of small- to medium-sized papionins have recently been diagnosed and described from East and South Africa respectively. Frost (2001) described a new species of papionin, *Pliopapio alemui*, from Aramis, Ethiopia (~4.4 Ma), which differs in facial morphology and overall size from *Parapapio*. Additional specimens tentatively attributed to this species from the Sagantole and Adu-Asa Formations in the Middle Awash region of Ethiopia may extend the taxon back to ~5.7 Ma (Haile-Selassie et al. 2004; Frost et al. 2009). Gilbert (2007) transferred *Parapapio antiquus* (Haughton 1925) from Taung (~2.3–2.0 Ma) to a new genus, *Procercocebus*, based on its inferred phylogenetic relationship with the *Cercocebus* + *Mandrillus* clade. Finally, Jablonski et al. (2008a) identified a small species of papionin from Koobi Fora (~1.9–1.4 Ma) as *Lophocebus* cf. *albigena*.

Parapapio ado (Hopwood, 1936)

This is the most common species of cercopithecid from Laetoli, representing 65.6% of the cranio-dental specimens (Table 6.2). All of the permanent teeth are represented in the collections, with the exception of I^2 (see Table 6.3 for dimensions). A number of mandibular specimens and cranial fragments are represented, but the lack of relatively complete skulls limits comparisons with other extant and fossil papionins. The most important new finds consist of a mandible of a large male individual with almost complete, but heavily worn, dentition (EP 700/00); a partial frontal bone (EP 1579/98), which, when combined with information from LAET 75-2966 (a previously unattributed frontal found by M.D. Leakey) provides the first evidence of the morphology of the upper face of *Pp. ado*; and a right maxilla of a juvenile individual with dP^3-dP^4 and M^1 (EP 900/03). Several postcranial remains ($n = 10$) are attributed to *Parapapio ado*, and they are represented proportionately in the Laetoli collections relative to the cranio-dental remains (see Table 6.11). A brief account of the morphology and functional/behavioral implications of the postcranial specimens is presented later in this chapter.

All but two of the specimens of known provenance were recovered from the Upper Laetolil Beds. The two isolated teeth from the Upper Ndolanya Beds at Loc. 7E (LAET 79-5472, M_3; EP 1215/03, dI^1) are morphologically and metrically indistinguishable from those from the upper Laetolil Beds, and are referred to the same species. When the samples of *Parapapio* from different stratigraphic units within the Upper Laetolil Beds are considered, there are significant differences in size (but apparently not morphology) between samples earlier and later in the sequence (i.e., below and above Tuff 5 respectively). The mesiodistal lengths of the upper and lower molars from below Tuff 5 ($n = 10$) are significantly smaller than those from above Tuff 5 ($n = 67$) (expressed as a standard deviation from the mean for each tooth type for the sample above Tuff 5; Student's t-Test, $t = 2.03$, $df = 75$, $p < 0.05$). It seems that the general size of the teeth increased through time during the Upper Laetolil sequence (with the length of the molars being 10.5% greater on average above Tuff 5). Nevertheless, consistency in the morphology of the teeth indicates that the entire sample from the Upper Laetolil Beds can be assigned to a single species. It is unclear whether this increase in body size was directly related to ecological changes (evidence from the gastropod fauna indicates that the paleoecology at Laetoli was less mesic above Tuff 5; Tattersfield 2011) or whether it was a consequence of more general evolutionary phenomena, such as Cope's rule or Bergmann's rule.

Table 6.2 List of cranio-dental specimens from Laetoli referred to *Parapapio ado*

Specimen[a]	Loc.[b]	Horizon[c]	Element and comments[d]
NHM. M14940			Rt mandible with P_3-M_3. Female. Holotype
NHM. M18774			Fragment of mandibular symphysis with rt and lt I_1
MB Ma 42441	Gar. 26		Complete rt and lt corpora with lt I_1-M_3, rt M_1-M_3, fragment of P_4. Female. [MB 1938.1]; Lectotype of *Papio (Simopithecus) serengetensis* Dietrich, 1942 (Leakey and Delson 1987)
MB Ma 42442	Vo.		Rt mandibular fragment with P_4-M_3, roots of C_1-P_3. Male. [MB 1938.2; same individual as Ma 42446]
MB Ma 42443	Vo. 670		Lt mandible with dP_3-dP_4, M_1, unerupted germs of I_2 and C_1. Female. [MB 1939.16.1; fits together with Ma 42457]
MB Ma 42444	Vo. 610		Lt mandibular fragment with P_4-M_2, roots of P_3, base of C_1. Male. [MB 1939.16.2; same individual as Ma 42445 and Ma 42458]
MB Ma 42445	Vo.		Rt mandibular fragment with M_2-M_3. [MB 1939.16.3; same individual as Ma 42444 and Ma 42458]
MB Ma 42446	Gar.		Lt mandibular fragment with M_1-M_3. [MB 1939.16.7; same individual as Ma 42442]
MB Ma 42447	Gar.		Rt. M_2. [MB 1939.16.8]
MB Ma 42448			Rt maxilla with P^4-M^1. [MB 1939.16.11; same individual as Ma 42456]
MB Ma 42450	Gar.		Rt. M^3. [MB 1939.16.14]
MB Ma 42451	De. Ost		Rt mandibular fragment with P_4-M_2. [MB 1939.16.15]
MB Ma 42452	Gar.		Lt mandibular fragment with M_1-M_2. [MB 1939.16.16]
MB Ma 42453	Gar.		Lt mandibular fragment with M_1-M_2, root of P_4. [1939.16.18]
MB Ma 42454	Vo. 670		Left mandibular fragment with roots of dP_3-dP_4, C_1 and P_3 erupting. Male
MB Ma 42455			Lt P_4. [MB 1939.16.22]
MB Ma 42456	Gar.		Rt M^2. [MB 1939.16.24; same individual as Ma 42448]
MB Ma 42457	Vo.		Fragment of symphysis with rt and lt I_1 germs [MB 1939.16.35; fits together with Ma 42443]
MB Ma 42458	Vo.		Symphyseal fragment with rt I_2-P_3, roots of I_1 and P_4; roots of lt I_1-I_2. Male. [MB 1939.16.2; fits together with Ma 42444, and belongs to same individual as Ma 42445]
MB Ma 42480			Lt M_1
LIT 59-197			Rt mandibular fragment with P_3-M_1. Female
LIT 59-363			Lt P_4
LIT 59-463			Lt premaxilla-maxilla with alveoli of I^1-I^2, and roots of C-P^4. Female
LIT 59-464			Lt M^2
LIT 59-598			Lt C^1. Male
LIT 59-599			Rt C^1. Male
LAET 64			Lt mandibular fragment with M_3
LAET 74-223	8		Crushed mandible with rt C_1-M_2, lt P_3-M_3. Female
LAET 74-235	8		Lt mandibular fragment with P_3-M_1, base of C_1. Female
LAET 74-240	8		Inferior margin of mandibular symphysis. Listed as indeterminate premaxillary fragment by Leakey and Delson (1987)
LAET 74-242/243/244	8		Associated lt I_1, lt mandibular fragment with P_3-M_2, rt mandibular fragment with C_1-M_3. Female
LAET 74-245	8		Rt I_2. Found with LAET 74-242-244, but not associated
LAET 74-315	7		Lt C_1. Male
LAET 74-316	7		Lt mandibular fragment with dC_1-dP_4, root dI_2
LAET 74-319	7		Rt C^1. Female
LAET 74-320	7		Lt dP^3
LAET 74-322	7		Associated lt maxilla with C^1 and P^4, rt maxilla with P^3-P^4, rt maxilla with M^2-M^3, lt M^2 and M^3. Male
LAET 75-419	10W		Rt M^2
LAET 75-453	6		Rt M^2
LAET 75-483	10		Rt mandibular fragment with M_2-M_3
LAET 75-812	7	Tuffs 7-8	Lt mandibular fragment with M_1-M_2; rt M_2
LAET 75-996	11		Lt mandibular fragment with M_1-M_2, fragment of M_3. Found with 75-997 and 75-998
LAET 75-997	11		Fragment of lower molar. Found with 75-996 and 75-998
LAET 75-998	11		Lt mandibular fragment with dP_3-dP_4. Found with 75-996 and 75-997
LAET 75-1207	10E		Lt C^1. Male
LAET 75-1209	10		Lt mandibular fragment with C_1-M_3. Female

(continued)

Table 6.2 (continued)

Specimen[a]	Loc.[b]	Horizon[c]	Element and comments[d]
LAET 75-1390	7		Lt M_3
LAET 75-1489	9		Lt M^1. Listed as from Loc. 9S in Leakey and Delson (1987)
LAET 75-2379	10		Associated rt M^1-M^3
LAET 75-2714	11		Damaged lt P^4 and molar fragment
LAET 75-2727	3		Lt mandibular fragment and symphysis with lt dP_3-dP_4, root of dC, broken crown of I_1, isolated M_1; rt I_1-I_2 exposed in crypts
LAET 75-2966	16		Fragment of frontal bone
LAET 75-3035	9 (N)		Rt mandibular fragment with P_3-M_3; alveoli I_1-C_1. Female. Listed as from Loc. 9S in Leakey and Delson (1987)
LAET 75-3228	11		Germ of lt dP_4. Found with 75-3229
LAET 75-3229	11		Rt M^2. Found with 75-3228
LAET 75-3372c	21		Rt M^2
LAET 75-3549	8		Fragment of rt dP^4
LAET 75-3614	3		Rt C_1. Male
LAET 75-3829	3		Rt mandibular fragment with M_1-M_3
LAET 76-3904	2		Lt P^4
LAET 77-4568	9		Rt mandibular fragment with M_3
LAET 77-4592	?		Rt M^3
LAET 77-4593	11		Lt M^2
LAET 77-4595	?		Rt mandibular fragment with P_3-M_3; inferior border of left corpus; associated isolated teeth rt I_1-I_2, lt I_1-I_2, P_3-M_1. Male
LAET 78-4602	6		Rt P^3
LAET 78-4667	1	60 cm above Tuff 7	Lt dP^3
LAET 78-4721	6	60 cm above Tuff 5	Mandibular symphysis with roots or lt I_1-P_3 and rt I_1-I_2
LAET 78-5269	10E?[e]	90 cm below Tuff 7	Associated rt C^1, P^3, M^2 and M^3. Male
LAET 78-5276	10E?[e]	30 cm below Tuff 7	Rt M^1
LAET 78-5288	10E?[e]	60 cm above Tuff 7	Rt mandibular fragment with P_3-P_4 erupting, M_1 in place, alveolus for M_2. Male
LAET 78-5307	10E?[e]	30 cm above Tuff 6	Rt mandibular fragment with dP_3, roots dI_1-dC
LAET 78-5352	21	60 cm below Tuff 6	Left C_1. Male
LAET 78-5373	10E?[e]	90 cm below Tuff 6	Rt P^4
LAET 78-5374	10		Rt M^2
LAET 78-5434	8	1.2 m below Tuff 7	Rt M^2
LAET 78-5439	8		Rt P^4
LAET 79-5441	6		Lt mandibular fragment with M_2-M_3
LAET 79-5442	2		Lt P_4
LAET 79-5465	11	Below Tuff 7	Lt M^2
LAET 79-5469	2		Lt P^3-P^4, root of C^1 in maxillary fragment. Male
LAET 79-5472	7E	U. Ndolanya	Rt M_3
LAET 79-5510	6		Rt mandibular fragment with P_4-M_1
EP 200/98	10E	Tuffs 5-7	Lt M^2
EP 400/98	10E	Tuffs 5-7	Rt P_4
EP 1083/98	9	Tuffs 5-7	Associated lt I_1-I_2
EP 1084/98	9	Tuffs 5-7	Lt C^1. Male
EP 1229/98	22	Tuffs 5-7	Lt mandibular fragment with M_2
EP 1578/98	10E	Tuffs 5-7	Lt maxillary fragment with M^3
EP 1579/98	10E	Tuffs 5-7	Frontal and portions of nasal bones and maxilla
EP 219/99	9	Tuffs 5-7	Rt mandibular fragment with P_3-P_4. Male
EP 161/00	16	Tuffs 7-8	Lt I_1
EP 211/00	1	Tuffs 6-8	Lt I_2
EP 332/00	8	Tuffs 5-7	Rt M^1
EP 467/00	20	Tuffs 6-8	Lt I^1
EP 562/00	22	Tuffs 5-7	Lt M_2
EP 700/00	2	Tuffs 5-7	Mandible with rt I_1-M_3, lt I_1-I_2, P_3-M_3, root of C_1 Male
EP 1371/00	6	Tuffs 5-7	Rt M_2
EP 1623/00	3	Tuffs 7-8	Rt M^2
EP 1624/00	3	Tuffs 7-8	Rt premaxilla-maxilla with dP^3-dP^4, root dC_1, alveolus dI^2; I^1-I^2 exposed in crypts

(continued)

Table 6.2 (continued)

Specimen[a]	Loc.[b]	Horizon[c]	Element and comments[d]
EP1762/00	2	Tuffs 5-7	Lt P^4
EP 1763/00	2	Tuffs 5-7	Left I_1
EP 2000/00	5	Tuffs 3-5	Rt maxilla with P^3-M^1
EP 2028/00	16	Tuffs 7-8	Rt M^3
EP 2076/00	13	Tuffs 5-8	Rt M^1
EP 2575/00	11	Tuffs 7-8	Lt M_2
EP 2884/00	10E	Tuffs 5-7	Lt dP_4, missing mesial portion of crown
EP 3011/00	1	Tuffs 6-8	Rt M_3
EP 3600/00	21	Tuffs 5-7	Fragment of lt M^2
EP 3733/00	22	Tuffs 5-7	Lt I_1
EP 500/01	2	Tuffs 5-7	Lt M^1
EP 928/01	7	Tuffs 5-8	Lt M^3
EP 929/01	7	Tuffs 5-8	Rt I^1
EP 1139/01	1	Tuffs 6-8	Lt I_1
EP 1441/01	21	Tuffs 5-7	Lt C^1. Male
EP 274/03	16	Tuffs 7-8	Fragment of lt M_2
EP 275/03	16	Tuffs 7-8	Mesial portion of lt dP_4
EP 572/03	2	Tuffs 5-7	Lt maxilla with P^3-P^4. Female
EP 712/03	2	Tuffs 5-7	Lt M^2
EP 898/03	10E	Tuffs 5-7	Associated lt I_2 and C_1, rt I_2. Female. [Same individual as 901/05]
EP 899/03	10E	Tuffs 5-7	Lt M_1
EP 900/03	10E	Tuffs 5-7	Rt maxilla with dP^3-dP^4 and M^1; germs of P^3-P^4 in crypts
EP 1215/03	7E	U. Ndolanya	Rt dI^1
EP 1411/03	8	Tuffs 5-7	Rt I_2
EP 1412/03	8	Tuffs 5-7	Rt P^4. Probably same individual as 1413/03
EP 1413/03	8	Tuffs 5-7	Rt P^3. Probably same individual as 1412/03
EP 1574/03	21	Tuffs 5-7	Tip of rt C^1. Male
EP 1763/03	22	Tuffs 5-7	Lt M^1
EP 2037/03	6	Tuffs 5-7	Germ of lt P_4
EP 2137/03	7	Tuffs 5-8	Rt M^1
EP 1137/04	13	Tuffs 6-8	Lt mandibular fragment with M_3
EP 1424/04	6	Tuffs 5-7	Lt M_1
EP 1628/04	17	Tuffs 7-8	Lt dI^1
EP 1714/04	2	Tuffs 5-7	Rt I^1
EP 1715/04	2	Tuffs 5-7	Rt M_2
EP 183/05	16	Tuffs 7-8	Rt dP_4
EP 597/05	7	Tuffs 5-8	Lt P^3
EP 900/05	10E	Tuffs 5-7	Rt P^4
EP 901/05	10E	Tuffs 5-7	Associated Rt I_1, C_1, P_3. [Same individual as 898/03]
EP 964/05	2	Tuffs 5-7	Lt P_4

[a] Specimen prefixes: NHM.M, Natural History Museum, London, 1935 Louis Leakey collections; MB Ma. Humboldt-Universität Museum für Naturkunde, Berlin, 1938–1939 Ludwig Kohl-Larsen collections; LIT, Kenya National Museum, Nairobi (on loan from Tanzanian National Museum), 1959 and 1964 Louis and Mary Leakey collections; LAET, Kenya National Museum, Nairobi (on loan from Tanzanian National Museum), 1974–1979 Mary Leakey Collections; EP, Eyasi Plateau Expedition, National Museum of Tanzania, Dar es Salaam, 1998–2005, Terry Harrison collections

[b] Localities: De. Ost, Deturi Ost (= Olaitole River Valley); Gar, Garusi; Marambu (= Olduvai Side Gorge, Loc. 1); Vo, Vogelfluss (= Garusi Valley). Otherwise, the localities listed by number are the collecting localities as designated by Leakey (1987a)

[c] Horizon: The stratigraphic provenience of the Kohl-Larsen collections and most of the specimens collected by Leakey are from unknown horizons within the Upper Laetolil Beds, except where indicated. The Harrison collections are mostly surface finds, and the stratigraphic provenience is recorded as a fossiliferous section between two marker tuffs within the Upper Laetolil Beds (unless more precise provenience is known for *in situ* specimens). All specimens are from the Upper Laetolil Beds, except those listed as U. Ndolanya, from the Upper Ndolanya Beds

[d] Element and comments: lt, left; rt, right. Sex is determined by the size and morphology of the canines and P_3. The Museum für Naturkunde in Berlin has recently provided new accession numbers for their fossil mammal collections; the previous numbers, listed by Leakey and Delson (1987), are cross-referenced here

[e] These specimens are listed as coming from Loc. 10 (between Tuffs 5 and 8), but the fossiliferous horizons exposed at this locality are between Tuffs 1 and 3. However, abundant fossils have been recovered from between Tuffs 5 and 8 at the neighboring Loc. 10E, and it is assumed here that the fossils were derived from this locality

Table 6.3 Measurements of teeth of *Parapapio ado* from Laetoli

Tooth	Dimension	N	Mean	SD	Range
UPPERS					
I1	MD	3	7.6	0.90	6.6–8.8
	BL	2	5.9	–	5.5–6.3
	BHT	–	–	–	–
I2	MD	–	–	–	–
	BL	–	–	–	–
	BHT	–	–	–	–
C (male)	MD	7	12.9	1.18	10.7–14.6
	BL	7	9.6	0.57	8.8–10.3
	BHT	–	–	–	–
C (female)	MD	1	6.6	–	6.6
	BL	1	6.3	–	6.3
	BHT	–	–	–	–
P3	MD	7	6.1	0.35	5.6–6.5
	BL	5	7.0	0.47	6.4–7.2
	BHT	4	6.5	0.53	5.9–7.3
	LHT	4	4.8	0.34	4.3–5.2
P4	MD	12	6.9	0.38	6.1–7.5
	BL	11	8.3	0.41	7.4–8.8
	BHT	6	7.3	0.65	6.3–8.1
	LHT	5	6.4	1.00	4.7–7.6
M1	MD	9	9.4	0.67	8.1–10.2
	BLmes	7	8.6	0.53	7.7–9.6
	BLdist	7	8.4	0.62	7.4–9.6
M2	MD	15	11.2	0.81	10.1–12.3
	BLmes	13	10.6	0.90	8.9–11.8
	BLdist	13	9.9	1.04	8.5–11.6
M3	MD	9	11.2	0.70	9.6–12.0
	BLmes	8	10.6	0.87	8.6–11.6
	BLdist	9	9.1	1.09	7.5–11.2
LOWERS					
I1	MD	9	5.8	0.37	5.2–6.4
	BL	12	5.7	0.41	5.3–6.9
	BHT	6	11.5	0.74	10.8–13.0
I2	MD	6	5.4	0.50	4.7–6.2
	BL	8	5.8	0.43	5.1–6.3
	BHT	4	11.6	2.03	9.5–14.9
C (male)	MD	6	10.9	0.69	10.3–12.4
	BL	5	7.2	0.55	6.5–8.0
	BHT	2	18.2	–	17.3–19.1
C (female)	MD	5	6.8	0.84	5.5–8.1
	BL	4	4.5	0.48	3.8–5.0
	BHT	1	11.8	–	11.8
P3	MD	16	9.5	2.07	7.2–13.0
	BL	16	5.0	0.58	3.9–6.1
	BHT	12	6.4	0.59	5.6–7.1
	HHT	11	10.5	2.63	7.2–16.0
P4	MD	22	7.2	0.48	6.1–8.2
	BL	17	6.5	0.45	5.4–7.6
M1	MD	26	9.6	0.64	8.0–10.9
	BLmes	14	7.5	0.51	6.6–8.4
	BLdist	18	7.7	0.47	6.9–8.8
M2	MD	27	11.3	0.72	9.7–12.9
	BLmes	18	9.3	0.71	8.0–10.2
	BLdist	17	9.1	0.45	8.4–9.9
M3	MD	19	14.5	0.79	12.7–15.4
	BLmes	14	9.6	0.81	7.9–10.8
	BLdist	14	8.8	0.58	7.2–9.8

BHT buccal height of crown, *BL* buccolingual breadth, *BLmes* buccolingual breadth mesially, *BLdist* buccolingual breadth distally, *LHT* lingual height of crown, *HHT* length of mesiobuccal face of P_3, *MD* mesiodistal length, *N* number of specimens, *SD* standard deviation

Description of Cranio-Dental Morphology

The subnasal clivus of the premaxilla is very short (only 8.6 mm deep in LIT 59–463), and the V-shaped inferior margin on the nasal aperture penetrates between the roots of the upper central incisors in the midline. The incisive foramen is not fully preserved in any of the specimens, but it was clearly an elongated lanceolate aperture as in extant African papionins. The anterior margin of the incisive canal lies opposite the C^1-I^2 diastema. The premaxillary suture passes between the I^2 and C^1 and courses almost directly medially across the palate to terminate midway along the length of the incisive foramen. Facially, the premaxillary-maxillary suture passes very close to the lateral margin of the nasal aperture, and it almost certainly continued superiorly to make contact with the nasal bones, as in extant African papionins.

The lower face above the premolars is relatively steep, and there is no indication of a maxillary fossa or maxillary ridge. In EP 1624/00, a maxillary fragment of an infant, there are at least 3 infraorbital foramina (Fig. 6.1). There is no evidence of a maxillary sinus. The anterior root of the zygomatic arch originates relatively low on the face (~9–10 mm above the alveolar margin in EP 1508/98 and LAET 74-322) opposite mesial M^3. The palate is relatively deep. The anterior portion of the palate is narrow, producing a rather slender snout. The diastema between I^2 and C^1 is relatively large, even in female individuals (3.5 mm in LIT 59–463). Overall, the lower face appears to have been moderately long and relatively narrow.

Two frontal bone fragments of *Pp. ado* are known – LAET 75-2966 and EP 1579/98 (Fig. 6.2). The frontal squama is mediolaterally convex and domes slightly behind the shallow supraorbital sulcus. It slopes posteriorly and superiorly at an angle of 125–137° relative to the infero-superior plane of the anterior margin of the nasal process of the frontal. The temporal lines are not preserved. In EP 1579/98 there is still a vestige of the metopic suture in the midline, represented as a shallow fold, just superior to the nasal bones. The supraorbital region has a slender (only 4.1 mm thick dorsoventrally at mid-length in LAET 75-2966), non-protruding costa above each orbit. The superior border of the orbit has a distinct supraorbital notch, with a small spicule forming its lateral margin. A remnant of the naso-lacrimal duct is preserved as a shallow groove on the medial face of the orbit. Judging

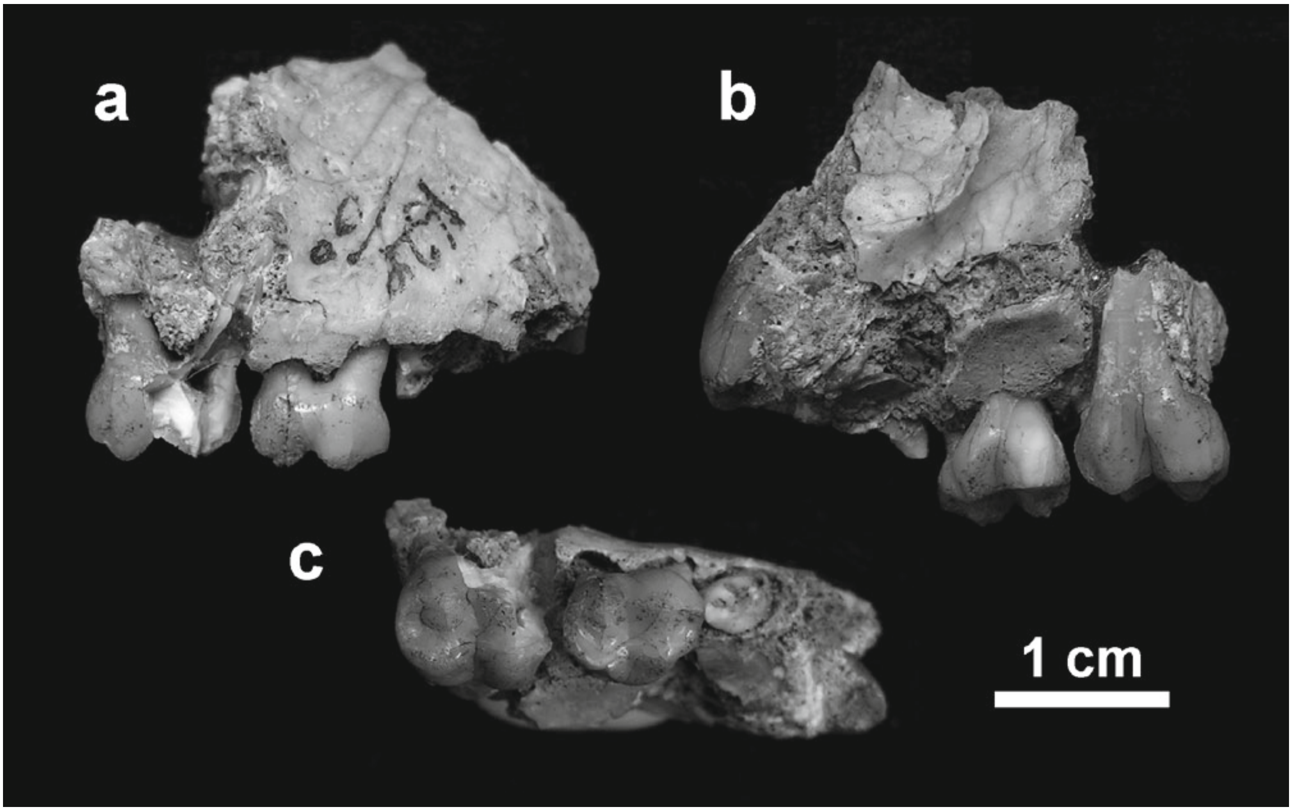

Fig. 6.1 *Parapapio ado*. EP 1624/00, right premaxilla-maxilla with dP^3-dP^4 and permanent incisors exposed in their crypts. (**a**) lateral view, (**b**) medial view, (**c**) occlusal view

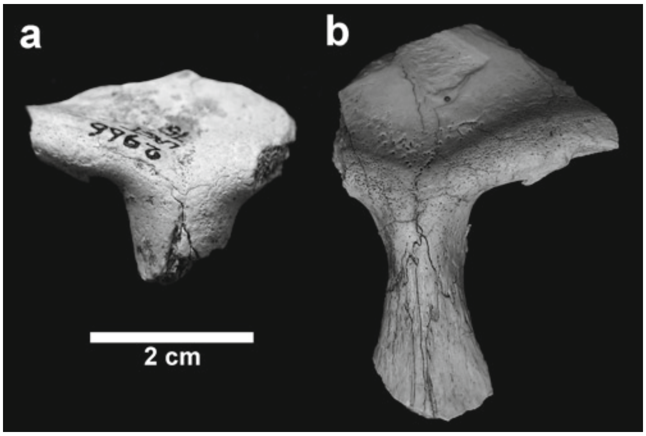

Fig. 6.2 *Parapapio ado*. (**a**) LAET 75-2966, fragment of frontal bone. Anterior view. (**b**) EP 1579/98, fragment of frontal bone, nasal bone and nasal process of maxilla

from the contour of its medial margin, the orbit was rectangular, with an angular medio-superior corner. The interorbital region is narrow (minimum breadth is 8.4 mm in EP 1779/98). In EP 1579/98 the nasal bones extend high on the face, reaching to within 3.8 mm of glabella and 5.5 mm superior to the fronto-maxillary suture. Superiorly, the nasals are very narrow in the interorbital region with a minimum breadth of only 1.5 mm. This is comparable to extant African papionins, which are characterized by long and narrow nasal bones. In lateral view, the interorbital region between glabella and the superior margin of the nasal aperture is straight or very gently concave, typical of *Parapapio*.

Some of the better-preserved mandibular specimens, including the recently recovered mandible EP 700/00 are illustrated in Figs. 6.3–6.6. The mandible has a relatively narrow symphyseal region associated with slender incisors. The incisors are set in a short arc, with the lateral incisors slightly more posteriorly placed than the central incisors. The cheek tooth rows diverge slightly posteriorly in occlusal view (5–15°, $n=3$), with gently convex lateral margins. Anteriorly, the symphysis is strongly convex infero-superiorly and medio-laterally. The contour of the external surface of the symphysis slopes posteriorly at about 50° to the occlusal surface of the cheek teeth in the superior portion, but midway down, below the canine roots, the external surface recedes more markedly posteriorly, at an angle of about 20°. Overall, the anterior face of the symphysis has a mean angulation of 36° ($n=5$, range = 29–46°). The external symphyseal region is delimited bilaterally by roughened irregular crests that originate inferiorly close to the base of the mandibular corpus below the molars, and then pass anteriorly and superiorly to terminate close to the

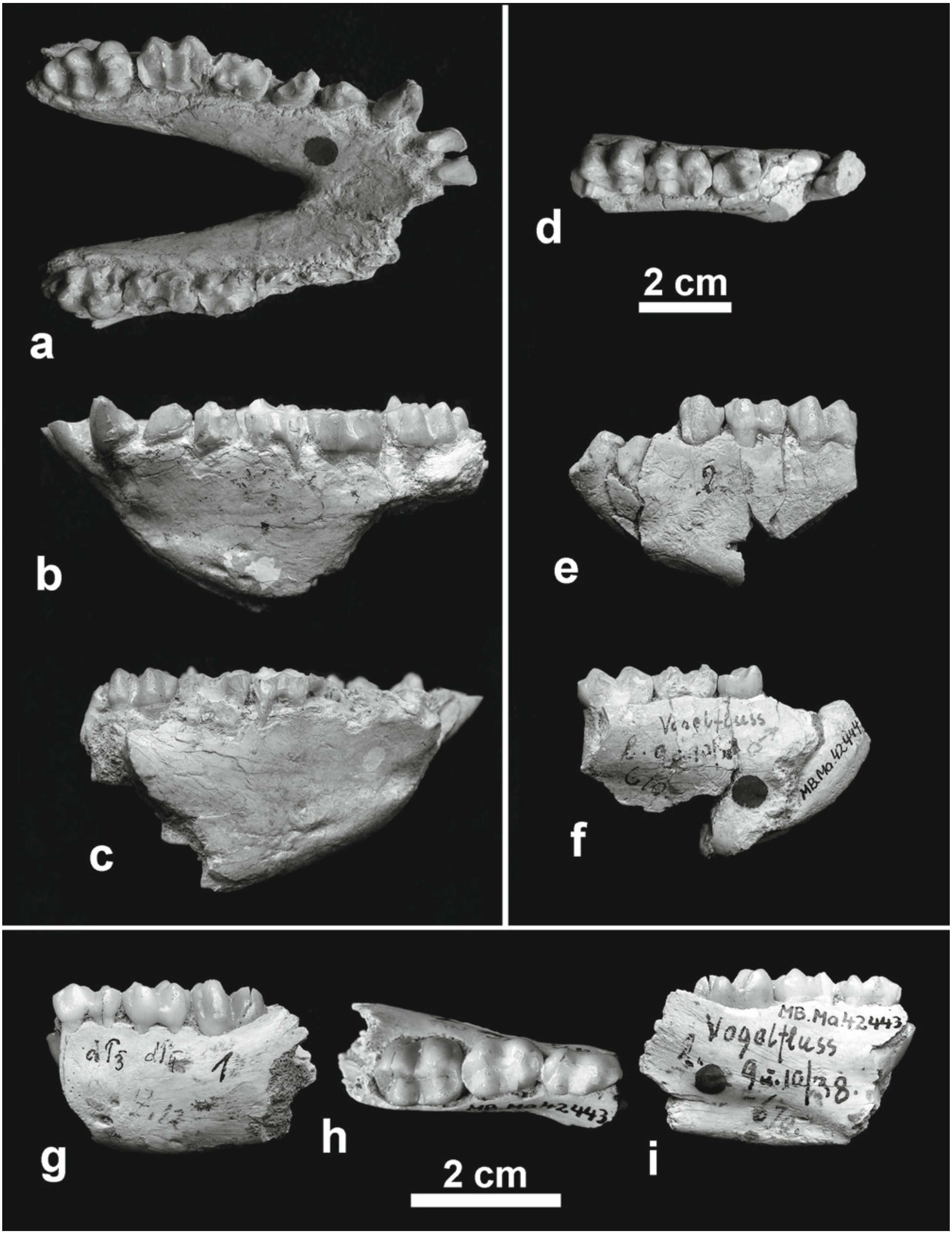

Fig. 6.3 *Parapapio ado*. Mandibular specimens from Laetoli collected by the Kohl-Larsen expedition, 1938–1939. (**a–c**) MB Ma 42441, mandible with left I_1-M_3 and right M_1-M_3. Female. (**a**) occlusal view, (**b**) left lateral view, (**c**) right lateral view. (**d–f**) MB Ma 42444, left mandibular fragment with P_4-M_2. Male. (**d**) occlusal view, (**e**) lateral view, (**f**) medial view. (**g–i**) MB Ma 42443, left mandibular fragment with dP_3-dP_4, M_1 and unerupted germs of I_2 and C. Female. (**g**) lateral view, (**h**) occlusal view, (**i**) medial view. *Top* scale bar refers to **a–f**; *bottom* scale bar refers to **g–i**

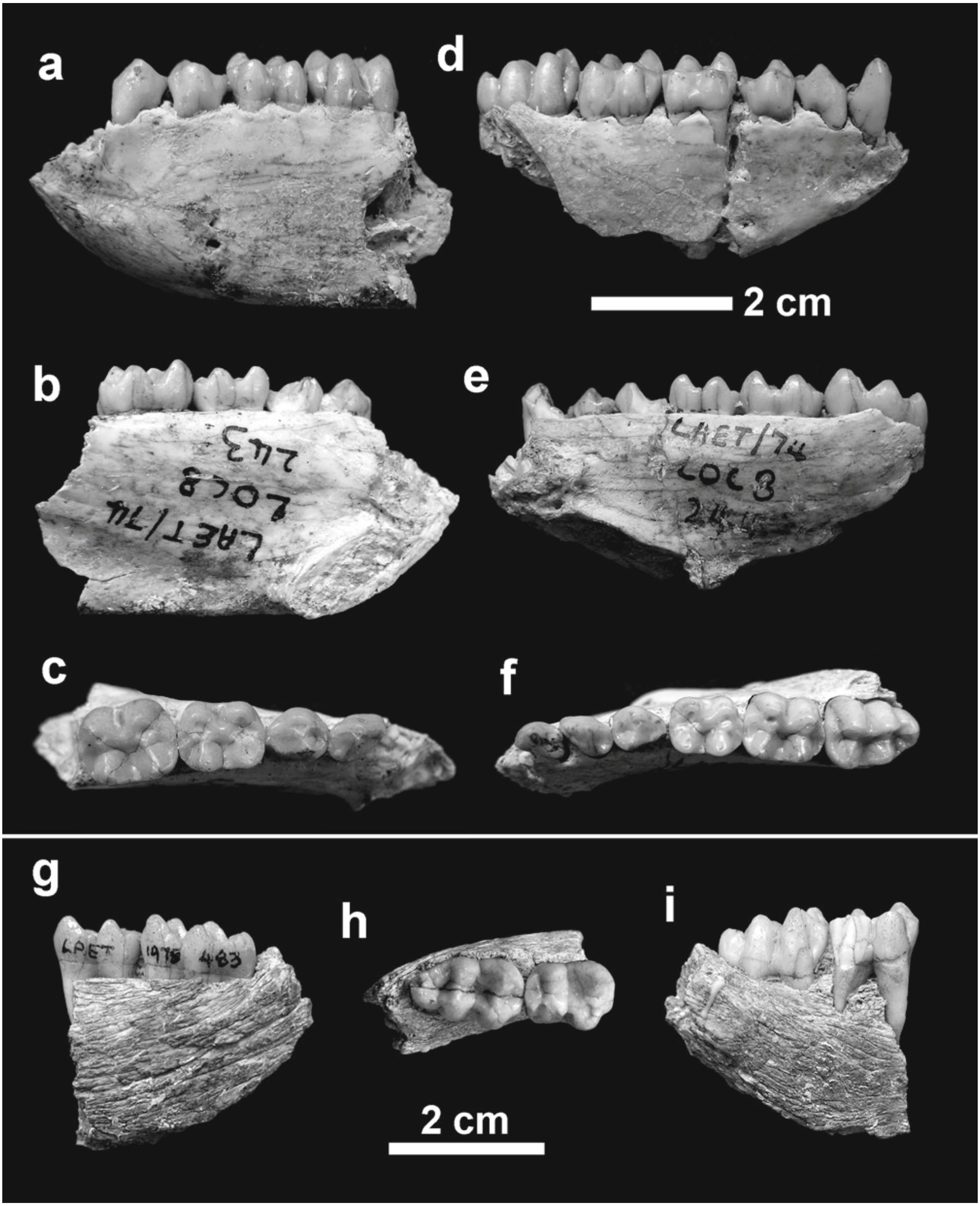

Fig. 6.4 *Parapapio ado*. Mandibular specimens from Laetoli collected by Mary Leakey expeditions, 1974–1979. (**a**–**c**) LAET 74-243, left mandibular fragment with P_3-M_2. Female. (**a**) lateral view, (**b**) medial view, (**c**) occlusal view. (**d**–**f**) LAET 74-244, right mandibular fragment with C-M_3 (associated with LAET 74-243). (**d**) lateral view, (**e**) medial view, (**f**) occlusal view. (**g**–**i**) LAET 75-483, right mandibular fragment with M_2-M_3. (**g**) medial view, (**h**) occlusal view, (**i**) lateral view. *Top* scale bar refers to (**a–f**); *bottom* scale bar refers to (**g–i**)

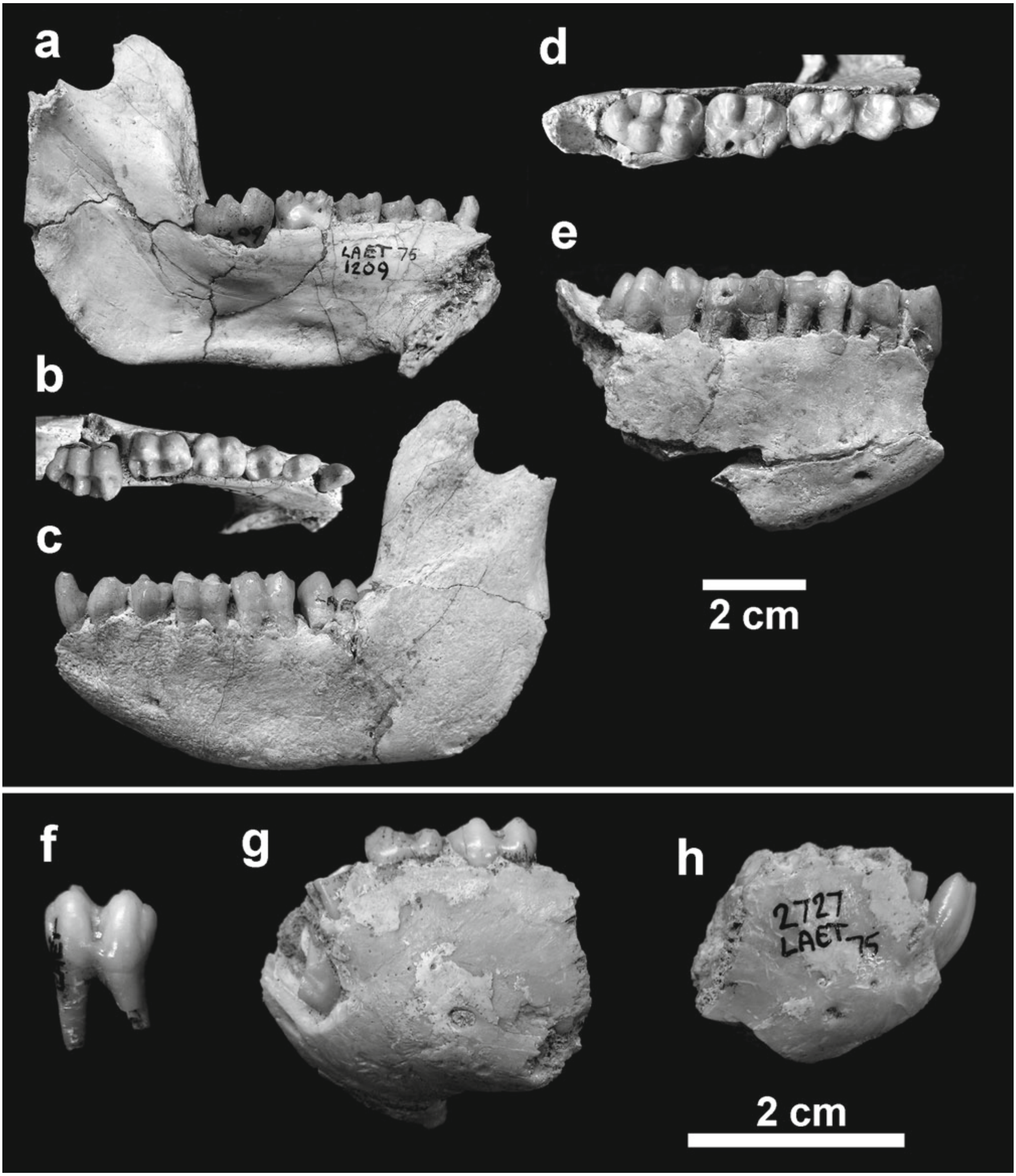

Fig. 6.5 *Parapapio ado*. Mandibular specimens from Laetoli collected by Mary Leakey expeditions, 1974–1979. (**a**–**c**) LAET 75-1209, left mandibular corpus and ramus with C-M_3. (**a**) medial view, (**b**) occlusal view, (**c**) lateral view. (**d**, **e**) LAET 77-4595, right mandibular fragment with P_3-M_3. (**d**) occlusal view, (**e**) lateral view. (**f**–**h**) LAET 75-2727. (**f**) left M_1, buccal view, (**g**) left mandibular corpus with left dP_3-dP_4, lateral view; (**h**) right mandibular corpus with I_1-I_2 germs exposed in their crypts, lateral view

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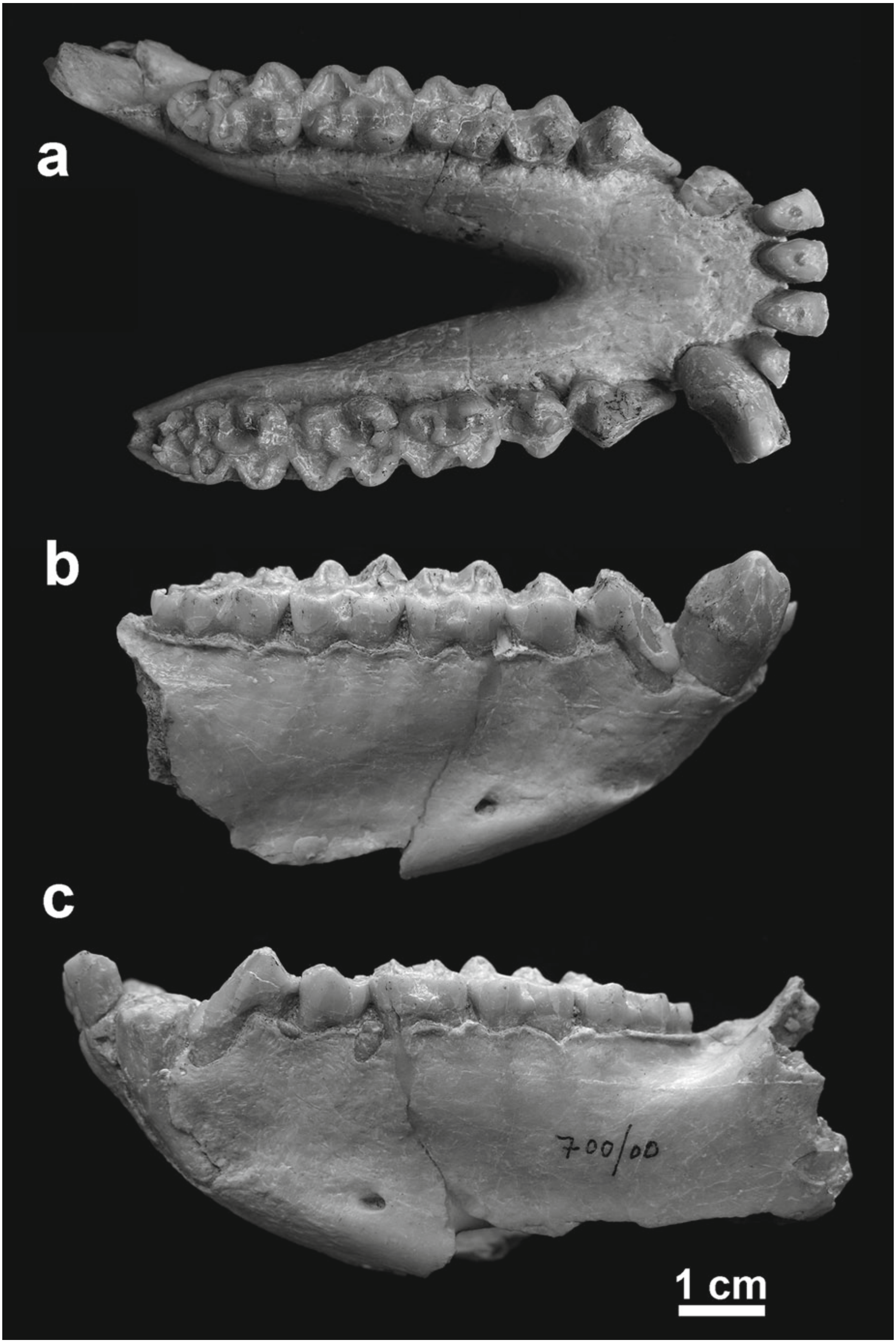
Fig. 6.6 *Parapapio ado*. EP 700/00, mandible with right I_1-M_3 and left I_1-I_2, P_3-M_3, root of C_1. Male. (**a**) occlusal view, (**b**) right lateral view, (**c**) left lateral view


a
b
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alveolar margin of the central incisors. These crests define a roughened triangular subcutaneous area on the front of the chin. About one-third down from the alveolar margin, the symphysis is perforated by an elliptical foramen, the median mental foramen, which exits internally at the genioglossal pit. Inferiorly, the symphysis extends posteriorly to below P_4/M_1 or the mesial aspect of M_1, where it terminates at a sharp margin.

The internal symphyseal contour is preserved in MB Ma 42441 and in EP 700/00. There is a well-developed superior transverse torus that extends posteriorly as far as mesial P_4. The subincisive planum is slightly concave and slopes posteriorly at an angle of 25° relative to the occlusal plane of the cheek teeth. The superior transverse torus forms a smoothly rounded buttress. The inferior transverse torus or simian shelf extends back as far as mesial M_1, and it is thicker and more shelf-like than the superior transverse torus. Between the two tori there is a deep depression forming the genioglossal pit. Along the superior margin of the genioglossal pit is the paired opening for the median mental foramen. On the inferior margin of the simian shelf is a shallow elliptical depression on either side of the midline that represents the sites of attachment for the anterior bellies of the digastric muscles. Inferiorly, the symphyseal margin forms a sharp crest.

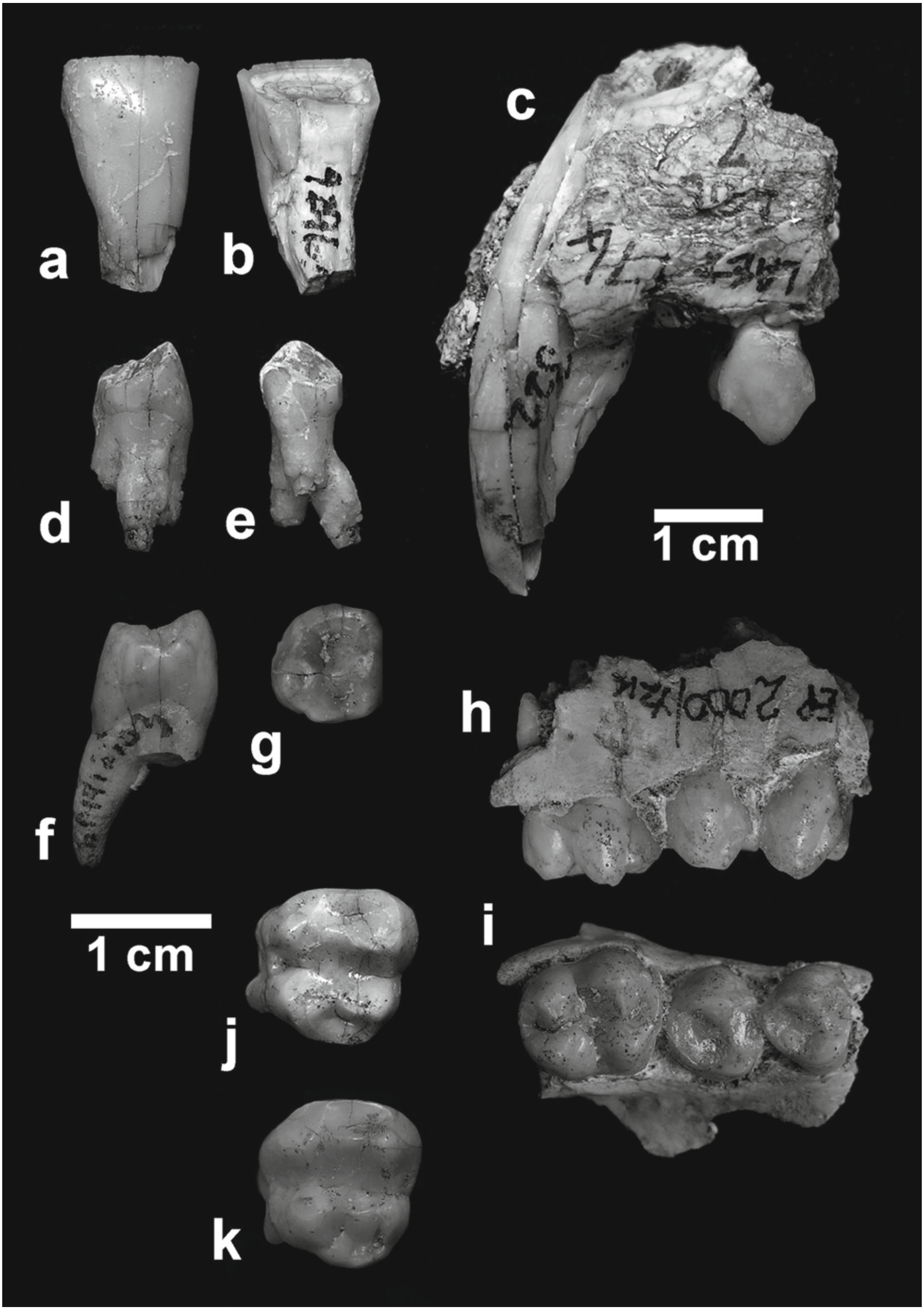
The mandibular corpus is moderately robust and quite shallow (the mean breadth-height index of the corpus at M_2 is 42.4, $n=4$). It maintains a relatively constant depth below the molars or deepens slightly posteriorly. The lateral surface of the corpus below the premolars and M_1 is slightly concave to almost flat, and there is little or no development of a mandibular fossa. Otherwise, the lateral face of the corpus is slightly convex supero-inferiorly, except for a shallow concavity that runs along the inferior border of the corpus below the molars. A well-defined, roughened depression (~12 × 8 mm) is situated midway down the lateral face of the mandible below the mesial aspect of P_3. It is bordered inferiorly by the rugose subcutaneous surface of the symphysis and superiorly by a rounded eminence. A similar feature is observed in male individuals of *Cercocebus*, but its function is unknown. The number of mental foramina ranges from 1 to 3, but a single foramen is most common (45.5%, $n=11$). The main mental foramen is situated relatively low on the mandible, about two-thirds down from the alveolar margin (mean = 66.6%, range = 62.2–71.5%, $n=10$), located below the P_4-M_1. The elliptical or triangular foramen is relatively large, up to 2.7 mm in diameter, and faces antero-laterally. The medial aspect of the corpus, like the lateral face, is convex in the alveolar region, but has a shallow convexity just superior to the inferior margin. This produces a flange-like inferior margin to the corpus in the region below the molars.

The ramus is best preserved in LAET 75-1209 (a subadult female), being complete except for the condyle (see Fig. 6.5). The root of the ramus originates opposite M_3, with little or no overlap with M_3 when seen in lateral view. The anterior margin of the ramus ascends steeply behind M_3, with a slope of 10° from the vertical. In most other papionins, there is a more pronounced posterior tilt (but this may simply reflect the relatively short face and subadult status of LAET 75-1209). The coronoid process is high and posteriorly curved. It is separated from the condylar process by a narrow, U-shaped mandibular incisure. The gonial region is rounded and well filled out. The lateral face of the ramus is convex inferiorly, but concave superiorly. Midway up the ramus is a rough oblique line that represents the site of insertion of the masseter muscle. Medially, the surface is generally concave, except for a low rounded buttress at the base of the condylar process. A distinct groove, the mylohyoid line, originates below the posterior root of M_3, midway down the corpus, and passes obliquely superiorly and posteriorly to end just inferior to the mandibular foramen. Although the condyle is not preserved, it can be estimated to have been located at a level slightly below the tip of the coronoid process, typical of papionins.

I^1 is a moderately high-crowned, relatively narrow and spatulate tooth (Fig. 6.7a–b). The lingual face is V-shaped, strongly concave with raised mesial and distal margins, which give it a slightly shoveled appearance. The lingual surface has a very thin coating of enamel. The buccal face is quite strongly convex mesiodistally and apico-basally. The root is short and robust, and slightly lingually recurved. The mean mesiodistal length of I^1 is 23.9% of the combined mean mesiodistal lengths of the lower molar series, which indicates relatively broad upper incisors. No examples of I^2 are known.

The upper canines are strongly sexually dimorphic. Males have canines that have tall, distally recurved and bilaterally compressed crowns, while females have much smaller, lower-crowned and less compressed canines (Fig. 6.7c). In males, the crown has a triangular cross-section at the base. The rounded mesial ridge is bordered lingually by a relatively deep mesial groove that reaches almost to the apex of the crown and continues basally onto the root. The mesial groove is bordered distally by a robust lingual pillar. The distolingual face of the crown is convex, and terminates at a sharp distal ridge. There is a faint trace of a cingulum around the base of the lingual face. The buccal face is smoothly convex mesiodistally and featureless, except for a faint apico-basal groove that continues onto the root.

Fig. 6.7 *Parapapio ado*. Upper dentition. (**a–b**) EP 929/01, Right I^1. (**a**) buccal view, (**b**) lingual view. (**c**) LAET 74-322, Left maxilla with C and P^4. Male. (**d–e**) EP 597/05, left P^3. (**d**) distal view, (**e**) lingual view. (**f**, **g**) EP 1412/03, right P^4. (**f**) mesial view, (**g**) occlusal view. (**h–i**) EP 2000/00, right maxilla with P^3–M^1. (**h**) buccal view, (**i**) occlusal view. (**j**) EP 712/03, left M^2, occlusal view. (**k**) EP 928/01, left M^3, occlusal view. *Top* scale bar refers to **c** only; *bottom* scale bar refers to all other specimens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The upper canines of females are low-crowned, only slightly distally recurved and rhomboidal in cross-section. The mesial ridge is short, and terminates basally at a narrow, but distinct lingual cingulum. Lingually, there is a very shallow mesial groove and a robust and rounded lingual pillar. The distal ridge is sharp, and slightly longer than the mesial ridge.

P^3 is broader than long, triangular in outline, and narrows lingually (see Fig. 6.7). The protocone is less elevated than the paracone and more conical in shape. A sharp transverse crest originates from the apex of the paracone, and passes lingually or slightly mesially to terminate at the base of the protocone. The pre- and postparacrista are long and sharp, and are aligned mesiodistally. The pre- and postprotocrista both curve buccally to become continuous with the mesial and distal marginal crest respectively. The mesial fovea is well-defined, and forms a small triangular basin. The distal fovea is much more capacious, being at least twice the area of the mesial fovea. The buccal aspect of the crown is convex and featureless. The enamel junction extends higher on the mesiobuccal root than the distobuccal root, especially in males.

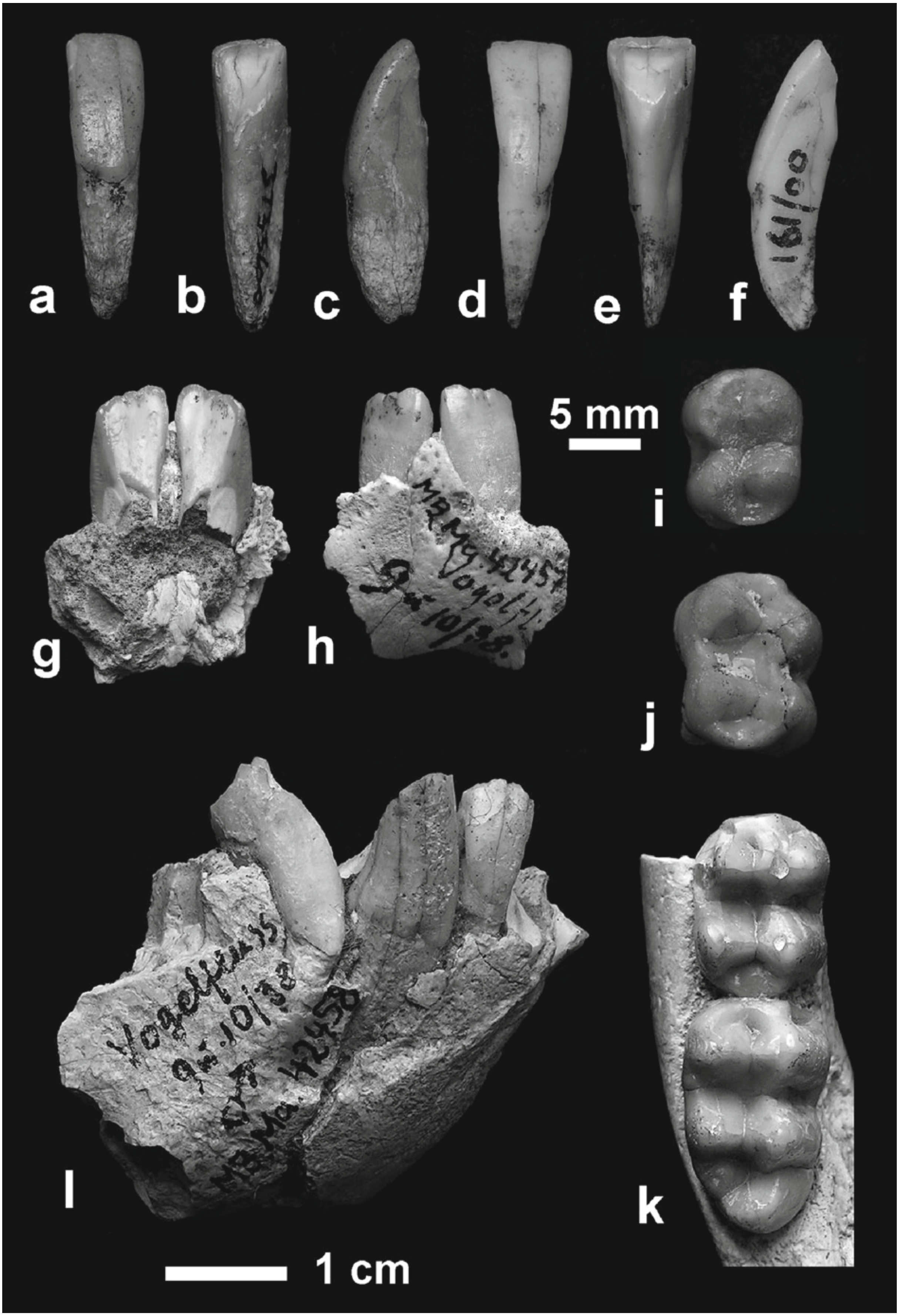
P^4 is larger than P^3, more ovoid in occlusal outline, and the two cusps are more similar in height (although the protocone is still somewhat lower than the paracone) (see Fig. 6.7). The mesial fovea is a well-defined D-shaped basin, about half the size of the distal basin. The two main cusps are joined by a transverse crest similar in development to that of the P^3. Both upper premolars have three roots that are closely appressed and fused at their base.

M^1 is longer than broad and subrectangular in outline, with slight distal narrowing and buccolingual waisting midway along its length (Fig. 6.7). The mean length-breadth index is 109.3. The degree of buccolingual flare is slight to moderate. The four main cusps are subequal in height, relatively low and voluminous. The protocone and hypocone are conical, and the paracone and metacone are pyramidal. The preprotocrista is short and terminates at the mesial marginal ridge at a protuberant beak. The postprotocrista joins the prehypocrista to form the lingual marginal ridge. The mesial lingual cleft is represented by a shallow groove. The posthypocrista curves distally and buccally to become continuous with the low distal marginal crest, and occasionally bears a small subsidiary tubercle. The preparacrista is short and ill-defined. It terminates mesially as a distinct tubercle. The postparacrista is better developed. The mesial fovea is restricted to a short crescentic groove, bordered by a well-developed mesial marginal ridge. The paraloph is well developed, but disrupted midway along its length by a groove connecting the mesial fovea and trigon basin. The metacone is slightly smaller than or subequal in size to the paracone, generally being the smallest of the main cusps. The premetacrista is shorter and less well-developed than the postparacrista. The two crests may occasionally meet at a small tubercle. A low rounded postmetacrista passes distally to meet the marginal ridge. The distal fovea is similar in size to the mesial fovea, forming a C-shaped basin around the base of the metacone. The metaloph is less well-developed than the paraloph, and is disrupted by a deep longitudinal fissure linking the trigon basin to the distal fovea. The hypocone is slightly more mesially placed than the metacone, so the metaloph is slightly obliquely oriented relative to the transverse axis of the crown. The trigon basin is almost square. It is bisected transversely by a deep groove that crosses from the median lingual cleft to the median buccal cleft. Midway along the transverse fissure is a longitudinal fissure that passes mesially into the mesial fovea and distally in the distal fovea. The buccal notch is relatively shallow.

M^2 is similar in morphology to M^1, except that it is larger and relatively longer (the mean length-breadth index is 118.7) (Fig. 6.7). M^3 is subequal in size to M^2, but differs in narrowing more strongly distally, and in having smaller distal cusps that are more closely associated, a reduced distal fovea, and a more crenulated distal margin (Fig. 6.7). The size ratio of the upper molars (mean areas of M^1:M^2:M^3) is 68:100:100.

The lower incisors are high-crowned and slender, with a narrow incisive apex (Fig. 6.8a–f). The buccal face has a thick covering of enamel, and is slightly mediolaterally convex and more strongly apico-basally convex. The lingual face has a very thin covering of enamel, as is typical of papionins (see Aimi and Nogami 1989), but this is rapidly lost through wear to expose the underlying dentine The crown of I$_1$ is mesiodistally bilaterally relatively symmetrical, although the distal margin is slightly steeper than the mesial margin. The mean mesiodistal length of I$_1$ is 16.4% of the combined mesiodistal lengths of the lower molar series, indicating relatively large incisors. The lingual aspect is mesiodistally slightly concave, and narrows basally to form a V-shaped lingual face. The crown is almost twice as high on the buccal face compared with the lingual face. Apical wear cuts down obliquely onto the lingual face to maintain a relatively sharp incisive cutting edge. The root is very short in relation to the height of the crown. Together the crown and root are strongly lingually recurved, with a marked apico-basal concavity of the lingual aspect. The crown of I$_2$ is less symmetrical than I$_1$, with a shorter distal margin lingually and a more mesiodistally convex buccal face.

Fig. 6.8 *Parapapio ado*. Lower dentition. (**a–c**) EP 3733/00, left I$_1$. (**a**) buccal view, (**b**) lingual view, (**c**) distal view. (**d–f**) EP 161/00, left I$_1$. (**d**) buccal view, (**e**) lingual view, (**f**) distal view. (**g, h**) MB Ma 42457, fragment of symphysis with germs of right and left I$_1$. Note the lack of enamel on the lingual surface of the incisors. (**g**) lingual view, (**h**) buccal view. (**i**) EP 899/03 left M$_1$, occlusal view. (**j**) EP 1371/00, right M$_2$, occlusal view. (**k**) MB Ma 42445, right mandibular fragment with M$_2$-M$_3$, occlusal view. (**l**) MB Ma 42458, symphyseal fragment with right I$_2$-P$_3$. Male. *Top* scale bar refers to (**a–k**); *bottom* scale bar refers to (**l**) only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The lower canine exhibits a high degree of sexual dimorphism, with males having much larger and higher crowned canines than in females. In females the crown is slightly distally recurved. The relatively short mesial crest terminates mesially at a narrow lingual cingulum. The distal crest is long and steeply inclined, and terminates basally at a small distobuccal tubercle. A low and narrow distal marginal ridge links the distobuccal crest to the lingual cingulum. The canine in male individuals is tall and slender, quite strongly bilaterally compressed, and distally recurved, with a slight apicobasal sinusoidal curvature of the crown when viewed from the mesial aspect. The mesial crest is relatively long and terminates basally at a narrow irregular lingual cingulum. The cingulum borders the base of the lingual face. The mesial crest is bordered lingually by a shallow mesial groove that interrupts the lingual cingulum. The distal heel of the canine is relatively short. The distal marginal ridge is low and terminates at a distobuccal tubercle. The buccal face of the crown is smoothly convex and featureless. The robust root is distally and buccally recurved, with a shallow mesial groove.

Like the canines, P_3 is strongly sexually dimorphic, in which male individuals have larger, more elongated crowns with extended mesiobuccal honing faces for occlusion with the upper canines. The female morph is quite short and relatively narrow, with only a slight degree of extension of the crown mesiobuccally. The long-axis of the crown is obliquely oriented relative to the C-P_4 midline (mean = 25°, range = 16–34°, $n = 9$). The crown has a single main cusp, the protoconid. The mesial crest is sharp and terminates at the lingual cingulum, sometimes at a distinct tubercle. The lingual cingulum encompasses the mesial portion of the lingual face only. The distal crest is also sharp, and descends steeply to become continuous with the distal marginal ridge. The latter curves lingually to terminate at a low rounded tubercle. The distal fovea forms a shallow elliptical basin. The lingual crest passes lingually and slightly distally. Midway along its length there is a low swelling that represents a vestigial metaconid.

P_4 is oval in occlusal outline, with a long axis that is slightly obliquely oriented to the long-axis of the cheek tooth row. It is a bicuspid tooth, with a conical protoconid and a pyramidal metaconid, which are subequal in height. The metaconid is positioned slightly more mesially than the protoconid. The cusps are linked by a high and sharp transverse crest, which like the protolophid in the molars, is oriented slightly oblique to the transverse axis of the crown. The mesiobuccal face of the crown extends more inferiorly than the distobuccal face, especially in male individuals. The preprotocristid and premetacristid are short and continuous with the mesial marginal ridge. These crests enclose a small pit-like mesial fovea. The postprotocristid arcs distolingually to join the distal marginal ridge. Lingually the distal marginal ridge terminates at a low rounded tubercle. The postmetacristid is separated from the latter by a fissure. The distal fovea forms a relatively deep and subcircular depression, which is much larger than the mesial fovea.

M_1 is long and narrow, and subrectangular in shape, with a slight degree of buccolingual waisting (Fig. 6.8). The crown tends to narrow slightly mesially, and exhibits moderate buccolingual flare. The mean breadth-length index is 80.2. The four main cusps are moderately tall and voluminous. The two buccal cusps, the protoconid and hypoconid, are conical, while the lingual cusps, the metaconid and entoconid, are more pyramidal in shape. In the unworn state the buccal cusps are only slightly less elevated than the lingual cusps, but this differential increases with wear. The protoconid and hypoconid are subequal in size. They are connected by a rounded longitudinal crest, composed of the postprotocristid and the prehypocristid, which bows lingually towards the talonid basin. The preprotocristid is relatively short, and passes mesiolingually to join the mesial marginal ridge at a small rounded protuberance, the protostylid, which forms the mesial point of the crown. On the mesiobuccal face of the protoconid there is a shallow groove, the mesial buccal cleft, which runs from the preprotocristid basally to terminate about two-thirds down the buccal face of the crown. The cleft serves to demarcate the protostylid from the protoconid, giving the former a beak-like configuration. The premetacristid arcs mesially and buccally to become continuous with the raised mesial marginal ridge. The premetacristid, preprotocristid, mesial marginal ridge and protolophid delimit a shallow D-shaped trigonid basin. The floor of the fovea has a Y-shaped fissure, of which the distal arm divides the paraprotocristid and the parametacristid portions of the protolophid. On the buccal side of the postprotocristid-prehypocristid is a U-shaped and receding platform, the median buccal cleft, separating the protoconid from the hypoconid. The buccal cleft generally has a flattened base, but sometimes it simply forms a shallow groove, and occasionally there are low, rounded secondary tubercles. The protolophid is slightly obliquely directed (~15°) relative to the transverse axis of the crown because the metaconid is placed more mesially than the protoconid. The distobuccal margin of the crown has a shallow distal buccal cleft. The posthypocristid arcs distally and lingually to become continuous with the low and ill-defined distal marginal ridge. The distal fovea is V-shaped, poorly delimited distally, with a Y-shaped fissure pattern that diverges distally. The distal fovea is slightly smaller than the trigonid basin. The metaconid and entoconid are subequal in height. The postmetacristid is ill-defined, and is formed by the angular distolingual margin of the metaconid. The same is true of the pre-entocristid and postentocristid on the entoconid. At the base of the postmetacristid there is occasionally a small mesostylid. The postmetacristid and pre-entocristid converge basally to form a shallow lingual notch that ends about 40% down the lingual face of the crown. The angle formed by the lingual notch is 65–75°. The hypolophid is more or less transversely aligned or only slightly oblique to the transverse axis of the crown. The talonid basin is relatively shallow. It is trapezoidal in shape, with a shorter buccal margin in relation to the lingual margin, because of the obliquity of the protolophid. The basin is transected by a Y-shaped groove system, in which the mesial and distal arms cross the lophids, and the lingual arm passes to the lingual notch, where it deviates around the mesostylid when present.

M_2 is identical in overall morphology to M_1, but differs in being much larger in size, and in having a relatively broader crown that tends to narrow less markedly mesially, with a narrower median buccal cleft, and, when present, a better developed mesostylid (Fig. 6.8). The mean breadth-length index is 82.3.

M_3 is broader and much longer than M_2, with a moderately long talonid that bears a well-developed hypoconulid (Fig. 6.8). The mean breadth-length index is 66.2. The portion of the talonid that extends distally beyond the distal buccal cleft averages 26% of the total crown length. The construction of the mesial portion of the crown is similar to that described above for M_1 and M_2. The median buccal cleft is generally restricted to a shallow groove or a narrow U-shaped gully. The mesostylid is weakly to moderately expressed. At the level of the hypolophid the crown narrows distally, so that, compared with M_2, the tips of the hypoconid and entoconid are situated closer together than the protoconid and metaconid. In addition, the distal pair of cusps is relatively reduced in size. The hypoconulid is a low pyramidal cusp situated on the distal margin of the crown. Its apex is positioned slightly buccally to the midline of the crown, but lingual to the line transecting the apices of the protoconid and hypoconid. The distal fovea is a large triangular basin, with a raised distal marginal ridge that occasional bears a distinct tuberculum sextum. The hypoconid and hypoconulid are separated buccally by a sharp groove that continues lingually into the distal fovea. The distal root of M_3 is typically trilobed, whereas in M_1 and M_2 it is bilobed. The lower molars exhibit a moderate degree of size differential between serial teeth, with a progressive increase in size from M_1 to M_3. The ratio of molar size (mean areas of M_1:M_2:M_3) is 70:100:132.

Comparisons

The mandible of *Pp. ado* differs from extant papionins in having well-developed symphyseal tori that extend further posteriorly and a more superiorly placed mental foramen (67% down from the alveolar margin, compared with mean values of 76% in *Lophocebus* and *Macaca*, 82% in *Papio*, and 88% in *Theropithecus*). In addition, it differs from *Papio* and *Mandrillus* in that the corpus does not shallow posteriorly, the intercanine distance is greater in males due to the relatively smaller canine roots, the cheek tooth rows diverge slightly posterior rather than being sub-parallel, the symphysis is more strongly inclined (50° compared with 68° in *Papio*), with a long subincisive planum and a more strongly developed inferior transverse torus (similar in *Mandrillus*), it lacks a lateral mandibular fossa, the ramus is taller and more vertical (with a posterior tilt from the vertical of only 10° versus 15–25° in *Papio* and *Mandrillus*), with a mesiodistally shorter intercondylar notch, and it lacks a distinct retromolar space posterior to M_3. These differences relate to the larger canines, the well-developed mandibular corpus fossae and the longer face in *Papio* and *Mandrillus*. In most of these respects *Pp. ado* is more similar to the medium-sized, shorter-faced papionins, such as *Macaca*, *Lophocebus* and *Cercocebus*. It differs from *Macaca nemestrina* in having more posteriorly diverging tooth rows in males, more pronounced symphyseal rugosity on the external surface of the symphysis, a more inferiorly placed mental foramen (76% in *Macaca*), a slightly less receding anterior symphyseal face (55° in *Macaca*), and a corpus that does not shallow posteriorly. In addition to the greater robusticity of the symphyseal region in *Pp. ado*, *Lophocebus* differs mainly in having a well-developed mandibular fossa, a more inferiorly placed mental foramen, and a more slender corpus. In the development of the mandibular corpus fossa, *Pp. ado* is more similar to *Cercocebus*, which has a shallow, indistinct depression in males and none in females.

The frontal of *Pp. ado* resembles the general morphology seen in extant papionins. It is similar in having a low, slightly domed frontal squama, slender supraorbital costae, a shallow supraorbital sulcus, a distinct supraorbital notch, a narrow interorbital region, a lacrimal duct located entirely within the lacrimal bone inside the orbit, an angular contour to the medio-superior aspect of the orbital outline, and mediolaterally slender nasal bones that extend superiorly past the fronto-maxillary suture and reaching almost to glabella. It differs from *Papio* in having more slender supraorbital costae, lacking an anteorbital drop and marked dorsoventral concavity along the midline of the nasals between glabella and nasion, and appears to have had relatively infero-superiorly taller orbits. It differs from *Mandrillus* in having a slightly narrower interorbital region and narrower nasal bones, lacking the anteorbital drop, midline glabella-nasion concavity, and strongly developed mediolateral doming of the nasals. *Parapapio ado* differs from *Macaca nemestrina* in having more slender and better-defined supraorbital costae, less pronounced supraorbital notch, broader interorbital region, and nasal bones that extend further superiorly. *Lophocebus* and *Cercocebus* differ in having more slender and less well-developed supraorbital costae, lack of a supraorbital sulcus, a weaker supraorbital notch, a narrower interorbital region, and nasal bones that extend only a short distance beyond the fronto-maxillary suture, and terminates well short of glabella (only *Lophocebus*).

The maxillary fragments of *Pp. ado* are too fragmentary to establish definitively that it lacked a facial fossa, but the available evidence certainly suggests that this was indeed the case. Relatively well-developed facial fossae are present in both sexes of *Papio* and *Lophocebus*, they are shallower in

Mandrillus and *Cercocebus*, and absent in *Macaca*. The anterior root of the zygomatic arch originates low on the face in *Pp. ado*, as in *Macaca*, *Cercocebus* and *Lophocebus*, whereas in the long-faced papionins, such as *Papio* and *Mandrillus*, it is much higher. The palate appears to have been relatively shallow in *Pp. ado* compared with all extant papionins.

The mean mesiodistal lengths of the upper and lower central incisor in relation to the mean mesiodistal lengths of the corresponding molar series combined is 23.9% and 16.4% respectively in *Pp. ado*. These values fall outside the range of most extant papionins (mean values for *Papio*, *Lophocebus*, *Cercocebus* and *Macaca* range from 28.2–38.0% for uppers and 18.2–25.4% for lowers), indicating that *Pp. ado* had relatively narrow incisors, similar to *Theropithecus gelada*. The upper central incisor in *Pp. ado* differs from that in *Papio* in being smaller, relatively narrower and with thicker enamel on the lingual surface of the crown. It differs from that in *Lophocebus* in not being as markedly mesiodistally convex buccally and being strongly shoveled lingually. The lower incisors of *Pp. ado* differ from the specialized condition in *Lophocebus* and *Cercocebus* in which the lateral incisors are much smaller than the central incisors. The index of mesiodistal length of $I_2 \times 100$/mesiodistal length of I_1 is 93.1 in *Pp. ado*, being similar to *Papio* (93.5) and *Macaca* (87.4), but distinct from *Cercocebus* (83.2) and *Lophocebus* (82.1), which have relatively smaller lateral incisors.

The upper canine in male individuals of *Pp. ado* is similar in form to that of *Papio*, *Mandrillus* and *Macaca*, but is mesiodistally relatively shorter, with a much shallower mesial groove. It differs from that in *Cercocebus* and *Lophocebus* in having a more robust and relatively mesiodistally longer crown. Similarly, the lower canines of males are relatively mesiodistally shorter than in *Papio*, *Mandrillus*, and *Macaca*. Upper and lower canines in females are similar in overall morphology to those of extant papionins. An important difference that distinguishes the canines of *Pp. ado* from extant papionins is the relatively high level of sexual dimorphism, especially compared to *Lophocebus* and *Cercocebus*. Lower canine mesiodistal length in females expressed as a percentage of male lower canine mesiodistal length gives an index of 62.4, compared with *Macaca* (64.2), *Papio* (68.6), *Cercocebus* (80.4) and *Lophocebus* (80.4). The sample of female upper canines is too small to calculate this index, but a similar relationship appears to hold for the upper canines.

P_3 in male individuals of *Pp. ado* has a much shorter mesiobuccal honing face than in all extant papionins, with the exception of *Lophocebus*. The breadth-length index in male *Pp. ado* has a mean value of only 49.1, compared with *Macaca* (36.7), *Papio* (38.0), and *Cercocebus* (38.0). The P_3 in *Lophocebus* is relatively much shorter, with an index of 63.5. Similarly, P_3 in female individuals of *Pp. ado* has a broader and shorter crown than in extant papionins. The upper premolars of *Pp. ado* are similar in morphology to those of extant papionins. Gilbert (2007) has shown that relative P4 size distinguishes major clades of extant papionins, with *Cercocebus* and *Mandrillus* having relatively larger premolars. The P4/M1 index (area) in *Pp. ado* is 70.9 for uppers and 63.3 for lowers, close to the mean values of *Macaca* (and probably close to the primitive condition), and intermediate between *Cercocebus*-*Mandrillus* and *Lophocebus*-*Papio*-*Theropithecus*.

The upper and lower molars of *Parapapio* have been described as being morphologically very similar to those of *Papio* and other extant papionins (Freedman 1957; Szalay and Delson 1979; Leakey and Delson 1987; Frost and Delson 2002), and, although they share a similar basic configuration, there are key differences that distinguish *Parapapio ado* from extant papionins. The upper and lower molars of *Pp. ado* are distinguished from all extant papionins by their taller cusps and generally more marked degree of buccolingual flare. The lower molars of *Papio* are larger in overall size, with more elongated crowns, deeper and better-defined foveae and clefts, relatively longer trigonid basin and distal fovea, more prominent mesostylids, a more pronounced size differential between the molars, M_3 narrows more strongly distally, and a better-developed hypoconulid, with the cusp apex positioned closer to the midline of the crown (rather than buccally displaced). Those of *Mandrillus* are slightly narrower, with better-developed clefts, more pronounced size differential between M_1 and M_2, and M_3 with smaller hypoconulid lobe and cusp apex positioned in the midline of the crown. *Macaca* has slightly narrower lower molars with shallower lingual notches, and a smaller hypoconulid lobe on M_3, but is otherwise quite similar. *Lophocebus* differs from *Parapapio* in having slightly narrower crowns, much lower and more rounded and voluminous cusps, weaker lophids, a shallower lingual notch, narrower mesial fovea, shorter and ill-defined talonid basin and distal fovea, lack of mesostylids, size differential between the molars less pronounced, M_3 relatively small in size with a reduced hypoconulid lobe in the midline of the crown. In *Cercocebus*, the lower molars differ in being relatively broader, with lower, more rounded and voluminous cusps, weaker lophids, a low lingual notch and slightly greater buccolingual flare, and M_3 is relatively smaller, with a reduced hypoconulid lobe.

The upper molars of *Papio* differ from *Pp. ado* in being relatively more elongated and lack the distal narrowing in M^1 and M^2. They also differ in having better-developed clefts along the lingual margin, less buccolingual flare and more elevated cusps. M^3 is relatively larger, and does not exhibit the same degree of reduction of the distal moiety. The upper molars of *Lophocebus* are much smaller and relatively broader, with lower cusps and greater buccolingual flare, but they have the same distal narrowing of the M^1 and M^2, and distal reduction of M^3. Compared with extant *Cercocebus*, *Lophocebus* and most species of *Macaca*, *Pp. ado* can be distinguished by the marked size differential between M1 and M2, a relatively large M^3 that is subequal in size to M^2, and an M_3 that is greater than 130% of the area of M_2. In these respects, the proportions of the molars are most similar to those seen in *Papio* and *Theropithecus*.

As noted by previous authors (Szalay and Delson 1979; Frost and Delson 2002), and highlighted in the diagnosis of the genus, *Parapapio* constitutes a cluster of primitive papionins that are distinguished by the lack of derived cranial features characteristic of other papionins. The face and mandible of *Pp. ado* corresponds closely to other species of *Parapapio* in retaining a suite of primitive features, and this is the basis for referring the taxon to this genus. Despite valid concerns that *Parapapio* might be paraphyletic, the included species do appear to represent a relatively homogeneous group, with a restricted range of morphological diversity. Compared with extant papionins, *Pp. ado* may be derived in having a relatively thick mandibular corpus, well-developed symphyseal tori, and posteriorly diverging tooth rows; part of a specialized dento-gnathic complex comprising relatively robust jaws and a moderately short face. Key features of the dentition of *Pp. ado* that distinguish it from extant papionins include relatively narrower incisors, a high degree of sexual dimorphism in canine size (except for *Macaca*), a short mesiobuccal honing face on P_3 (except *Lophocebus*), taller molar cusps, and molar crowns that are relatively broader, with a greater degree of buccolingual flare (except *Cercocebus*). A more detailed comparative analysis of these features is needed to determine their phylogenetic polarity, but they do highlight that *Pp. ado* has a unique suite of anatomical features of the face and dentition that serves to distinguish it from all extant papionins.

Comparisons between *Pp. ado* and the South African species of *Parapapio* are limited by the fragmentary nature of the cranial remains from Laetoli. However, in the preserved parts of the frontal region and maxilla *Pp. ado* is very similar in morphology to *Pp. broomi* (Freedman 1957), except that the latter species has nasals that are raised to form a midline keel. The facial specimens from Laetoli lack the thickened supraorbital tori and the distinctive protruding and keeled nasals seen in the male cranium of *Pp.* cf. *jonesi* from Hadar (A.L. 363-1a), and to a lesser degree in male individuals of this species from South Africa, but they do resemble the contour seen in female individuals. The morphology of the maxilla and frontal in *Pp. lothagamensis* is similar to that of *Pp. ado*, except that the supraorbital torus is more slender, the interorbital breadth is relatively narrower, and the frontal squama is somewhat less domed. The mandible of *Pp. lothagamensis* differs from *Pp. ado* in having a longer and more receding symphysis, with a strongly convex anterior dental arcade, a shallower corpus, with a distinct fossa below P_4-M_1. The upper face and mandible of *Pp. ado* can be distinguished from that of *Pliopapio alemui* in that the latter has a well-developed supraorbital sulcus or ophryonic groove, a distinct anteorbital drop, and more steeply inclined symphysis (Frost 2001). Most of the characteristic features of the cranium of *Procercocebus antiquus* are not preserved in *Pp. ado*, but the former can be distinguished by its more pronounced maxillary ridges and facial fossae (Gilbert 2007).

Comparisons of the size (i.e., area) of the lower molar in species of *Parapapio, Procercocebus* and *Pliopapio* are presented in Table 6.4. *Parapapio ado* is intermediate in size between *Pp. broomi* and *Pp. jonesi* (the lower molar area in *Pp. ado* is 10.2% smaller and 12.2% larger respectively). It is much smaller than *Pp. whitei* and considerably larger than *Pp. lothagamensis* and *Pliopapio alemui*, although their ranges do overlap. Overall, *Pp. ado* is most similar in size to *Pp.* cf. *jonesi* from Hadar and *Procercocebus antiquus* from Taung (see Table 6.4).

Generally, the proportions of the molar series in *Pp. ado* are similar to those of other species of *Parapapio*, with a marked size differential between M1 and M2, M^3 subequal in size to M^2, and M_3 more than 130% the area of M_2. However, *Pp. ado* does differ in having relatively narrower upper and

Table 6.4 Relative size of the lower molars in *Parapapio* and other small fossil African papionins

		Mean area (length × breadth)				
Species	Locality	M1	M2	M3	Total	% ±
Pliopapio alemui	Aramis	46.0	67.7	87.4	201.1	−36.8
“Parapapio” lothagamensis	Lothagam	48.6	69.3	87.8	205.7	−35.4
“Parapapio” sp.	Kanapoi	53.7	84.8	104.1	242.6	−23.8
“Parapapio” sp.	Allia Bay (Area 261–1)	58.3	97.1	119.3	274.7	−13.7
Parapapio jonesi	Sterkfontein	64.5	96.7	118.1	279.3	−12.2
Parapapio cf. jonesi	Hadar	60.0	98.7	129.3	288.0	−9.5
Parapapio sp. indet. C	Koobi Fora	70.7	103.0	121.9	295.6	−7.1
Parapapio sp. indet. B	Koobi Fora	84.9	99.1	126.0	310.0	−2.6
Parapapio ado	**Laetoli**	**73.9**	**105.1**	**139.2**	**318.2**	**–**
Procercocebus antiquus	Taung	79.4	117.6	139.7	336.7	+5.8
Parapapio broomi	Sterkfontein	85.6	115.1	149.9	350.6	+10.2
Parapapio whitei	Sterkfontein	82.5	133.6	182.0	398.1	+25.1

Data: Freedman (1957), Freedman and Stenhouse (1972), Frost (2001), Frost and Delson (2002), Harris et al. (2003), Leakey et al. (2003), Jablonski et al. (2008a); Harrison, unpublished data lower molars (as noted by Leakey and Delson 1987). It also differs from *Pp. jonesi* and *Procercocebus antiquus* in having a relatively larger M_3, and from the latter in having relatively smaller P4s (although the distinction may not be as profound as in other species of *Parapapio*).

The dentition of *Pp. lothagamensis* (~5.0–7.4 Ma) differs in a number of important respects from that of *Pp. ado*. These include: being much smaller in overall size; P_3 with the frequent occurrence of a metaconid; obliquely oriented P_4; upper premolars relatively broader; upper and lower molars with lower cusps and greater buccolingual flare; relatively broader M_1 (mean breadth-length index is 84.2, compared with 80.2 in *Pp. ado*); M_3 narrows more strongly distally, often with a smaller hypoconulid lobe; upper molars relatively shorter (mean length-breadth index of M^2 is 98.9, compared with 105.7 in *Pp. ado*), with weaker loph development; M^3 relatively large compared to M^2; dP^4 with a weakly developed crista obliqua; dP_4 occasionally with vestigial hypoconulid (Leakey et al. 2003; Harrison, unpublished data). Given that *Pp. lothagamensis* differs from *Pp. ado* (and from other species of *Parapapio*) in an extensive suite of dental and cranial features, many of which appear to be more primitive, the attribution of these species to the same genus would seem to be unwarranted. Transfer to a new genus is probably justified, but it should await a thorough and much-needed taxonomic revision of *Parapapio*. In addition, Benefit et al. (2008) have recently noted important similarities between *Pp. lothagamensis* and specimens of similar age from As Sahabi in Libya, and this serves to further highlight the primitive nature and distinctiveness of the species from Lothagam.

Parapapio specimens from Kanapoi and Allia Bay (Area 261-1) in Kenya (~4.0–4.1 Ma) have been assigned to *Pp. ado* (Leakey et al. 1995, 2003; Jablonski et al. 2008a). However, the material is smaller in dental size, and differs in a number of respects from *Pp. ado* from Laetoli that preclude it from being assigned to the same species. These features include: narrower symphyseal region, mandibular corpus shallower and more gracile, with a more distinct fossa below P_4-M_1; lower cheek teeth relatively buccolingually broader, with lower cusps and greater buccolingual flare; P_4 more obliquely oriented; M_1 relatively smaller in relation to M_2, and M_3 not as large; size differential between the lower molars (area of M1:M2:M3) is 66:100:127, compared with 70:100:132 in *Pp. ado* from Laetoli; M_3 narrows strongly distally, with smaller hypoconulid lobe (hypoconulid occasionally vestigial). Although somewhat larger in dental size than *Pp. lothagamensis*, the material from Kanapoi and Allia Bay shares a number of distinctive features with the geologically older material from the Nawata Fm. at Lothagam. It likely represents a different species, but referral to the same genus as "*Parapapio*" *lothagamensis* may be appropriate. A partial mandible (KNM-WT 16752), assigned to *Pp. ado* by Harris et al. (1988), from the Lower Lomekwi Mb. (~3.4 Ma) has the same suite of distinctive characteristics as the material from Kanapoi and Allia Bay, and can probably be assigned to the same taxon.

These preliminary comparisons confirm that *Pp. ado* can be distinguished from the somewhat younger species of *Parapapio* from South Africa, at least in its dental characteristics. It is also distinct from *Parapapio* specimens provisionally referred to *Pp.* cf. *jonesi* and *Pp.* cf. *whitei* from localities in East Africa. Material referred to *Pp. lothagamensis* and *Pp. ado* from the late Miocene and early Pliocene localities Lothagam (Nawata Mb.), Kanapoi, and Allia Bay are morphologically distinct, and probably represent an unnamed genus. If this proves to be the case, then *Pp. ado* from Laetoli would represent the earliest record of the genus. In fact, there are surprisingly few matches with *Pp. ado* from Laetoli with specimens from other Plio-Pleistocene localities, but a maxillary fragment with M^1-M^3 (KNM-LT 26369) from the Kaiyumung Mb. at Lothagam (~3.5–3.9 Ma), described as cf. *Parapapio* species indet. by Leakey et al. (2003), confirms that *P. ado* did occur contemporaneously in northern Kenya.

Table 6.5 List of cranio-dental specimens from Laetoli referred to large papionins

Specimen[a]	Loc.[b]	Horizon[c]	Element and Comments[d]
MB Ma 42449	Gar.	Pleistocene	Rt maxillary fragment with M^2. *Papio* sp. [MB 1939.16.13]
MB Ma 42473	Lem.	Pleistocene	Mandibular symphysis with left P_3-P_4, base of C_1. Male. *Papio* sp. [MB 1939.16.33]
MB Ma 42474	Lem.	Pleistocene	Lt maxilla with M^3. *Papio* sp. [MB 1939.16.34]
LAET 78-4765	11	Tuff 7B	Rt dP^4. Papionin gen. et sp. indet.
EP 2075/00	13	Tuffs 5-8	Rt C^1. Papionin gen. et sp. indet.

[a] Specimen prefixes: MB Ma. Humboldt-Universität Museum für Naturkunde, Berlin, 1938–1939 Ludwig Kohl-Larsen collections; LAET, Kenya National Museum, Nairobi (on loan from Tanzanian National Museum), 1974–1979 Mary Leakey collections; EP, Eyasi Plateau Expedition, National Museum of Tanzania, Dar es Salaam, 1998–2005 Terry Harrison collections

[b] Localities: Gar., Garusi; Lem., Lemagrut Korongo; numbers refer to the collecting localities designated by Leakey (1987a)

[c] Horizon: The stratigraphic provenience of the Kohl-Larsen collections and most of the specimens collected by Leakey are from unknown horizons within the Upper Laetolil Beds, except where indicated. The Harrison collections are mostly surface finds, and the stratigraphic provenience is recorded as a fossiliferous section between two marker tuffs within the Upper Laetolil Beds (unless more precise provenience is known for *in situ* specimens). All specimens are from the Upper Laetolil Beds, except those listed as Pleistocene

[d] Element and comments: lt, left; rt, right. Sex is determined by the size and morphology of the canines and P_3. The Museum für Naturkunde in Berlin has recently provided new accession numbers for their fossil mammal collections; the previous numbers, listed by Leakey and Delson (1987), are cross-referenced here

Papionini gen. et sp. indet.

As recognized by Leakey and Delson (1987), an isolated dP^4 and a distal humerus from Laetoli belong to a large species of papionin, which they referred to cf. *Papio* sp. The 1998–2005 collections include an isolated upper canine of a papionin, too large to be attributed to *Pp. ado*, which is provisionally attributed here to the same taxon as the dP^4 and distal humerus (Table 6.5). The two teeth are briefly described below, and the distal humerus is discussed with the other postcranial remains from Laetoli in a later section of this chapter.

Description of Cranio-Dental Morphology

LAET 78-4765 is a right upper dP^4. It is heavily worn, with some weathering and etching of the enamel surface. The crown is longer than broad (mesiodistal length = 11.0 mm, buccolingual breadth mesially = 9.4 mm), and it narrows distally. It is relatively low crowned, with a marked degree of buccolingual flare. Morphologically, the tooth is similar to that of extant *Papio*, but it is larger in size. It exceeds the maximum mesiodistal and buccolingual dimensions of the dP^4 in male *Papio cynocephalus* by 3.8% and 13.3% respectively (data from Koppe and Swindler 2004). Its dimensions are similar to the corresponding tooth of the large extinct papionin, *Dinopithecus ingens* from South Africa (Freedman 1957; Leakey and Delson 1987).

EP 2075/00 is a right upper canine of a male individual, missing the tip of the crown (Fig. 6.9). It is a distally recurved, blade-like tooth, with a strongly bilaterally compressed crown. The length and breadth dimensions of the crown are 15.3 mm and 11.1 mm respectively. The minimum height of the crown is ~25 mm, but it can be estimated to have exceeded 30 mm when intact. The deep mesial groove extends onto the root. The buccal surface is generally smooth, except for fine grooves that extend from the apex of the crown onto the base of the root. The root is relatively stout. Overall, it is similar in morphology to the upper male canines of *Papio*, but differs in having a somewhat shallower mesial groove. It differs from upper canines of males of *Parapapio* in having a more robust crown and root, a less distally recurved crown, a shallower mesial groove, and a lightly grooved buccal face. It differs from the upper canines of cf. *Rhinocolobus* sp. from Laetoli in being much more robust and more markedly distally recurved. The linear dimensions exceed that of the largest male canine attributed to *Pp. ado* and cf. *Rhinocolobus* sp. by 7.9% and 43.2% respectively. It falls within the upper end of the range of male canines of *Papio cynocephalus* and *Papio anubis*, as well as *Papio robinsoni* from Swartkrans (Freedman 1957). The canine is smaller than that of *Dinopithecus ingens* from Swartkrans (Freedman 1957), but is similar in size to that of *Dinopithecus quadratirostris* from the Turkana Basin (Iwamoto 1982).

Fig. 6.9 Papionin gen. et sp. indet. EP 2075/00, right upper canine. *Left*, buccal view. *Right*, lingual view

Based on these two isolated teeth it is evident that the cercopithecid community at Laetoli included a second species of papionin, larger in dental size than *Pp. ado*. The teeth are similar in morphology to extant *Papio* sp., but are larger or fall in the upper end of the range of variation. They are comparable in size to *Dinopithecus*, which is represented by specimens from the Turkana Basin dating from ~3.3–1.9 Ma (Frost 2007). There are no postcranial specimens of *Dinopithecus* with which to compare the distal humerus from Laetoli. Unfortunately, the material from Laetoli is too fragmentary and too poorly represented to establish its taxonomic identity. It could belong to *Dinopithecus*, to a large species of *Papio*, or to a previously unrecorded species of large papionin. The best course of action is to leave the material unassigned as Papionini gen. et sp. indet. until more material is recovered.

In addition to the three specimens from the Upper Laetolil Beds, the Kohl-Larsen collection includes two papionins of large size from Lemagrut Korongo, a locality just to the northeast of Laetoli on the northwestern flanks of the Lemagurut volcano (Dietrich 1942). These include a left maxilla with M^3 (MB Ma 42474) and a mandibular fragment with P$_3$-P$_4$, and the base of the lower canine (MB Ma 42473) (Fig. 6.10, Table 6.5). The specimens are lightly mineralized, and, based on the adhering matrix, were preserved in a reddish-brown tuffaceous sediment. The associated fauna indicates a Pleistocene age. Similarly, a right maxillary fragment with M^2 from Laetoli (MB Ma 42449) is poorly mineralized and has white enamel, and was probably derived from the late Pleistocene Ngaloba

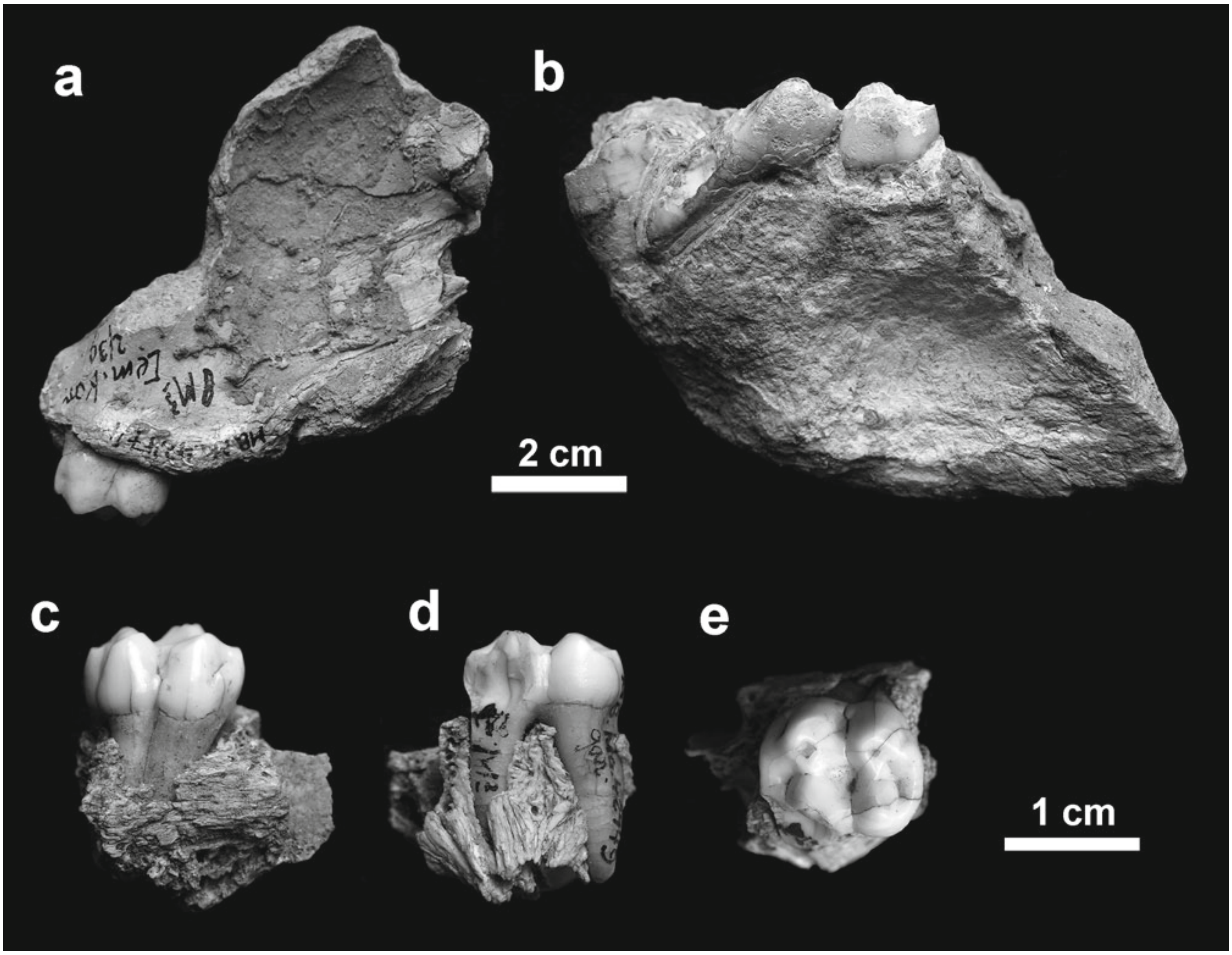


Fig. 6.10 *Papio* sp. from Pleistocene sediments at Laetoli. (**a**) MB Ma 42449, right maxillary fragment with M^2. (**b**) MB. Ma 42473, mandibular fragment with left P_3-P_4 and base of canine. Male. (**c**–**e**) MB Ma 42474, left maxilla fragment with M^3. (**c**) lingual view, (**d**) buccal view, (**e**) occlusal view. *Top* scale bar refers to **a** and **b**; *bottom* scale bar refers to **c**–**e**

Beds (Fig. 6.10). The teeth are morphologically indistinguishable from those of extant *Papio anubis*, and, in terms of their dimensions, they fall in the upper end of the size range or slightly exceed those of *Papio cynocephalus* and *Papio anubis*.

Subfamily Colobinae Jerdon, 1867
Tribe Colobini Jerdon, 1867

Rhinocolobus Leakey, 1982

Diagnosis: Face generally airorhynchous. Interorbital pillar relatively narrow. Rostrum long, at least subnasally. Nasals extremely short. Nasal aperture wide and very long anteroposteriorly, with its margin oriented at a low angle relative to the alveolar plane. In profile, the nasal aperture and face are concave. Relatively small orbits. Supraorbital tori slender, but prominent and projecting, with deep supraorbital sulcus. Neurocranium long and narrow, with small sagittal crest posteriorly in males. Extensive nuchal crest present in males and females. Posteriorly inclined foramen magnum. Mandibular symphysis slightly obliquely inclined, and lacking mental ridges. Corpus relatively deep and narrow, and deepens posteriorly, with expanded gonial angle (at least in males) and lack of fossae and *prominentia laterales*. Ramus tall and vertical or slightly posteriorly inclined. Incisors small relative to molars. P^3 with prominent protocone. P_4 with distinct metaconid. Lower molars long and narrow. M_3 with distal lophid generally equal in breadth or wider than mesial lophid. Postcranial morphology indicates specialization for arboreal locomotion. Humeral head broad, spherical and higher than greater tuberosity. Distal humerus with short medial trochlear keel, spherical capitulum, relatively well-developed zona conoidea, and long and medially projecting medial epicondyle. Proximal ulna with short, slightly retroflexed olecranon process (Adapted from Leakey 1982; Birchette 1982; Frost and Delson 2002; Jablonski et al. 2008b).

Distribution and Taxonomy

Rhinocolobus turkanaensis is known principally from the Koobi Fora and Omo Shungura Fms. of the Turkana Basin in Kenya and Ethiopia, from horizons ranging in age from ~3.4–1.5 Ma (Jablonski 2002; Frost 2007; Jablonski et al. 2008b). More recently, it has provisionally been recognized as occurring in contemporary horizons in the Hadar Fm. (~3.4–3.2 Ma) (Frost and Delson 2002). It is part of a diverse community of large colobines from the Plio-Pleistocene of East Africa that includes *Paracolobus* (*Pc. chemeroni* and *Pc. mutiwa*) and *Cercopithecoides* (*C. kimeui*, *C. williamsi*, and *C. meavae*), dating to at least 3.4–1.5 Ma (Jablonski 2002; Frost and Delson 2002; Frost 2007; Jablonski et al. 2008b). The only large colobine currently recognized from South African Plio-Pleistocene localities is *Cercopithecoides williamsi* (~3.2–1.0 Ma) (Jablonski 2002; El-Zaatari et al. 2005). The early Pliocene localities of Asa Issie (~4.1–4.2 Ma), Aramis (~4.4 Ma) and As Duma (~4.3–4.5 Ma) each have a single species of *Kuseracolobus* (i.e., *K. hafu* and *K. aramisi*) (Frost 2001; Semaw et al. 2005; Hlusko 2006). Frost et al. (2009) have recently reported isolated teeth attributable to *K. aramisi* from the Kuseralee Member of the Sagantole Formation in the Middle Awash region in Ethiopia, dating back to at least 5.2 Ma. A small and relatively primitive species of *Cercopithecoides*, *C. kerioensis*, from Lothagam (possibly from the Apak Member, ~4.2–5.0 Ma), may represent the earliest representative of this genus (Leakey et al. 2003). Similarly, the recently described *Paracolobus enkorikae*, from the late Miocene of Lemudong'o (~6 Ma) in Kenya, represents the earliest record of *Paracolobus* (Hlusko 2007). The large colobine from Laetoli occurs in a temporal window (~3.8–3.4 Ma) that is poorly represented in the fossil record of Africa, occurring at the transition between the earlier cercopithecid faunas with *Kuseracolobus* and the later and more diverse faunas from Hadar and the Turkana Basin.

Although comparisons are limited by the fragmentary nature and paucity of the material, it is evident that the specimens from Laetoli cannot be assigned to any of the currently recognized colobine taxa from the later Neogene of Africa. Leakey and Delson (1987) tentatively attributed the material from Laetoli to *Paracolobus*, based on the morphology of the mandible and proximal femur. Unfortunately, most of the diagnostic features of the genus are not preserved, making a more definitive allocation impossible. Nevertheless, detailed comparisons of the dentition, mandible and lower face highlight important differences that distinguish the Laetoli material from *Paracolobus*, and indicate a closer resemblance to *Rhinocolobus turkanaensis*. These features are described in the comparison section below, and are used here to tentatively reassign the material to the latter genus. However, it is important to emphasize that while the Laetoli specimens have their closest morphological and metrical similarity to *Rhinocolobus turkanaensis*, their unique suite of features confirms that they belong to a distinct species, and it is quite likely, with the recovery of more complete material, that the Laetoli taxon may even represent a new genus. Until such time, the large colobine from Laetoli is recognized here as cf. *Rhinocolobus* sp.

cf. Rhinocolobus sp.

This species is represented by 28.8% of the cranio-dental specimens from Laetoli, being slightly less than half as common as *Parapapio ado* (Table 6.1). All of the permanent teeth are represented in the collections, except for I^2, I_2 and the lower canine of females (Table 6.6). As for *Pp. ado*, the lack of relatively complete skulls or crania hampers comparisons with colobines from other Plio-Pleistocene localities in East and South Africa, and prevents a more precise taxonomic designation. Nevertheless, a number of maxillary and mandibular specimens are known, as well as associated tooth rows, and these provide adequate evidence from the lower face and dentition to determine that the material does not belong to any of the named fossil colobine species from Africa. Most of the new finds consist of isolated teeth, jaw fragments, and isolated postcranials. The best new specimen (EP 412/00) consists of associated lower cheek teeth (see Table 6.6). The increased sample does allow an improved understanding of the anatomy and paleobiology of the large colobine from Laetoli. Unfortunately, without more complete cranial specimens it is not possible to diagnose a new species. Moreover, while the number of fossil colobine species recognized from East and South Africa seems to be well-established, I am not convinced that all of the species are attributable to the four currently recognized extinct genera – *Rhinocolobus*, *Paracolobus*, *Cercopithecoides*, and *Kuseracolobus* (e.g., a good case could probably be made to recognize several new genera based on the species currently included in *Paracolobus* and *Cercopithecoides*). Given these uncertainties, and in the absence of a detailed revision of the African fossil colobines, the taxonomic status of the large colobine from Laetoli must be regarded as provisional at best.

All of the specimens of known provenience are from the Upper Laetolil Beds, except for an upper central incisor from the Upper Ndolanya Beds (Loc. 7E) that appears to be referable to this species (Table 6.6). None of the specimens collected by Harrison since 1998 are from horizons below Tuff 5, so it is uncertain whether this species shows the same temporal increase in size that occurs in *Pp. ado*. One specimen from the Mary Leakey collection is possibly derived from below Tuff 5 (LAET 75-2011 from Loc. 10), if the locality information is correct. This isolated M_2 is slightly larger than the others attributed to this species, but obviously larger samples of known stratigraphic provenience are needed to test possible temporal trends.

Table 6.6 List of cranio-dental specimens from Laetoli referred to cf. *Rhinocolobus* sp.

Specimen[a]	Loc.[b]	Horizon[c]	Element and Comments[d]
MB Ma 42454	Vo. 670		Lt mandibular fragment with C_1, P_3-P_4 exposed in crypts. Male. [MB 1939.16.19]
MB Ma 42459	Vo. 670		Lt mandibular fragment with M_2-M_3. [MB 1939.16.4]
MB Ma 42460	Gar.		Lt mandibular fragment with M_2-M_3. [MB 1939.16.5]
MB Ma 42461	Gar.		Lt maxilla with P^3-M^1. [MB 1939.16.10]
MB Ma 42462	Marambu		Rt mandibular fragment with M_3. [MB 1939.16.6]
MB Ma 42463	Marambu		Lt maxilla with P^4-M^1. Unassociated lt M^1 and fragment of lt upper molar. [MB 1939.16.9]
MB Ma 42464			Lt P^4. [MB 1939.16.23]
MB Ma 42465			Lt M^2 fragment. [MB 1939.16.21]
MB Ma 42466			Rt maxillary fragment with M^1. [MB 1939.16.25]
MB Ma 42467			Lt M^1. [MB 1939.16.26]
MB Ma 42468	Gar.		Lt M^2. [MB 1939.16.28]
MB Ma 42469			Rt M_3. [MB 1939.16.29]
MB Ma 42470			Rt. M^3. [MB 1939.16.30]
MB Ma 42471			Rt M^2. [MB 1939.16.31]
MB Ma 42472			Rt M^1. [MB 1939.16.32]
MB Ma 42475	Gar.		Rt maxilla with C^1-P^3. Female. [MB 1939.16.12]
MB Ma 42476	Gar.		Lt maxilla with C_1-P_4. Female. [MB 1939.16.17]
LIT 59-462			Lt C^1. Male
LAET 74-247	3		Rt maxilla with M^1-M^2, roots of P^4, alveoli C^1-P^3; lt maxilla with P^3, M^2, roots of C^1, P^4-M^1, alveoli I^2, M^3; rt C^1, female; fragment of left temporal bone
LAET 74-295	6		Rt maxilla with I^1, P^3-M^3, roots I^2-C^1. Female
LAET 74-321	7		Rt premaxilla-maxilla with dP^3-dP^4, M^1, alveoli of dI^1-dC^1, crown of I^1 in crypt; left premaxilla-maxilla with I^2 exposed in crypt; germ lt I^1; lateral margin of rt orbit; unassociated rt M_1
LAET 75-990	11		Rt dC^1
LAET 75-3372b	21		Rt M_3
LAET 75-1469	9		Rt mandibular fragment with C_1-M_2. Male
LAET 75-1560	9S		Lt C_1-P_3. Male. Associated with a temporal bone and a cranial vault fragment of non-primates. Probable antimere of LAET 75-1469
LAET 75-1915	2		Fragment of lt M_3
LAET 75-1974	1		Rt M_2
LAET 75-2011	10		Rt M_2
LAET 75-2523	2		Associated P_3-M_2
LAET 75-2847	2		Fragment of rt M^2
LAET 75-3740	3		Rt M_2. Listed as from Loc. 2 in Leakey and Delson (1987)
LAET 76-3861	3		Lt maxillary fragment with roots of M^3
LAET 76-4126	11		Rt maxilla with P^3-M^1. Listed as from Loc. 10W in Leakey and Delson (1987)
LAET 76-4156	21		Rt M_2
LAET 77-4566	11		Lt M_1
LAET 78-4596	17		Rt mandibular fragment with C_1, M_1-M_3, roots P_3-P_4; lt mandibular fragment with M_2-M_3; associated lt I_1, P_3-M_1. Male
LAET 78-4693	6		Lt M_1
LAET 78-5123	7E	U. Ndolanya	Rt I^1
LAET 79-5340	21		Associated rt M_1 and fragment of lt M_1
LAET 79-5509	11		Fragment of rt M_3
EP 204/98	10E	Tuffs 5-7	Rt C_1. Male
EP 1508/98	9	Tuffs 5-7	Lt M_1
EP 220/99	9	Tuffs 5-7	Rt M^1
EP 221/99	9	Tuffs 5-7	Lt M^3
EP 222/99	9	Tuffs 5-7	Rt P^4
EP 223/99	9	Tuffs 5-7	Maxillary fragment with germ of lt M^3 preserved in crypt.
EP 105/00	11	Tuffs 7-8	Rt mandibular fragment with M_3
EP 333/00	8	Tuffs 5-7	Rt P^4
EP 412/00	12/12E	Tuffs 5-8	Associated lt P_3-M_2
EP 2314/00	17	Tuffs 7-8	Lt mandibular fragment with M_1
EP 2410/00	16	Tuffs 7-8	Rt C^1. Male
EP 2740/00	3	Tuffs 7-8	Rt M_3. Missing distal part of crown

(continued)

Table 6.6 (continued)

Specimen[a]	Loc.[b]	Horizon[c]	Element and Comments[d]
EP 115/01	6	Tuffs 5-7	Lt P_3. Male
EP 630/03	2	Tuffs 5-7	Rt M^3
EP 773/03	9	Tuffs 5-7	Lt P_3. Female
EP 1517/03	12E	Tuffs 5-7	Rt M^2
EP 1573/03	21	Tuffs 5-7	Lt M^3
EP 1949/03	7	Tuffs 5-8	Germ of lt M^2
EP 2274/03	13	Tuffs 5-8	Lt M_3
EP 120/05	8	Tuffs 5-7	Rt P^3
EP 1098/05	1	Tuffs 6-8	Lt M^2

[a] Specimen prefixes: NHM.M, Natural History Museum, London, 1935 Louis Leakey collection; MB Ma, Humboldt-Universität Museum für Naturkunde, Berlin, 1938–1939 Ludwig Kohl-Larsen collection; LIT, Kenya National Museum, Nairobi (on loan from Tanzanian National Museum), 1959 and 1964 Louis and Mary Leakey collections; LAET, Kenya National Museum, Nairobi (on loan from Tanzanian National Museum), 1974–1979 Mary Leakey Collections; EP, Eyasi Plateau Expedition, National Museum of Tanzania, Dar es Salaam, 1998–2005, Terry Harrison collections

[b] Localities: De. Ost, Deturi Ost (= Olaitole River Valley); Gar, Garusi; Marambu (= Olduvai Side Gorge, Loc. 1); Vo, Vogelfluss (= Garusi Valley). Otherwise, the localities listed by number are the collecting localities as designated by Leakey (1987a)

[c] Horizon: The stratigraphic provenience of the Kohl-Larsen collections and most of the specimens collected by Leakey are from unknown horizons within the Upper Laetolil Beds, except where indicated. The Harrison collections are mostly surface finds, and the stratigraphic provenience is recorded as a fossiliferous section between two marker tuffs within the Upper Laetolil Beds (unless more precise provenience is known for *in situ* specimens). All specimens are from the Upper Laetolil Beds, except those listed as U. Ndolanya, from the Upper Ndolanya Beds

[d] Element and comments: lt, left; rt, right. Sex is determined by the size and morphology of the canines and P_3. The Museum für Naturkunde in Berlin has recently provided new accession numbers for their fossil mammal collections; the previous numbers, listed by Leakey and Delson (1987), are cross-referenced here

Description of Cranio-Dental Morphology

The premaxilla-maxilla is best preserved in LAET 74-295, a female individual (Fig. 6.11). The subnasal clivus is relatively short, with a supero-inferior height of 10.6 mm. The inferior margin of the nasal aperture is V-shaped, narrowing between the roots of the central incisors. To accommodate this configuration, the root of I^1 is much shorter than that of I^2, as is typical of most cercopithecids. The anterior recess of the incisive fossa is located far anteriorly, only 3.5 mm from the posterior margin of the I^1 alveolus. The aperture itself is located 9.2 mm posterior to I^1. Unfortunately, only the anterior margin of the incisive foramen is preserved, so it is not possible to determine its overall size or shape. The premaxillary suture passes obliquely across the anterior aspect of the palate from the lateral margin of the incisive fossa to the anterior margin of the upper canine, and then onto the lower face.

The full extent of the premaxillary suture on the lower face is not preserved, so it is not known whether it contacted the lateral margin of the nasal aperture or made contact with the nasal bones. In LAET 74-321, an infant specimen, the premaxillary suture approaches to within 1.7 mm of the margin of the nasal aperture at mid-aperture height, so it is possible that it did not extend superiorly as far as the nasal bones (Fig. 6.12). Anteriorly, the facial aspect of the premaxilla has a gently undulating surface for the roots of the incisors. The canine root produces a low or indistinct jugum in female individuals, bordered posteriorly by a shallow canine fossa. Otherwise, the lateral aspect of the lower face is relatively flat and rises steeply above the cheek teeth.

The damaged maxilla exposes a voluminous maxillary sinus. The floor of the sinus forms an undulating surface situated just above the level of the molar root tips. In LAET 74-295 it extends anteriorly as far as M^1, and extends laterally into the anterior root of the zygomatic arch and posteriorly beyond M^3. In LAET 74-247 the sinus extends anteriorly as far as mid-P^4 and in LAET 76-3861 it extends 7.5 mm posteriorly beyond M^3 into the maxillary tuberosity (Fig. 6.13).

The inferior margin of the orbit and the infraorbital foramina are not preserved in any adult specimens, but a small fragment of the lateral margin of the right orbit is associated with an infant specimen, LAET 74-321. The facial aspect of the malar process meets the temporal fossa laterally at a sharp keel. There are paired zygomaticofacial foramina, located above the inferior margin of the orbit. The lateral orbital margin has a sharp rim. A portion of the lacrimal duct is preserved on the left maxillary fragment of LAET 74-321, and appears to have been located inside the orbit (see Fig. 6.12).

The alveolar region of the maxilla is quite steep laterally, and is antero-posteriorly convex. The anterior root of the zygomatic arch is situated low on the face and originated opposite M^1-M^2. The palate is shallow, relatively short, and U-shaped with outwardly curving tooth rows. The maximum breadth of the palate occurs opposite M^2. A small diastema, 1.6 mm in length, separates the alveoli of the upper canine and lateral incisor in LAET 74-295, but it was presumably larger in males (see Fig. 6.11). A groove leading to the greater

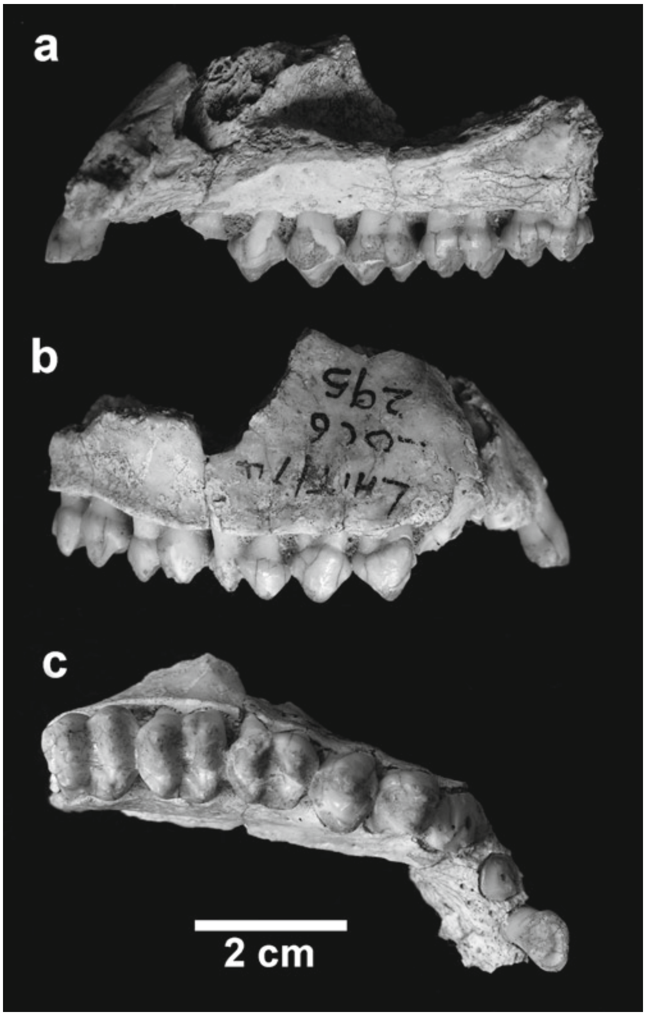


Fig. 6.11 cf. *Rhinocolobus* sp. LAET 74-295. Right maxilla with I^1, P^3-M^3. (**a**) medial view, (**b**) lateral view, (**c**) occlusal view

palatine foramen begins opposite M^2, and the foramen itself is a narrow slit located opposite the posterior portion of M^3. A small lesser palatine foramen is located posterior to M^3 on the pyramidal process of the palatine. The posterior margin of the maxillary tuberosity is angled back superiorly at an angle of ~120° relative to the alveolar plane, and meets the stout pyramidal process at a right angle.

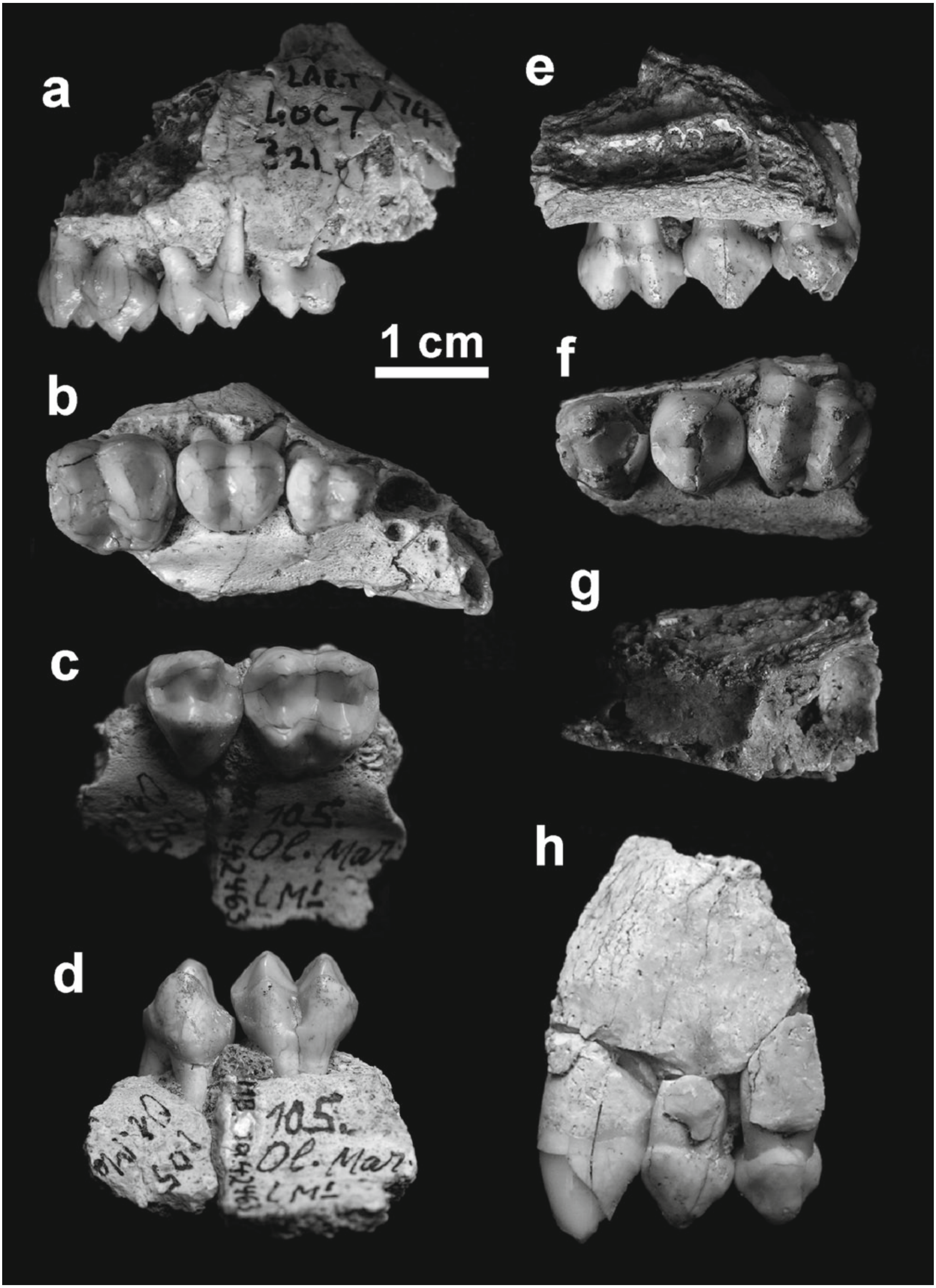
A fragment of the temporal bone is associated with LAET 74-247. Inferiorly, there is a well-defined triangular articular surface for the mandibular condyle, which measures 19.6 mm wide by at least 13.5 mm long. The articular facet is slightly antero-posteriorly convex and mediolaterally concave. The postglenoid process is a tall triangular plate, slightly anteriorly recurved, with a sharp lateral margin. It is a height of 6.9 mm above the posterior margin of the articular surface. This is much more elevated than is typically found in extant African colobines. The external auditory meatus is not preserved, but the raised margin for its external aperture is visible posterior to the medial aspect of the postglenoid process. This suggests that the ectotympanic was a relatively short tube set back from the lateral margin of the temporal bone, as in extant African colobines. Two tiny foramina, located just posterior to the articular surface, mark the limit of the tympanosquamosal fissure. Two large, incompletely preserved foramina, located on the lateral side of the lateral pterygoid plate, represent the closely paired foramen spinosum and foramen ovale. Dorsally, the anterior plate of the articular process of the temporal forms the slightly concave and triangular posterior root of the zygomatic arch. Laterally, the wall of the temporal above the posterior root of the zygomatic arch bows outwards, suggesting a relatively inflated base to the cranial vault.

The mandible has a relatively deep symphysis, with a long and posteriorly sloping subincisive planum (Figs. 6.14 and 6.15). There is a well-developed and angular superior transverse torus and a strongly projecting simian shelf, which extends posteriorly to the level of P$_4$-M$_1$. Between the two tori is a deep genioglossal pit. The inferior surface of the simian shelf has well-developed scars on either side of the mid-line for the anterior bellies of the digastric muscles. Externally, the symphysis bears a low rounded crest that begins inferiorly below the premolars and passes obliquely upwards to terminate in the midline just below the incisors. The ridges are smooth as in extant colobines, rather than rugose as in cercopithecines. The triangular region enclosed by these ridges has a finely crenulated subcutaneous surface. Although the symphyseal region is only partial preserved, there is no evidence of a median mental foramen.

The corpus is moderately deep and slender (the mean breadth-height index of the corpus at M$_2$ is 42.4, $n = 2$), and it deepens somewhat posteriorly. The lateral face of the corpus is slightly concave below the premolars, but convex below the molars. One or two mental foramina are located below P$_4$. The medial surface of the corpus is infero-superiorly slightly convex. There is a low buttress two-thirds down from the alveolar region of the P$_4$-M$_2$ that blends into the simian shelf. Laterally, the anterior root of the ramus originates midway down the lateral surface of the corpus below M$_3$, and rises steeply posterior to it to create a short retromolar space. It lacks distinct *prominentia laterales* (see Figs. 6.14 and 6.15).

I^1 is relatively small compared to the size of the cheek teeth. The mean mesiodistal length of I^1 is 20.2% of the combined mean lengths of the lower molar series. It is high-crowned and

Fig. 6.12 cf. *Rhinocolobus* sp. Maxillary specimens from Laetoli. (**a**, **b**) LAET 74-321, right maxilla with dP^3–dP^4 and M^1. (**a**) lateral view, (**b**) occlusal view. (**c**, **d**) MB Ma 42463, left maxilla with P^4-M^1. (**c**) occlusal view, (**d**) medial view. (**e–g**) MB Ma 42461, left maxilla with P^3-M^1. (**e**) medial view, (**f**) occlusal view, (**g**) dorsal view, showing the floor of the maxillary sinus. (**h**) MB Ma 42476, left maxilla with C-P^4, lateral view. Female


a
LAET
LOC 7/74-
321
1 cm
b
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10.5.
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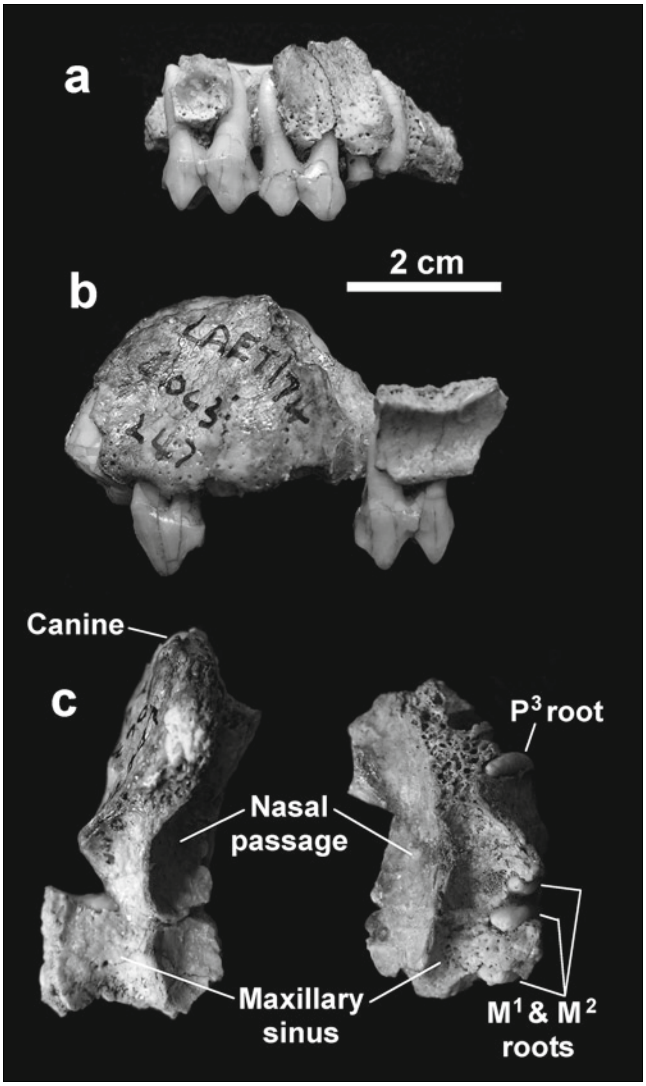

Fig. 6.13 cf. *Rhinocolobus* sp. LAET 74-247. (**a**) right maxilla with M^1-M^2, lateral view. (**b**) left maxilla with P^3 and M^2, lateral view. (**c**) right and left maxilla, superior view, showing the extent of the maxillary sinus

relatively narrow. The lingual face is concave and it is bordered mesially and basally by a well-developed marginal ridge and lingual cingulum. This gives the crown a distinctive shoveled form. The lingual face is devoid of a lingual pillar or any secondary wrinkling. Enamel is present on the lingual face, but it is only about half as thick as that on the buccal face. The apex bows buccally and it continues mesially onto the lingually projecting mesial marginal ridge, creating a scythe-shaped occlusal apex. In its unworn state, the apex bears a series of mammelons, but these are soon worn flat. The mesial and distal margins are both apico-basally convex, so that the greatest mesiodistal width of the tooth is at mid-crown height.

There are no examples of I^2 known. Judging from the size of the root in LAET 74-295, it would have been a sizeable tooth, not much smaller than I^1.

The upper canines listed by Leakey and Delson (1987) all belong to female individuals. However, several canines of male individuals, included as indeterminate specimens by Leakey and Delson (1987) are here reassigned to this taxon. They can be distinguished from those of *Pp. ado* in being mesiodistally shorter, with less recurved crowns and roots, a shallower mesial groove, a less inflated lingual pillar, and a smaller root, and they closely resemble those of other extinct and extant colobines.

The canines of males are tall, slightly distally recurved, and bilaterally compressed. The mesial crest is sharp, with a shallow mesial groove and a well-developed lingual pillar. The root is more slender, straighter and probably relatively longer than in *Pp. ado*. The upper canine of female individuals is much smaller and relatively lower crowned than those of males, but the degree of sexual dimorphism is not as marked as in *Pp. ado*. The crown has an ovoid to subtriangular section basally, with a convex buccal face and a V-shaped lingual face. It has a shallow mesial groove, a broad, rounded lingual pillar, and a narrow lingual cingulum, which does not continue around the pillar.

P^3 is a high-crowned relatively narrow tooth. It is triangular in occlusal outline, narrowing strongly lingually. The two main cusps are closely associated, and linked by an elevated and sharp transverse crest. The protocone is lower than the paracone, and this differential in elevation increases with wear. The pre- and postparacrista are long and sharp. The mesial fovea is a small triangular basin, usually well delimited by the mesial crests of the paracone and protocone, and the raised mesial marginal crest. The distal margin is convex, and the D-shaped distal fovea is much larger than the mesial fovea. On the buccal face of the crown, the enamel junction extends further down onto the mesiobuccal root than on the distobuccal root.

P^4 is morphologically similar to P^3, but it is larger, with a more ovoid occlusal outline, a larger distal fovea, and a less marked extension of the enamel junction onto the mesiobuccal root. The paracone is much more elevated than the protocone, but the difference in elevation is not as marked as it is in P^3. The mesial margin is convex and it borders a crescentic mesial fovea. A trace of the distal lingual cleft may be present. Both upper premolars have three distinct roots.

M^1 is almost square in outline, being only slightly longer than broad, and narrowing slightly distally. The mean length-breadth index is 106.7. The crown exhibits a moderate degree of buccolingual flare. The protocone and hypocone are subequal in size. The preprotocrista is directed mesiobuccally, where it meets the low mesial marginal ridge at a tiny tubercle. The postprotocrista runs obliquely distobuccally. The mesial lingual cleft is narrow and irregular. The median lingual cleft forms a triangular ledge between the protocone and hypocone, sometimes bearing small subsidiary tubercles. The distal lingual cleft is restricted to a dimple on the distolingual face of the hypocone. The preparacrista meets the postprotocrista to form the lingual

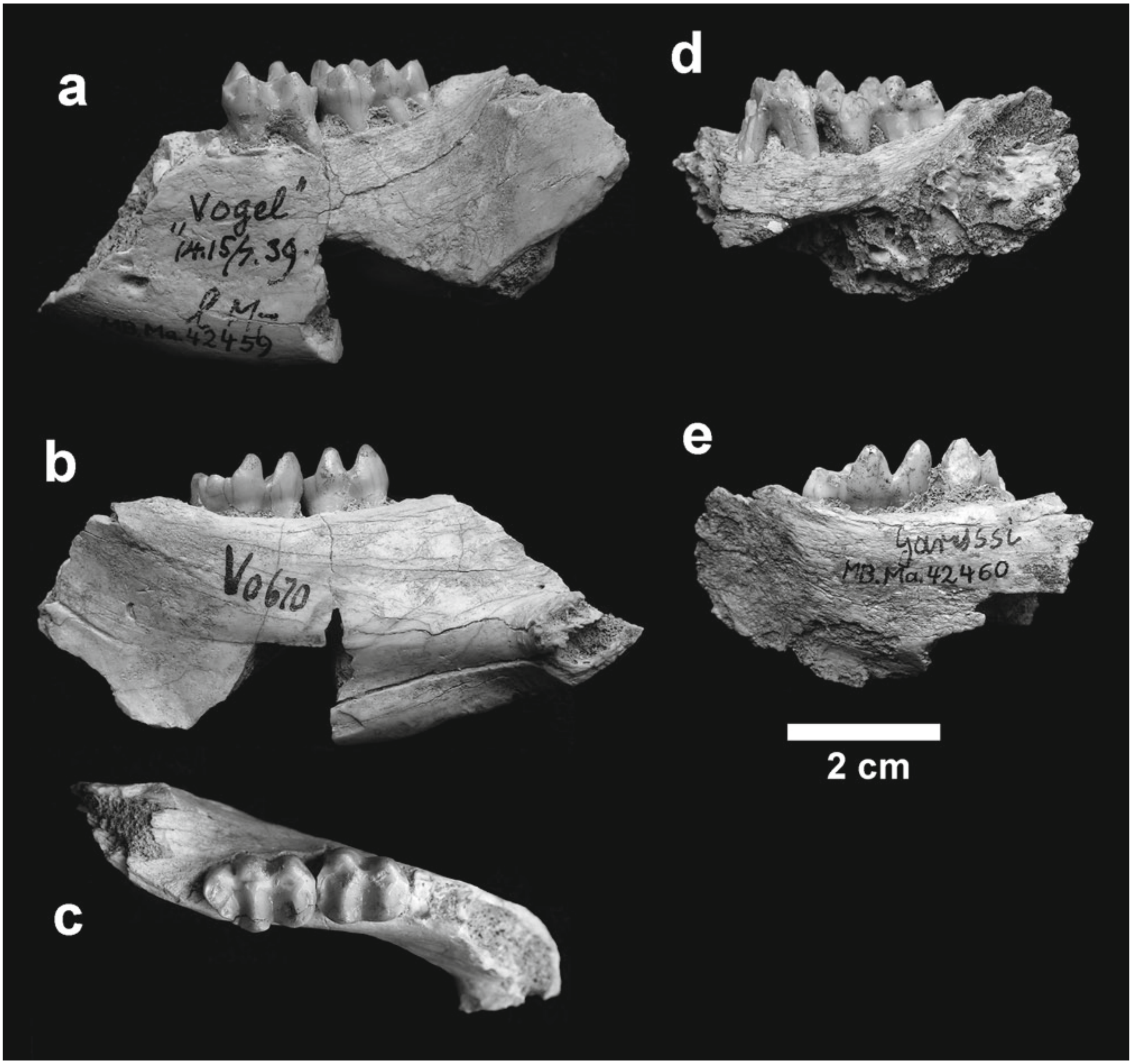

Fig. 6.14 cf. *Rhinocolobus* sp. Mandibular specimens from Laetoli collected by the Kohl-Larsen expedition, 1938–1939. (**a**–**c**) MB Ma 42459, left mandibular fragment with M_2-M_3. (**a**) lateral view, (**b**) medial view, (**c**) occlusal view. (**d**, **e**) MB Ma 42460, left mandibular fragment with M_2-M_3. (**d**) lateral view, (**e**) medial view

marginal crest. The paracone is slightly more elevated than the protocone, with a larger basal area. The metacone is smaller than the paracone, and subequal in size to the hypocone. The paraloph and metaloph are sharp and well developed. The paraloph is more obliquely oriented than the metaloph, so that the two lophs converge slightly towards the buccal side of the crown. The mesial fovea is a broad D-shaped basin, bordered mesially by a weak marginal crest. The postparacrista and the premetacrista are quite long and sharp, and are separated by a moderately deep V-shaped buccal notch that extends about half way up the crown. The distal fovea is longer and broader than the mesial fovea. The trigon basin is square and relatively deep. A distinct transverse fissure passes from the median lingual cleft across the trigon basin to the median buccal cleft. A longitudinal fissure bisects the paraloph and metaloph and arcs around the base of the paracone and metacone respectively. Otherwise, the occlusal fissures are weakly expressed, and secondary wrinkling is absent.

M^2 is larger than M^1, the crown is relatively broader (with the breadth generally exceeding the length), and the lingual and buccal clefts are better developed. M^3 is larger than M^2 and relatively broader. The crown narrows distally, with reduction of the distal pair of cusps, the length of the metaloph and the

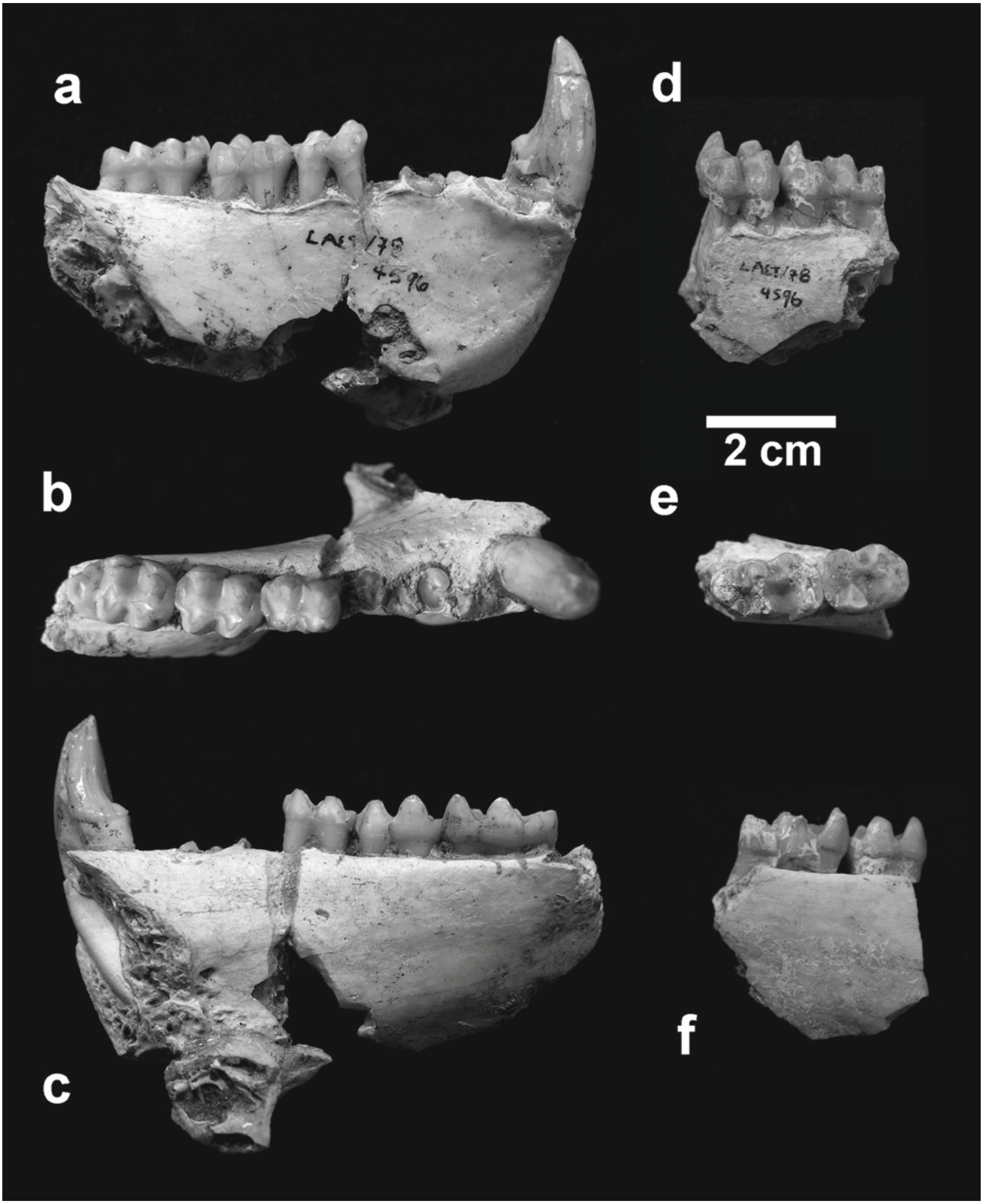

Fig. 6.15 cf. *Rhinocolobus* sp. LAET 78-4596. (**a**–**c**) right mandibular fragment with C, M_1-M_3. (**a**) lateral view, (**b**) occlusal view, (**c**) medial view. (**d**–**f**) left mandibular fragment with M_2-M_3. (**d**) lateral view, (**e**) occlusal view, (**f**) medial view

size of the distal fovea. Occasionally it bears a small V-shaped heel with subsidiary tubercles. The mean length-breadth index is 102.9 and 108.7 for M^2 and M^3 respectively. The size ratio of the upper molars (mean areas of M^1:M^2:M^3) is 77:100:106, with an increase in size posteriorly and a marked size differential between M^1 and M^2. As in the lower molars, the upper molars exhibit a strong wear differential between the buccal and lingual cusps, with the lingual cusps exposing dentine at a much earlier wear stage than the buccal cusps.

I_1 is small in relation to the size of the cheek teeth. The mean mesiodistal length of I_1 is 14.2% of the combined mean mesiodistal lengths of the lower molar series. The crown is relatively low and broad. The crown has relatively thin enamel covering the lingual face, and much thicker enamel buccally. The crown is spatulate, with convex mesial and distal margins. The lingual face is scooped or shoveled, bordered by raised mesial and distal margins and the lingual cingulum. There is no lingual pillar. The buccal face is mesiodistally strongly convex and featureless. Wear tends to be restricted to the narrow incisive apex. However, moderately worn specimens exhibit fine apico-basally oriented striations on the apical portion of the buccal face, implying a certain degree of overbite. The root is narrow and bilaterally compressed. No examples of I_2 are known.

The lower canine is known only from male individuals. It is high-crowned and slender, and only slightly distally recurved. It has a shallow mesiobuccal groove. The root is slender and has a distinct buccal curvature.

P_3 exhibits marked sexual dimorphism, with males having a larger crown and a much longer mesiobuccal honing face. However, the degree of dimorphism is less than is seen in *Pp. ado*. The crown is long and narrow, and obliquely oriented in relation to the long-axis of the cheek tooth row. In males, the mesiobuccal face of the crown is extended to form a long and steep honing face. In female individuals it is much shorter. The protoconid is high and bilaterally compressed. The mesial crest is long and sharp, and it terminates mesially at a small tubercle at the junction with the lingual cingulum. The lingual cingulum is represented by a narrow ledge of enamel that continues distally around the lingual face of the crown as far as the distolingual crest. The latter is an obliquely oriented crest, with a slight swelling along its length that represents the metaconid. The distal crest is short, and it arcs lingually to become continuous with the distal marginal crest. The distal fovea is small and shallow.

P_4 is relatively long and narrow, and obliquely oriented in relation to the long axis of the cheek tooth row. The two main cusps are similar in height and closely associated, but the protoconid is slightly more voluminous than the metaconid. The transverse crest linking the two cusps is short and quite elevated. The preprotocristid is well-developed, and it passes mesiolingually to end at a small tubercle on the mesial marginal ridge. The premetacristid is low, rounded and ill-defined. The mesial fovea is small and pit-like. The buccal face is convex, with slight traces of mesial and distal buccal clefts. The enamel junction on the buccal face extends down onto the mesiobuccal root of the tooth in male individuals. The postmetacristid and postprotocristid each terminate at the distal margin in a small tubercle. The distal fovea is a relatively large rectangular basin.

M_1 is long and narrow, subrectangular with quite marked buccolingual waisting and slight distal narrowing. The mean breadth-length index is 75.5. The cusps are relatively high, with sharp and fine occlusal crests. The protoconid and hypoconid are lower, but more voluminous than the metaconid and entoconid. The short mesial ridges of the protoconid and metaconid meet the low mesial marginal crest to delimit a short mesial fovea. A well-developed protolophid connects the apices of the protoconid and metaconid. The protoconid and hypoconid are linked by a convex longitudinal crest, comprising the postprotocristid and prehypocristid. The median buccal cleft forms an ill-defined sloping surface or sometimes a distinct platform. The mesial buccal cleft is represented by a rounded fold on the mesiobuccal face of the protoconid. The vestigial distal buccal cleft is represented by a shallow dimple on the distobuccal face of the hypoconid. The hypoconid is smaller and lower than the protoconid. It is connected to the entoconid by a slightly obliquely oriented hypolophid. The pre-entocristid and postentocristid are poorly defined. The distal marginal ridge is convex, and it delimits a small distal fovea, which is broader and longer than the mesial fovea. The lingual notch is deep, and reaches to at least mid-crown. The talonid basin is rectangular, being longer than broad. It has a simple Y-shaped fissure pattern, with the lingual arm passing through the lingual notch, and the mesial and distal arms bisecting the lophids. Otherwise, the occlusal surface is relatively smooth, with no secondary wrinkling or tubercles.

M_2 is similar to M_1 except that it is larger and relatively broader (the mean breadth length index is 80.9), and it has a square talonid basin and better developed buccal clefts. M_3 is much larger than M_2 and it tapers distally to form a well-developed heel. The mean breadth-length index is 62.7. The mesial fovea is represented by a broad crescentic groove. The hypoconid and entoconid are more closely associated, due to the distal narrowing of the crown. The hypoconid is a little smaller than the protoconid, and the entoconid is reduced in size. The distal lophid is narrower than the mesial lophid. The hypoconulid has a large basal area, but is relatively low. It is connected to the hypoconid by a low, rounded crest. The tip of the hypoconulid is situated in the midline of the crown, or slightly towards the buccal side. The distal fovea is a large triangular basin. The postentocristid usually bears a large tuberculum sextum. The lower molars exhibit a strong wear differential between the lingual and buccal cusps, with the buccal cusps wearing more strongly and exposing dentine well ahead of the lingual cusps. The size ratio of the lower molars (mean areas of M_1:M_2:M_3) is 74:100:129. Dimensions of the teeth are presented in Table 6.7.

Comparisons

The upper and lower incisors of cf. *Rhinocolobus* sp. are relatively small compared to those of extant colobines. The mean mesiodistal lengths of the upper and lower central incisor

Table 6.7 Measurement of teeth of cf. *Rhinocolobus* sp. from Laetoli

Tooth	Dimension	N	Mean	SD	Range
UPPERS					
I1	MD	3	6.4	0.09	6.3–6.5
	BL	3	5.6	0.42	5.2–6.2
	BHT	1	9.3	–	9.3
I2	MD	–	–	–	-
	BL	–	–	–	–
	BHT	–	–	–	–
C (male)	MD	1	10.9	–	10.9
	BL	1	7.6	–	7.6
	BHT	–	–	–	–
C (female)	MD	3	8.9	0.59	8.1–9.5
	BL	3	7.0	0.29	6.6–7.3
	BHT	–	–	–	–
P3	MD	5	7.2	0.35	6.8–7.7
	BL	5	8.2	0.56	7.5–9.1
	BHT	4	6.8	0.33	6.5–7.3
	LHT	2	6.3	–	6.1–6.5
P4	MD	6	7.4	0.39	6.9–8.1
	BL	7	8.8	0.54	8.2–9.7
	BHT	4	7.3	0.30	6.9–7.7
	LHT	3	7.7	0.36	7.2–8.0
M1	MD	9	9.6	0.42	9.0–10.2
	BLmes	4	9.0	0.33	8.6–9.4
	BLdist	5	8.8	0.18	8.5–9.0
M2	MD	8	10.7	0.71	9.7–11.6
	BLmes	7	10.4	0.58	9.9–11.4
	BLdist	5	9.4	0.67	8.7–10.7
M3	MD	5	11.3	0.98	10.0–13.0
	BLmes	4	10.4	0.52	9.8–11.2
	BLdist	4	9.1	0.53	8.7–10.0
LOWERS					
I1	MD	1	5.0	–	5.0
	BL	1	5.7	–	5.7
	BHT	–	–	–	–
I2	MD	–	–	–	–
	BL	–	–	–	–
	BHT	–	–	–	–
C (male)	MD	5	11.0	0.35	10.5–11.6
	BL	4	7.7	0.87	6.8–8.9
	BHT	3	21.8	2.97	19.6–26.0
C (female)	MD	–	–	–	–
	BL	–	–	–	–
	BHT	–	–	–	–
P3	MD	3	11.0	1.31	9.4–12.6
	BL	2	6.2	–	6.0–6.3
	BHT	2	6.9	–	6.2–7.6
	HHT	2	12.0	1.01	10.6–12.8
P4	MD	3	8.5	1.13	7.6–10.1
	BL	3	6.3	0.42	5.9–6.9
M1	MD	10	9.8	0.48	9.0–10.7
	BLmes	5	7.1	0.69	6.4–8.0
	BLdist	6	7.4	0.56	6.9–8.3
M2	MD	8	11.0	0.51	10.3–11.9
	BLmes	6	8.3	0.46	7.7–9.5
	BLdist	7	8.8	0.39	8.1–9.1
M3	MD	8	14.2	0.77	13.4–15.8
	BLmes	6	9.1	0.95	7.8–10.5
	BLdist	5	8.8	0.50	8.1–9.6

BHT buccal height of crown, *BL* buccolingual breadth, *BLmes* buccolingual breadth mesially, *BLdist* buccolingual breadth distally, *LHT* lingual height of crown, *HHT* length of mesiobuccal face of P_3, *MD* mesiodistal length, *N* number of specimens, *SD* standard deviation

in relation to the mean mesiodistal lengths of the corresponding molar series combined are 20.2% and 14.2% respectively. These values fall below or at the lowest end of the range of extant Asian and African colobines (mean values range from 23.0–27.2% and 13.7–19.0%). Compared with other fossil colobines, the proportions of the incisors are similar to those of *Pc. chemeroni, Pc. enkorikae*, *R. turkanaensis*, and *Cercopithecoides meavae*, whereas the incisors of *Kuseracolobus* are relatively larger.

P^3 of cf. *Rhinocolobus* sp. has a well-developed protocone, as in *R. turkanaensis*, *Paracolobus* and *Kuseracolobus*, and contrasts with the derived condition in *Cercopithecoides* and extant African colobines in which the protocone is highly reduced.

The molars of cf. *Rhinocolobus* sp. can be distinguished from most extant colobines in having a marked size differential between M1 and M2, an M^3 that is larger in area than M^2, and an M_3 that is almost 130% larger in area than the M_2. However, this is the typical pattern for the large Plio-Pleistocene colobines from Africa, and there is much less diversity in molar proportions than among extant colobines. The main exceptions are *Cercopithecoides meavae* and *C. kimeui*, which have a less pronounced size differential between M1 and M2, and *Cercopithecoides kerioensis* and *C. kimeui*, with an M_3 area that is only 114% of that of M_2. The length-breadth proportions of the upper and lower molars of the large colobine from Laetoli are most similar to those of *Kuseracolobus*, and differ from those of *Rhinocolobus* and *Cercopithecoides*, which are relatively longer, while the upper molars of *Paracolobus* are distinguished by being relatively broader.

In terms of overall dental size, using combined lower molar area as a proxy for size, cf. *Rhinocolobus* sp. from Laetoli is most similar to *Rhinocolobus turkanaensis* from the Turkana Basin and Hadar, and *Cercopithecoides kimeui* from Koobi Fora (Table 6.8). The teeth are much larger in *Paracolobus chemeroni* and *Pc. mutiwa.* All other fossil colobines from East and South Africa are generally smaller in size (see Table 6.8 for comparisons).

The material from Laetoli does not preserve much of the face, so many of the diagnostic features distinguishing *Rhinocolobus* from other large fossil colobines cannot be determined. Nevertheless, some useful comparative information can be discerned from the palate, lower face and mandible. The key characteristics of the Laetoli maxilla and premaxilla are a V-shaped inferior margin to the nasal

Table 6.8 Relative size of the lower molars in fossil African colobines

Species	Locality	Mean area (length × breadth) M1	M2	M3	Total
Cercopithecoides kerioensis	Lothagam	–	52.9	60.5	–
Paracolobus enkorikae	Lemudong'o	44.4	58.0	73.3	175.7
Colobinae species C	Lothagam	46.1	55.2	75.9	177.2
Colobinae species B	Lothagam	41.0	71.5	>72.5	>185.0
Kuseracolobus aramisi	Aramis	49.0	64.2	85.0	198.2
Cercopithecoides meavae	Hadar & Leadu	57.3	66.3	86.6	210.2
***Cercopithecoides* sp.**	**Laetoli**	**52.7**	**68.3**	**95.0**	**216.0**
Cercopithecoides williamsi	Sterkfontein	57.4	72.8	95.9	226.1
Cercopithecoides williamsi	East Turkana	62.5	76.3	111.0	249.8
Kuseracolobus hafu	Asa Issie	72.0	90.5	115.6	278.1
Rhinocolobus turkanaensis	East Turkana & Omo	69.6	85.6	123.8	279.0
cf. *Rhinocolobus turkanaensis*	Hadar	66.8	93.5	123.1	283.4
Cercopithecoides kimeui	Koobi Fora	81.7	98.0	111.9	291.6
cf. *Rhinocolobus* sp.	**Laetoli**	**72.5**	**96.8**	**129.2**	**298.5**
Paracolobus chemeroni	Chemeron	94.9	125.0	158.4	378.3
Paracolobus mutiwa	Omo	84.2	115.9	158.7	358.8

Data: Freedman (1957), M.G. Leakey (1982, 1987c), Frost (2001), Frost and Delson (2002), Leakey et al. (2003), Hlusko (2006, 2007), Jablonski et al. (2008b); Harrison, unpublished data

aperture, anterior root of the zygomatic process situated opposite M^1-M^2, laterally curved cheek tooth row, and a relatively short palate, and in these respects it matches well with *R. turkanaensis*, *Kuseracolobus*, and *Cercopithecoides.* It differs from *Rhinocolobus turkanaensis* in having a shallower subnasal clivus, a less robust frontal process of the zygoma, and a shorter rostrum. *Paracolobus mutiwa and Pc. chemeroni* differ in having a U-shaped inferior margin to the nasal aperture, a relatively longer palate, a more posteriorly placed anterior root to the zygomatic arch (opposite M^3 in *Pc. mutiwa* and M^2 in *Pc. chemeroni*), relatively straight-sided tooth rows, and a broader muzzle with distinct facial fossae. The large maxillary sinus present in the Laetoli specimens also occurs in *Cercopithecoides williamsi* from South Africa (absent in specimens from the Turkana Basin), *C. kimeui*, and possibly *C. alemayehui*, as well as *Libypithecus* and *Mesopithecus*, but is absent in *Rhinocolobus* and *Paracolobus* (Rae 2008; Gilbert and Frost 2008; Harrison, unpublished observation).

The mandible of cf. *Rhinocolobus* sp. from Laetoli resembles *Rhinocolobus turkanaensis* in having a relatively long and sloping symphysis, no median mental foramen (absent in *R. turkanaensis* from Hadar, but present in the Turkana Basin material), a corpus that deepens posteriorly, a narrow extramolar sulcus, and absence of *prominentia laterales*. It differs from *Paracolobus* and *Kuseracolobus* in having a less vertical symphysis, a corpus that does not deepen posteriorly to such a marked extent (similar to *Pc. enkorikae*), and absence of *prominentia laterales*. The Laetoli large colobine differs from *Cercopithecoides* in having a more sloping symphysis with a long subincisive planum, absence of a median mental foramen (present in *C. williamsi* and *C. kimeui*), a deeper and more slender corpus that deepens slightly posteriorly, and absence of *prominentia laterales* (except *C. meavae*).

In sum, the large colobine from Laetoli bears its closest similarity in its dentition and lower face to *Rhinocolobus turkanaensis*. It differs mainly in having a shorter rostrum, a shallower subnasal clivus, a more gracile frontal process of the maxilla, a maxillary sinus, a slightly shallower mandibular corpus, and relatively shorter upper and lower molars. Based on these comparisons, the taxon represented at Laetoli is tentatively retained in *Rhinocolobus*, although it clearly represents a distinct species from *R. turkanaensis*. With the recovery of more complete material, it is possible that the Laetoli specimens could belong to a novel genus. While my own comparisons (see below) agree with the observations of Leakey and Delson (1987) that the proximal femur corresponds closely in morphology to that of *Pc. chemeroni* (although it differs from that of *Pc. mutiwa*), without comparative material of *Rhinocolobus turkanaensis*, it is not possible to conclude that the proximal femur from Laetoli provides grounds for attribution to any particular genus of colobine.

Cercopithecoides Mollett, 1947

Diagnosis: Medium-sized to very large colobines with globular calvaria. Rostrum short in relation to neurocranial length. Frontal process of zygomatic bone narrow. Interorbital region broad. Supraorbital tori thick, with deep supraorbital sulcus. Sagittal crest absent, at least anteriorly. Mandibular symphysis steep, but shallow with a median mental foramen (except *C. meavae*). Mandibular corpus shallow and thick, with slightly expanded or unexpanded gonial region. P^3 protocone reduced (Adapted from Freedman 1957; Leakey 1982; Szalay and Delson 1979; Frost and Delson 2002).

Taxonomy and Distribution

Five species of *Cercopithecoides* are recognized – *C. williamsi* Mollett, 1947; *C. kimeui* Leakey, 1982; *C. meavae* Frost and Delson, 2002; *C. kerioensis* Leakey et al., 2003; and *C. alemayehui* Gilbert and Frost, 2008. *Cercopithecoides williamsi* is the only large colobine represented at Plio-Pleistocene localities (~3.2–1.0 Ma) in South Africa (Freedman 1957; Jablonski 2002). This same species occurs contemporaneously at Koobi Fora (~3.4–1.5 Ma) in Kenya, but is much less common. *Cercopithecoides kimeui* is known from Koobi Fora, West Turkana, Hadar (Pinnacle Locality), Olduvai Beds II-III, and Rawi in eastern Africa, dating from ~3.4–0.8 Ma (Leakey 1982; Frost and Delson 2002; Jablonski 2002; Frost et al. 2003; Frost 2007; Jablonski et al. 2008b). A third species, *C. meavae* from Leadu and Hadar (~3.4–3.3 Ma), occurs contemporaneously in eastern Africa. A small species of *Cercopithecoides*, *C. kerioensis*, from Lothagam (possibly from the Apak Member, ~4.2–5.0 Ma), may represent the earliest representative of the genus (Leakey et al. 2003). Finally, a recently named species, *C. alemayehui* (Gilbert and Frost 2008), known only from the type specimen from the Daka Member, Bouri Formation in the Middle Awash region of Ethiopia (~1.0 Ma), is apparently a late surviving species in eastern Africa.

As indicated in the diagnosis, all of these species are characterized by a distinctive suite of specialized cranio-dental features, including a short rostrum, a steep mandibular symphysis, a shallow and robust mandibular corpus that maintains a constant depth below the cheek teeth, a slightly expanded gonial region, and a P^3 with a reduced protocone (Frost and Delson 2002; Jablonski 2002; Jablonski et al. 2008b). In addition, all of the known species for which postcranials are known (not *C. kerioensis* or *C. alemayehui*) are apparently specialized for terrestrial locomotion (Frost and Delson 2002; Jablonski et al. 2008b).

Cercopithecoides sp.

Material assigned to this genus from Laetoli was first attributed to Colobinae gen. et sp. indet. by Leakey and Delson (1987). The sample consisted of two upper premolars from the Kohl-Larsen collection and two upper premolars from the Leakey collection, as well as a cuboid and a proximal femur assigned on the basis of size. The teeth were recognized as smaller than those assigned to cf. *Rhinocolobus* sp. Although only a few additional specimens of the small colobine from Laetoli have been recovered since 1998 (see Table 6.9), the sample now includes a partial mandible with P_3-M_3 of a female individual (EP 1425/04), which helps to resolve its taxonomic affinities (Fig. 6.16). The mandibular corpus in EP 1425/04 is low and robust, and does not increase in depth posteriorly, with a slightly convex inferior margin. In addition, the P^3 has a very reduced protocone, and the lower molars exhibit a very marked wear differential between the lingual and buccal cusps. This combination of morphological features is typical of *Cercopithecoides*, and serves to distinguish it from all other Plio-Pleistocene colobines. Attribution of the smaller colobine from Laetoli to *Cercopithecoides* seems well justified. However, the Laetoli material has a unique set of characters that distinguish it from all of the currently recognized species (see comparisons below). It certainly represents a different species of *Cercopithecoides*, but unfortunately the current material is not adequate to diagnose a new taxon. It is recognized here as *Cercopithecoides* sp.

Table 6.9 List of cranio-dental specimens from Laetoli referred to *Cercopithecoides* sp.

Specimen[a]	Loc.[b]	Horizon[c]	Element and comments[d]
MB Ma 42477			Rt P^4. [MB 1939.16.20]
MB Ma 42478			Rt P^3. [MB 1939.16.27]
LAET 75-3372a	21		Rt P^3
LAET 77-4565	?		Rt M_3
LAET 77-4578	7		Lt P^4
EP 201/98	10E	Tuffs 5-7	Rt M_3
EP 202/98	10E	Tuffs 5-7	Rt M_1
EP 1079/04	11	Tuffs 7-8	Rt M_3
EP 1425/04	6	Tuffs 5-7	Lt mandibular fragment with P_3-M_3. Female

[a] Specimen prefixes: MB Ma, Humboldt-Universität Museum für Naturkunde, Berlin, 1938–1939 Ludwig Kohl-Larsen collection; LAET, Kenya National Museum, Nairobi (on loan from Tanzanian National Museum), 1974–1979 Mary Leakey collections; EP, Eyasi Plateau Expedition, National Museum of Tanzania, Dar es Salaam, 1998–2005 Terry Harrison collections

[b] Localities: Numbers refer to the collecting localities designated by Leakey (1987a)

[c] Horizon: The stratigraphic provenience of the Kohl-Larsen collections and most of the specimens collected by Leakey are from unknown horizons within the Upper Laetolil Beds, except where indicated. The Harrison collections are mostly surface finds, and the stratigraphic provenience is recorded as a fossiliferous section between two marker tuffs within the Upper Laetolil Beds (unless more precise provenience is known for *in situ* specimens). All specimens are from the Upper Laetolil Beds

[d] Element and comments: lt, left; rt, right. Sex is determined by the size and morphology of the canines and P_3. The Museum für Naturkunde in Berlin has recently provided new accession numbers for their fossil mammal collections; the previous numbers, listed by Leakey and Delson (1987), are cross-referenced here

Description of Cranio-Dental Morphology

No cranial specimens of this taxon have been recovered from Laetoli. The mandibular corpus, known only from EP 1425/04, is quite low and robust (see Fig. 6.16). Mandibular robusticity at M_2 is 50.8 (mean breadth-height index of corpus at M_2).

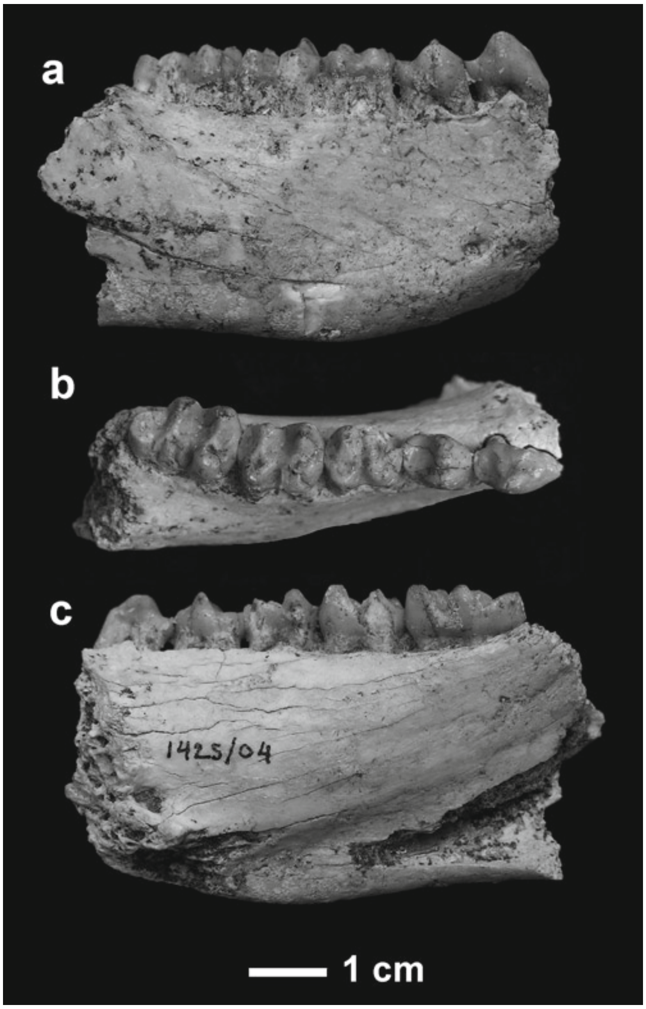

Fig. 6.16 *Cercopithecoides* sp. EP 1425/04, right mandibular corpus with P_3–M_3. (**a**) lateral view, (**b**) occlusal view, (**c**) medial view

It shallows slightly posteriorly below the cheek teeth. Laterally, the corpus is slightly concave below P_3-M_1, and dorsoventrally convex below M_2-M_3. There is no mandibular corpus fossa. The root of the ramus originates below M_3, and judging from the preserved portion it ascended just posterior to M_3 without overlap in lateral view. It lacks a distinct *prominentia laterales*. A single large elliptical mental foramen occurs below P_3/P_4, about two-thirds down the corpus from the alveolar margin. The inferior margin of the corpus is quite thick and well rounded, with a slightly convex anteroposterior contour. It curves medially as it passes posteriorly.

The symphyseal region is incompletely preserved, with the inferior margin missing. There is a low, rounded superior transverse torus, separated from the simian shelf by a well-defined genioglossal pit. A low rounded ridge, the mylohyoid line, originates from the simian shelf and passes posteriorly and superiorly along the medial face of the corpus, and eventually fades midway below M_3. The area superior to the mylohyoid line is generally convex. Below the line is a deeply concave area, at least anteriorly, representing the submandibular fossa.

The posterior wall of the alveolus for the lower canine is preserved anterior to P_3. It is evident that the root was short and slender, characteristic of female individuals, and that it abutted directly against the root of P_3, without a diastema. The cheek tooth row shows a slight lateral curvature.

Examples of the dentition are limited to the upper premolars and the lower cheek teeth (P_3-M_3) (Fig. 6.17, Table 6.9). Measurements of the dentition are presented in Table 6.10. P^3 is a narrow, subtriangular tooth with two cusps that are markedly different in elevation. The paracone is very tall, and cristodont, while the protocone is reduced to a tiny conical tubercle. The pre- and postparacrista are long and sharp, and subequal in length. The mesial and distal crests of the protocone are short and rounded. A transverse crest descends from the apex of the paracone and passes mesiolingually to terminate midway along the mesial marginal ridge. It does not reach the protocone. As a consequence, a deep longitudinal valley separates the cusps, and the mesial fovea is restricted to a small triangular basin along the mesial margin of the paracone. The distal fovea is expansive. The lingual face of the crown is narrow and strongly convex. The buccal face is remarkably tall, and mesiodistally convex, except for a shallow apico-basal groove mesially. The enamel margin extends further down on the mesiobuccal root than the distobuccal root.

P^4 shows the same suite of distinctive traits as P^3. The crown is ovoid to sub-triangular in shape with two main cusps. The paracone is well-developed, very tall, with sharp pre- and postparacrista. The protocone is weakly expressed, forming a small triangular tubercle on the lingual margin. A fine transverse crest descends from the apex of the paracone and passes lingually and slightly mesially to terminate at the base of the preprotocrista. It does not meet the protocone. The mesial fovea is a small, shallow triangular basin. In both upper premolars there are three roots that are partially or fully fused (unlike the separate roots seen in cf. *Rhinocolobus* sp.).

P_3 is relatively small, with a short mesiobuccal honing face for occlusion with the upper canine, at least in female individuals. The enamel junction of the honing face extends only a short distance onto the mesial root. The crown is relatively narrow, and the long-axis is aligned with the posterior cheek teeth. The protoconid is relatively low, and positioned almost centrally on the occlusal surface. The mesial crest is short and sharp. The lingual face is triangular and slightly convex, and is bordered by an indistinct lingual cingulum. The distolingual crest is low and rounded, and terminates basally at the lingual cingulum. The distal basin is a narrow, relatively small and shallow depression, bordered by a low distal marginal ridge.

P_4 is relatively long and narrow, with its long-axis aligned with the lower molar row. The protoconid and paraconid are

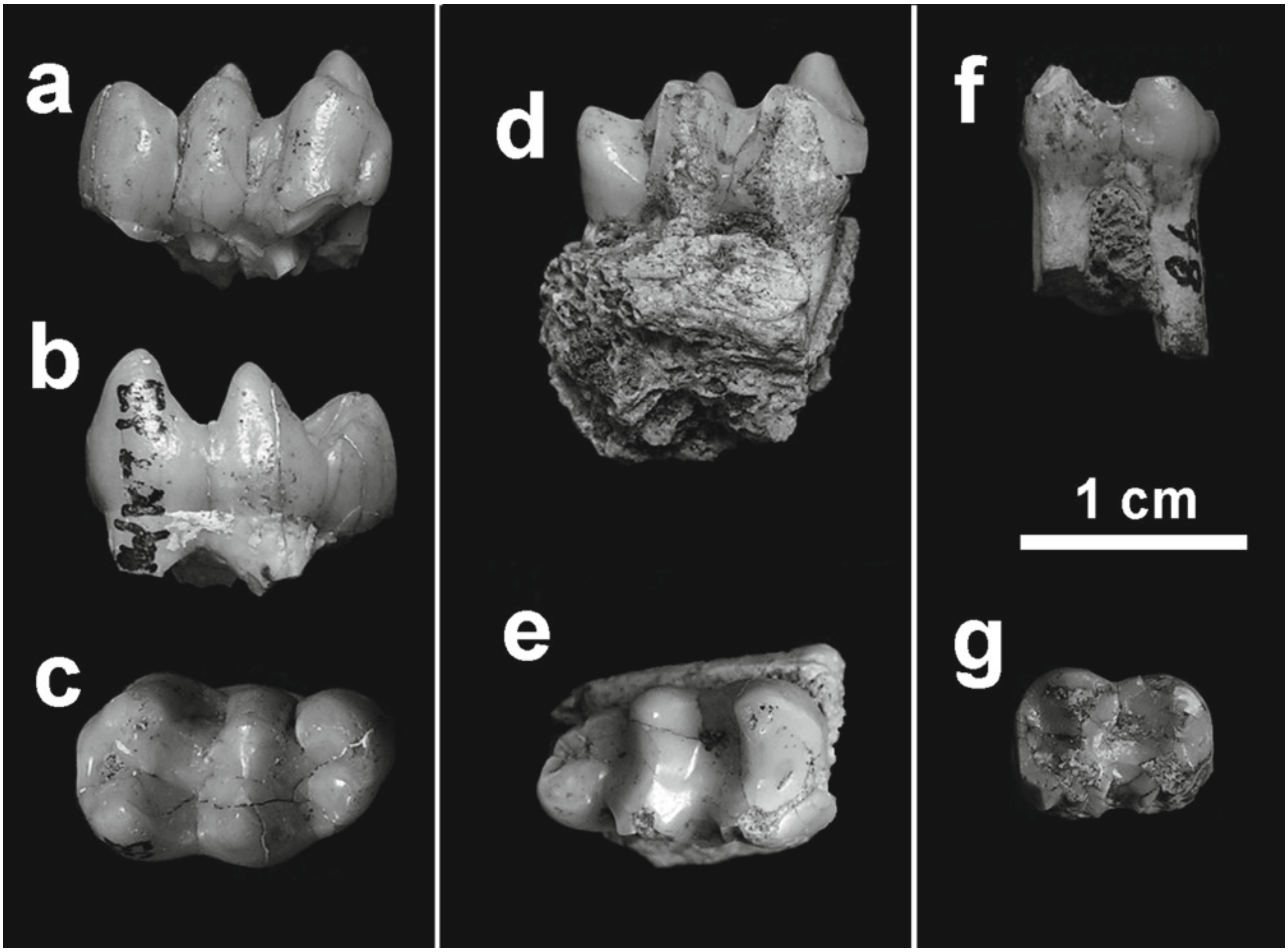

Fig. 6.17 *Cercopithecoides* sp. (**a**–**c**) EP 201/98, right M_3. (**a**) buccal view, (**b**) lingual view, (**c**) occlusal view. (**d**–**e**) EP 1079/04, right M_3. (**d**) buccal view, (**e**) occlusal view. (**f**, **g**) EP 202/98, right M_1. (**f**) lingual view, (**g**) occlusal view

transversely aligned, and connected by a well-developed crest. The protoconid is slightly more elevated than the paraconid. The mesial fovea is very short, so the cusps are positioned far mesially. There is a strong preprotocristid, but no preparacristid, so the mesial fovea opens lingually. The talonid basin is long and narrow. Crests descend distally from the apices of the two main cusps to meet the distal marginal ridge. There are no distal tubercles.

M_1 is a long and narrow tooth (the mean breadth-length index is 80.2), with relatively pronounced buccolingual waisting (see Figs. 6.16 and 6.17f–g). The lingual cusps are quite low for colobines, and are separated by a moderately deep V-shaped lingual notch that extends about halfway down the crown. The buccal cusps are lower, and exhibit a stronger wear differential than the lingual cusps. The protolophid and hypolophid are sharp, elevated and well-developed. The latter is slightly obliquely oriented relative to the transverse axis of the crown. The median buccal cleft forms a well-defined triangular platform between the protoconid and hypoconid. The mesial and distal buccal clefts are weakly expressed. The buccal marginal crest linking the protoconid and hypoconid is relatively low and rounded, but well-developed. The mesial and distal foveae are relatively small. The talonid basin is rectangular, being longer than broad, and relatively deep. The floor of the basin is transected by an ill-defined Y-shaped groove system, in which the main arm passes through the lingual notch and subsidiary arms pass towards the protoconid and hypoconid. Otherwise, the thin enamel covering is smooth and devoid of secondary wrinkling.

M_2 is much larger in size than M_1, with a marked size differential between them, but they are similar in overall proportions (the breadth-length index is 82.4). M_2 differs from M_1 in having less marked buccolingual waisting of the crown, broader and more expansive mesial and distal foveae, a deeper talonid basin, more elevated cusps and a deeper lingual notch that extends below mid-crown height.

M_3 is much longer and slightly broader than M_2 (with a mean breadth-length index of 60.8), with only a slight degree

Table 6.10 Measurements of teeth of *Cercopithecoides* sp. from Laetoli

Tooth	Dimension	N	Mean	SD	Range
UPPERS					
P3	MD	3	5.9	0.19	5.8–6.2
	BL	3	7.2	0.54	6.6–7.9
	BHT	3	8.1	1.07	6.9–9.5
	LHT	3	4.8	0.46	4.3–5.4
P4	MD	1	5.0	–	5.0
	BL	1	6.2	–	6.2
	BHT	1	6.8	–	6.8
	LHT	1	5.1	–	5.1
LOWERS					
P3	MD	1	9.5	–	9.5
	BL	1	5.2	–	5.2
	BHT	1	6.1	–	6.1
	HHT	1	9.2	–	9.2
P4	MD	1	7.8	–	7.8
	BL	1	6.1	–	6.1
M1	MD	2	8.1	–	7.9–8.2
	BLmes	1	6.3	–	6.3
	BLdist	2	6.5	–	6.3–6.6
M2	MD	1	9.1	–	9.1
	BLmes	1	7.5	–	7.5
	BLdist	1	7.2	–	7.2
M3	MD	4	12.5	0.38	12.1–13.0
	BLmes	3	7.6	0.31	7.3–8.0
	BLdist	4	7.4	0.46	6.8–8.0

BHT buccal height of crown, *BL* buccolingual breadth, *BLmes* buccolingual breadth mesially, *BLdist* buccolingual breadth distally, *LHT* lingual height of crown *HHT* length of mesiobuccal face of P$_3$, *MD* mesiodistal length *N* number of specimens, *SD* standard deviation

of buccolingual waisting of the crown (see Figs. 6.16 and 6.17a–e). The lingual cusps are moderately tall, and the lingual notch extends well below mid-crown height. The protolophid and hypolophid are well-developed, being elevated and sharp. The lophids are subparallel, and oriented distinctly obliquely to the transverse axis of the tooth. The mesial fovea is short, broad and very shallow, being restricted to a small crescentic fissure. The talonid basin is deep and rectangular in shape, being slightly longer than broad. It has a simple Y-shaped fissure pattern as in the other lower molars. The median buccal cleft is quite restricted compared with M$_2$, and forms an elliptical pit. Distally there is a short and relatively narrow heel, dominated by a low rounded, but voluminous hypoconulid. The hypoconulid is positioned to the buccal side of the midline, almost in line with the protoconid and hypoconid. It is connected to the hypoconid by a short, low and rounded crest. The distal marginal crest is low and indistinct, and it terminates at the base of the entoconid. There is no tuberculum sextum or other subsidiary tubercles. The distal fovea is a small triangular basin, which opens lingually at a shallow notch between the entoconid and the distal marginal crest. The size ratio of the lower molars (mean areas of M$_1$:M$_2$:M$_3$) is 77:100:139.

Comparisons

Although this taxon is poorly represented, it can be readily distinguished from cf. *Rhinocolobus* sp. based on its size and on its distinctive suite of morphological features. Although there is slight overlap in size of the lower premolars in female individuals, the lower molars in *Cercopithecoides* sp. are absolutely smaller (the combined molar area is 27.6% smaller on average), the upper premolars are relatively broader and higher crowned with a transverse crest that does not reach the protocone, a very reduced and more lingually positioned protocone, and a more convex distal margin, the P$_3$ and P$_4$ are relatively narrower and more longitudinally aligned with the long axis of the molar row, the lower molars are less hypsodont with shallower lingual notches, and M$_3$ has more obliquely oriented lophids, a longer distal heel and a more strongly buccally off-set hypoconulid. The mandibular corpus is more robust (breadth-height index of corpus at M$_2$ is 50.8 compared with 42.4 in cf. *Rhinocolobus* sp.) and it shallows slightly posteriorly rather than deepens.

As noted above, the very reduced P^3 protocone, the marked wear differential between the lingual and buccal cusps on the lower molars, and the specialized morphology of the mandibular corpus allow the Laetoli material to be assigned to *Cercopithecoides*. However, the taxon can be distinguished from all of the currently recognized species of the genus by its unique combination of features. It differs from *C. williamsi* in being smaller in overall dental size (see Table 6.8), having a relatively larger M$_3$, relatively broader lower molars, and lacking *prominentia laterales* on the mandibular corpus. *Cercopithecoides kimeui* is much larger in dental size, with much broader lower molars, less marked size differential between M$_1$ and M$_2$, relatively much smaller M$_3$ (the ratio of M$_1$:M$_2$:M$_3$ area is 83:100:114 in *C. kimeui* compared with 77:100:139 in *Cercopithecoides* sp.), and relatively lower and more inflated cusps. The Laetoli species is similar in overall dental size to *C. meavae* (Table 6.8), but differs in having a narrower P$_3$ with a shorter mesiobuccal honing face, broader and relatively larger P$_4$, less elevated lower molar cusps with shallower lingual notches and less well-developed lophids, greater size differential between M$_1$ and M$_2$, a narrower and slightly smaller M$_3$ with a shorter hypoconulid heel, and a mandibular corpus that is shallower and not as robust. *Cercopithecoides kerioensis* is much smaller in dental size than *Cercopithecoides* sp. from Laetoli, and differs in having a narrower P$_4$ with a small metaconid, relatively broader lower molars, a relatively smaller M$_3$ (the ratio of M$_2$:M$_3$ area is 100:114 in *C. kerioensis*, compared with 100:139 in *Cercopithecoides* sp.) with a reduced hypoconulid lobe, and a more slender mandibular corpus. Comparisons with *C. alemayehui* are hampered by the fact that few overlapping anatomical elements are preserved; only the upper premolars can be compared. The P^3 is significantly smaller in

C. alemayehui than in *Cercopithecoides* sp. from Laetoli. As discussed below, if the isolated postcranials from Laetoli referred to *Cercopithecoides* sp. are appropriately attributed, then this species is more arboreal than other species of *Cercopithecoides*.

Postcranial Remains of Fossil Cercopithecids from Laetoli

A small collection of cercopithecid postcranials has been recovered from Laetoli (Table 6.11). All of the specimens come from the Upper Laetolil Beds, with the exception of EP 1366/01, a proximal humerus from the Lower Laetolil Beds at Emboremony, and LAET 75-415, a metatarsal fragment from the Upper Ndolanya Beds at Loc. 14. Most of the finds are isolated and fragmentary, but two specimens are associated with cranio-dental specimens (LAET 74-247 and LAET 76-3904), and can be attributed with certainty to a particular taxon. Nevertheless, many of the other specimens can be provisionally assigned taxonomically, based on their size and morphology (see Table 6.11). Delson et al. (2000) have provided reasonable body mass estimates for *Pp. ado* and cf. *Rhinocolobus* sp. from Laetoli, based on dental dimensions (mean of 21 kg [19–25 kg] for males and 12 kg [11–13 kg] for females of *Pp. ado*, and mean of 34 kg [28–41 kg] for males and 17 kg [15–19 kg] for females of cf. *Rhinocolobus* sp.). Leakey and Delson (1987) briefly commented on many of the postcranial specimens recovered by Mary Leakey. The aim here is to provide a brief account of the anatomy, functional morphology, and taxonomic affinities of the postcranial specimens from Laetoli, including a number of new specimens recovered since 1998.

Table 6.11 List of cercopithecid postcranial specimens from Laetoli

Specimen[a]	Loc.[b]	Horizon[c]	Element and comments[d]
LAET 74-247	3		Lt proximal femur. Associated with cranio-dental remains of cf. *Rhinocolobus* sp.
LAET 74-327	7		Rt distal femur. According to Leakey catalogue, possibly same individual as 74-322. *Parapapio ado*
LAET 75-415	14	U. Ndolanya	Rt proximal metatarsal IV
LAET 75-672	1		Lt cuboid. *Parapapio ado*
LAET 75-744	1		Lt calcaneum missing the tuber calcis. Probably cf. *Rhinocolobus* sp.
LAET 75-1177	6		Rt talus, missing the head and neck. cf. *Rhinocolobus* sp.
LAET 75-1817	10W		Lt proximal femur. *Cercopithecoides* sp.
LAET 75-2283	10E		Lt calcaneus. Distal portion only. *Parapapio ado*
LAET 75-3611	22		Associated rt proximal metatarsal IV and V. *Parapapio ado*
LAET 76-3870	16		Lt talus. cf. *Rhinocolobus* sp.
LAET 76-3904	2		Associated lt cuboid, lt capitate, lt metacarpal I, lt metacarpal V, proximal phalanx (probably lt manual phalanx IV). Associated with P^4 of *Parapapio ado*
LAET 78-4907	22S		Rt proximal radius
LAET 78-4911	22	6.1 m below Tuff 7	Proximal manual phalanx (probably lt ray IV). *Parapapio ado*
LAET 78-4925	5	4.6 m above Tuff 3	Lt distal humerus. Papionin gen. et sp. indet.
EP 399/98	10E	Tuffs 5-7	Rt proximal humerus. *Parapapio ado*
EP 1001/98	9S	Below Tuff 2	Rt talus. *Parapapio ado*
EP 067/99	10E	Tuffs 5-7	Rt proximal humerus. *Cercopithecoides* sp.
EP 1052/00	10	Below Tuff 2	Distal end of proximal pedal phalanx. Probably from ray V
EP 210/01	3	Tuffs 7-8	Lt scaphoid. Probably cf. *Rhinocolobus* sp.
EP 1366/01	Emb. 1	L. Laetolil	Rt. proximal humerus. *Cercopithecoides* sp.
EP 896/03	10E	Tuffs 5-7	Rt proximal metatarsal IV. *Cercopithecoides* sp.
EP 774/03	9	Tuffs 5-7	Distal end of middle pedal phalanx
EP 142/04	22	Tuffs 5-7	Rt proximal radius. *Parapapio ado*
EP 902/05	10E	Tuffs 5-7	Terminal phalanx. *Parapapio ado*
EP 963/05	2	Tuffs 5-7	Distal end of proximal phalanx. Probably lateral manual digit

[a] Specimen prefixes: LAET, Kenya National Museum, Nairobi (on loan from Tanzanian National Museum), 1974–1979 Mary Leakey collections; EP, Eyasi Plateau Expedition, National Museum of Tanzania, Dar es Salaam, 1998–2005 Terry Harrison collections

[b] Localities: Emb. 1, Emboremony 1. Numbers refer to the collecting localities designated by Leakey (1987a)

[c] Horizon: The stratigraphic provenience of the Kohl-Larsen collections and most of the specimens collected by Leakey are from unknown horizons within the Upper Laetolil Beds, except where indicated. The Harrison collections are mostly surface finds, and the stratigraphic provenience is recorded as a fossiliferous section between two marker tuffs within the Upper Laetolil Beds (unless more precise provenience is known for *in situ* specimens). All specimens are from the Upper Laetolil Beds, except those listed as U. Ndolanya from the Upper Ndolanya Beds and L. Laetolil from the Lower Laetolil Beds

[d] Element and comments: lt, left; rt, right. Provisional taxonomic attributions are based on size and morphological comparisons

Postcranials Attributed to *Parapapio*

LAET 76-3904 consists of several postcranial elements – left cuboid, left capitate, left metacarpal I, left metacarpal V, and proximal phalanx (probably a left manual phalanx from ray IV) – associated with a P^4 belonging to *Pp. ado* (Fig. 6.18a, Table 6.11). The postcranial elements are much smaller than those of male *Papio anubis* and slightly larger than male *Lophocebus aterrimus*, and are therefore consistent in size with female *Pp. ado*.

The cuboid in LAET 76-3904 is relatively long proximodistally, with narrow proximal and distal facets. It is quite similar in proportions to the cuboid of *Lophocebus* and *Macaca*, and contrasts with the relatively short cuboid seen

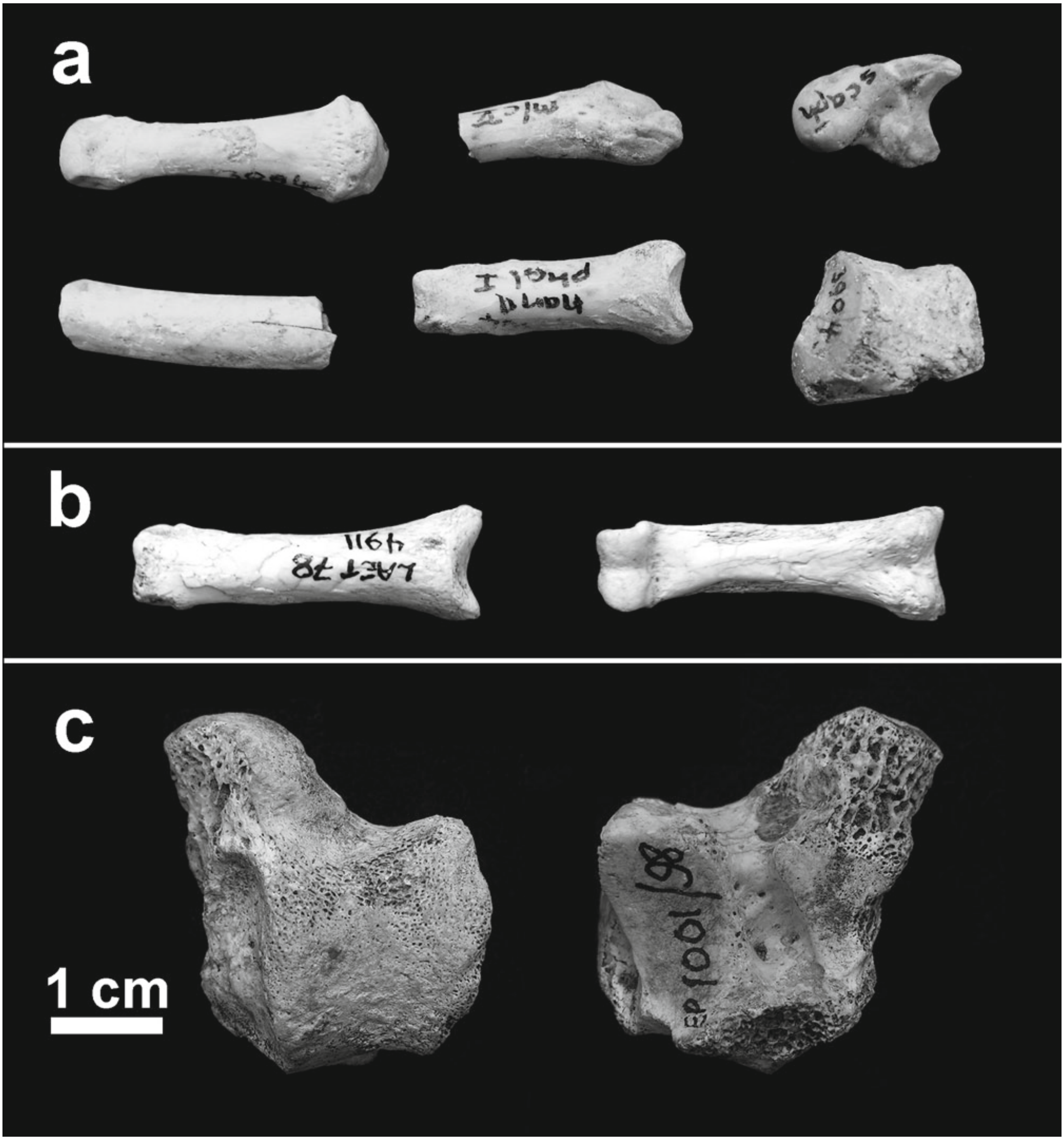

Fig. 6.18 *Parapapio*. Postcranial remains. (**a**) LAET 76-3904. Associated bones of left manus and left pes. *Top* row, left to right, metacarpal I, metacarpal V, capitate. *Bottom* row, left to right, metacarpal shaft fragment, proximal phalanx (probably ray IV), cuboid. (**b**) LAET 78-4911, proximal manual phalanx (probably left ray IV). *Left*, dorsal view. *Right*, ventral view. (**c**) EP 1001/98, right talus. *Left*, dorsal view. *Right*, ventral view

in *Papio*, *Nasalis* and *Colobus*. The relatively short cuboid in extant colobines is associated with proximodistal abbreviation of the tarsus in general (Strasser 1988). In dorsal view, the bone is subrectangular, narrowing slightly proximally, with a shallow waisting of the bone towards the proximal end. Again, this matches well with the pattern seen in *Lophocebus*, and it can be distinguished from those of *Papio* and *Colobus*, which taper more strongly proximally, and exhibit a more marked degree of waisting. In dorsal view, the facets for metatarsals IV and V are offset at a slight angle of about 20°. In proximal view, the dorsal surface is strongly convex and the proximal articular facet is U-shaped and quite narrow, similar to the pattern seen in *Lophocebus*. *Papio* and *Colobus* by contrast have wider proximal articular facets with a low arc of curvature. This indicates that the foot of *Pp. ado* had a relatively wide range of rotation at the calcaneocuboid joint, suggestive of a relatively mobile foot in pronation-supination. The calcaneal facet protrudes slightly proximally, as in *Lophocebus* and *Colobus*, but is less protuberant than in *Papio*. The plantar tubercle on the ventral surface is relatively well-developed as in *Papio*. In distal view, the two facets for metatarsals IV and V are similar in breadth, but the latter is slightly dorsoventrally shorter due to the tapering of the bone laterally. This is similar to the configuration seen in extant cercopithecids, except that the fossil tends to have a more squared-off rather than convex lateral margin. Medially, there are confluent articular facets for the navicular and the lateral cuneiform. Along the disto-dorsal margin of the medial aspect there is a second small D-shaped facet for the lateral cuneiform. The proximal facet for the lateral cuneiform is slightly larger than the distal facet, as is typical of cercopithecines (in colobines, the proximal facet is smaller or absent) (Strasser and Delson 1987; Strasser 1988). The configuration of the facets on the medial side of the cuboid is quite similar to that in *Lophocebus*. Laterally, there is a shallow groove for the peroneus longus tendon, as in *Lophocebus* and *Colobus*, which is not as deep as in *Papio*. There is a large reniform facet on the proximal aspect of the lateral face for contact with a sesamoid (*os peroneum*) in the tendon of peroneus longus (Le Minor 1987; Strasser 1988). Overall, the cuboid is very similar in morphology to that of *Lophocebus*; the main difference being the somewhat better developed plantar tubercle.

An isolated left cuboid (LAET 75-672), similar in size and morphology to the specimen described above, can also be attributed to *Pp. ado*. It differs, however, in being slightly shorter, having a slightly wider distal articular surface, and a more concave dorsal surface. These differences prompted Leakey and Delson (1987) to refer this specimen to the small indeterminate colobine (here recognized as *Cercopithecoides* sp.), but the two fossil cuboids are structurally and functionally so similar that there can be little doubt that they belong to the same taxon. Besides, LAET 75-672 has a relatively large proximal articular facet for the lateral cuneiform, typical of cercopithecines (Strasser and Delson 1987).

LAET 75-2283 is a fragmentary left calcaneus, lacking much of the tuber calcis. The bone is quite heavily weathered and abraded, and there appears to be a carnivore bite mark (2 mm in diameter) on the medial side of the heel process. The calcaneus is larger than that of male *Colobus gueреza*, and similar in size to male *Lophocebus albigena*, being consistent in size with female individuals of *Pp. ado*. Distally, the cuboid articular facet is lunate in shape, and markedly concave, with a deep ligamentous pit as in *Colobus* and *Lophocebus*. In *Papio*, by contrast, the facet is relatively shallower. The cuboid facet is tilted obliquely (28°) to the mediolateral plane of the sustentaculum tali, as in *Papio* (30°) and *Lophocebus* (33°), whereas in *Colobus* it is more horizontally aligned (10°). The distal segment of the calcaneus, anterior to the posterior talar facet, is moderately long as in extant papionins. The anterior and middle talar articular surfaces consists of two elliptical facets separated by a distance of only 1.5 mm, as in *Papio* and *Lophocebus*, whereas colobines have facets that are more widely separated. The middle talar facet forms an elongated ellipse as in papionins, rather than a small circular facet typical of colobines. There is a prominent roughened tubercle on the superior surface of the distal segment, just proximal to the cuboid facet, for the attachment of a well-developed talo-calcaneal ligament. The sustentaculum tali forms a small triangular platform. On its inferior surface there is a broad and shallow groove for the flexor hallucis longus. The posterior talar facet is short and broad, and quite elevated. The lateral margin of the calcaneus bows outwards, and is roughened for the peroneal tubercle. Inferiorly, there is a large anterior tubercle for attachment of the plantar ligament. In general, the morphology in LAET 75-2283 is most similar to papionins among extant cercopithecids in having a relatively long anterior segment, closely associated anterior talar facets, an elongated middle talar facet, an obliquely oriented cuboid facet, and a relatively large anterior tubercle on the plantar surface. It differs from terrestrial papionins, however, in having a shallower cuboid articular facet. Overall, the fossil calcaneus is a good match for that of *Lophocebus albigena*, and functionally it implies that *Pp. ado* was less specialized for terrestrial locomotion than *Papio*.

EP 1001/98 consists of a right talus in which the medial aspect is weathered and incomplete (Fig. 6.18c). Based on its size and general morphological similarity to extant *Papio*, it is assigned to *Pp. ado*. The head is incomplete, but it appears to have had a relatively strongly convex articular surface for the navicular. A short articular tail extends from the head onto the lateral margin of the neck. The neck is short and quite robust, with a neck angle of 22° relative to the long axis of the tibial trochlear facet and 46° to the posterior calcaneal facet, more similar to *Papio* than arboreal cercopithecids.

The cup-like facet for the medial malleolus of the tibia is deep and well defined, as in extant cercopithecines (Harrison 1982; Strasser 1988). Lateral to this facet, on the distal margin of the tibial trochlear facet is a small protuberance that acts as a bony "stop" for the distal tibia in full dorsiflexion of the foot (Harrison 1982; Conroy and Rose 1983). On the medial side, there is a weakly developed tubercle for the deltoid ligament. The tibial trochlear facet is quite broad, with a shallow midline groove and a moderate degree of posterior tapering. The lateral margin of the tibial facet is much more elevated than the medial margin, and more sharply keeled. The flange for the lateral malleolus of the fibula is relatively small. On the plantar surface the posterior calcaneal facet is quite narrow and is strongly arched. The anterior calcaneal facet is missing, and the middle facet is only partially preserved. The sinus tarsi is broad and relatively deep. A small lateral tubercle is present posteriorly. The posteromedial margin is damaged, so the development of the groove for the flexor tibialis is unknown (see Strasser 1988). There are well-developed pits on the plantar surface of the neck and on the lateral side of the talar body for strong talo-calcaneal and posterior talofibular ligaments respectively.

EP 1001/98 can be distinguished from the fossil tali attributed to cf. *Rhinocolobus* sp. (LAET 75-1177 and LAET 76-3870) in a number of important features. These include: lateral margin of tibial trochlear facet relatively more elevated and sharply keeled; cup for medial malleolus of tibia deeper and more extensive medially; a relatively small lateral flange for the medial malleolus (larger in *Papio*); neck relatively shorter and less medially angled (similar angulation in *Papio*, but the neck is longer); the talar body narrows more strongly posteriorly (even more pronounced in *Papio*); the sinus tarsi is broad and deep; and the deltoid tuberosity is less prominent. Among extant cercopithecids, the talus is most similar to *Papio*, but it does differ in having a shallower groove on the tibial trochlear facet, presence of a lateral tail on the articular surface of the head, a more strongly arched posterior calcaneal facet, a smaller flange for the medial malleolus, and a shorter neck. The elevated lateral margin and the degree of wedging of the tibial facet, the deep cup-like depression for the medial malleolar facet, and the short lateral malleolar flange all help to enhance stability of the talocrural joint during rapid parasagittal excursions. The angulation of the talar neck may relate functionally to a more adducted neutral position for the hallux. Overall, the morphology of the talus is consistent with *Pp. ado* being a semi-terrestrial or terrestrial cercopithecid, but somewhat less specialized in this direction than *Papio*.

LAET 75-3611 consists of associated right proximal metatarsals IV and V. The former is more complete, preserving more than half of the shaft (total length of fragment is 42.8 mm). Metatarsal V preserves only the base of the shaft (total length of fragment is 17.4 mm). Both metatarsals are slightly weathered and abraded. They correspond in size to male *Papio anubis*, so they could be attributed to either *Pp. ado* or cf. *Rhinocolobus* sp. based on size alone. However, morphologically they are most similar to extant papionins, which makes attribution to *Pp. ado* more likely.

In metatarsal IV, the proximal articular surface for the cuboid is a dorsoventrally tall and rectangular facet. It has an unusual tubercle on the dorsolateral margin that is not seen in extant cercopithecids. Laterally there is a single lunate-shaped facet for metatarsal V. Medially there is a pair of ovoid facets for metatarsal III, of which the superior facet is about twice the size of the inferior facet. This resembles the pattern seen in extant papionins, whereas in *Colobus* the two facets are united. Inferiorly there is a broad rectangular facet for articulation with a sesamoid. The interosseus pits on the medial and lateral side are relatively shallow. Based on the preserved portion of the shaft, the metatarsal appears to have been relatively robust, as in *Papio* and *Lophocebus*, compared with the relatively slender shaft in *Colobus*.

Metatarsal V in LAET 75-3611 bears a triangular facet for the cuboid that occupies the supero-medial corner of the proximal face, similar to that in *Lophocebus*. Laterally there is a well-developed and rugose tuberosity, which matches that in *Papio*. The tuberosity is smaller in *Colobus* and *Lophocebus*. Inferiorly and laterally there is a secondary tubercle with a smooth face for articulation with a sesamoid. Medially there is a large bilobed facet for metatarsal IV, which resembles that of *Papio* and *Lophocebus*. In *Colobus* the facet has a much smaller inferior lobe.

EP 399/98 consists of a slightly weathered right proximal humerus (Fig. 6.19 a–d). In terms of overall size, it falls in the lower end of the range for *Papio anubis*, and is consistent in size with *Pp. ado*. The head is globular, and implies relatively wide ranges of excursion at the shoulder joint in the parasagittal plane as well as in abduction-adduction. The mediolateral breadth of the head (25.0 mm) is subequal to its antero-posterior length (25.1 mm). In posterior view, the head of the humerus is egg-shaped, with a relatively broad and convex articular surface proximally in the mediolateral plane, but one that narrows and becomes less convex distally. In lateral view, the articular surface of the head has a relatively strong antero-posterior curvature. Proximally, the head extends very slightly above the level of the greater and lesser tuberosities, and the distance between the two tuberosities is quite wide (14.1 mm), which is most similar to the pattern seen in arboreal cercopithecids (Jolly 1967; Harrison 1989; Rose 1989; Larson 1993). The lesser tuberosity forms a rectangular, slightly rugose protuberance. The greater tuberosity is almost circular in outline and more rugose. The greater and lesser tuberosities are subequal in elevation, but the former is much larger (the maximum diameter of the lesser tuberosity is only 67% of the diameter of the greater tuberosity). The bicipital groove is shallow and broad compared with

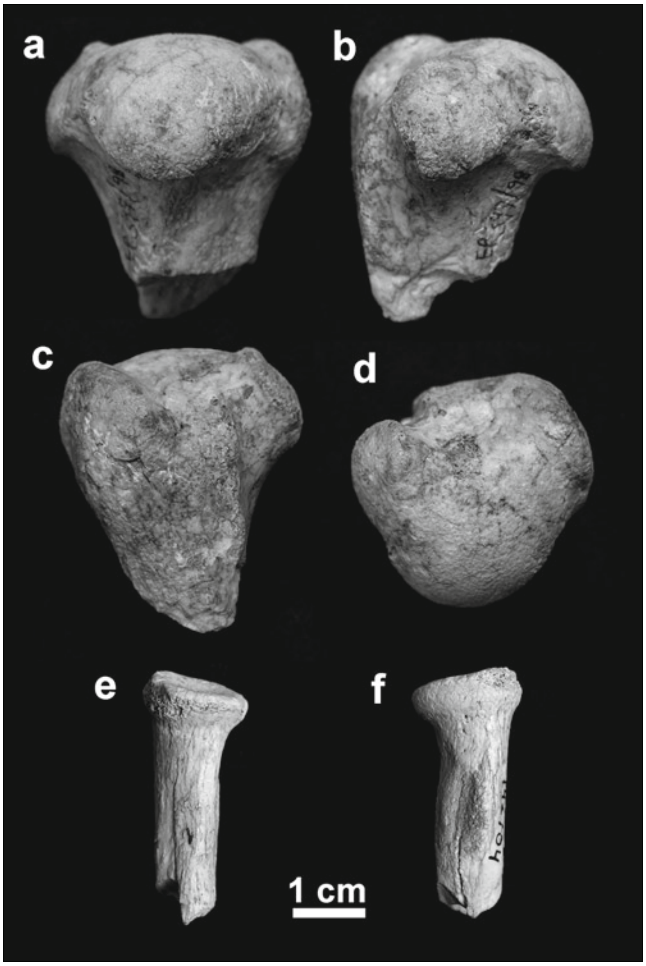

Fig. 6.19 *Parapapio*. Forelimb postcranial remains. (**a**–**d**) EP 399/98, right proximal humerus. (**a**) posterior view, (**b**) medial view, (**c**) anterior view, (**d**) proximal view. (**e**–**f**) EP 142/04, right proximal radius. (**e**) posterior view, (**f**) anterior view

Papio, and it is located relatively far laterally. It is bordered medially by a sharp keel that runs the length of the preserved portion of the shaft. The configuration of the articular surface of the head and the tuberosities indicate that *Pp. ado* was less specialized for terrestrial locomotion than extant *Papio,* being most consistent with semi-terrestrial or arboreal cercopithecids.

EP 142/04 represents the proximal end of a right radius (Fig. 6.19e–f). The specimen is slightly smaller than those of male individuals of *Lophocebus albigena*, but is quite similar morphologically. It is much smaller and differs in a number of important respects from LAET 78-4907 assigned to cf. *Rhinocolobus* sp. Attribution to a female individual of *Pp. ado* is reasonable given the size and morphology. The head is ovoid in shape, with a maximum diameter of 13.7 mm. and a perpendicular breadth of 12.5 mm. The breadth-length index of the radial head is 91.2, similar to that in extant cercopithecines and less elliptical than in colobines (Harrison 1989; Ciochon 1993). The articular surface of the head is tilted obliquely towards the antero-lateral side at an angle of 10° to a plane perpendicular to the long axis of the shaft. It has a deep, circular depression placed centrally on the proximal articular surface for articulation with the capitulum of the humerus. The rim surrounding the depression is broadest and most rounded antero-laterally. The posteromedial rim is narrower, and raised to form a sharply elevated lip. The tilt of the head and the raised rim provide enhanced stability of the elbow joint in semi-flexed and pronated positions (Harrison 1989; Rose 1993). The collar of the radial head forms a rim of uneven thickness, being thickest antero-medially (4.8 mm) and shallowest laterally (1.8 mm) (see Rose 1993).

The neck is relatively slender and elliptical in cross-section. It has a maximum diameter of 9.4 mm and a perpendicular breadth of 7.8 mm. The length of the neck, from the inferior rim of the head to the superior margin of the bicipital tuberosity, is relatively short (6.5 mm). The index of radial neck length (length of the neck x100/maximum breadth of the head) is 47.4, which falls within the ranges for *Macaca*, *Papio*, and *Mandrillus*, and is less than in *Lophocebus*, colobines and cercopithecins (which have relatively longer radial necks) (Harrison 1989). The bicipital tuberosity is represented by an ovoid roughened protuberance, with a slit-like central depression. The shaft below the tuberosity is subcircular in cross-section. The long-axis of the shaft is directed at an angle of 16° to the long-axis of the neck, implying a relatively bowed radial shaft. Curvature of the radius shaft tends to be pronounced in arboreal cercopithecids, associated with relatively well-developed forearm rotators (Rose 1993; Ciochon 1993).

Few features serve to distinguish extant cercopithecids in the proximal radius, so it has proved difficult in the past to deduce functional differences (Jolly 1967; Birchette 1982). Nevertheless, the proportions of the head, the length of the radial neck, and the bowing of the shaft are of some significance in this regard (Harrison 1989). EP 142/04 is most similar to *Lophocebus*, except that the neck is relatively longer in the latter. It differs from that of *Colobus* in having a more robust shaft, which is less strongly laterally bowed, and in having a shorter radial neck. Compared to that of *Papio*, the capitular depression on the head is deeper in EP 142/04, the neck is slightly longer, the bicipital tuberosity is less protuberant, and the shaft appears to be more strongly bowed laterally.

The left capitate of LAET 76-3904 is generally similar in morphology to that of *Lophocebus*. It differs primarily in being relatively proximo-distally longer, having a less globular scaphoid facet and less concave facet for metacarpal III. On the medial side of the distal end, there is a single continuous B-shaped facet for metacarpal II as in *Lophocebus*, whereas in *Papio* and *Colobus* it is subdivided into separate superior and inferior facets. The facet for metacarpal III on the distal aspect of the bone is strongly concave, most similar to *Lophocebus*, but relatively more pronounced. Ventral tapering of the metacarpal III facet is marked, being most similar in this respect to *Papio*. The palmar tubercle is weakly developed, as in *Lophocebus*. The articular facet for the hamate is only slightly convex.

Metacarpal I in LAET 76-3904 shows that the first manual ray in *Pp. ado* was relatively long and well-developed. The metacarpal is 23.5 mm long. The metacarpal length:capitate proximodistal length ratio in LAET 76-3904 is 1.87, compared with 1.69, 1.61 and 1.59 in *Papio*, *Lophocebus* and *Colobus* respectively. The presence of a relatively long first metacarpal adds support to the attribution of these associated postcranials to *Pp. ado* rather to one of the colobines, which presumably had reduced thumbs as in extant colobines. The distal articular surface for the proximal phalanx is low and broad, and narrows slightly dorsally. It is dorsoventrally shallower than in *Lophocebus* and *Papio*. The shaft is relatively stout compared to extant cercopithecids. The proximal articular surface is relatively broad with a strong mediolateral convexity, most similar to *Lophocebus*, suggesting a wide range of abduction of the thumb. It lacks the pronounced palmar beak of *Papio*. Overall, the impression is that *Pp. ado* had a well-developed and mobile thumb that was capable of wide ranges of motion in flexion-extension, and especially in abduction-adduction.

Only the proximal end of metacarpal V in LAET 76-3904 is preserved. The proximal facet is more similar to *Colobus* than *Papio* and *Lophocebus* in being relatively broad. The dorsoventral height and mediolateral breadth of the facet are 8.7 mm and 6.6 mm respectively. It differs from *Papio* in having a greater mediolateral convexity of the hamate facet and a relatively longer facet for articulation with metacarpal IV.

The proximal phalanx in LAET 76-3904 is probably from ray IV of the left manus. It is short and stout, with an index of phalangeal robusticity (mid-shaft breadth × 100/maximum length of phalanx) of 25.1. This falls outside the range of extant cercopithecids, with the exception of *Theropithecus gelada* (Harrison 1989). As noted by Jolly (1967, 1972) and Harrison (1989), relative phalangeal length is a good indicator of substrate utilization in cercopithecids, with short stout phalanges, such as those in *Pp. ado*, implying a high degree of terrestriality in their locomotor behavior. An index relating the length of proximal phalanx IV against the length of the first metacarpal discriminates terrestrial forms with long thumbs and short lateral digits, such as *Theropithecus gelada* (62.0), *Erythrocebus patas* (81.9), and *Papio anubis* (86.6), from arboreal and semi-terrestrial cercopithecids with short thumbs and long lateral digits, such as *Chlorocebus aethiops* (120.2), *Lophocebus* spp. (121.0), *Cercopithecus mitis* (123.1) and *Colobus guereza* (136.3). The index in the fossil is 83.9, most similar to terrestrial cercopithecids. The distal articulation is dorsoventrally low and narrow, being mediolaterally narrower than the midshaft diameter. It does not narrow dorsally, being most similar to *Papio* in this respect, implying joint stability in both flexion and extension. The midline groove of the trochlea of the distal articulation is relatively shallow, as in *Lophocebus*, and much shallower than in *Colobus* and *Papio*. The shaft is broad and quite flattened dorsoventrally, with a slight degree of curvature comparable to that in *Papio*. The flanges on the plantar surface for the flexor sheaths are strongly developed and located far distally, as in *Papio*. The proximal end is relatively broad, again as in *Papio*. Overall, the phalanx is most similar to those of terrestrial cercopithecids.

LAET 78-4911 is an isolated proximal phalanx, again probably from the ray IV of the left manus (Fig. 6.18b). It is morphologically similar to the previous specimen, but is somewhat larger, being comparable in size to the corresponding phalanx in male *Papio anubis*, and less robust. It is identifiable as a manual phalanx by its relatively narrow distal articulation with a shallow trochlear groove. The index of phalangeal robusticity is 19.7, which falls in the upper extreme of the range for arboreal cercopithecids, but most closely corresponds to terrestrial monkeys (Harrison 1989). The distal articular surface is relatively narrow, with a shallow trochlear groove, especially on the palmar aspect. The slight degree of curvature of the shaft matches that of *Papio*. The palmar surface of the shaft has long and deep grooves bordered by narrow crests extending along the medial and lateral sides for attachment of the flexor sheaths. These flanges are similar in location to those in *Papio*, but are longer and more strongly developed in the fossil. The proximal articular surface is similar to that in *Papio*, except that it is slightly narrower with a greater mediolateral concavity. Overall, the stout shaft and strong flexor sheaths are features that the fossil shares with the phalanges of *Papio*, while the shallow trochlear groove of the distal articulation and the more concave proximal articular facet are similar to arboreal cercopithecids, such as *Colobus* and *Lophocebus*. On balance, the morphology implies that *Pp. ado* was a semi-terrestrial form, less committed to terrestriality than *Papio*.

Trails of cercopithecid footprints are known from three sites (C, D, and F) at Laetoli Locs. 7, 11 and 10E respectively (Leakey 1987b). A total of 21 prints from the foot were complete enough to measure, and these ranged in length from 130–185 mm (from toe tip to center of heel; the total foot length would have been somewhat greater). This falls just below or in the lower end of the range of total foot length of extant adult male and female *Papio anubis* (152–229 mm for total hindfoot length; Berger 1972). Several prints also show clear impressions of the thumb. They closely resemble those of prints made by modern-day yellow baboons (*Papio cynocephalus*) (Bird 1987). Although there is some variation in overall size (exaggerated by the preservation), the prints are consistent with belonging to a single species. Based on size, the presence of a sizeable thumb, and their overall similarity to those of extant baboons, the prints were most likely made by *Pp. ado*. They confirm that at least one species of cercopithecid at Laetoli, presumably *Pp. ado*, spent time moving quadrupedally on the ground.

In summary, the postcranial specimens attributed to *Pp. ado*, when viewed collectively, exhibit a mosaic of features that are found in extant arboreal and semi-terrestrial papionins. It clearly was not as specialized for terrestriality as *Papio* or *Theropithecus*. Some aspects of the foot, especially the morphology of the cuboid and calcaneus, most closely resemble *Lophocebus*. The functional anatomy of the proximal humerus and proximal radius indicates specialization of the forelimb for semi-terrestrial and arboreal behaviors. In contrast, the talus and especially the robusticity of the phalanges indicate a greater degree of specialization for terrestrial quadrupedalism. The footprints at Laetoli provide additional support for this type of behavior. Overall, the balance of evidence suggests that *Pp. ado* was a relatively slender and agile semi-terrestrial monkey (generally similar, in terms of positional behavior, to *Cercocebus* and some species of *Macaca*), which was adept in the trees (where it probably spent the majority of its time), but frequently traveled on the ground to forage and to move between woodland and forest patches. Given its size and the short digits, *Pp. ado* would probably have preferred walking and running on large diameter supports in arboreal settings, but it was certainly capable of climbing into the upper part of the canopy to forage and to sleep at night.

Postcranial material, presumably of *Parapapio*, has been recovered from Plio-Pleistocene localities in South Africa, but they are all unassociated and have not yet been attributed taxonomically. Based on ecomorphological comparisons, Elton (2001) suggested that the different species of *Parapapio* in South Africa might have had different ecological preferences, with *Pp. jonesi* being more terrestrial than the larger *P. broomi*. The postcranial morphology (i.e., distal humerus and proximal femur) in *Pp.* cf. *jonesi* from Hadar is most comparable to that of extant arboreal macaques and mangabeys (Frost and Delson 2002), and was probably similar in its inferred locomotor behavior to that presented here for *Pp. ado*. Additional work is needed to document the diversity of positional behavior in *Parapapio* spp., but at least two species from the Pliocene of East Africa, *Pp. ado* (Laetoli) and *Pp.* cf. *jonesi* (Hadar), were apparently semiterrestrial papionins, more arboreally adapted than *Papio*, *Theropithecus* and *Mandrillus*, but still highly proficient as terrestrial quadrupeds.

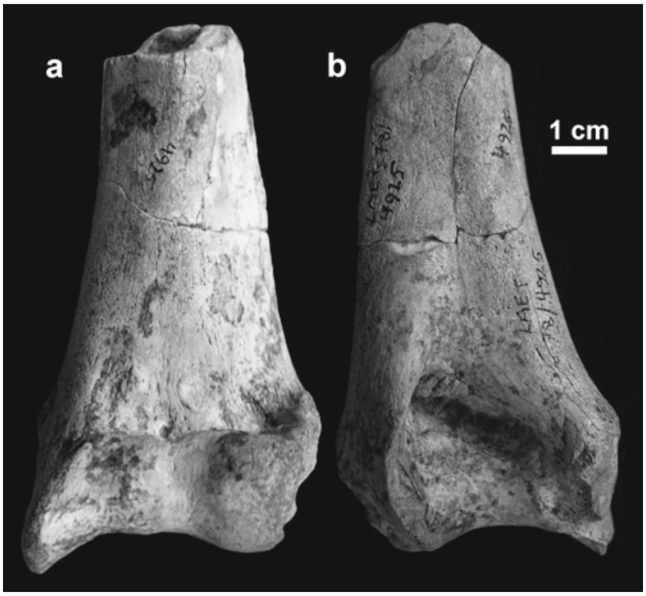

Fig. 6.20 Papionin gen. et sp. indet. LAET 78-4925. Left distal humerus. (**a**) anterior view, (**b**) posterior view

Postcranials Attributed to the Large Papionin

LAET 78-4925 is a left distal humerus (Fig. 6.20). It is somewhat larger than *Papio anubis* specimens (with average linear dimensions that exceed that of a large male anubis baboons by more than 12%). The size and morphology of the specimen indicate that it belonged to a large species of papionin, as initially suggested by Leakey and Delson (1987). However, it differs from *Papio* in the following respects: the distal articular surface is mediolaterally broader in relation to its proximo-distal height; the medial trochlear keel is less projecting distally (the index of relative flange projection, following Frost and Delson (2002), is 59.0 in LAET 78-4925, which is intermediate between extant colobines and terrestrial cercopithecines), and its medial margin is aligned more obliquely to the long-axis of the shaft; the lateral trochlear keel is better defined (although still relatively low), and positioned more medially; the capitulum is similar in degree of convexity, but the articular surface is more expanded distally, allowing greater stability in extended positions of the elbow; the medial epicondyle is slightly shorter and more posteriorly directed (directed posteriorly at an angle of 65° to the transverse axis of the distal articulation; this falls outside the values of extant arboreal cercopithecids, just within the range of semi-terrestrial monkeys, but close to the mean values for terrestrial cercopithecines, such as *Papio* and *Theropithecus* [Harrison 1989; Frost and Delson 2002]); the lateral epicondyle is better developed; the trochlear keel projects more distally in relation to the medial epicondyle; the olecranon fossa is proximodistally lower and it lacks the perforation commonly seen in *Papio*, thereby limiting full extension of the elbow joint; the fossa is not excavated under the lateral olecranon margin; the medial border of the olecranon is wider than the lateral border, whereas in *Papio* it is the opposite; the shaft is more stoutly constructed; the lateral supracondylar ridge, which runs along the length of the shaft fragment, is more weakly developed; the coronoid fossa is slightly shallower; and the radial fossa is not perforated.

The size and morphology of LAET 78-4925 clearly points to it belonging to a large terrestrial cercopithecid. The key functional features that indicate terrestrial behavior are as follows: projecting and sharply developed medial trochlear keel, a narrow trochlea, a less globular capitulum, a short and posteriorly directed medial epicondyle, a short lateral epicondyle, a deep and well delimited olecranon fossa, shallow radial and coronoid fossae, and a weakly developed lateral supracondylar keel (Jolly 1967, 1972; Harrison 1989; Ciochon 1993). However, it is less specialized in this direction than extant *Papio*, especially in the less projecting medial trochlear keel, the greater development of the capitular surface distally, and the less specialized morphology of the olecranon fossa for stabilizing the elbow joint in maximal extension.

Postcranials Attributed to cf. *Rhinocolobus* sp.

LAET 74-247 is a left proximal femur, lacking most of the shaft (Fig. 6.21a, b). The proximal femur is associated with cranio-dental specimens of cf. *Rhinocolobus* sp., and this seems to be a reasonable association based on its size and morphological characteristics. The maximum diameter of the head (24.8 mm) falls in the upper end of the range of male *Papio anubis* and *Nasalis larvatus*, and is, therefore, consistent in size with cf. *Rhinocolobus* sp.

The superior and inferior surfaces of the head are mediolaterally convex, with a marked extension of the articular surface laterally onto the dorsal surface of the femoral neck. There is a well-developed fovea capitis, 11.0 mm by 6.2 mm in diameter, which is relatively centrically placed. In anterior view, the head was positioned almost at the level of the apex of the greater trochanter, being only 1.9 mm lower. The height of the greater trochanter above the femur neck in relation to the diameter of the head yields an index of 27.8, most similar to modern-day arboreal colobines (Harrison 1982; Frost and Delson 2002; Frost 2007). The degree of projection of the greater trochanter influences the mechanical advantage of the gluteus medius and piriformis muscles acting about the hip joint (Smith and Savage 1956). A relatively low projection of the greater trochanter, as seen in LAET 74-247 and extant colobines, permits rapid extension of the hindlimb, important in arboreal leaping (Walker 1974). The neck is moderately short, as in extant colobines, with the marginal lip of the head being separated from the superior margin of the greater trochanter by 11.7 mm and from the inferior margin of the lesser trochanter by 24.1 mm. The neck is quite robust, with a minimum antero-posterior breadth of 13.9 mm. A short and stout femoral neck is an adaptation to resist greater bending stresses during arboreal leaping and climbing (Fleagle 1977; Fleagle and Meldrum 1988; Harrison and Harris 1996). The neck angle is difficult to measure precisely because much of the shaft is lacking, but it can be estimated to have been 123° relative to the long axis of the shaft, being most similar to extant colobines and arboreal cercopithecins (Harrison and Harris 1996; Frost and Delson 2002; Frost 2007). This feature is presumably functionally related to increased use of the hindlimb in abducted positions during arboreal climbing (Harrison 1982; Harrison and Harris 1996).

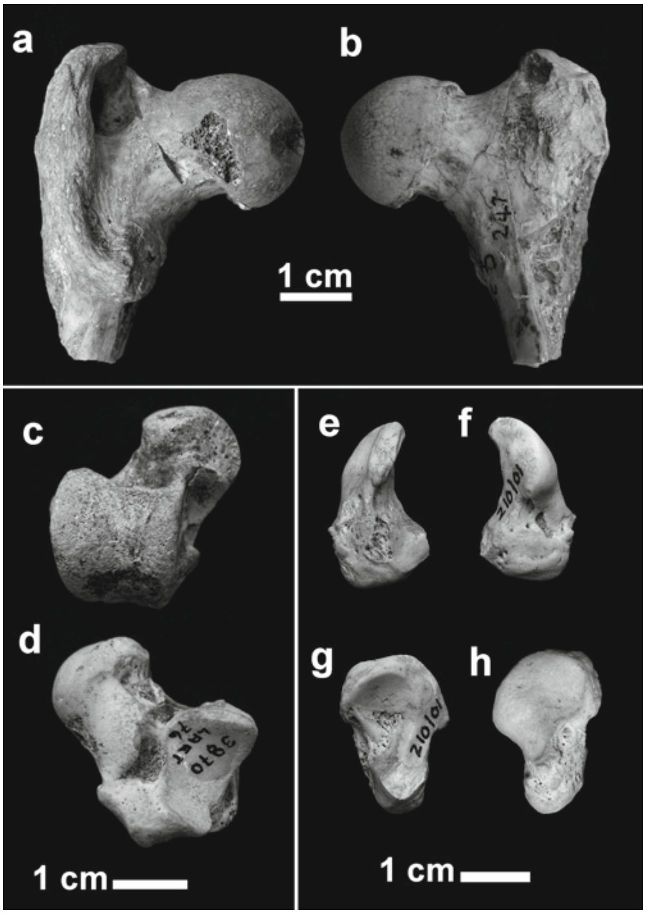

Fig. 6.21 cf. *Rhinocolobus* sp. Postcranial remains. (**a**, **b**) LAET 74-247, left proximal femur. (**a**) posterior view, (**b**) anterior view. (**c**, **d**) LAET 76-3870, left talus. (**c**) dorsal view, (**d**) ventral view. (**e–h**) EP 210/01, left scaphoid. (**e**) proximal view, (**f**) distal view, (**g**) medial view, (**h**) lateral view

The specimen differs from the proximal femur of *Papio* in having a more globular femoral head, a relatively lower greater trochanter in relation to the head, a slightly shorter neck with a greater neck angle, and a less prominent lesser trochanter. These features indicate that the femur belonged to a more arboreally adapted cercopithecid. Morphologically, it is quite similar to *Colobus* and *Piliocolobus*, but differs in having a slightly lower greater trochanter and a less globular femoral head. LAET 75-247 differs from the proximal femur of *Paracolobus mutiwa* (KNM-WT 16827), *Cercopithecoides williamsi* (KNM-ER 4420) and *Cercopithecoides meavae* (A.L. 2–70) in having a shorter and more robust neck, a higher neck angle, and a much less elevated greater trochanter. It is much more similar to *Paracolobus chemeroni* (KNM-BC 3), which is slightly larger, but corresponds in having a short neck and a low greater trochanter in relation to the position of the head. It differs, however, in having a higher neck angle. It appears to have been more specialized for arboreal behaviors than most of the other Plio-Pleistocene East African large colobines, with the exception of *Paracolobus chemeroni* (Birchette 1982).

LAET 74-327 is a right distal femur lacking the medial condyle. It is of comparable size to thsssse previous specimen, being as large as an extant male *Papio anubis*. The general morphology is comparable to that of *Colobus* in being relatively antero-posteriorly short in relation to the mediolateral width, and in having a low and broad patella groove, a low rounded lateral keel to the patella groove, and a lateral condyle that narrows distally. These features all indicate that the joint was less effectively stabilized during rapid flexion-extension at the knee compared to terrestrial cercopithecids.

LAET 76-3870 consists of a complete, but slightly weathered and abraded, left talus (Fig. 6.21c, d). It is slightly larger than the talus of a male *Papio anubis*, and thus conforms to the expected size for cf. *Rhinocolobus* sp. LAET 75-1177 is a more fragmentary right talus, lacking the head and neck, as well as the proximal portion of the talar body. Morphologically it is very similar to LAET 76-3870, but slightly smaller (the linear dimensions are on average 10.9% smaller).

The head of the talus has a strong mediolateral curvature as in extant colobines, and extends more medially than in *Papio* and *Lophocebus*. In distal view, the mediolateral long-axis of the head is relatively strongly obliquely tilted in relation to the subtalar plane (20° in LAET 76-3870) as in *Colobus*, and much more so than in terrestrial cercopithecids, such as *Papio*. The neck is moderately long and quite robust, being more similar in this respect to *Papio* and *Lophocebus*, than to *Colobus*, which has a relatively shorter neck. The talar neck in LAET 76-3870 is oriented mediolaterally at an angle of 34° to the long axis of the tibial articular facet and 63° to the posterior calcaneal facet. The head and neck are directed more medially than in *Papio* and *Lophocebus*, but are comparable to the orientation in *Colobus*. The orientation of the head and neck in LAET 76-3870 implies that the foot was well adapted for inverted positions during climbing. There is a well-developed cup-like articular facet on the medial side of the neck for articulation with the medial malleolus of the distal tibia. It is similar to that in *Colobus* and *Lophocebus*, and slightly shallower than that in *Papio*. The articular surface for the distal tibia has a relatively low and rounded lateral margin and a broad, shallow trochlear groove, as in arboreal cercopithecids, such as *Colobus* and *Lophocebus*. In *Papio*, by contrast, the lateral margin of the tibial facet is sharp and more elevated, with a deeper trochlear groove.

The tibial facet tapers proximally with a low degree of wedging (index of wedging = breadth of the tibial facet proximally × 100/ breadth of the tibial facet distally, including the malleolar cup; index = 65.8 in LAET 76-3870, compared to mean values of 50.8 in *Papio anubis*, 55.4 in *Cercopithecus aethiops*, and 54.9 in *Colobus guereza*; Harrison 1982). Wedging of the tibial facet is highest in terrestrial cercopithecids to maintain greater stability of the talocrural joint during parasagittal excursions, especially in positions of extreme dorsiflexion. The fibular flange on the lateral side of the talus for articulation with the malleolus of the fibula is only moderately developed, being intermediate between the short flange of *Colobus* and *Lophocebus*, and the strongly developed flange in *Papio*. The ligamentous pits on the posterolateral and posteromedial aspects of the talar body for the posterior talofibular and posterior talotibial ligaments are well developed compared with those in *Colobus*, but are not as strongly pitted as in *Papio*. The tubercle for the deltoid ligament is prominent as in *Colobus*, and more strongly developed than in *Lophocebus* and *Papio*. Proximally, the groove for the tendon of the flexor hallucis longus is broad and shallow compared with that in *Papio* and *Lophocebus*, and is more similar to the configuration in *Colobus*. There is a well-developed medial tubercle and a low lateral tubercle. On the plantar surface, the sulcus tali is quite deep and broad. The middle calcaneal facet is long and narrow, and gently convex. The posterior calcaneal facet is relatively wide, strongly concave dorsoventrally, and in LAET 76-3870 its long-axis is oriented at an angle of 83° to the long-axis of the tibial articular surface.

LAET 76-3870 and LAET 75-1177 share a number of key structural features with *Colobus* that distinguish it from terrestrial cercopithecids. These include: talar head with strong mediolateral convexity and marked dorso-ventral tilt; shallow articular depression for the medial malleolus of the tibia; relatively narrow flange for the lateral malleolus of the fibula; tibial articular surface that is only slightly wedged, with shallow trochlear groove, and less elevated lateral margin; shallow and broad groove for the flexor hallucis longus; well-developed deltoid tubercle; and moderately developed medial and lateral ligamentous pits. These features indicate that the foot of *Rhinocolobus* was similar to *Colobus* in being less specialized for stability during fast, parasagittal actions of the talocrural joint, and better adapted for inversion of the foot in arboreal climbing.

LAET 75-744 consists of a left calcaneus lacking the proximal end of the heel process. The specimen is slightly larger in size than male *Papio anubis*, and is much larger in size than LAET 75-2283 assigned to *Pp. ado*. Based on the size of the specimen an attribution to cf. *Rhinocolobus* seems reasonable. The cuboid facet is quite deep, as in *Colobus* and *Lophocebus*, compared with the relatively shallow depression in *Papio*. Its mediolateral alignment (6°) in relation to the plane of the sustentaculum tali, is much more similar to that of *Colobus* (10°), than to *Papio* (30°) and *Lophocebus* (33°). The anterior segment of the calcaneus distal to the posterior facet is moderately long, as in *Papio* and *Lophocebus*, and longer than in *Colobus*. Disposition of the anterior talar articular surface is obscured by weathering. The middle articular facet is long and elliptical as in cercopithecines, rather than subcircular as in colobines. The peroneal tubercle on the lateral side is massively developed, most similar to that of *Papio*. The sustentaculum tali is mediolaterally relatively short. Inferior to the sustentaculum tali is a shallow groove for the flexor hallucis longus. Inferiorly, there is a weakly developed anterior tubercle. The heel process is short and relatively deep dorsoventrally. Superiorly, a well-developed ridge runs from the posterior margin of the posterior talar facet onto the superior aspect of the heel process.

LAET 74-744 exhibits a mosaic of features found in extant cercopithecids, but several key aspects of the anatomy link it structurally and functionally to the calcanei of colobines: the low angle of mediolateral tilt of the cuboid articulation, the weakly developed anterior tubercle, and the short and deep heel process. It differs from the calcaneus of *Paracolobus mutiwa* (KNM-WT 16827) in being slightly smaller in overall size, and in having a slightly less concave cuboid facet, a smaller and less proximally positioned peroneal tuberosity, a narrower sustentaculum tarsi and a deeper heel process, but overall it is functionally similar.

EP 210/01 is a left scaphoid, missing the tip of the mediodistal beak (Fig. 6.21e–h). It is slightly larger in overall size than male specimens of *Papio anubis*, so it is consistent in size with the other postrcranial elements of cf. *Rhinocolobus* sp. The radial facet is dorsoventrally relatively wide, and reniform in shape. The inferior margin of the facet is smoothly rounded, while the superior margin is lipped. The remainder of the proximal surface to the medial side of the radial facet is a roughened subcutaneous surface, which forms a rounded, but stout prominence medially for the attachment of the abductor pollicis brevis. Distally, there is a crescent-shaped facet on the lateral margin for articulation with the lunate. Medial and inferior to the lunate facet is a deep, tear-drop shaped concavity for the capitate. Superior to the capitate facet is a smooth articular surface for the os centrale. Medially there is a distally directed beak-like process, which, although incomplete, was clearly a well-developed process. The superior face of the beak has the remnant of an elliptical facet for articulation with the trapezoid. Compared with the similar-sized scaphoid in *Papio*, EP 210/01 differs in having a mediolaterally broader and more convex articular surface for the radius, a more concave facet for the capitate, and a stouter proximo-medial tubercle for attachment of the abductor pollicis brevis. These features suggest that cf. *Rhinocolobus* sp. had a greater range of abduction-adduction of the wrist, a more mobile scaphoid-capitate joint, and an enhanced capability for abduction of the thumb.

The postcranials attributed to cf. *Rhinocolobus* sp. are readily distinguishable from those assigned to the two species of papionins at Laetoli, and they most closely resemble those of extant colobines, as well as some of the large extinct colobines from the Mio-Pliocene of East Africa. Although the material is too scanty to reconstruct its locomotor behavior, the large colobine from Laetoli was evidently specialized for arboreal quadrupedalism, including adaptations for climbing and leaping. The postcranials are generally similar to those of *Rhinocolobus turkanaensis*, *Paracolobus chemeroni* and *Paracolobus enkorikae,* which were apparently predominantly arboreal quadrupeds (Birchette 1982; Leakey 1982; Ciochon 1993; Frost and Delson 2002; Hlusko 2007), and they differ from those of the more specialized terrestrial fossil colobines belonging to *Cercopithecoides* spp. and *Pc. mutiwa* (Birchette 1982; Leakey 1982; Harris et al. 1988; Frost and Delson 2002; Jablonski et al. 2008b; Harrison, unpublished). Unfortunately, there are no overlapping skeletal elements to compare with *Kuseracolobus*, but the postcranial morphology does indicate that, like *Rhinocolobus* and *Paracolobus*, *Kuseracolobus* was predominantly arboreal (Hlusko 2006).

Postcranials of **Cercopithecoides sp.**

LAET 75-1817 is a left proximal femur (Fig. 6.22g, h). It is slightly smaller than the femur of female individuals of *Colobus guereza*, and, therefore, consistent in size with *Cercopithecoides* sp. The head is relatively globular, as in *Colobus* and *Lophocebus*, with a more extensive articular surface than *Papio*. The head is relatively small (diameter = 15.1 mm) in relation to the stout shaft, as in *Colobus*. The maximum diameter of the fovea capitis is 6.6 mm. The neck is relatively long, as in arboreal and semi-terrestrial cercopithecines. The length of the neck from the base of the head to the proximal margin of the lesser trochanter is 11.1. It is quite stout, with a minimum antero-posterior and mediolateral diameter of 8.8 and 12.5 respectively. The neck angle is 128° relative to the long-axis of the shaft, similar to that of extant colobines and arboreal cercopithecins (Frost 2007). *Papio*, *Mandrillus* and terrestrial cercopithecins differ in have a shorter neck with a lower neck angle (Harrison and Harris 1996; Frost and Delson 2002). The greater trochanter is not preserved, but it probably extended proximally to a level slightly above that of the head. There is a well-developed intertrochanteric line that reaches the lesser trochanter as in

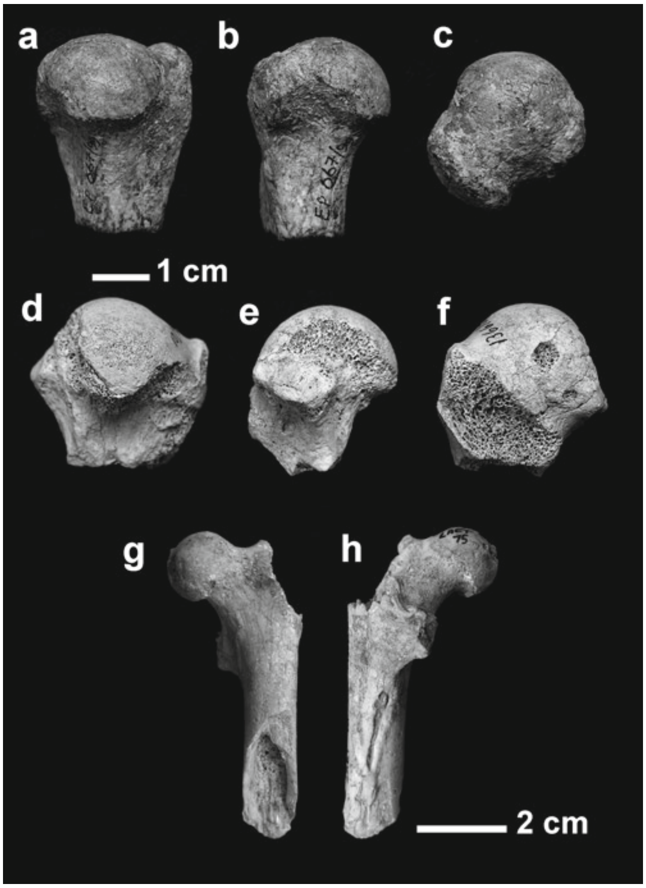

Fig. 6.22 *Cercopithecoides* sp. (**a**–**c**) EP 067/99, right proximal humerus. (**a**) posterior view, (**b**) medial view, (**c**) proximal view. (**d**–**f**) EP 1366/01, right proximal humerus. (**d**) posterior view, (**e**) medial view, (**f**) proximal view. (**g**–**h**) LAET 75-1817, left proximal femur. (**g**) anterior view, (**h**) posterior view. *Top* scale bar refers to **a–f**; *bottom* scale bar refers to **g–h**

Papio and *Cercocebus*, and is more distinct than in *Colobus*. Unlike *Colobus*, there is no indication of an intertrochanteric tubercle. The lesser trochanter is prominent, providing a mechanical advantageous insertion for the iliacus. Inferior to the lesser trochanter is a well-developed crest for the vastus medialis and pectineus muscles. On the posterior surface of the shaft, just distal to the greater trochanter, there are strong muscle markings leading down to the linea aspera, presumably for attachment of the quadratis femoris and adductor brevis muscles (Howell and Straus 1933). The shape of the head and orientation and length of the neck indicate a wide range of abduction and rotation at the hip, typical of arboreal cercopithecids. This inference is further supported by the strong muscle markings for thigh abductors, adductors and lateral rotators in the fossil. Overall, the impression is one of a small arboreal cercopithecid, quite similar in its overall morphology to extant African colobines.

EP 067/99 is a slightly weathered right proximal humerus (Fig. 6.22a–c). It is similar in size to male *Lophocebus albigena* and slightly larger than male *Colobus guereza*, and consistent in size either with female *Pp. ado* or *Cercopithecoides* sp. However, it is much smaller (average linear measurements are 23.7% smaller) and morphologically distinct from EP 399/98 assigned to *Pp. ado*, and it shares key features with extant colobines that indicate that the specimen is best attributed to *Cercopithecoides* sp. The head is globular, with a sub-circular shape in posterior view, and a strong degree of convexity in both the mediolateral and anteroposterior planes (see Harrison 1989). Compared with EP 399/98 of *Pp. ado*, the head is much more spherical, with a greater curvature of the articular surfaces. Estimated maximal ranges of motion in each plane (based on the angle of convergence of lines perpendicular to the margins of the articular surface) are 144° in the antero-posterior plane and 110° in the mediolateral plane. This compares to values in EP 399/98, assigned to *Pp. ado*, of 123° and 62° respectively. The articular surface of the head extends proximally well above the greater and lesser tuberosities (at least 2 mm), as seen in arboreal cercopithecids (Harrison 1989). Clearly, the humero-scapular joint was highly mobile and accommodated a wide range of flexion-extension, abduction-adduction and circumduction, typical of arboreal cercopithecids. The greater and lesser tuberosities are relatively low, elliptical protuberances. The greater tuberosity is slightly more elevated proximally than the lesser tuberosity. The bicipital groove is shallow and ill-defined.

EP 1366/01 is a right proximal humerus that is rather badly weathered, but the main morphological features are still discernable (Fig. 6.22d–f). This is the only cercopithecid specimen known from the Lower Laetolil Beds (from Emboremony 1). It is similar in size and morphology to EP 067/99, and it likely belongs to the same species. The head is globular with strong convexity of the articular surface in the mediolateral and proximodistal planes. Estimated maximal ranges of motion in each plane (based on the angle of convergence of lines perpendicular to the margins of the articular surface) are 144° in the antero-posterior plane and 95° in the mediolateral plane, similar to those of EP 067/99. The head projects proximally 6 mm above the level of the greater tuberosity, so is even more elevated than in EP 067/99. The bicipital groove is broad and shallow. It differs slightly from EP 067/99 in the shape of the head, in that it is relatively longer in the proximodistal diameter than in the mediolateral breadth, and the head narrows slightly posteriorly, rather than being sub-circular.

EP 896/03 consists of the proximal end and much of the shaft of a right metatarsal IV. The proximal articular surfaces are slightly abraded. The fossil is identical in size and similar in morphology to the corresponding element in male individuals of *Colobus guereza*. Based on its size it can be attributed with confidence to *Cercopithecoides* sp. The cuboid facet is not fully preserved, but it was evidently a rectangular facet that was dorsoventrally taller than wide. It is generally quite strongly convex in the dorsoventral plane, and the facet is tilted at an angle of 18° to the vertical plane relative to the long-axis of the shaft, so that it faces slightly dorsally. The facet also has a 10° mediolateral obliquity, with the medial margin being more distally placed than the lateral margin. A long and narrow crescent-shaped facet occurs on the lateral side of the proximal end for articulation with metatarsal V. It is dorsoventrally concave. Superiorly, the facet has a distinct beak, which allows greater stability at the metatarsal IV-V joint. Medially, the proximal end preserves the remnants of two distinct facets for metatarsal III. The superior facet is preserved almost intact. The inferior facet is abraded, leaving only a roughened ridge. The shaft is slender with a relatively strong dorsoventral curvature and a slight degree of curvature to the lateral side.

The postcranial specimens attributed to the smaller species of colobine from Laetoli are morphologically very similar to those of extant *Colobus*, and clearly indicate that this taxon was fully arboreal in its locomotor behavior. If this is the case, *Cercopithecoides* sp. from Laetoli contrasts with *C. williamsi*, *C. kimeui* and *C. meavae*, which all appear to have postcrania that indicate a relatively high degree of terrestrial specialization (Birchette 1982; Leakey 1982; Elton 2001; Frost and Delson 2002; Jablonski et al. 2008b). It is conceivable that the Laetoli species represents the primitive sister taxon of these three species (consistent with its greater antiquity), and that it retains the primitive postcranial morphology and arboreal habitus that was subsequently modified to allow increased terrestriality in the last common ancestor of later species of *Cercopithecoides*. This hypothesis could be tested with the recovery of postcranial material of *Cercopithecoides kerioensis* from Lothagam, which may represent the earliest and most primitive known member of this lineage (Leakey et al. 2003). Alternatively, if the postcranial distinctions are confirmed by additional associated discoveries, they might provide sufficient evidence to recognize the Laetoli taxon as a separate genus.

Unassigned Cercopithecid Postcranials

LAET 78-4907 is a right proximal radius. It is comparable in size to male *Papio anubis*, so it could be assigned to either *Pp. ado* or cf. *Rhinocolobus* based on size alone. The maximum length of the fragment is 45.3 mm. The head is elliptical in shape, with a shallow central depression, and a raised posterior lip. Although the head is weathered and abraded, it is possible to estimate its maximum diameter and perpendicular breadth at 21.0 mm and 17.3 mm respectively. The breadth-length of the radial head is 82.4, which indicates a relatively elliptical shape, most similar to extant colobines (Harrison 1989). The antero-posterior tilt of the head is quite marked (9°). The tilt of the head and the lipping provide for greater stability of the humero-radial joint in semi-flexed and pronated postures (Harrison 1989; Rose 1993). The neck is slender and appears to be relatively short. The bicipital tuberosity is well developed and rugose as in *Papio* and *Lophocebus*, and better developed than in *Colobus*. There is a strong ridge and depression on the antero-lateral side of the shaft for the attachment of the supinator.

LAET 75-415 consists of the proximal end and shaft of a right metatarsal IV. This is the only postcranial element of a cercopithecid known from the Upper Ndolanya Beds (Loc. 14). It is larger and more robust than the corresponding bone in *Papio*. Comparisons with LAET 75-3611, assigned to *Pp. ado*, show that LAET 75-415 is much larger (linear dimensions are almost 27% larger) and more robust. The specimen could belong to cf. *Rhinocolobus* sp., which has been provisionally identified from the Upper Ndolanya Beds, but given that we know so little about the cercopithecid community from this stratigraphic unit, it is probably best to leave the specimen unassigned.

The proximal end is eroded, so the details of the articular surfaces for the cuboid and metatarsals cannot be determined. The cuboid facet is subrectangular in shape. The elliptical superior facet for metatarsal III is separated from the cuboid facet by a distance of 1.6 mm. The inferior facet for metatarsal III is not preserved. Inferiorly there is a small rectangular facet for a sesamoid. The facet for metatarsal V on the lateral side is only preserved superiorly. Judging from its eroded base, it was a bilobed facet. The shaft appears to be very stout, being more robust even than in *Papio*.

EP 1052/00 is the distal end and portion of the shaft of a pedal proximal phalanx, probably from ray V. The distal end is relatively broad, with a trochleiform articular surface that narrows dorsally. The midline groove is quite deep. The shaft appears to have been relatively slender, with minimal dorsoventral curvature, and weak development of the flanges for the flexor sheaths. It is most similar to the morphology seen in *Lophocebus albigena*, except that the shaft is more slender and the flexor sheaths are less pronounced.

EP 963/05 is the distal end of a manual proximal phalanx from a lateral ray. The distal articular surface is relative broad and narrows dorsally, with a moderately well-developed midline groove. Medially and laterally, there are shallow depressions for the collateral ligaments. The shaft is dorsoventrally flattened, with sharp keels medially and laterally for the attachment of the flexor sheaths.

EP 774/03 is the distal end of a middle phalanx from the pes. The distal end is relatively broad, with a wide V-shaped trochlear groove separating the articular condyles. The shaft is quite slender, dorsoventrally compressed, and elliptical in section. It is very slightly dorsoventrally curved. It differs from *Papio* in having a dorsoventrally shallower distal articulation and a more slender shaft, and differs from *Colobus* in having a less curved shaft. Overall, like the previous three specimens, it is metrically and morphologically similar to the corresponding phalanges of *Lophocebus albigena*. It is likely that all of these phalanges belong to *Pp. ado* based on size alone, but without associated comparative material an attribution to cf. *Rhinocolobus* sp. cannot be entirely discounted.

EP 902/05 is a complete, slightly weathered terminal phalanx. It is from a lateral digit, but it is not possible to discern whether it is from the pes or manus. It is intermediate in size between those of male *Colobus guereza* and *Papio anubis*. It is a relatively quite long and slender phalanx. The proximal end is mediolaterally narrow. The articular surface for the middle phalanx is sellar, being dorsoventrally concave and mediolaterally convex. The shaft narrows distally. The inferior surface of the shaft has strongly developed ridges for the flexor sheaths that run the entire length of the shaft. The distal end has a well-developed but slender apical tuft. It differs from the terminal phalanges in *Papio* in being relatively longer, with a narrower apical tuft and less well-developed ridges for the flexor sheaths. By contrast, the terminal phalanges of *Colobus* are longer and more slender than in EP 902/05, with a narrower apical tuft, and more strongly developed flexor sheath ridges. An index of proximal breadth x100/maximum length of terminal phalanges (pedal and manual lateral digits combined) discriminates extant cercopithecids according to their substrate preference. Arboreal cercopithecids have relatively longer terminal phalanges (mean index: *Presbytis* spp. 44.9; *Colobus guereza*, 46.4; *Cercopithecus mitis*, 47.5) than terrestrial cercopithecids (*Theropithecus gelada,* 52.0; *Papio anubis*, 58.0; *Erythrocebus*, 63.2), with semi-terrestrial taxa broadly intermediate (*Macaca nemestrina*, 48.7; *Mandrillus sphinx,* 50.1; *Chlorocebus aethiops*, 55.1). The value for this index in EP 902/05 (53.0) falls into the ranges of all three categories, but it is most consistent with the breadth-length proportions of semi-terrestrial cercopithecids.

Temporal and Spatial Distribution of Fossil Cercopithecids at Laetoli

As noted in the “Materials and Methods” section, few cercopithecids have been recovered from the Lower Laetolil Beds ($n=1$) and Upper Ndolanya beds ($n=4$). The apparent rarity of cercopithecids from the Lower Laetolil Beds (>3.8 Ma) can probably be explained as a consequence of the relative paucity of vertebrate fossils from this stratigraphic unit. The same cannot be said for the Upper Ndolanya Beds (~2.6–2.7 Ma), which have yielded abundant fossils and a diverse fauna. Cercopithecids are clearly a rare component of the Upper Ndolanya assemblage, and this may be a true reflection of their relative abundance in the fauna during the late Pliocene. Different taphonomic variables operating in the Upper Ndolanya Beds compared with the Upper Laetolil Beds (i.e., the Upper Ndolanya fauna is much more taxonomically biased against small and medium-sized mammals) may have been a contributing factor, but it is unlikely to provide a full explanation for the difference (Su and Harrison 2008). Contrasting ecological settings, with the Upper Ndolanya Beds inferred to be more arid and less tree covered than the Upper Laetolil Beds (Kingston and Harrison 2007; Kovarovic and Andrews 2007; Su and Harrison 2008), may have been a more important factor in determining the relative abundance of cercopithecids. It may also be significant that all of the Upper Ndolanya cercopithecids are known from Loc. 7E, despite the fact that large samples of fossil vertebrates from these beds have been recovered from other localities, such as Locs. 14 and 18. The cercopithecids from the Upper Ndolanya Beds can be referred to *Pp. ado* and cf. *Rhinocolobus* sp., and based on the very limited samples available, they appear to be metrically and morphologically indistinguishable from those from the Upper Laetolil Beds.

Cercopithecids have been recovered from all of the main collecting localities at Laetoli, with the exception of Locs. 4, 15, 19 and 22E. This is presumably an issue of sampling, since cercopithecids only comprise 0.75% of the total mammalian assemblage (based on the Harrison collections), and these localities have yielded relatively small collections of fossil mammals (fewer than 250 specimens). In fact, most localities have cercopithecid counts that are close to the average representation relative to the total number of fossil mammals collected. A few localities (i.e., Locs. 9, 10E, 16, 21 and 22) have a significant over-representation of cercopithecids, and this may imply some ecological or taphonomic heterogeneity in the Upper Laetolil Beds. More importantly, perhaps, is the observation that cercopithecids are significantly under-represented in the lowermost horizons of the Upper Laetolil Beds below Tuff 5. Only two cercopithecid teeth were recovered by the author from horizons below Tuff 5 (i.e., at Locs. 5, 9S, 10, and 10W), whereas the expected count at these sites, based on the average representation of cercopithecids in the total mammalian samples from the Upper Laetolil Beds, should be 19. The rarity of cercopithecids in the Upper Laetolil Beds below Tuff 5 is confirmed when the samples from the Leakey and Harrison collections are combined, since only 4.3% ($n=10$) of the total cercopithecid sample comes from below Tuff 5, compared with over 20% of all mammals. Clearly, cercopithecids are relatively and absolutely rarer in the earlier part of the sequence of the Upper Laetolil Beds, and this presumably relates to an important ecological difference. Paradoxically, however, the evidence from the fauna and sedimentology indicates that the paleoecology was more mesic and probably more densely wooded below Tuff 5 compared to the upper part of the sequence, and this should presumably have provided ideal habitats for cercopithecids.

As noted above there is apparently a significant metrical trend in the cercopithecid samples from the Upper Laetolil Beds through time. Although the number of specimens from the early part of the stratigraphic sequence is relatively small, there does appear to be a significant increase in the size of the teeth in *Pp. ado* above Tuff 5 (see above for details). This may imply an evolutionary change in this lineage over the ~200 kyr duration of the deposition of the Upper Laetolil Beds. The samples are too small to examine temporal trends in cf. *Rhinocolobus* sp., but the single lower molar from below Tuff 5 is larger than all of the corresponding teeth from above Tuff 5.

Parapapio ado is the most common taxon at Laetoli, comprising almost two thirds (65.6 %) of the cercopithecid specimens. *Rhinocolobus* sp. is the next most common (28.8%), followed by *Cercopithecoides* (4.2%) and Papionini gen. et sp. indet. (1.4%) (Table 6.1). The small sample sizes do not allow an assessment of the representation of the different species at the various localities, but the two most common species appear to have co-occurred in approximately the same proportions (*Parapapio:* cf. *Rhinocolobus* = 69:31) at different localities throughout the Upper Laetolil Beds.

When compared with cercopithecid faunas from other Plio-Pleistocene localities in East Africa, there are two important observations that can be made about the composition of the Laetoli community. First is the absence of *Theropithecus*, which occurs as a common and ubiquitous species at Pliocene localities in East Africa.[1] Second is the relatively large proportion of colobines in the fauna. As has been noted previously, these two observations are linked, since it is the success of *Theropithecus* in the mid-Pliocene, from ~3.4 Ma onwards, that leads to the much greater dominance of papionins and the relative decline in the proportion of colobines (Frost 2007). Although the earliest recorded occurrence of *Theropithecus* is ~3.9 Ma, it does not become widely distributed in East Africa until ~3.4 Ma (Frost 2007; Leakey et al. 2008). Data on the relative abundance of colobines (in terms of specimen counts) in the late Miocene and Pliocene cercopithecid faunas from East Africa, show that colobines were an important component of the communities until around ~3.5 Ma (Table 6.12). From 3.5 Ma to 1.5 Ma, during the so-called "*Theropithecus* zone", *Theropithecus* becomes the dominant cercopithecid at all localities, and the proportion of colobines declines accordingly (Frost 2007; Leakey et al. 2008). The Upper Laetolil Beds sample the time period (~3.5–3.8 Ma), just preceding the appearance of *Theropithecus* at localities throughout East Africa, when colobines and *Parapapio* were still the dominant cercopithecids. However, Haile-Selassie et al. (2010) have recently reported that the cercopithecid fauna from Woranso-Mille, dating to 3.6–3.8 Ma, and contemporary with the Upper Laetolil fauna, was dominated by *Theropithecus oswaldi* aff. *darti* (see Am-Ado in Table 6.12). This might imply that there were important regional differences in the turnover of the cercopithecid fauna during the mid-Pliocene. Although cercopithecids are rare in the Upper Ndolanya Beds (~2.6–2.7 Ma), it is interesting that *Theropithecus* has not yet been recorded from this unit, even though it is very common at other late Pliocene localities in East Africa. Therefore, the absence of *Theropithecus* at Laetoli might not be simply a matter of time, but may reflect the lack of suitable habitats, including a requirement for closed woodland and/or permanent bodies of water.

Table 6.12 Relative proportion of colobines in the cercopithecid faunas from East African localities

Age	Locality	% Colobines
~6.5–7.4 Ma	Lower Nawata Mb., Lothagam, Kenya	21
~6 Ma	Lemudong'o, Kenya	100
~5.7 Ma	Adu-Asa Fm., Ethiopia	87
~5.2 Ma	Kuseralee Mb., Sagantole Fm., Ethiopia	31
~5.0–6.5 Ma	Upper Nawata Mb., Lothagam, Kenya	36
~4.4 Ma	Aramis, Ethiopia	56
~4.3–4.5 Ma	As Duma, Gona, Ethiopia	35
~4.1–4.4 Ma	Lonyumun Mb., Nachukui Fm., Kenya	31
~3.8–4.4 Ma	Asa Issie, Ethiopia	86
~4.1–4.2 Ma	Kanapoi, Kenya	23
~3.5–4.0 Ma	Upper Lonyumun, Moiti and Lower Lokochot Mb., Koobi Fora Fm., Kenya	28
~3.5–3.8 Ma	**Upper Laetolil Beds, Laetoli, Tanzania**	**33**
~3.5–3.8 Ma	Am-Ado, Ethiopia	9
~3.5 Ma	Kaiyumung Mb., Nachukui Fm., Kenya	7
~3.3–3.4 Ma	Sidi Hakoma Mb., Hadar Fm., Ethiopia	3
~3.2–3.3 Ma	Denan Dora Mb., Hadar Fm., Ethiopia	0
~2.5–3.5 Ma	Upper Lokochot and lower Burgi Mb., Koobi Fora Fm., Kenya	16
~2.5–3.4 Ma	Omo Shungura Mb. B-C, Ethiopia	5
~1.9–2.4 Ma	Omo Shungura Mb. E-G, Ethiopia	7
~1.6–2.0 Ma	Upper Burgi to KBS Mb., Koobi Fora Fm., Kenya	18

The line in the middle of the Table separates those localities (bottom of Table) with *Theropithecus*

Data sources: Eck 1976; Harris et al. 1988; Frost 2001, 2007; Feibel 2003; Leakey et al. 2003; Leakey et al. 2008; McDougall and Feibel 2003; Semaw et al. 2005; White et al. 2006; Hlusko 2007; Reed 2008; McDougall and Brown 2008; Frost et al. 2009; Haile-Selassie et al. 2010; Harrison, unpublished

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[1] Ndessokia (1990: 175, 177) added *Theropithecus darti* to the faunal list of the Upper Laetolil Beds, based on material from his 1987–1988 collections. The location of these collections is unknown, so the identification cannot be verified. Given the absence of *Theropithecus* from the extensive Leakey and Harrison collections, it seems unlikely that this taxon was present in the Upper Laetolil Beds. It is possible that the material on which the identification is based is intrusive from the Ngaloba Beds, in which *Theropithecus* is known to occur (Harrison, personal observation).

Conclusions

New fossil cercopithecids recovered from Laetoli since 1998 have increased the available sample to 237 specimens. Most of the material consists of isolated teeth, jaw fragments and postcranial bones from the Upper Laetolil Beds (~3.5–3.8 Ma), but four specimens are known from the Upper Ndolanya Beds (~2.6–2.7 Ma) and a proximal humerus has been recovered from the Lower Laetolil Beds (~3.8–4.3 Ma). The enlarged sample now available for study has helped to clarify the taxonomic affinities and paleobiology of the Laetoli cercopithecids. However, it has not been possible to assign most of the taxa to known species because of the lack of relatively complete cranial material and because of the fact that the Laetoli taxa appear to be unrecorded or poorly represented at other African Pliocene localities. Four species are represented at Laetoli: *Parapapio ado*, Papionini gen.et sp. indet., cf. *Rhinocolobus* sp., and *Cercopithecoides* sp.

Parapapio ado is the most common species at Laetoli, representing about two-thirds of the specimens. Comparisons of the dentition, mandible and face confirm that *Pp. ado* shares a suite of primitive features with other species of *Parapapio*, which distinguish it from all other genera of extant and extinct papionins. In terms of dental size and proportions, and features of the face, *Pp. ado* can be distinguished from all other species of *Parapapio* from the Plio-Pleistocene of East and South Africa. *Parapapio lothagamensis* and material referred to *Pp. ado* from Kanapoi and Allia Bay in Kenya appear to be morphologically quite distinct from other species of *Parapapio*, and probably represent a distinct genus. In this case, *Pp. ado* from Laetoli would represent the earliest record of the genus. Other than Laetoli, the only confirmed record of *Pp. ado* is from the contemporary Kaiyumung Mb. at Lothagam in northern Kenya (Leakey et al. 2003; Harrison, unpublished observation). The postcranial specimens attributed to *Pp. ado* indicate that it was a relatively slender and agile semi-terrestrial monkey (generally similar, in terms of positional behavior, to *Cercocebus* and some species of *Macaca*), adept in the trees, but frequently traveled on the ground (as confirmed by the fossil footprint evidence).

A second species of papionin, larger in dental size than *Pp. ado*, is represented at Laetoli by several isolated teeth. The teeth are similar in morphology to extant *Papio* sp., but are larger or fall in the upper end of the range of variation. They are most comparable in size to *Dinopithecus*. Unfortunately, the material is too fragmentary and too poorly represented to establish its precise taxonomic identity. It could belong to *Dinopithecus*, to a large species of *Papio*, or to a previously unrecorded species of large papionin. The material is left unassigned as Papionini gen. et sp. indet. A distal humerus attributed to this species indicates that it was large terrestrial cercopithecid, probably less specialized for terrestriality than extant *Papio*.

The colobines attributed to cf. *Rhinocolobus* sp. comprise 28.8% of the cranio-dental specimens from Laetoli. The lack of relatively complete skulls or crania hampers comparisons with other fossil colobines, and prevents a more precise taxonomic designation. Nevertheless, the material does provide adequate evidence to determine that the material does not belong to any of the previously recognized fossil colobine species from Africa, but without more complete cranial specimens it is not possible to diagnose a new species. In many aspects of the dentition, lower face and mandible it matches well with *Rhinocolobus turkanaensis*, but differs in having a shallower subnasal clivus, a less robust frontal process of the zygoma, a shorter rostrum, a maxillary sinus, a slightly shallower mandibular corpus, and relatively shorter upper and lower molars. With the recovery of more complete material, it is possible that this taxon could be assigned to a new genus. Although the postcranial material is insufficient to reconstruct its locomotor behavior, the large colobine from Laetoli was specialized for arboreal quadrupedalism, similar to *Rhinocolobus turkanaensis*, *Paracolobus chemeroni* and *Paracolobus enkorikae*.

The somewhat smaller species of colobine from Laetoli was initially attributed to Colobinae gen. et sp. indet. (Leakey and Delson 1987). With the recovery of additional specimens since 1998, including a partial mandible, the taxonomic affinities of this species have been clarified. Specialized features of the dentition and mandible serve to link it to *Cercopithecoides* and to distinguish it from all other Plio-Pleistocene colobines. However, the Laetoli material has a unique set of characters that distinguish it from all of the currently recognized species of *Cercopithecoides*, and it certainly represents a new species. Unfortunately, the current material is not adequate to diagnose a new species, so it is recognized here as *Cercopithecoides* sp. The postcranial specimens attributed to this species are very similar to those of extant *Colobus*, and clearly indicate that it was fully arboreal in its locomotor behavior. If this is the case, *Cercopithecoides* sp. from Laetoli contrasts with later species of this genus, which all appear to have had postcrania that indicate a relatively high degree of terrestriality.

Analysis of the distribution of fossil cercopithecids at Laetoli provides some provisional evidence of spatial patterning and temporal trends. Taking into account sampling differences, it appears that the two most common species of cercopithecids at Laetoli, *Pp. ado* and cf. *Rhinocolobus* sp., are represented in approximately the same relative proportion (ratio of 69:31) across the individual collecting localities. There is also evidence that cercopithecids are relatively underrepresented components of the mammalian fauna below Tuff 5 compared with later in the Upper Laetolil sequence. This presumably relates to key ecological differences through time during the deposition of the Upper Laetolil Beds. However, the evidence available indicates that the paleoecology below Tuff 5 was possibly slightly more mesic and more densely wooded than above Tuff 5, and this would presumably have provided equally suitable habitats for cercopithecids (Tattersfield 2011). Although the samples are relatively small, there is apparently a significant increase in size of the dentition of *Pp. ado* above Tuff 5, implying an evolutionary trend in this lineage over the course of the ~200 kyrs represented by the Upper Laetolil Beds.

Compared with the faunas from other Plio-Pleistocene localities in East Africa, two important and related observations can be made about the composition of the Laetoli cercopithecid community: the absence of *Theropithecus* and the relatively large proportion of colobines in the fauna. Colobines represent an important component of cercopithecid communities from East Africa during the late Miocene and early Pliocene. From 3.5 to 1.5 Ma, *Theropithecus* becomes the dominant cercopithecid at all localities, and the proportion of colobines declines accordingly. The Upper Laetolil Beds sample the time period, just preceding the appearance of *Theropithecus* at localities throughout East Africa, when colobines and *Parapapio* were still the dominant cercopithecids.

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Chapter 7

Hominins from the Upper Laetolil and Upper Ndolanya Beds, Laetoli

Terry Harrison

Abstract Renewed investigations at Laetoli in northern Tanzania have led to the recovery of a number of new fossil hominins. A lower canine and a mandibular fragment from the Upper Laetolil Beds (3.63–3.85 Ma) are referred to *Australopithecus afarensis*, and an edentulous maxilla and a proximal tibia from the Upper Ndolanya Beds (2.66 Ma) are attributed to *Paranthropus aethiopicus* and Hominini gen. et sp. indet., respectively. Additional hominin specimens from earlier collections are described here for the first time, including three specimens of *A. afarensis*, probably from the Upper Laetolil Beds, and a possible cranial fragment of an infant from the Upper Ndolanya Beds. The chronology and provenance of the Laetoli hominins are reconsidered. The species *afarensis* is provisionally retained in *Australopithecus* to reflect its anatomical and paleobiological similarities to the other species of *Australopithecus sensu lato*, but a reasonable case could be made on phylogenetic grounds to transfer it to *Praeanthropus*. It has been argued that the Laetoli sample of *A. afarensis* is morphologically and temporally intermediate between *A. anamensis* and the Hadar sample of *A. afarensis*, and that *A. anamensis* and *A. afarensis* represent a single anagenetically evolving lineage. However, the new specimens from the Upper Laetolil Beds help to close the gap between the Laetoli and Hadar samples, and a critical assessment of the morphological variation in the two samples indicates that there are few consistent differences separating them. Rather than being intermediate in morphology, the Laetoli sample appears to represents an earlier population of *A. afarensis*, with almost the full complement of derived features that characterizes the Hadar sample, but still retaining a few primitive traits. The morphological features that distinguish *A. anamensis* from *A. afarensis* are much more extensive, and these provide adequate justification for the recognition of a species distinction. The evidence best fits an evolutionary model involving a cladogenetic event rather than a simple anagenetic transformation of a single unbranched *anamensis-afarensis* lineage through time. The *Paranthopus aethiopicus* specimen from the Upper Ndolanya Beds represents the oldest securely dated specimen definitively attributable to this taxon and the first definitive record outside of the Turkana Basin. The *Paranthropus* clade probably immigrated into eastern Africa before 2.7 Ma, and became widely distributed throughout the region soon thereafter. The timing and biogeographic patterning of the occurrence of *Paranthropus* and *Homo* suggest that their respective dispersals into eastern Africa were not coincident or synchronous. *Homo* appeared somewhat later than *Paranthropus* across most of eastern Africa, except in the Awash region of Ethiopia where *Homo* makes its first appearance in the absence of *Paranthropus*. These differences in the timing and distribution suggest that *Paranthropus* and *Homo* may have had different biogeographic histories, and that their ancestral species may have had different ecological requirements at the time of their initial influx into eastern Africa.

Keywords Pliocene • Tanzania • *Australopithecus afarensis* • *Paranthropus aethiopicus* • Laetoli • Hadar • Taxonomy

Introduction

Laetoli in northern Tanzania has yielded a relatively small but important collection of early hominins from the mid-Pliocene Upper Laetolil Beds, dated from ~3.63–3.83 Ma (Weinert 1950; White 1977, 1980a, 1981; Leakey 1987a, b; Kyauka and Ndessokia 1990). Although there has been debate about the number of taxa represented at Laetoli, and what these taxa should be named (Tobias 1980a, b; Johanson 1980a; Day et al. 1980a; White et al. 1981; Olson 1981, 1985; Logan et al. 1983; Ferguson 1986, 1987, 1988; Falk et al. 1995; Groves 1996; Senut 1996; Kimbel et al. 2004; Grine et al. 2006), there is current consensus that the remains can all be attributed to a single species, *Australopithecus afarensis* (or *Praeanthropus afarensis*) (see Table 7.1). The Laetoli sample of *A. afarensis* ($n=33$) is not as large as the collections from Hadar (330 specimens; Kimbel and Delezene 2009), and the specimens tend to be isolated elements and

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Table 7.1 Taxonomy and synonymy list of *Australopithecus afarensis*

Superfamily: Hominoidea Gray, 1825
Family: Hominidae Gray, 1825
Subfamily: Homininae Gray, 1825
Tribe: Hominini Gray, 1825
Genus: *Australopithecus* Dart, 1925
Species: *A. afarensis* Johanson, 1978

Synonymy
1948 – *Praeanthropus* Hennig, 1948 – Hennig (1948) [*nomen nudum*, no fixation of type species]
1950 – *Meganthropus africanus* Weinert, 1950 – Weinert (1950)
1954 – *Australopithecus africanus transvaalensis* Broom, 1936 – Robinson (1954) [*partim*]
1955 – *Praeanthropus africanus* (Weinert 1950) – Senyürek (1955)
1978 – *Australopithecus afarensis* Johanson, 1978 – Hinrichsen (1978)
1978 – *Australopithecus afarensis* Johanson, White and Coppens, 1978 – Johanson et al. (1978)
1980 – *Australopithecus africanus afarensis* Johanson, 1978 – Tobias (1980b)
1980 – *Australopithecus africanus aethiopicus* Tobias, 1980 – Tobias (1980b) [*nomen nudum*, conditionally proposed]
1980 – *Australopithecus africanus tanzaniensis* Tobias, 1980 – Tobias (1980b) [*nomen nudum*, conditionally proposed]
1981 – *Paranthropus africanus* (Weinert 1950) – Olson (1981)
1981 – *Homo* (*Australopithecus*) sp. indet. – Olson (1981)
1983 – *Dryopithecus* (*Sivapithecus*) *sivalensis* (Lydekker, 1879) – Ferguson (1983)
1984 – *Homo antiquus* Ferguson, 1984 – Ferguson (1984) [junior homonym, name preoccupied by *Homo antiquus* Adloff, 1908]
1985 – *Homo* (*Australopithecus*) *aethiopicus* (Tobias 1980b) – Olson (1985) [junior homonym, name preoccupied by *Homo aethiopicus* Bory de Saint-Vincent, 1825]
1987 – *Australopithecus africanus miodentatus* Ferguson, 1987 – Ferguson (1987)
1996 – *Australopithecus antiquus* (Ferguson 1984) – Senut (1996)
1996 – *Australopithecus bahrelghazali* Brunet et al., 1996 – Brunet et al. (1996)
1999 – *africanus* Weinert, 1950 – name suppressed by the International Commission on Zoological Nomenclature for the purposes of the Principle of Priority but not for those of the Principle of Homonymy, Opinion 1941
2000 – *Praeanthropus afarensis* Johanson, 1978 – Wood and Richmond (2000)

more fragmentary. However, the sample does represent the second largest sample of *A. afarensis*, and perhaps more significantly derives from an earlier time period (the hominins from Hadar date from ~3.0–3.4 Ma; Kimbel et al. 2004; Campisano and Feibel 2008). The fossil hominins from Woranso-Mille (~3.57–3.8 Ma) in Ethiopia, with 30 specimens recovered to date, including a partial skeleton (Haile-Selassie et al. 2007, 2010), have not yet been formally taxonomically assigned, but if they later prove to belong to *A. afarensis* they would provide another important sample of this taxon contemporary with Laetoli.

The site of Laetoli is unique for the remarkable preservation of trails of footprints, presumably of *A. afarensis* (see Leakey and Hay 1979; Clarke 1979; Day and Wickens 1980; White 1980b; Charteris et al. 1981, 1982; Hay and Leakey 1982; Leakey 1978, 1979, 1981, 1987c; White and Suwa 1987; Tuttle 1985, 1987, 1990, 1994, 2008; Tuttle et al. 1990, 1991a, b, 1992; Feibel et al. 1996; Agnew and Demas 1998; Meldrum 2004; Sellers et al. 2005; Berge et al. 2006; Raichlen et al. 2008). This evidence has been used to confirm earlier inferences based on functional morphology of the skeletal remains that bipedalism was an important component of the terrestrial locomotor behavior of mid-Pliocene hominins (e.g., Johanson et al. 1982; Stern and Susman 1983; Susman et al. 1984, 1985; Latimer et al. 1987; Latimer 1991; Susman and Stern 1991; McHenry 1986, 1991, 1994; Stern 2000; Ward 2002).

Fossil hominins have not yet been recovered from the Lower Laetolil Beds (~4.4–3.85 Ma; Deino 2011), and are rare in the younger stratigraphic units that overlie the Upper Laetolil Beds, although indirect evidence of their presence is provided by the occurrence of stone tools in the Olpiro Beds (~2.0 Ma; Deino 2011) and Ngaloba Beds (Late Pleistocene) (Harris and Harris 1981; Leakey 1987a; Hay 1987; Ndessokia 1990). Mary Leakey's expeditions did recover a relatively complete cranium of *Homo sapiens* from the Late Pleistocene Upper Ngaloba Beds. Most recently, Harrison (2002) reported specimens attributable to *Paranthropus aethiopicus* from the Upper Ndolanya Beds, dated to 2.66 Ma (Deino 2011) (see Fig. 7.1). The history of discovery of *A. afarensis* and the other hominin finds from Laetoli is briefly reviewed below.

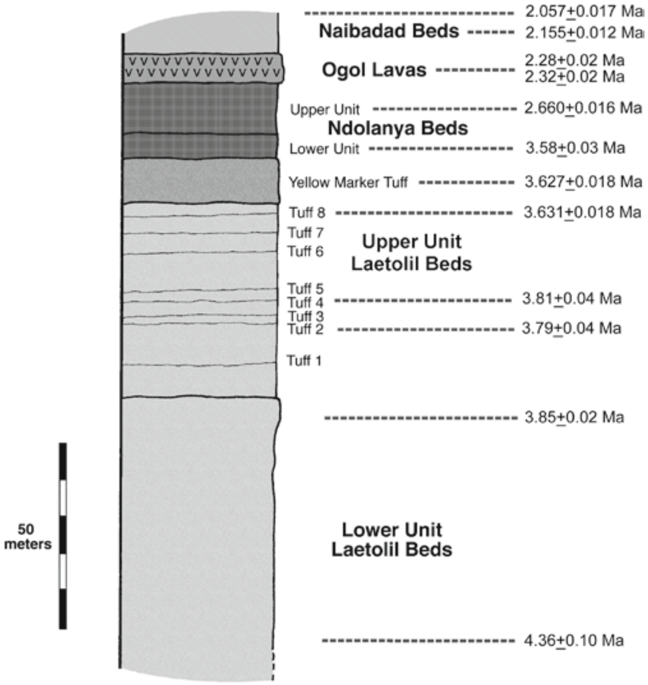


Fig. 7.1 Stratigraphic column and radiometric dating of the lower part of the sequence at Laetoli (After Hay 1987; Drake and Curtis 1987; Ndessokia 1990; Manega 1993; Mollel et al. 2011; Deino 2011)

The fossil collections made by Louis and Mary Leakey at Laetoli in 1935 included a hominin lower canine (M.42323, formerly M.18773), which is housed in the Natural History Museum in London. This was the first Pliocene hominin to be recovered from East Africa, although the specimen was not identified as such until some decades later (White 1981). In 1939 Kohl-Larsen's expedition to Garusi (= Laetoli) included a hominin maxilla with P^3 and P^4 (Garusi I) and an isolated M^3 (Garusi II) (Weinert 1950; Remane 1950, 1954; Robinson 1953, 1955; Protsch 1976, 1981). Both of these specimens are housed in the Institut für Ur- und Frühgeschichte und Archäologie des Mittelalters, Tübingen. An undescribed occipital fragment (Garusi III), apparently of a fossil hominin from Pleistocene sediments, has been lost (Protsch 1976, 1981; Ullrich 2001). In the late 1970s, Eric Delson identified a previously unrecognized hominin lower incisor among the fossil cercopithecids in Berlin that had been collected by Kohl-Larsen (White 1981; Delson, personal communication), and this specimen has been briefly described (Ullrich 2001).

The most extensive collection of hominins from the Upper Laetoli Beds (n = 25) was recovered by expeditions led by Mary Leakey from 1974 to 1979 (Leakey 1987b). These comprise 14 isolated teeth, 10 cranial/jaw fragments or associated dentitions, and a partial skeleton of an immature individual. Of these, 23 have been described previously (White 1977, 1980a; Leakey 1987b), and two are identified here as belonging to *A. afarensis* for the first time. These include a weathered and heavily rolled mandibular fragment (L.H. 29), initially referred to *Homo* cf. *H. erectus*, and a weathered isolated upper canine (LAET 79-5447), which were found the same field season at Loc. 8. At the time of their discovery these surface finds were presumed to be derived from the deflated Pleistocene sediments, because they have the black and orange staining typical of the fossils from these beds. However, specimens that erode out of the Upper Laetolil Beds and are reworked into the superficial lag deposits can often develop similar preservational characteristics. Since their morphology is entirely consistent with material from the Upper Laetolil Beds, these two specimens are reassigned here to *A. afarensis*. A further undescribed specimen (LAET 75-3817) of a possible hominin was excavated by Mary Leakey's team at Loc. 7E from the Upper Ndolanya Beds. This is a zygomatic process of a right frontal of an infant, recorded in the catalogue as a cercopithecid. The only other hominin recovered by Mary Leakey's expeditions is a hominin cranium (L.H. 18) from the Late Pleistocene Upper Ngaloba Beds, referrable to *Homo sapiens* (Day et al. 1980b; Magori and Day 1983).

Renewed investigations at Laetoli by the Institute of Human Origins, directed by D.C. Johanson from 1985 to 1988, succeeded in recovering a single hominin specimen, an isolated right M^3 (L.H. 31) (Ndessokia 1990; Kyauka and Ndessokia 1990). The specimen was recovered from the Upper Laetolil Beds at Loc. 10 in 1987, but the precise stratigraphic provenance is unknown. Unfortunately, the author has not been an able to relocate the specimen.

The resumption of full-scale paleontological and geological research at Laetoli and at other sites on the Eyasi Plateau in 1998, under the direction of the author, led to the recovery of four additional hominins. Two specimens, an isolated lower canine (EP 162/00) and a mandibular fragment with P_3-M_1 (EP 2400/00), were recovered from the Upper Laetolil Beds at Loc. 16 (see Harrison and Kweka 2011; Fig. 7.2). Both specimens are referable to *A. afarensis*. In addition, two hominins were recovered from the Upper Ndolanya Beds – a proximal tibia (EP 1000/98) and an edentulous maxilla (EP 1500/01). These are the first hominins to be recovered from this stratigraphic unit, and have proven to be of exceptional interest. EP 1500/01 was found in 2001 at the newly recorded locality of Silal Artum, just to the north of the main fossiliferous outcrops at Laetoli (see Harrison and Kweka 2011; Fig. 7.2). As is discussed below, the maxilla can be confidently attributed to *Paranthropus aethiopicus*. EP 1000/98 was found during the first season of renewed fieldwork at Laetoli in 1998, at yet another new locality, Loc. 22S, this time at the southern edge of the main Laetoli outcrops (see Harrison and Kweka 2011; Fig. 7.2). Attribution of isolated postcranial specimens to early hominin taxa is obviously problematic, but given the occurrence of *P. aethiopicus* as the only hominin known from the Upper Ndolanya Beds it is likely that the proximal tibia belongs to this species. However, since there is no direct association and the hominins from the Upper Ndolanya Beds are few, the proximal tibia is conservatively identified here as Hominini gen. et sp. indet. Further discussion concerning the affinities of EP 1000/98 is presented below.

The aim of this contribution is to present a descriptive account of the morphology of the newly collected hominin specimens from the Upper Laetolil and Upper Ndolanya Beds, as well as of the previously undescribed specimens from the Kohl-Larsen and Mary Leakey collections. The study also provides an opportunity to clarify aspects of the chronology and provenance of the Laetoli hominins, and to discuss their implications for understanding the evolutionary history of *Australopithecus afarensis* and *Paranthropus aethiopicus*.

Material

A list of hominins recovered from Laetoli between 1935 and 1979 was presented in Leakey (1987b: 116–117), and the individual specimens have been figured and described in

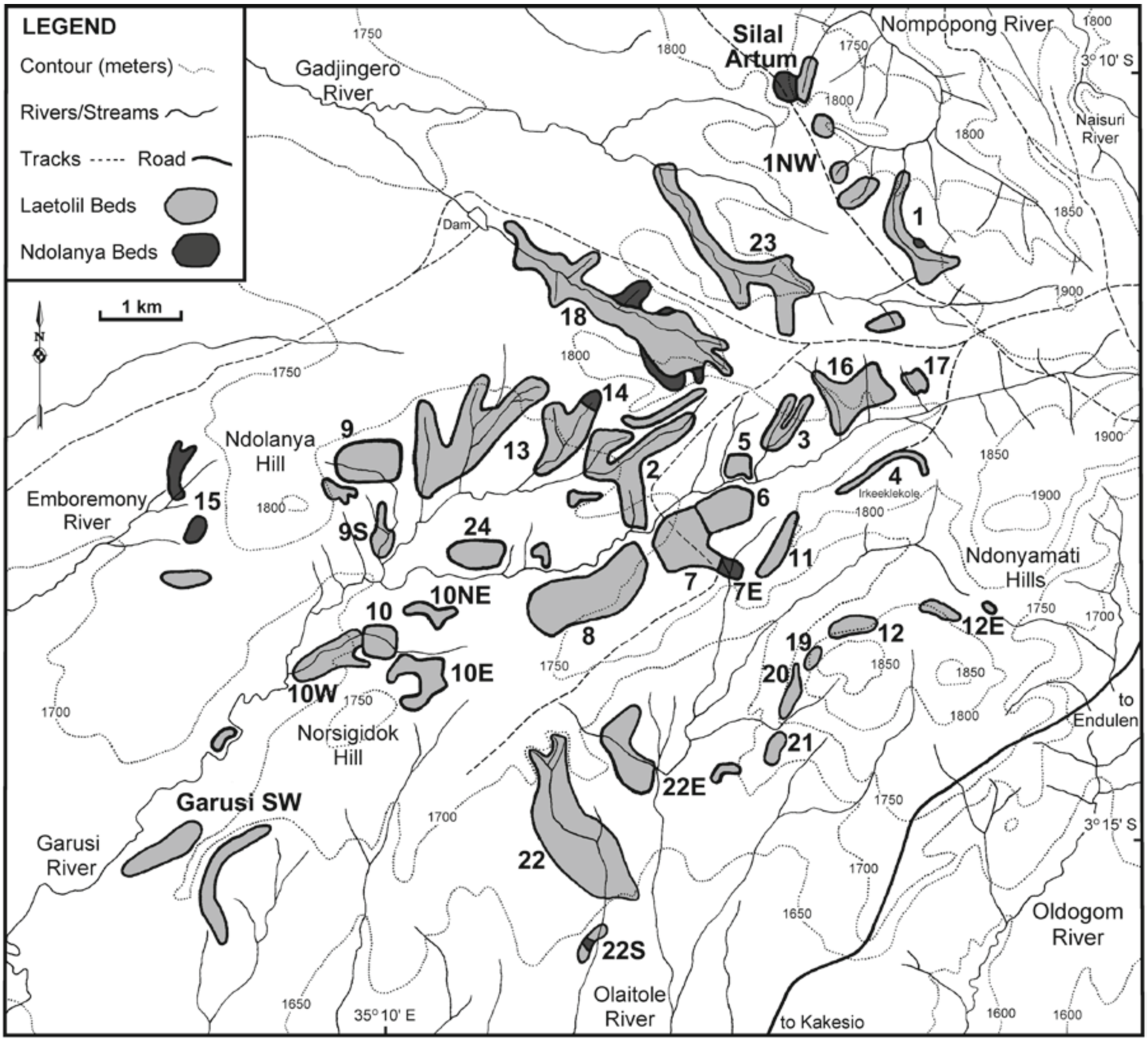


Fig. 7.2 Map of the Laetoli area showing the main outcrops of the Upper Laetolil and Upper Ndolanya Beds and the paleontological collecting localities

some detail (Leakey et al. 1976; White 1977, 1980a, 1981; Day et al. 1980b; Magori and Day 1983; Leakey 1987b). An updated list is presented in Table 7.2, which includes a number of emendations and corrections to the original list, as well as the addition of new specimens recovered or identified since 1987. All of the hominins recovered from the Upper Laetolil Beds can be referred to *Australopithecus afarensis*. The only taxon so far identified in the Upper Ndolanya Beds is *Paranthropus aethiopicus*.

The Laetoli hominins are housed in the Natural History Museum in London (NHM.M; 1935 Leakey collection), Humboldt-Universität Museum für Naturkunde in Berlin (MB Ma.; 1938–1939 Kohl-Larsen collection), Institut für Ur- und Frühgeschichte und Archäologie des Mittelalters, Tübingen (Garusi hominins; 1938–1939 Kohl-Larsen collection), Kenya National Museum in Nairobi (LAET; 1974–1979 Leakey collections on loan from Tanzania), and National Museum of Tanzania (EP, Eyasi Plateau expedition; 1998–2005 Harrison collection). Comparisons with original specimens and casts of *Australopithecus afarensis*, *A. anamensis*, *Paranthropus boisei, P. robustus*, and *P. aethiopicus* were carried out at the Kenya National Museum (KNM), National Museum of Tanzania (TNM), American Museum of Natural History (AMNH), and Natural History Museum in London (NHM).

Provenance

Most of the hominins from Laetoli, including the new specimens described here, are surface finds that had already eroded out of their original stratigraphic context at the time of their discovery. In most cases, based on the position of the find spot, the local topographic and stratigraphic context, and the occurrence of associated fossils, it is possible to determine the

Table 7.2 Catalogue of fossil hominin specimens recovered from Laetoli

Specimen	Year	Collector	Locality	Stratigraphic position	Anatomical part	Taxon	Comments
M.42323	1935	L.S.B. Leakey Expedition	Unknown	Upper Laetolil Beds	Lt C_1	*A. afarensis*	Published as M.18773 (White 1980a, 1981)
Garusi I	1939	Kohl-Larsen Expedition	Unknown	Upper Laetolil Beds	Rt maxilla frag. with P^3-P^4	*A. afarensis*	Holotype of *Praeanthropus* (see Table 7.1)
Garusi II	1939	Kohl-Larsen Expedition	Unknown	Upper Laetolil Beds	Lt M^3	*A. afarensis*	
MB Ma. 8294 (Garusi 4)	1939	Kohl-Larsen Expedition	Unknown	Upper Laetolil Beds	Lt I_1	*A. afarensis*	
L.H. 1	1974	M. Mwoka	Loc. 1	~1.2 m above Tuff 7	Rt P^4 frag.	*A. afarensis*	Found by M. Muoka in Leakey et al. (1976)
L.H. 2	1974	M. Muluila	Loc. 3	~0.5 m above Tuff 7	Mandible (infant) with rt and lt dP_4, unerupted crowns of rt and lt I_1, C, P_3; damaged crowns of rt and lt dC, dP_3 and M_1	*A. afarensis*	
L.H. 3	1974–75	M. Mwoka	Loc. 7	Between Tuffs 7 and 8, just above xenolith horizon	Partial upper and lower dentition: (a) rt dP^4, (b) lt I^1, (c) rt I^2, (d) lt I^2, (e) lt C^1, (f) lt P^3, (g) lt P^4, (h) rt M^1, (i) lt M^1 frag., (j) lt dI_2, (k) rt dC_1, (l) rt dP_3, (m) rt I_1, (n) rt C_1, (o) lt C_1, (p) rt P_3, (q) rt P_4 (r) lt P_4, (s) rt M_1 frag., (t) lt M_1	*A. afarensis*	
L.H. 4	1974	M. Muluila	Loc. 7	1.2 m below Tuff 7	Mandible with rt C-M_3, lt P_4-M_2, roots lt C-P_3, alveoli rt and lt incisors	*A. afarensis*	Lectotype of *A. afarensis* (see Table 7.1)
L.H. 5	1974	M. Muluila	Loc. 8	~1.8 m below Tuff 7	Rt maxilla frag. with I^2-M^1	*A. afarensis*	Same individual as L.H. 27 and 28
L.H. 6	1974–75	M. Mwoka	Loc. 7	~0.5 m above Tuff 7	Associated upper teeth: (a) rt I^2, (b) rt C^1, (c) rt P^3, (d) rt dP^4 and unerupted P^4, (e) rt M^1	*A. afarensis*	
L.H. 7	1975	M. Mwoka	Loc. 5	~0.6 m above Tuff 5	Rt M^3	*A. afarensis*	
L.H. 8	1975	E. Kandindi	Loc. 11	~0.9 m above Tuff 7	Rt M^2 and M^3	*A. afarensis*	Same individual as L.H. 22
L.H. 10	1975	E. Kandindi	Loc. 10W	5.5 m below Tuff 3	Lt mandibular frag., edentulous with broken roots C-M_1	*A. afarensis*	Incorrectly stated as 5.5 m above Tuff 3 in White (1980a)
L.H. 11	1975	E. Kandindi	Loc. 10W	7.3 m below Tuff 3	Lt M^2	*A. afarensis*	
L.H. 12	1975	E. Kandindi	Loc. 5	1.8 m below Tuff 4	Lt M^3	*A. afarensis*	
L.H. 13	1975	M. Jackes	Loc. 8	~3 m below Tuff 7	Rt mandibular frag., edentulous with roots of M_1-M_3	*A. afarensis*	
L.H. 14	1975–76	E. Kandindi	Loc. 19	~0.3 m above Tuff 5	Associated lower dentition: (a) rt I_1, (b) lt I_1, (c) rt I_2, (d) lt I_2, (e) rt C_1, (f) lt C_1, (g) lt P_4, (h) rt M_2, (i) rt P_3, (j) lt P_3, (k) lt M_1	*A. afarensis*	Incorrectly stated as 3 m above Tuff 5 in Leakey (1987a); see White (1980a: 503)
L.H. 15	1976	Mrs. Luce	Loc. 1	0.9 m above Tuff 8	Lt M_2	*A. afarensis*	Incorrectly stated as 9 m above Tuff 8 in Leakey (1987a); see White (1980a: 503). Previously identified as M_3 (White 1980a)
L.H. 16	1976	L. Kangiran	Loc. 6	Just below Tuff 6	Rt M_1	*A. afarensis*	Lt M_1 in Leakey (1987a)
L.H. 17	1976	A. Mwongela	Loc. 9	Between Tuffs 5 and 8	Lt M^1	*A. afarensis*	
L.H. 18	1976	E. Kandindi	Loc. 2	Upper Ngaloba Beds	Cranium	*Homo* cf. *H. sapiens*	Incorrectly listed as Loc. 25 in Leakey (1987a)

(continued)

Table 7.2 (continued)

Specimen	Year	Collector	Locality	Stratigraphic position	Anatomical part	Taxon	Comments
L.H. 19	1976	M. Mwoka	Loc. 8	Between Tuffs 5 and 6	Lt M_2	*A. afarensis*	
L.H. 20	1976	C. Kamau	Loc. 1	Between Tuffs 7 and 8	Lt I^1	Non-hominin, *Rhinocolobus*	Initially identified as a hominin, but subsequently recognized as a cercopithecid
L.H. 21	1976	M. Mwoka	Loc. 12E	Between Tuffs 6 and 7	Partial skeleton (juvenile): (a) rt maxilla, (b) lt maxilla frag., (c) lt maxilla frag, (d) lt dP^4, (e) rt zygomatic, (f) lt frontal frag., (g) frontal frag., (h) parietal frag., (i) rt parietal frag., (j) parietal frag., (k) rt temporal frag., (l) temporal frag., (m) rt occipital frag., (n) lt occipital frag., (o) rt occipital frag., (p) rt clavicle frag., (q) rib sternal end, (r) lt proximal ulna, (s) ulna frag., (t) distal ulna frag., (u) rt femur shaft and neck, (v) lt femur shaft frag., (w) intermediate phalanx, (x) proximal phalanx, (y) proximal phalanx, (z) metacarpal II frag., (a-1) metapodial head, (a-2) phalanx epiphysis	*A. afarensis*	Incorrectly stated as from Loc. 12 (White 1980a)
L.H. 22	1977	E. Kandindi	Loc. 11	~0.9 m above Tuff 7	Lt P^4 and M^1	*A. afarensis*	Same individual as L.H. 8
L.H. 23	1978	M. Mwoka	Loc. 8	~1.3 m below Tuff 7	Lt M_2	*A. afarensis*	2 m below Tuff 7 according to the field catalogue entry
L.H. 24	1978	E. Kandindi	Loc. 10E	~2.1 m below Tuff 7	Lt P_3	*A. afarensis*	
L.H. 25	1978	M. Mwoka	Loc. 2	15 cm above Tuff 6	Rt P^3	*A. afarensis*	From Loc. 14 according to White (1980a). Incorrectly listed as Rt P_3 in Leakey (1987a)
L.H. 26	1978	J. Masovo	Loc. 6	~3.7 m below Tuff 7	Rt M^2	*A. afarensis*	Finder is J. Masobo according to White (1980a)
L.H. 27	1979	N. Mbuika	Loc. 8	~2 m below Tuff 7	Rt M^3	*A. afarensis*	Same individual as L.H. 5 and 28
L.H. 28	1979	P. Sila	Loc. 8	~2 m below Tuff 7	Rt M^2	*A. afarensis*	Same individual as L.H. 5 and 27
L.H. 29	1979	M. Mwoka	Loc. 8	Unknown	Lt mandibular frag. with M_1-M_3	*A. afarensis*	Published as *Homo* cf. *H. erectus* (Leakey 1987a)
L.H. 30	1975	M.D. Leakey Expedition	Loc. 7	Probably between Tuffs 6 and 8	Lt dC^1	*A. afarensis*	Synonymous with L.H. 3/6 (c)
L.H. 31	1987	L. Dotha	Loc. 10	Unknown	Rt M^3	*A. afarensis*	Specimen lost
LAET 75–3817	1975	M.D. Leakey Expedition	Loc. 7E (strip 8)	Upper Ndolanya Beds	Rt zygomatic process of frontal; two associated bone frags. (infant)	cf. Hominini indet.	Previously identified as a cercopithecid
LAET 79–5447	1979	M.D. Leakey Expedition	Loc. 8	Unknown	Rt C^1	*A. afarensis*	Previously undescribed
EP 1000/98	1998	C. Robinson	Loc. 22S	Upper Ndolanya Beds	Lt proximal tibia	Hominini gen. et sp. indet.	
EP 162/00	2000	A. Kweka	Loc. 16	Between Tuffs 7 and 8	Lt C_1	*A. afarensis*	
EP 2400/00	2000	M. Mbago	Loc. 16	51 cm above Tuff 8	Rt mandibular frag. with P_3-M_1	*A. afarensis*	
EP 1500/01	2001	T. Harrison	Silal Artum	Upper Ndolanya Beds	Rt maxillary frag., edentulous	*P. aethiopicus*	

Sources: White (1977, 1980a, 1981); Day et al. (1980b); Magori and Day (1983); Leakey (1987a); Kyauka and Ndessokia (1990); Kyauka (1994); Ullrich (2001); Harrison (2002, unpublished data) original stratigraphic unit from which the hominin fossil was derived (usually narrowly constrained between two sequential marker tuffs, such as between Tuffs 7 and 8 in the case of EP 2400/00). However, except for those rare instances of hominins being found *in situ* (i.e., L.H. 2, L.H. 3 and L.H. 6), it is important to make a distinction between the finding spot and the presumed original stratigraphic placement of the specimens. For example, Leakey (1987b) recorded precise information on the stratigraphic location of the hominins recovered by her team, but this represents the stratigraphic level of the surface on which specimens were found rather than that of the level from which they eroded. Although long distance transportation can be largely discounted at Laetoli, the displacement of surface finds by livestock and game animals and by seasonal run-off over short distances is certainly conceivable, and can be shown to have occurred for some associated dental remains (Leakey 1987b). The main point is that all surface finds, including those recovered by Mary Leakey for which precise stratigraphic locations have been published, are at best derived from narrow stratigraphic horizons between marker tuffs.

The three hominin specimens recovered by Kohl-Larsen are certainly derived from the Upper Laetolil Beds based on their preservation, but otherwise the published and archival information does not permit a more precise geographic or stratigraphic provenance (Kohl-Larsen 1943; Protsch 1981). Garusi Hominid I and II were apparently recovered from the same locality, 16 days apart. Protsch (1981: 12) has described the location as being "the most northwesterly corner of the Garusi River", but Kohl-Larsen's sketch map (published in Protsch 1981: 4) marks the find spot to the *northeast* of the head of the Garusi River, between the Garusi and Gadjingero river valleys. Protsch (1981: 12) further indicates that "the finds were located about 500 m west of Kohl-Larsen's campsite at a tributary of the Garusi River, at the foot of [a] … sandstone plateau" (see also Kohl-Larsen 1943: 386). From the sketch map published by Kohl-Larsen (1943), we know that his camp (Lagerplätze) was situated in the vicinity of Loc. 4 on the southern side of the Garusi valley. All of the evidence, which is admittedly rather scanty, appears to be consistent with the Garusi hominins having come from Loc. 16. Protsch (1981: 10–11) published photographs from the Kohl-Larsen expedition that identify the location of the Garusi I and II finds. Unfortunately, I have not been able to relocate the exact spots where these photographs were taken because there are no distinguishable landmarks, but the photos are not inconsistent with them having been taken at Loc. 16.

Another issue pertaining to the provenance of the hominin fossils collected by Mary Leakey is the stratigraphic placement of the marker pedestals at Laetoli. The hominin find spots were marked by stones embedded in a concrete block with the L.H. number inscribed on top (Leakey 1987b). Most of these pedestals are still traceable today, but the original structures have been damaged to varying degrees, and in some cases they have been repaired or replaced by subsequent workers (Mabulla 2000). The problem is that the locations of the pedestals do not always match the recorded stratigraphic position of the hominin find. According to new observations in the field (see Ditchfield and Harrison 2011) there is a discrepancy in the stratigraphic location of at least seven pedestals (Table 7.3). There are two possible

Table 7.3 Discrepancies between the published stratigraphic position of hominins at Laetoli and the placement of the marker pedestals

Specimen	Locality	Recorded stratigraphic position of hominin (Leakey 1987b)	Stratigraphic position of marker pedestal	Additional comments
L.H. 3/6	Loc. 7	Between Tuffs 7 and 8	On top of Tuff 6	See Ditchfield and Harrison (2011)
L.H. 4	Loc. 7	1.2 m below Tuff 7	1.25 m below Tuff 6	See Ditchfield and Harrison (2011)
L.H. 7	Loc. 5	~0.6 m above Tuff 5	On top of Tuff 3	See Ditchfield and Harrison (2011). The main fossil-bearing horizon at Loc. 5 is between Tuffs 3 and 5
L.H. 10	Loc. 10W	5.5 m below Tuff 3	Not located	Incorrectly stated as 5.5 m above Tuff 3 in White (1980a). Based on the section in Hay (1987) the hominin is from between Tuffs 1 and 2. This is the main fossil-bearing horizon at Loc. 10W
L.H. 11	Loc. 10W	7.3 m below Tuff 3	Not located	Based on the section in Hay (1987) the hominin is from between Tuffs 1 and 2. This is the main fossil-bearing horizon at Loc. 10W
L.H. 12	Loc. 5	1.8 m below Tuff 4	Just below Tuff 3	The main fossil-bearing horizon at Loc. 5 is between Tuffs 3 and 5
L.H. 14	Loc. 19	~0.3 m above Tuff 5	~0.3 m above Tuff 5	Incorrectly stated as 3 m above Tuff 5 in Leakey (1987a); see White (1980a: 503)
L.H. 15	Loc. 1	9 m above Tuff 8	~0.9 m above Tuff 8	Typographic error in Leakey (1987a); see White (1980a: 503)
L.H. 16	Loc. 6	Just below Tuff 6	1.5 m below Tuff 6	
L.H. 21	Loc. 12E	Between Tuffs 6 and 7	7.6 m above Tuff 7	Incorrectly stated as from Loc. 12 (White 1980a)
L.H. 23	Loc. 8	~1.3 m below Tuff 7	Between Tuffs 6 and 7	2 m below Tuff 7 according to the catalogue entry
L.H. 25	Loc. 2	15 cm above Tuff 6	Not located	From Loc. 14 according to White (1980a)
L.H. 26	Loc. 6	~3.7 m below Tuff 7	5 m below Tuff 6	See Ditchfield and Harrison (2011)

explanations for these inconsistencies: (1) the stratigraphic placement of the hominin is incorrectly recorded; or (2) the pedestals were placed in the wrong positions. Without evidence to the contrary, I am inclined to accept that the recorded position of the hominins is accurate, and that the pedestals are incorrectly placed.

Given these considerations, as well as what is known about the occurrence of fossiliferous horizons in the Upper Laetolil Beds (see Harrison and Kweka 2011), most of the fossil hominins can be placed into their appropriate statigraphic context (see Table 7.4). It can be seen that *A. afarensis* specimens occur throughout the Upper Laetolil Beds, with dates ranging from 3.63 Ma to 3.83 Ma. When their stratigraphic placement is taken into consideration, it can be seen that most of the hominins from the Upper Laetolil Beds (*n*=23; 88.5%) are derived from above Tuff 5, and there are relatively few specimens from the lower part of the sequence. However, this is largely a reflection of the number of exposures and the frequency of occurrence of fossil vertebrates throughout the sequence. The percentage of fossil mammals recovered from above Tuff 5, between Tuffs 3 and 5, and below Tuff 3 are 80.6%, 5.5% and 13.9% respectively. By comparison the corresponding percentages of hominin finds are 88.5%, 3.9% and 7.7%, which implies that their frequency of occurrence is quite close to that expected given variations in paleontological productivity throughout the sequence. However, the relative rarity of hominins obtained from the productive localities that sample the sequence below Tuff 3 (i.e., Locs. 10, 10W and 9S) may eventually prove to be of some significance.

Table 7.4 Stratigraphic distribution of hominins in the Upper Laetolil Beds

Marker Tuff	Age (Ma)[a]	*In situ* finds[b]	Surface finds[b]
Yellow Marker Tuff	3.63		
			L.H. 15, EP 2400/00
Tuff 8	3.63		
		L.H. 2, 3/6	L.H. 1, 8, 22, EP 162/00
Tuff 7	3.66		
			L.H. 4, 5, 13, 21, 23, 24, 25, 26, 27, 28
Tuff 6	3.70		
			L.H. 7, 14, 16, 19
Tuff 5	3.79		
Tuff 4	3.79		
			L.H. 12
Tuff 3	3.80		
Tuff 2	3.81		
			L.H. 10, 11
Tuff 1	3.83		
Lower Laetolil Beds	3.85–4.36		

[a] Data from Deino (2011)

[b] Data from Leakey (1987a) and Harrison (unpublished)

New Hominins from the Upper Laetolil Beds

Since 1998, two additional specimens of *A. afarensis* have been recovered, both derived from the upper part of the Upper Laetolil Beds at Loc. 16: EP 2400/00, a right mandibular fragment with P_3-M_1, and EP 162/00, a left lower canine. In addition, two specimens recovered by Mary Leakey's expeditions are described here for the first time: L.H. 29, a left mandibular fragment with M_1-M_3, and LAET 79-5447, an isolated upper canine. An isolated lower incisor, MB Ma. 8294 (Garusi 4), in the Kohl-Larsen collections of the Museum für Naturkunde in Berlin, briefly discussed by Ullrich (2001), is also formally described here for the first time.

EP 2400/00

Right mandibular fragment with P_3-M_1 (Fig. 7.3).

Location and Stratigraphic Provenance

This specimen was discovered by Michael Mbago at Loc. 16 on August 7, 2000. The specimen was found on the surface in a shallow drainage channel on the western flank of the main gully, 51 cm above Tuff 8 (see Harrison and Kweka 2011). Although EP 2400/00 had been displaced from it original location at the time of discovery, its original stratigraphic provenance can be interpreted to be 0.5–1.3 m above Tuff 8. The absolute age of specimen can be constrained by the bracketing radiometric dates for Tuff 8 (3.631 ± 0.018 Ma) and the overlying Yellow Marker Tuff (3.627 ± 0.018 Ma) (Deino 2011), and can inferred to have an age of ~3.63 Ma (see Fig. 7.1). It is one of the youngest specimens of *A. afarensis* known from Laetoli.

Preservation

The mandibular corpus is partially preserved below the cheek teeth; the inferior portion of the corpus is missing below the level of the mental foramen. Anteriorly, the posterior margin of the alveolus for the lower canine is preserved. Posteriorly there is a pair of indentations that represents the anterior margin of the alveolus for the mesial root of M_2. Laterally, the bone is quite weathered and the surface is marked by numerous fine cracks oriented anteroposteriorly in line with the bone fibers. Thin flakes of bone have been lost from the surface immediately over the mesial roots of P_3 and P_4, and to a lesser extent on the M_1 anterior root. As a consequence, the roots are exposed to a greater degree than they would

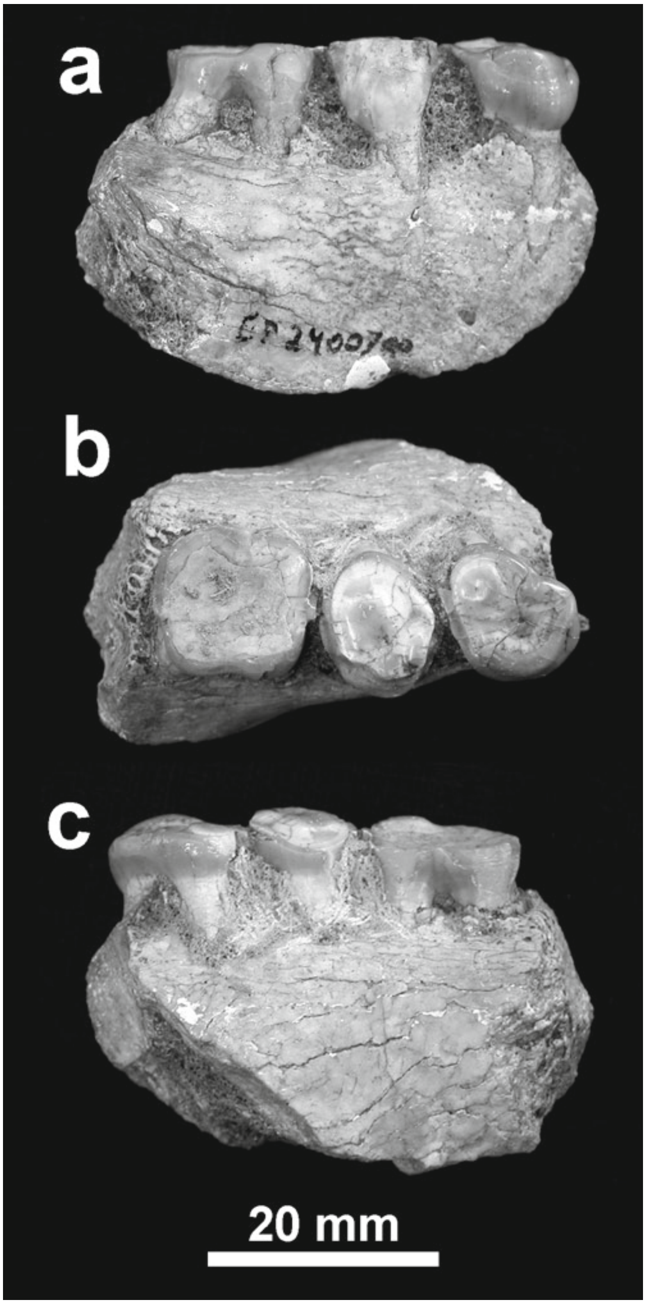


Fig. 7.3 EP 2400/00, right mandibular fragment with P_3-M_1 of *Australopithecus afarensis*. (**a**) lateral view; (**b**) occlusal view; (**c**) medial view

have in life. Posteriorly, a large triangular flake of bone has been removed by abrasion from the lateral side of the corpus from just below M_1, at the point where the corpus is beginning to expand for the anterior root of the ramus. The medial side of the corpus also shows fine longitudinal cracking of the surface bone, with a relatively sharp break anteriorly, and a feathered surface posteriorly below and behind M_1, which may be the result of pre-fossilization weathering. None of the broken edges are fresh, and it seems likely that the mandible was fragmented prior to fossilization, although the sharp breaks inferiorly and anteriorly suggest that additional breakage occurred after it was fossilized and exposed on the surface. There are no indications of carnivore or rodent gnawing.

The teeth are very worn occlusally. P_3 has lost a small flake of enamel from its distolingual margin. P_4 has lost the enamel from its entire buccal face, and the marginal enamel is chipped and flaked. No enamel remains on the occlusal surface of M_1. In addition, enamel has been chipped from the mesiobuccal corner of the crown, as well as from the mesial and lingual faces. However, preservation is adequate to allow accurate measurements of the original dimensions of the teeth.

Morphology

The mandibular fragment consists of the alveolar portion of the corpus below P_3-M_1. The inferior portion of the corpus is missing, with only a maximum depth of 18.6 mm remaining below P_4-M_1. The corpus appears to be relatively thick in relation to the size of the teeth. The thickness of the alveolar portion of the corpus is 18.3 mm at mid-P_3, 18.9 mm at mid-P_4, and at least 22.2 mm at mid-M_1.

The lateral surface of the corpus below P_3 is relatively flat. A small accessory mental foramen, with a diameter of 1.7 mm, is located vertically 15.2 mm below mid-P_3. There is a shallow groove posterior to the aperture indicating that a branch of the mental nerve exited in this direction. The corpus is broken at the level of the main mental foramen, but its superior and posterior margins of the mental foramen are preserved. It was quite large and elliptical in shape, with a minimum anteroposterior diameter of 4.8 mm. The preserved margins are sharply defined. The dorsal margin of the foramen is located 19.4 mm below the cemento-enamel junction (and 17.5 mm below the alveolar margin) of the mesial margin of P_4. The accessory foramen is situated superior and anterior to the main foramen, and separated from it by a distance of 6.3 mm. Directly superior to and slightly posterior to the main foramen is a distinct, but shallow depression, which occurs just inferior to the root apices of P_4. Superior to this the lateral aspect of the corpus is slightly convex infero-superiorly. Below M_1 the lateral wall is more markedly convex, where the lateral prominence of the anterior root of the ramus originates. In inferior view, the broken surface shows that the bony wall of the corpus was thick, up to 3.6 mm thick both medially and laterally.

Medially the surface of the corpus is evenly convex infero-superiorly; more markedly so below P_3 than M_1. Posteriorly the alveolus for the mesial root of M_2 indicates that it was a relatively broad tooth buccolingually. The minimum breadth of the alveolus is 13.7 mm, which compares with the equivalent dimension in M_1 of only 12.1 mm. The alveolus for the lower canine is partially preserved. It has a minimum diameter of 8.0 mm, but judging from its contour it would have exceeded 9 mm in diameter. It was clearly a sizeable root, although it did not exceed the span of the roots for P_3. The inferosuperior length of the canine alveolus is incomplete, but at its point of breakage, 12.3 mm below the superior margin of the alveolus, it still accommodated a stout root. Judging from the relatively small size of the alveolus for the canine root EP 2400/00 likely belonged to a female individual. The minimum distance between the alveoli of the canine and the mesial root of P_3 is only 1.6 mm, so there was effectively no diastema. In occlusal view, the preserved cheek tooth row exhibits a very slight lateral convexity. Judging from the preserved portion of the canine alveolus, the canine crown would have been positioned slightly medial to the long-axis of the postcanine tooth row, as is typical of *A. afarensis* compared to the more primitive lateral position in *A. anamensis* (Ward et al. 2001).

The P_3 is larger in overall size than P_4. It is obliquely oriented, with its long-axis oriented at 44° to the line of P_3-M_1. The maximum length of the crown is 11.9 mm and its perpendicular breadth is 9.0 mm. The mesiodistal and buccolingual dimensions are given in Table 7.6. In occlusal view, the crown is trapezoidal in shape, with the greatest breadth mesially and narrower distally. The occlusal surface of the crown is worn nearly flat, with much of the enamel worn away and an extensive area of dentine exposed (more than 50% of the occlusal surface). Apart from the enamel around the margin of the crown, there is a small area retained at the base of the crown mesiobuccally and a small circular area (3.5×3.2 mm) of very thin enamel retained in the talonid basin. The protoconid is worn flat, and is represented by a large area of exposed dentine, but was almost centrally positioned on the crown. The mesiobuccal face of the crown bulges outwards beyond the lateral surface of the corpus, but then tapers apically. The inferior enamel junction on the mesiobuccal face extends slightly more inferiorly onto the root than it does in the rest of the crown. The worn height of the mesiobuccal face is 6.1 mm, compared with only 3.3 mm lingually. The small size and morphology of the P_3 confirms the observation from the size of the alveolus for the canine root that EP 2400/00 belongs to a female individual.

Occlusal contact between the upper canine and the mesiobuccal face of P_3 was evidently concentrated on the apex of the protoconid, and did not extend far down onto the mesiobuccal face of the crown. An obliquely oriented furrow in the enamel at the base of the crown mesially represents a trace of the buccal cingulum. A vestige of cingulum is also present along the buccal margin of the crown, and these two sections are linked by a shallow and irregular indentation in the enamel surface that arcs mesiodistally around the mesiobuccal face, about 4 mm up from the base of the crown. The buccal face of the crown is evenly convex, except for a slight angulation midway along its length, presumably representing the point where the postprotocristid would have converged with the distal marginal ridge. Mesiolingually, the crown has a prominent protuberant beak, which represents the mesial termination of the preprotocristid. The mesiolingual margin of the crown is slightly concave. Distolingually there is a small triangular area of dentine exposure, continuous with that produced by the worn protoconid, located between the island of enamel preserved in the talonid basin and a small fold of enamel along the mesial margin that represents a remnant of enamel between the preprotocristid and hypoprotocristid. This area of dentine exposure represents the location of the metaconid, which, in the unworn state, would have been very small judging from the size of the dentine exposure. The talonid heel was narrow. Distally, where the enamel wall is exposed, the enamel is 1.1 mm thick. The tooth is two-rooted, with the mesial and distal roots subequal in size. The mesial root is placed more laterally than the distal root, and it is cylindrical in shape rather than mesiodistally compressed. The exposed portion of the mesial root has a length of 10.2 mm, but it cannot have been longer than 15 mm, otherwise it would be visible inferiorly where the corpus is broken.

The P_4 is oval in occlusal outline, with a long-axis directed at 72° to the line of P_3-M_1. The crown is broader than long. The tooth is heavily worn, with dentine exposure over more than 50% of the occlusal surface. The protoconid and metaconid have been worn flat and are represented by contiguous areas of dentine exposure. The two cusps were apparently subequal in size. Two thin layers of enamel are retained on the flattened occlusal surface. A large rectangular remnant is located centrally and distally, corresponding to the floor of the talonid basin, and a much smaller oval-shaped remnant occurs along the mesiolingual margin of the crown, corresponding to the floor of the mesial fovea. The mesiobuccal face of the crown bulges laterally, and its cemento-enamel junction extends inferiorly below that of P_3 and M_1. Even in its very worn state, the buccal face of the crown is much higher than the lingual face (7.4 mm as opposed to 2.4 mm). The tooth has two subequal roots, both transversely aligned.

M_1 is very heavily worn, with no enamel remaining on the occlusal surface. The specimen evidently belonged to an aged individual. The dentine surface is smoothly concave, with no residual topography of the cusps, surrounded by an elevated rim of enamel. The broken enamel suggests that the sides of the teeth were coated with relatively thin enamel, although no measurements can be taken. The crown is relatively broad and rectangular in shape, with a slight degree of buccolingual waisting midway along its length (slightly more pronounced on the buccal side). There are no observable traces of cingulum, but if originally present they likely would have been removed by the excessive wear.

Comparisons

The corpus of EP 2400/00 is similar in contour and size to that of L.H. 4, and of the larger mandibles from Hadar, such as A.L.

400-1 and A.L. 266-1, and more robust than the smaller Hadar mandibles, such as A.L. 128-23 and A.L. 198-1. The mean mediolateral breadth of the corpus below M_1 in the Hadar sample ($n=22$) is 19.8 mm, with a range of 15.8 mm to 24.7 mm (Lockwood et al. 2000; Kimbel et al. 2004) (Table 7.5). EP 2400/00 with a minimum breadth at M_1 of 22.2 mm places the Laetoli specimen in the upper end of the range for *A. afarensis* and *A. anamensis*, and close to the mean value for *A. africanus* (Tobias 1991; Ward et al. 2001; Kimbel et al. 2004).

Judging from the contour of the broken anterior margin of the medial surface of the corpus, the mandible would have had an anteroposteriorly elongated subincisive planum, as in other specimens of *A. afarensis*, such as A.L. 400-1 and A.L. 198-1, and more pronounced than in A.L. 266-1 and A.L. 288-1. However, it was clearly not as posteriorly inclined as in *A. anamensis* (Ward et al. 2001). The medial surface of the corpus below M_1 is strongly convex, indicating that it was heavily buttressed medially as in A.L. 400-1. The root of the ramus on the lateral side of the corpus is situated below M_1, as in L.H. 4, MAK-VP-1/12, and most of the mandibular specimens from Hadar (White et al. 2000; Kimbel et al. 2004), but it does occur more posteriorly in A.L. 400-1 (mesial M_2) and A.L. 198-1 (distal M_2).

EP 2400/00 has a small elliptical depression located below mid-P_4, just superior and posterior to the mental foramen. A similar small depression occurs in A.L. 207-13, A.L. 288-1i, A.L. 333w-60, A.L. 400-1a, A.L. 437-2, A.L. 438-1 g, A.L. 444-2, L.H. 4 and MAK-VP-1/12, and the general area is concave in A.L. 198-1, but otherwise mandibles of *A. afarensis* are uniformly convex in this area. The mental foramen is positioned below mesial P_4. The modal position in *A. afarensis* and *A. africanus* is below P_4, although it varies in location from below distal P_3 to P_4/M_1 (Ward et al. 1982; Tobias 1991). A similar pattern characterizes the small sample of mandibular specimens of *A. anamensis* (Ward et al. 2001). The occurrence of a main foramen and a smaller accessory foramen in EP 2400/00 is commonly observed among *A. afarensis*. Robinson (2003) recorded multiple mental foramina in 36.0% of the specimens from Hadar. Paired foramina also

Table 7.5 Comparison of dimensions (mm) of the mandibular corpus in EP 2400/00 with other specimens of *A. afarensis* from Laetoli, Hadar and Maka

Locality	Specimen	Breadth at P_4	Breadth at M_1	Height mental foramen to alveolar margin
Laetoli	EP 2400/00	18.9	22.2(–)	17.5
	L.H. 4	18.5	19.7	21.4
Hadar	A.L. 128-23	16.6	18.0	17.4
	A.L. 145-35	18.9	21.1	18.0
	A.L. 198-1	15.8	15.8	18.4
	A.L. 207-13	17.4	18.1	21.0
	A.L. 228-2	16.0	16.3	20.1
	A.L. 266-1	19.9	21.7	18.4
	A.L. 277-1	17.8	17.9	23.0
	A.L. 288-1i	16.6	17.1	20.0
	A.L. 311-1	22.0	–	26.3
	A.L. 315-22	17.3	19.2	21.1
	A.L. 330-5	18.5	20.9	19.7
	A.L. 333w-12	16.8	17.4	19.0
	A.L. 333w-1a,b	18.9	19.4	18.7
	A.L. 333w-32+60	22.0	23.6	24.1
	A.L. 400-1a	18.5	18.7	20.1
	A.L. 417-1a	18.4	18.0	21.5
	A.L. 433-1a	20.3	20.2	17.0
	A.L. 437-1	21.2	20.0	25.0
	A.L. 437-2	22.2	22.2	23.2
	A.L. 438-1 g	25.0	24.7	20.5
	A.L. 444-2	21.1	23.0	21.6
	A.L. 582-1	22.6	21.4	21.1
	A.L. 620-1	19.5	20.5	23.5
Maka	MAK-VP 1/12	17.7	18.7	18.8

Dimensions: Maximum mediolateral breadth of corpus at mid-P_4; maximum mediolateral breadth of corpus at mid-M_1; vertical inferosuperior height of the corpus between the alveolar margin and the mental foramen

Data: Laetoli (Harrison, unpublished); Maka (White et al. 2000); Hadar (Kimbel et al. 2004). Where both sides are measurable, the value is the average of the right and left sides.

occur in the MAK-VP-1/12 mandible from Maka and in L.H. 4 from Laetoli. In EP 2400/00 the mental foramen is located 17.5 mm below the alveolar margin (Table 7.5). This falls at the low end of the range for the *A. afarensis* sample from Hadar (17.0–26.3 mm, $n=23$), which has a mean value of 20.8 mm (Kimbel et al. 2004). The distance in L.H. 4 is 20.4 mm and 22.4 mm on the left and right sides of the corpus respectively.

Although incomplete, the canine alveolus in EP 2400/00 is consistent in size with the canine root in EP 162/00, which has a mesiodistal length of 9.3 mm and breadth of 6.3 mm. The small size of the alveolus for the canine root would suggest that EP 2400/00 belonged to a female individual. This is supported by the size and morphology of P_3.

P_3 in EP 2400/00 is the smallest known example of this tooth from Laetoli (Table 7.6). It is slightly smaller than that in L.H. 4 and L.H. 2, which have occlusal areas 1.6% and 2.0% larger respectively, but it is much smaller (18.8% smaller in area) than the very large P_3 in L.H. 3. The morphology of the crown in EP 2400/00 is quite similar to that in L.H. 4 and L.H. 24, but it does differ in a number of respects: more pronounced mesiolingual beak, narrower distal basin, smaller metaconid, more pronounced buccal cingulum, and greater extension of the cemento-enamel junction mesiobuccally onto the base of the mesial root. EP 2400/00 is similar in occlusal outline to L.H. 3, but it is much smaller, and has a more prominent mesiolingual beak, a less convex distal margin, and probably a much smaller metaconid. However, the latter is similar in having distinct traces of the buccal cingulum mesially and distally. Also, the P_3 in L.H. 4 is oriented less obliquely to the long axis of the cheek tooth row (28°) than in EP 2400/00 (44°), which is close to the mean value (43°, range = 32–52°) for the Hadar sample. Judging from the orientation of the distal contact facet in L.H. 24, the crown was positioned more obliquely in the tooth row than in EP 2400/00. The configuration of the roots appears to match that in L.H. 4 (and the majority of specimens from Hadar), with a large cylindrical mesial root and a mesiodistally compressed distal root. However, as noted by White et al. (2000) and Kimbel and Delezene (2009) there is variation in P_3 root number and structure at Laetoli and Hadar, ranging from a pair of roots as in EP 2400/00, to a Tome's root (e.g., L.H. 14, A.L. 145-35, A.L. 288-1, A.L. 400-1a), and divided distal root (e.g., L.H. 24)

The P_3 in EP 2400/00 is quite similar in size and shape to the smaller examples of P_3 from Hadar, such as A.L. 128-23 and A.L. 288-1, which presumably belonged to female individuals. It differs from A.L. 288-1 in being slightly larger in size, mesiodistally longer, and with a more distinct lingual cingulum, especially mesially. EP 2400/00 is similar in shape, proportions and general morphology to A.L. 128-23, but it is slightly larger in size. The specimens are a good match in the development of the mesiobuccal beak and the apparent small size of the metaconid. A.L. 128-23 differs in having a more protuberant distal tubercle and a less well-developed buccal cingulum mesially. EP 2400/00 is also larger than the P_3 in A.L. 207-13, but similar in proportions. It differs in having a more pronounced mesiolingual beak, a less protuberant distal tubercle, a more distinct buccal cingulum mesially, and probably a smaller metaconid. A.L. 400-1 is similar in overall size to EP 2400/00, but it had a larger metaconid, a less-well-developed buccal cingulum, and it lacks the mesiolingual beak. A.L. 277-1 is slightly larger, with a smaller mesiolingual beak, a somewhat larger metaconid, and a less shelf-like buccal cingulum. EP 2400/00 is similar in size to A.L. 266-1, but it has a narrower and longer crown, a more prominent mesiolingual beak, a less protuberant distal tubercle, and a slightly smaller metaconid.

As noted by White (1985), the full range of metaconid expression, from absent to well developed, is present in the sample from Hadar. A weak or absent metaconid is found in 40.0% of P_3s from Hadar. In the previously collected hominins from Laetoli, a large metaconid is present in L.H. 2, L.H. 3, L.H. 4, and L.H. 14, whereas it is weakly developed in L.H. 24 (20.0% of the sample). EP 2400/00 adds a second example of P_3 from Laetoli with a weakly expressed metaconid, bringing the incidence to 33.3%. It may be that a lower proportion of P_3s with a well-developed metaconid does occur at Hadar compared with the specimens from Laetoli, but the samples are still too small to adequately test the significance of the difference. Overall, the P_3 of EP 2400/00 does not appear to have any morphological features that can be used to consistently discriminate it from the sample from Hadar, except that the crown is relatively longer.

Lockwood et al. (2000) and Kimbel et al. (2006) have demonstrated that the length of P_3 in the Laetoli sample is significantly greater than that in the Hadar sample, and that this is part of a temporal trend in *A. afarensis*. The more primitive condition, in which the P_3s are relatively longer than in *A. afarensis* from Laetoli, is seen in *Australopithecus anamensis* (Ward et al. 2001). With the recovery of EP 2400/00, a relatively small P_3, which is more similar in overall size to examples from Hadar, the magnitude of the temporal trend is somewhat diminished. Nevertheless, the mesiodistal length and the maximum length of the P_3 crown are still significantly greater in the Laetoli sample than in the sample from Hadar (see Discussion).

The P_4 in EP 2400/00 is consistent in length and breadth dimensions to previously described specimens of *A. afarensis* (Table 7.6). In terms of its occlusal area (mesiodistal length × buccolingual breadth; 103.7 mm^2) EP 2400/00 falls in the lower end of the range for the Hadar sample (mean = 106.9 mm^2; range = 77.0–134.5 mm^2; Kimbel et al. 2004), being most comparable in size to A.L. 228-2, A.L. 266-1 and A.L. 400-1a. EP 2400/00 is also smaller than the P_4 in L.H. 3 and L.H. 14. It is similar in size those of L.H. 4, but the crown is slightly shorter. The long-axis of the P_4 in EP 2400/00 relative

Table 7.6 Dimensions (mm) of EP 162/00 and EP 2400/01 compared with other *A. afarensis* teeth from Laetoli, Hadar, Dikika and Maka

			Laetoli[b]			Hadar and Dikika[c]			Maka[d]		
Tooth	Dimension	EP[a]	N	Mean	Range	N	Mean	Range	N	Mean	Range
C_1	MD	8.5	2	10.5	9.3–11.7	10	8.6	7.5–9.5	1	9.5	9.5
	BL	8.0	3	10.3	10.1–10.4	11	10.6	8.8–12.4	1	10.2	10.2
P_3	MD	10.8	6	10.9	9.8–12.2	19	9.2	7.9–11.4	2	9.5	9.3–9.7
	BL	10.0	6	10.9	9.8–12.3	19	10.4	8.9–12.6	2	11.3	11.2–11.3
P_4	MD	9.1	5	10.4	9.6–11.1	20	9.7	7.7–11.4	2	9.4	9.0–9.7
	BL	11.4	5	11.5	10.8–12.1	17	11.0	9.8–12.8	2	10.4	9.9–10.8
M_1	MD	12.3	5	13.4	12.2–14.2	23	13.0	10.1–14.8	3	13.2	13.0–13.6
	BL	11.4	5	13.1	12.5–13.5	17	12.5	11.0–13.5	3	12.2	12.1–12.4

MD mesiodistal length, *BL* buccolingual breadth

[a] New specimens collected from Laetoli by the Eyasi Plateau expedition (1998–2005): EP 162/00 (lower canine) and EP 2400/00 (mandible with P_3-M_1). Canine measurements follow method used by White (1977), but discrepancies reflect differences in tooth orientation

[b] Specimens from Laetoli collected by Louis Leakey (1935) and Mary Leakey (1974–1979). Canine data from White (1977, 1980a); all other measurements by the author

[c] Data from Kimbel et al. (2004) and Alemseged et al. (2006)

[d] Data from White et al. (2000). The data include estimated and maximum values, as well as teeth from both sides of the MAK-VP-1/12 mandible

to the line of the cheek teeth (72°) is more obliquely directed than the majority of P_4s from Hadar, which have a mean orientation of 61°, but it does fall in the upper end of the range (43°–85°). At noted by White (1985), and confirmed by further comparisons of EP 2400/00, there appear to be no consistent differences in the morphology of P_4 in the Hadar and Laetoli samples.

M_1 in EP 2400/00 is heavily worn and prevents detailed comparison of the occlusal morphology. In terms of its mesiodistal and buccolingual dimensions it represents the smallest example from Laetoli, and falls in the low end of the range of the series of first lower molars from Hadar (Table 7.6). The crown is relatively narrow, with a breadth-length index of 92.7, which again falls at the low end of the range for the sample from Hadar (mean = 95.8, range = 88.5–103.1; Kimbel et al. 2004).

EP 162/00

Left lower canine (Fig. 7.4).

Location and Stratigraphic Provenance

This specimen was found by Amandus Kweka at Loc. 16 on January 17, 2000. It was recovered as a surface find between Tuffs 7 and 8 (see Harrison and Kweka 2011). The absolute age of EP 162/00 can be constrained by the new radiometric dates for Tuff 7 (3.67 ± 0.04 Ma) and Tuff 8 (3.631 ± 0.018 Ma) (Deino 2011), giving the specimen an inferred age of ~3.63–3.67 Ma (see Fig. 7.1).

Fig. 7.4 EP 162/00, left lower canine of *Australopithecus afarensis*. (**a**) buccal view; (**b**) lingual view

Preservation

The crown is damaged by abrasion and slightly worn. A section of enamel 3.7 mm wide has been lost from the distal margin around the base of the crown, so that the distal tubercle is incompletely preserved. In addition, a large flake of enamel has been lost from the mesial and mesiobuccal face of the crown from the tip of the apex to half way down the crown. The lingual face is moderately pitted by weathering, and an apico-basally directed crack originates at the base of the crown distolingually and continues for much of the length of the root. The mesial and buccal faces of the crown are lightly pitted by weathering, with a series of fine cracks running apico-basally around the base of the crown. Mesiolingually there is a prominent crack that extends almost to the apex of the crown and runs almost the full length of the root. The root is complete, but the distal margin of the apex shows clear signs of having been gnawed by a small rodent. It is evident from the weathering and rodent gnawing that the isolated canine was exposed on the Pliocene land surface prior to being buried. The loss of enamel from the crown appears to be relatively fresh, and was likely caused by the trampling of livestock.

Morphology

The crown is relatively short and distally recurved. The height of the crown is estimated to be 11.7 mm (with the chipped apex it has a minimum height of 11.4 mm). The mesiodistal length and buccolingual breadth of the crown are given in Table 7.6, along with comparative data on other specimens of *A. afarensis* from Laetoli and Hadar. It is oval in occlusal outline, and markedly buccolingually compressed. The breadth-length index is estimated to have been 80.9. The apex is situated distal to the midline axis of the root in the mesiodistal plane. The lingual face of the crown is apico-basally slightly concave and mesiodistally convex. It is bordered basally by a low, rounded and ill-defined lingual cingulum, which is best developed mesially. The distal margin, and most of the distal tubercle on the distobuccal margin have been lost through abrasion, but it is evident that the latter was quite prominent. A low rounded distal crest descends from the apex to terminate at the distal tubercle. Just lingual to the distal crest, and slightly better developed, is a low distolingual crest that descends from the apex to the base of the crown. The two crests are separated by a shallow crescent-shaped groove, which is deepest and broadest basally. Both crests have been flattened by slight wear along their apical aspects. Mesially the lingual cingulum curves apically. The enamel at the mesial junction of the lingual cingulum is damaged, but presumably it would have become continuous mesially with the relatively short mesial ridge. The mesial ridge itself is not preserved. The enamel in this region has been sheared away to expose a narrow strip of dentine running obliquely across the crown from the apex to the mesiolingual margin of the crown. The exposed enamel has a maximum thickness of 0.7 mm. The buccal surface is mesiodistally convex and curves distolingually towards the apex. It is generally smooth and featureless, except for a shallow groove around the base of the mesiobuccal face, representing a vestige of the buccal cingulum. In addition, skirting the base of the buccal face of the crown from the mesial margin to the distal tubercle is a hypoplasia, represented by a distinct band of thin enamel, 0.8 mm wide and originating about 2.4 mm up from the base of the crown.

The root is apico-basally much taller than the crown (the length of the root buccally is 22.1), and relatively stout. It is elliptical in cross-section, with a slightly concave mesiolingual face. In lateral view the distal margin is relatively straight, while the mesial margin is convex and curves distally. In distal view the root is relatively straight, although the apex shows a slight curvature towards the lingual side.

Comparisons

EP 162/00 is comparable in size and morphology to the smaller lower canines from Hadar, which presumably belonged to female individuals (Table 7.6). EP 162/00 is most similar to A.L. 198-1, but the latter is slightly larger (although the crown height is comparable), and has a less strongly bilaterally compressed crown and a thicker and more rounded lingual pillar. The specimen also matches quite well with the incomplete crown in A.L. 128-23, which is among the smallest lower canines of *A. afarensis*. EP 162/00 is slightly larger and has a somewhat broader distal face, but is otherwise similar in proportions and overall dimensions. They also share a similarly placed hypoplastic feature on the buccal aspect of the crown. The larger canines from Hadar, such as A.L. 333w-58, A.L. 333-90 and A.L. 277-1, presumably from male individuals, differ in being relatively higher crowned and less bilaterally compressed, with more profound mesial and distal grooves, a more strongly developed and rounded lingual pillar, a better-defined lingual cingulum mesially, and a more prominent distal tubercle. EP 162/00 is much smaller and relatively lower-crowned than the five examples of lower canines previously recovered from Laetoli (L.H. 2, L.H. 3n, L.H. 14e, L.H. 14f and M.42323) (Table 7.6). Compared with the range of size variation and morphology seen in the larger sample from Hadar, the latter canines from Laetoli are all likely to have belonged to male individuals. EP 162/00 represents, therefore, the first canine from Laetoli that can be assigned to a female individual, and shows that the size range of *A. afarensis* canines from Laetoli is comparable to that at Hadar.

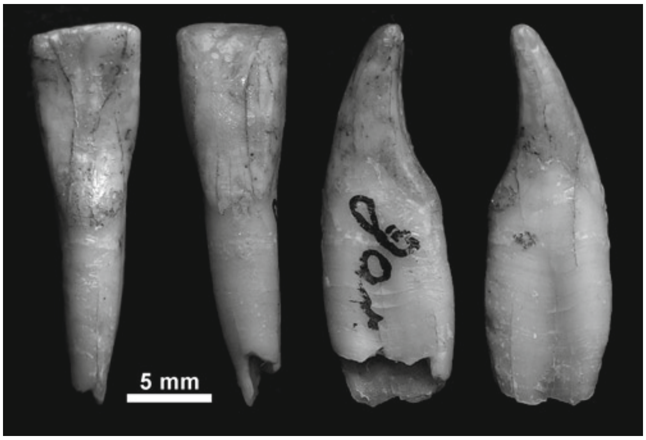


Fig. 7.5 MB Ma. 8294, left I_1 of *Australopithecus afarensis*. From *left* to *right*: lingual view; buccal view; distal view; mesial view

MB Ma. 8294

Unerupted left I_1 (Fig. 7.5).

Location and Stratigraphic Provenance

The specimen was first identified as that of a hominin in the late 1970s by Eric Delson, while studying the Laetoli cercopithecids from the Kohl-Larsen collection in Berlin (White 1981). The root bears an original field abbreviation "gar.", which signifies that it came from the Garusi Valley (= Laetoli). Preservation of the specimen is consistent with it being derived from the Upper Laetolil Beds, but otherwise its geographical and stratigraphic provenance is unknown.

Preservation

The crown is well preserved, with no indication of wear. The enamel surface is slightly pitted due to weathering, and there are a number of fine cracks, some of which extend onto the base of the root. There are no mesial or distal interproximal contact facets. It is evident that the tooth was unerupted. The tip of the root is missing, with loss of small flakes from the distal apect of the root apex, but the mesial aspect of the root is relatively complete. Judging from the preserved portion of the root and the size of the root canal, the root was still open, but the tooth was otherwise close to being completely formed. Fine striations on the buccal, mesiobuccal and distobuccal faces of the root appear to have been produced by gnawing by a small rodent. This indicates that the tooth was isolated and exposed on the Pliocene landsurface prior to burial and fossilization.

Morphology

The tooth has been briefly described by Ullrich (2001), who refers to the specimen as Garusi 4, although use of the museum accession number is preferable. The specimen is described as a lateral incisor, but the narrowness and symmetry of the crown makes it a better match with the lower central incisors from Hadar.

As noted above, the specimen is well preserved and unworn. The crown is tall and relatively narrow (see Table 7.7 for dimensions). The apical margin is mesiodistally narrow, with a fine incisive edge that becomes buccolingually slightly thicker where it meets the mesial and distal margins. There are two small swellings on the distolingual aspect of the apical margin, which presumably represent traces of mammelons. The crown is mesiolingually broadest at the apex and narrows basally. The mesial and distal margins are both slightly convex, producing a relatively symmetrical crown bilaterally. The mesial margin is slightly longer than the distal margin, so the incisive apex slopes inferiorly as it passes distally. The lingual face is apicobasally strongly concave, but slightly convex mesiodistally. A low and indistinct swelling, a trace of the lingual pillar, descends the lingual face obliquely from just below the apex in the midline to blend in with the general surface of the lingual aspect of the crown about two-thirds down and to the distal side of the midline. The lingual pillar is separated from the rounded mesial and distal marginal rims by shallow grooves. There is no lingual cingulum around the base of the lingual face of the crown.

In mesial view, the crown tapers apically with a concave lingual face and a slightly convex buccal face. The base of the crown meets the root at an inverted V-shaped cemento-enamel junction. The root is lingually recurved, such that when the incisive apex is oriented as in tip-to-tip occlusion with its upper counterpart, the apicobasal long axis of the root would have been directed lingually at an angle of 21°. This angling of the root reflects the posterior inclination of the mandibular symphysis in *A. afarensis*.

The buccal face of the crown is generally featureless. It is biconvex apico-basally and mesiodistally. The mesial and distal margins taper slightly in the apical half of the crown, then more abruptly in the basal half. This gives the mesial and distal margins their convexity. Overall, the crown is

Table 7.7 Dimensions (mm) of I_1 of *Australopithecus afarensis*

		Laetoli[a]		Hadar and Dikika[b]		
Dimensions	MB Ma. 8294	N		N	Mean	Range
MD	6.3	1	7.8	6	6.3	5.6–7.1
BL	7.1	1	7.8	5	7.3	6.9–7.6
BHT	11.7(e)	1	13.0			

MD mesiodistal length, *BL* buccolingual breadth, *BHT* buccal height of crown, *(e)* estimated value

[a] Data collected by author

[b] Data from Kimbel et al. (2004) and Alemseged et al. (2006)

bilaterally almost symmetrical, apart from the slightly shorter distal margin and the slightly distally receding apex. There are no evident anomalies in the surface of the enamel associated with hypoplasias or other developmental disturbances.

The root is mostly complete, except for the tip, which has lost some flakes from the mesial face. The root canal was apparently still open, with a dumbbell-shaped lumen, 4.3 mm wide in the buccolingual plane. The root is mesiodistally compressed, with shallow grooves on the mesial and distal faces. The buccal margin is slightly broader than the lingual face. The length of the root (11.4 mm) is subequal to the height of the crown, but when complete would have been slightly longer.

Comparisons

MB Ma. 8294 is morphologically similar to the I_1 germ in L.H. 2, the only other complete lower central incisor from Laetoli, but it is much smaller in its overall dimensions (16.9% smaller on average in its linear dimensions) (see Table 7.7). Moreover, L.H. 2 differs in being relatively broader, having a distinct median groove on the lingual face, and a greater number of mammelons on the incisive apex. L.H. 3(m) consists of the distal half of I_1 only. It appears to be similar in size and morphology to L.H. 2, but slightly higher crowned, and somewhat larger in overall size than MB Ma. 8294. The I_1s from Hadar are consistent in morphology and dimensions to MB Ma. 8298 (see Table 7.7) (Johanson et al. 1982; Kimbel et al. 2004).

L.H. 29

Left mandibular corpus with M_1-M_3 (Fig. 7.6).

Location and Stratigraphic Provenance

The specimen was found on July 21, 1979 by Mwongela Mwoka at Loc. 8 (field number LAET 79-5487). According to Leakey (1987b) the heavily weathered and rolled specimen was recovered from the surface of the lower part of the exposures near the Garusi River. It was assumed at the time to be derived from the Pleistocene Lower Ngaloba Beds (Leakey 1987b: 108), because of the dark staining and patination. As a consequence, the specimen was attributed to *Homo* cf. *H. erectus* (Leakey 1987b: Table 5.1). However, the specimen is heavily mineralized, unlike the Pleistocene fossils from Laetoli, which tend to be more lightly mineralized. It is much more likely that the specimen was originally derived from the fossil-rich Upper Laetolil Beds, and that it developed a similar coloration to that typical of Pleistocene fossils at Laetoli after eroding out onto the surface and becoming secondarily associated with the superficial sediments. Moreover, the morphology of L.H. 29 is entirely consistent with that of *A. afarensis*, and it seems most plausible to assume that the specimen was originally derived from the Upper Laetolil Beds. Regardless of its provenance, the morphological evidence alone supports reassignment of L.H. 29 to *Australopithecus afarensis*.

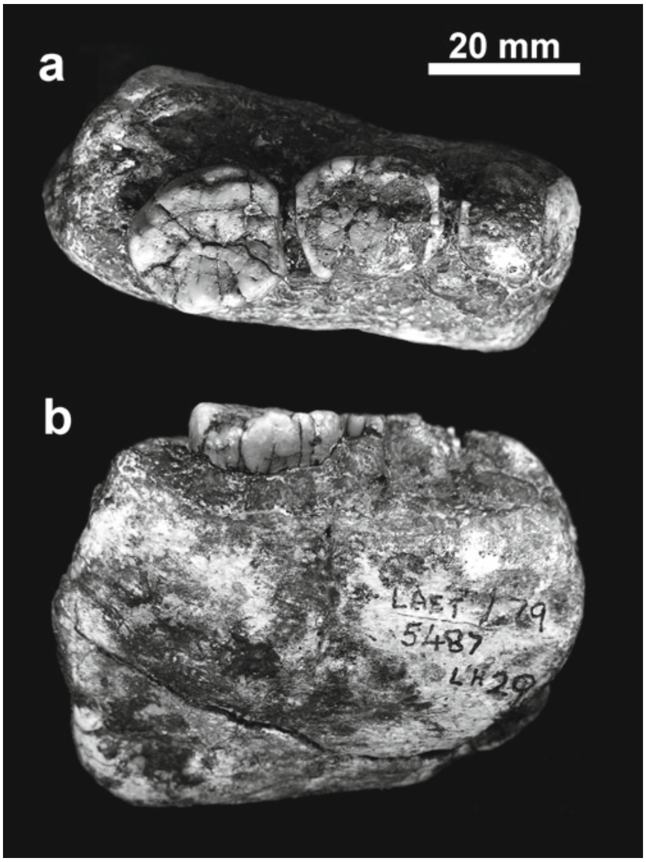


Fig. 7.6 L.H. 29, left mandibular corpus with M_1-M_3 of *Australopithecus afarensis*. (**a**) occlusal view; (**b**) medial view

Preservation

The specimen preserves the mandibular corpus below the lower molars, but it is quite heavily weathered and smoothed by rolling, especially at the broken edges. A deep longitudinal crack in the corpus runs anteroposteriorly along the inferior one-third of the medial face. The lower molars are damaged, eroded and moderately to heavily worn. M_1 has been almost entirely obliterated by weathering and rolling, leaving only a well-rounded dentine core and a small fragment of enamel, 4 mm long, along the distal margin of the crown. M_2 has a rounded mesiolingual face that has been eroded and rolled.

A large crack passes transversely across the crown at an oblique angle, passing through the hypoconid and entoconid. The enamel rim from the buccal margin of the protoconid has been chipped away. The M_3 is complete, but several cracks have caused slight expansion of the dimensions of the crown. Mesially there is a transverse fracture that passes across the mesial aspect of the protoconid and metaconid to skirt the distal margin of the mesial fovea. A second fracture originates from the midpoint of the transverse crack and passes distally in the midline into the center of the talonid basin, where it deviates buccally to pass through the distal margin of the hypoconid. A third fracture passes mesiolingually across the mesiobuccal face of the hypoconulid at an oblique angle to join the midline fracture. A finer crack passes between the hypoconulid and entoconid.

The bone of the mandibular corpus is yellow-grey in coloration with a black tar-like staining, the enamel of the teeth is dark grey with orange staining, and the exposed dentine is black. This resembles the coloration of fossils from late Pleistocene sediments, but given the degree of weathering and rolling, the specimen clearly spent a long period of time on the surface prior to being recovered, and it is very likely that the fossil developed a coloration and patination associated with the rare fossil material derived from the surface lag.

Morphology

The mandibular corpus is poorly preserved. It is robust, being thickest in the alveolar region and narrowing inferiorly, and increases in thickness posteriorly. The corpus maintains a relatively constant depth below the molars or deepens slightly posteriorly. The lateral face of the corpus is slightly convex inferosuperiorly. The root of the ramus originates opposite M_3. The medial face is relatively flat.

The M_1 is poorly preserved; it comprises a rounded stump of dentine, with a small segment of the enamel rim preserved along the distal margin. The occlusal surface of the enamel remnant is worn flat, indicating that the molar was probably very worn with much of the enamel cap missing. The dimensions of M_1 cannot be measured or accurately estimated, but preservation of the enamel distally and the mesial root does indicate that the tooth was at least 10 mm in length.

The M_2 is mostly complete, but the mesiolingual corner and much of the lingual face have been damaged and smoothed as a result of erosion and rolling. The length of the crown can be measured with precision, but only a minimum and estimated buccolingual breadth can be obtained (see Table 7.8). The crown appears to have been mesiodistally longer than broad and rectangular in shape with rounded corners. The enamel cap is worn flat and large areas of dentine are exposed on the protoconid and hypoconid and a smaller area is exposed on the hypoconulid. Damage to the lingual side of the crown does not permit determination of the extent of dentine exposure on the metaconid and entoconid. The crown is too worn and damaged to provide any information on the detailed morphology of the occlusal surface. In terms of its size, proportions, cusp distribution, and enamel thickness it appears to be consistent in morphology with other M_2s of *A. afarensis* (see below).

The M_3 is complete, but the crown is cracked and moderately worn. The crown is longer than broad and ovoid in shape, with well-rounded corners. The mesial margin of the crown has a broad and concave interproximal facet for contact with M_2. The length of the tooth is currently 14.1 mm, but its original length can be estimated to have been 14.8 mm (Table 7.8). M_3 was clearly larger in area than M_2. Based on the estimated dimensions of the molars, the occlusal area (mesiodistal length × buccolingual breadth) of M_3 is 9.8% larger than that of M_2.

The protoconid is larger than the hypoconid, which is situated immediately distally. The hypoconulid is a small triangular cusp situated just to the buccal side of the midline of the crown. The three buccal cusps are closely approximated, being separated by fine fissures that radiate out from the talonid basin. The metaconid is smaller in area than the protoconid. A short groove running obliquely along the mesiobuccal margin of the metaconid represents the remnant

Table 7.8 Dimensions (mm) of lower molars in L.H. 29 compared with other *A. afarensis* teeth from Laetoli, Hadar, and Maka

			Laetoli[b]			Hadar[c]			Maka[d]		
Tooth	Dimension	L.H. 29[a]	N	Mean	Range	N	Mean	Range	N	Mean	Range
M_2	MD	13.2 (13.8)	4	14.3	14.0–14.9	25	14.2	12.1–16.5	3	14.4	14.0–15.0
	BL	(12.9)	4	13.4	12.7–14.1	21	13.4	11.1–15.2	3	13.2	13.0–13.3
M_3	MD	14.1 (14.8)	1	16.2	16.2	19	15.1	13.4–17.4	4	15.6	15.2–16.2
	BL	13.4	1	13.9	13.9	16	13.4	11.3–15.3	4	13.4	13.0–13.8

MD mesiodistal length, *BL* buccolingual breadth

[a] Estimated values are in parentheses. Data collected by the author

[b] Specimens collected by Mary Leakey (1974–1979), excluding L.H. 29. Data collected by the author

[c] Data from Kimbel et al. (2004)

[d] Data from White et al. (2000). The data include estimated and maximum values, as well as teeth from both sides of the MAK-VP-1/12 mandible

of the mesial fovea. The entoconid is similar in size to the metaconid. Interposed between the metaconid and entoconid is a small wedge-shaped metastylid, separated from the main buccal cusps by deep fissures. A V-shaped distal basin separates the entoconid from the hypoconulid. A small area of dentine is exposed on the protoconid, and the other buccal cusps are worn flat but without exposed dentine. The metaconid and entoconid exhibit a moderate degree of wear, but they retain greater topographic relief than the buccal cusps. Bordering the buccal face of the protoconid and the mesiobuccal face of the hypoconid is a rounded, but well-developed buccal cingulum (or protostylid, expression state 6 of Hlusko 2004), as is typically found in the lower molars of *A. afarensis* from Laetoli. The cingulum is better developed than on L.H. 4, but is comparable to that seen on M_1 and M_2 of L.H. 14h.

Comparisons

The height and breadth dimensions of the mandibular corpus below mid-M_2 can be compared with data on *A. afarensis* mandibles from Hadar (see Table 7.9). The breadth of the corpus in L.H. 29 is 22.8 mm, compared with a mean value of 21.8 mm in the sample from Hadar (range = 18.1-30.5 mm; $n=24$) (Kimbel et al. 2004). The height of the corpus at M_2 is 38.4, which exceeds the deepest mandible known from Hadar (A.L. 444-2). The mean corpus height at M_2 in the Hadar sample is 31.7 mm (range = 25.3–37.6; $n=19$) (Kimbel et al. 2004). L.H. 29 is similar in corpus breadth to L.H. 4, but is somewhat deeper (Table 7.7). The size of the corpus indicates that L.H. 29 was probably a male individual. It also indicates that there was a good deal of variation in corpus dimensions in the Laetoli sample, comparable to that from Hadar. If L.H. 29 does derive from the Upper Laetolil Beds, then it may have important implications for inferences about evolutionary change in *A. afarensis*. Lockwood et al. (2000) have demonstrated a shift toward larger corpus size in the youngest *A. afarensis* mandibles from Hadar, but the recovery of an individual with a relatively large mandibular corpus from Laetoli, earlier in time than the Hadar sample, may call into question whether this was a temporal trend in the species as a whole or a more localized phenomenon uniquely characteristic of the Hadar sample.

Table 7.9 Comparison of dimensions (mm) of the mandibular corpus in L.H. 29 with other specimens of *A. afarensis*

Locality	Specimen	Ht at M_2	Br at M_2
Laetoli	L.H. 29	38.4	22.8
	L.H. 4	30.3	22.6
	L.H. 13	–	23.6
Hadar	A.L. 128-23	–	22.9
	A.L. 145-35	–	24.8
	A.L. 188-1	34.3	18.8
	A.L. 198-1	30.8	18.1
	A.L. 198-22	34.0	20.9
	A.L. 207-13	25.3	18.4
	A.L. 225-8	28.1	21.4
	A.L. 266-1	27.6	24.2
	A.L. 315-22	28.0	20.0
	A.L. 330-5	28.3	19.5
	A.L. 333w-1a, b	32.4	23.0
	A.L. 333w-32+60	35.4	23.6
	A.L. 417-1a	32.8	18.4
	A.L. 432-1	–	20.3
	A.L. 433-1a, b	–	20.8
	A.L. 436-1	26.0	19.6
	A.L. 437-1	–	19.6
	A.L. 437-2	37.0	24.2
	A.L. 438-1 g	37.1	28.1
	A.L. 444-2	37.6	30.5
	A.L. 620-1	34.5	22.6
Maka	MAK 1/12	29.6	20.6
	MAK 1/2	32.6	21.4

[a] Dimensions: Inferosuperior height of corpus at mid-M_2; mediolateral breadth of corpus at mid-M_2

[b] Data: Laetoli (Harrison, unpublished); Maka (White et al. 2000); Hadar (Kimbel et al. 2004). Where both sides are measurable, the value is the average of the right and left sides

The M_1 and M_2 are too worn and damaged to allow detailed comparisons of the occlusal morphology. In its shape, proportions, cusp size and distribution, and enamel thickness, the M_2 in L.H. 29 matches well with the corresponding tooth in L.H. 4, but is slightly smaller. In terms of its estimated occlusal area (178.2 mm^2) it represents the smallest M_2 so far recovered from Laetoli (previous finds range in occlusal area from 180.3 to 197.4 mm^2). However, the estimated occlusal area does fall well within the range of variation for the Hadar sample ($n=21$, range = 137.6–234.1 mm^2, mean = 189.0; Kimbel et al. 2004). The M_2 crown is relatively narrow with an estimated breadth-length index of 93.5, which falls within the range of variation of the previously collected specimens from Laetoli ($n=4$, range = 89.4–100.7, mean = 93.6) and the Hadar sample ($n=21$, range = 84.6–107.7, mean = 95.6; Kimbel et al. 2004).

The M_3 in L.H. 29 is similar to L.H. 4, the only other M_3 previously recovered from Laetoli (L.H. 15 is considered here to be an M_2 rather than M_3, *contra* White 1980a), but it differs in being smaller in size (the occlusal area in L.H. 29 is 198.3 mm^2 versus 225.2 mm^2 in L.H. 4) and relatively broader (the breadth-length index in L.H. 29 is 90.5 versus 85.8 in L.H. 4), with more convex buccal and lingual margins, a larger hypoconulid, a larger distal fovea, a more pronounced metastylid, and a better developed buccal cingulum. The occlusal morphology of M_3 in L.H. 29 corresponds well with examples from Hadar. The occlusal area and breadth-length index fall close to the mean values for the Hadar sample (occlusal area: $n=15$, range = 151.4–266.2 mm^2, mean = 200.0; breadth-length index: $n=15$, range = 82.4–100.7, mean = 89.0; Kimbel et al. 2004).

In L.H. 29 M_3 is slightly larger (11.4% larger) in its occlusal area than M_2. A similar relationship occurs in L.H. 4 (17.4% larger than M_2) and the Hadar sample (the occlusal area of M_3 exceeds that of M_2 in associated teeth by an average of 9.4%), but there is a good deal of variation in the latter sample, with some specimens having M_3 slightly smaller than M_2 (up to 9.0% smaller) or much larger (up to 50.4% larger) (Kimbel et al. 2004).

LAET 79-5447

Right upper canine (Fig. 7.7).

Location and Stratigraphic Provenance

According to Mary Leakey's field catalogue this specimen was found on July 6, 1979 at Loc. 8, but details of its stratigraphic provenance and the identity of the collector of the specimen are not recorded. Although identified as a "hominid" in the catalogue, it presumably remained undescribed and unpublished because of the weathering and dark staining, similar to L.H.29, which gives it a superficial resemblance to the preservation typical of late Pleistocene fossils at Laetoli (see below).

Preservation

The specimen preserves a complete crown and most of the root, except for the tip. It is quite heavily weathered. The crown has a prominent crack that runs from the apex along the mesial ridge and margin and continues along the mesial face of the root to terminate at the broken root tip. A similar crack runs perpendicular, passing from the apex onto the buccal and lingual faces where it terminates at mid-crown. A series of smaller hairline cracks disrupt the enamel around the base of the crown, especially on the buccal aspect. The buccal face of the crown is eroded and pitted by weathering. The lingual face is more heavily etched, and much of the enamel from the base of the lingual aspect of the crown has been lost. A small chip of enamel is missing from the mesial marginal ridge on the lingual face.

Fig. 7.7 LAET 79-5447, right upper canine of *Australopithecus afarensis*. (**a**) distal view; (**b**) mesial view; (**c**) buccal view; (**d**) lingual view

The enamel in the unweathered state was grey-brown, as is common among fossil teeth from the Upper Laetolil Beds, but most of the enamel surface has developed a white patination, with orange staining and smaller areas of black patination. The root was originally grey-brown, but is now stained black and orange with light grey patches. This black and orange mottling is typical of Late Pleistocene fossils, and this probably accounts for why the specimen has previously been overlooked. However, as noted above for L.H. 29, specimens that erode out of the Upper Laetolil Beds and become reworked with the superficial sediments often secondarily develop a patination and stain resembling Late Pleistocene fossils. The original coloration of the fossils does indicate that it was derived from the Upper Laetolil Beds, and this is supported by the anatomy and size of the tooth, which is identical to that of upper canines of *A. afarensis* (see Table 7.10).

Morphology

The entire crown and most of the root are preserved. The crown is relatively tall, with an angular apex. The apicomesial margin runs for 6.5 mm from the apex to form a long and relatively sharp ridge. It is angled at 23° to the apicobasal axis of the crown. Light wear is evident along the mesiolingual aspect of the apex, where a small area of dentine is exposed, and it continues mesially as a flattened facet along the apicomesial margin of the crown. This wear facet is produced by occlusion with the apex of the lower canine. The apicomesial margin meets the mesial margin at an obtuse angle of 126°, and forms the mesial shoulder situated about two-thirds down from the base of the crown. From the mesial

Table 7.10 Dimensions (mm) of upper canines of *Australopithecus afarensis*

		Laetoli[a]			Hadar and Dikika[b]		
Dimensions	LAET 79-5447	N	Mean	Range	N	Mean	Range
MD	10.3	3	10.4	9.5–11.7	12	9.7	8.8–10.4
BL	9.3	3	10.0	9.1–11.5	11	10.9	9.3–12.4
BHT	14.2	2	14.0	13.9–14.0			

MD mesiodistal length, *BL* buccolingual breadth, *BHT* buccal height of crown

[a] Data collected by author

[b] Data from Kimbel et al. (2004) and Alemseged et al. (2006)

shoulder, the mesial margin ascends at a slightly oblique angle towards the base of the crown. The distal margin forms a relatively straight and sharp ridge that meets the apicomesial margin at an angle of 82°. Basally, the distal margin ridge terminates at a small distal tubercle, forming the distal shoulder, situated about one-third down from the base of the crown.

The buccal face of the crown is apicobasally and mesiodistally strongly convex and generally featureless. The distal tubercle is bordered mesially by a shallow apicobasally oriented groove. A very shallow groove is also evident bordering the mesial margin. Despite the weathered enamel there is no evidence of any developmental disturbances, such as hypoplasias.

The mesial face of the crown forms a flattened V-shaped surface. The enamel junction at base of the mesial aspect of the crown is U-shaped. Although the mesial face is weathered and eroded, traces of the original enamel surface confirm that the base of the crown had a large interproximal contact facet for I^2 and that there was no maxillary diastema (absent in 50% of *A. afarensis* specimens according to Kimbel et al. 2004).

In lingual view, the mesial shoulder is much more apically placed than the distal shoulder, producing a rhomboidal shaped crown with a strong mesiodistal asymmetry. The lingual face is mesiodistally slightly convex. An eroded remnant of a narrow and sharp lingual pillar is preserved in the middle one-third of the crown. It presumably ran from the base of the crown to the apex in its original state. A small subsidiary ridge originates from the base of the crown, close to the origin of the lingual pillar, and passes obliquely mesially across the lingual face of the crown to join the distal ridge midway along its length. Mesial to the lingual pillar, the lingual face is generally quite flat, although some fine crenulations in the weathered enamel surface may indicate that there was originally some secondary wrinkling. A shallow groove and a raised rim border the mesial margin of the lingual face. A narrow and shallow groove separates the lingual pillar from the distal margin. The base of the crown of the buccal face is damaged, so the morphological details are not discernable.

The root is almost complete except for the missing apex. It is quite short. The preserved portion is 14.8 mm long, but it was probably 18.5 mm long when complete. The root is mesiodistally compressed, and its maximum cross-sectional dimensions are 10.3 mm by 6.9 mm. The mesial face of the root is flattened, with a shallow groove running along its length. The buccal face is convex and thicker than the lingual face, giving the root a triangular cross-section.

Comparisons

LAET 79-5447 is very similar in overall size and crown height to the unerupted upper canine, L.H. 6b from Laetoli, which is inferred to have belonged to a male individual. L.H. 6b does differ, however, in a few features, including: (a) a steeper and more convex apicomesial ridge that grades smoothly into the mesial margin, without the sharp angulation seen in LAET 79-5447; (b) a slightly more prominent lingual pillar; (c) a less pronounced distal tubercle; and (d) the mesial margin of the lingual face lacking the distinct marginal rim. The largest of the upper canines from Laetoli, LH 3e, is quite a bit larger than LAET 79-5447. The mesiodistal length and buccolingual breadth of the crown in LAET 79-5447 are 13.6% and 23.7% smaller than in L.H. 3e, respectively, but the crown height was slightly higher. LAET 79-5447 also differs from L.H. 3e in the following features: (a) the apicomesial ridge and the mesial margin are angled as in LAET 79-5447, but the angulation occurs at mid-crown height, rather than one-third up from the apex as in LAET 79-5447; (b) the lingual pillar is better developed and positioned closer to the mesial margin; (c) the distal margin is shorter and less steep, giving the crown in L.H. 3e greater mesiodistal symmetry in lingual view; and (d) there is more strongly developed secondary wrinkling on the buccal face. LAET 79-5447 is larger and relatively higher crowned than the worn upper canine in L.H. 5, inferred to have belonged to a female individual, although it is generally similar in morphology. The root is longer and more slender in L.H. 5.

The sample of upper canines of *A. afarensis* from Hadar ($n=11$; Kimbel et al. 2004) exhibits metrical variation that can be interpreted as sexual dimorphism in overall size (i.e., cross-sectional area and crown height). Metrically, LAET 79-5447 falls in the lower end of the size range of canines inferred to belong to male individuals (being most similar in dimensions and morphology to A.L. 200-1) (Table 7.10). LAET 79-5447 is morphologically similar to A.L. 333x-3 in the shape and degree of symmetry of the crown, but somewhat smaller in its overall dimensions (see Fig. 7.8). The latter specimen is the largest of the upper canines from Hadar, and is reasonably interpreted as belonging to that of a male individual, but it is still smaller than L.H. 3e, which is the largest upper canine attributed to *A. afarensis*. A.L. 333x-3 also differs from LAET 79-5447 in the following features: (a) the apicomesial ridge is slightly steeper; (b) the lingual pillar is similar in development, but slightly more mesially placed; and (c) the distal tubercle is less prominent. These relatively minor differences are outweighed by the striking similarities. Kimbel et al. (2004: 207) suggest that the small sample of upper canines from Laetoli can be distinguished from those from Hadar in having more symmetrical crowns with a more cervically positioned mesial shoulder, being more similar in height to the distal shoulder. This is the case for L.H. 3e and possibly also for L.H. 5, but not for L.H. 6b or LAET 79-5447, which have the pattern typically found in the upper canines from Hadar. This can be considered a variable feature in the *A. afarensis* sample from Laetoli, and claims about the

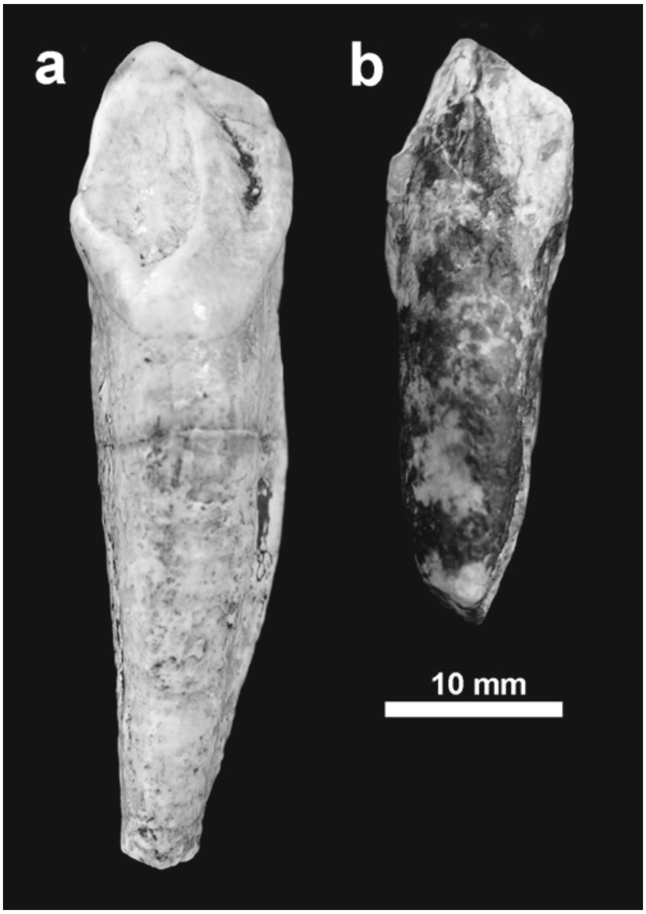


Fig. 7.8 Comparison of LAET 79-5447 with upper canine A.L. 333x-3 from Hadar. (**a**) A.L. 333x-3 (cast), lingual view, left upper canine (reversed image). (**b**) LAET 79-5447, lingual view, right upper canine

purported difference between the two samples have been influenced by the extreme morphology represented by the very large canine, L.H. 3e, from Laetoli. Nevertheless, it is true that the configuration seen in L.H. 3e and to some extent L.H. 5 is not matched by any specimens in the large sample of upper canines from Hadar, thereby implying that a discernable difference may exist in the relative frequency of different upper canine morphs between the samples from Laetoli and Hadar.

New Hominins from the Upper Ndolanya Beds

Since the resumption of systematic fieldwork at Laetoli in 1998 fossil hominins have been recovered for the first time from the Upper Ndolanya Beds, which are dated to 2.66 Ma. In 1998 a proximal tibia (EP 1000/98) was discovered at Nenguruk Hill at Loc. 22S. At the time, its taxonomic affinities could not be determined because hominin craniodental specimens were not known from the Upper Ndolanya Beds, and several potential candidate taxa in eastern Africa were penecontemporaneous (i.e., *Paranthropus aethiopicus*, *Australopithecus garhi*, and *Homo* sp.). In 2001 a maxillary fragment was recovered from the Upper Ndolanya Beds at Silal Artum that was identifiable as *Paranthropus aethiopicus*. This is the only specimen definitively attributed to this species from outside the Turkana Basin of northern Kenya and southern Ethiopia (see Table 7.11 for a summary of the taxonomy and nomenclature of this species).

Table 7.11 Taxonomy and synonymy list of *Paranthropus aethiopicus*

Superfamily: Hominoidea Gray, 1825
Family: Hominidae Gray, 1825
Subfamily: Homininae Gray, 1825
Tribe: Hominini Gray, 1825
Genus: *Paranthropus* Broom, 1938
Species: *P. aethiopicus* (Arambourg and Coppens 1968)

Synonymy
1967 – “Paraustralopithecus aethiopicus” – Arambourg and Coppens (1967) [unavailable, conditionally proposed]
1968 – *Paraustralopithecus aethiopicus* Arambourg and Coppens, 1968 – Arambourg and Coppens (1968)
1978 – *Australopithecus africanus* Dart, 1925 – Howell (1978) [*partim*]
1986 – *Australopithecus aethiopicus* (Arambourg and Coppens 1968) – Walker et al. (1986)
1988 – *Paranthropus aethiopicus* (Arambourg and Coppens 1968) – Clarke (1988)
1989 – *Australopithecus walkeri* Ferguson, 1989 – Ferguson (1989)

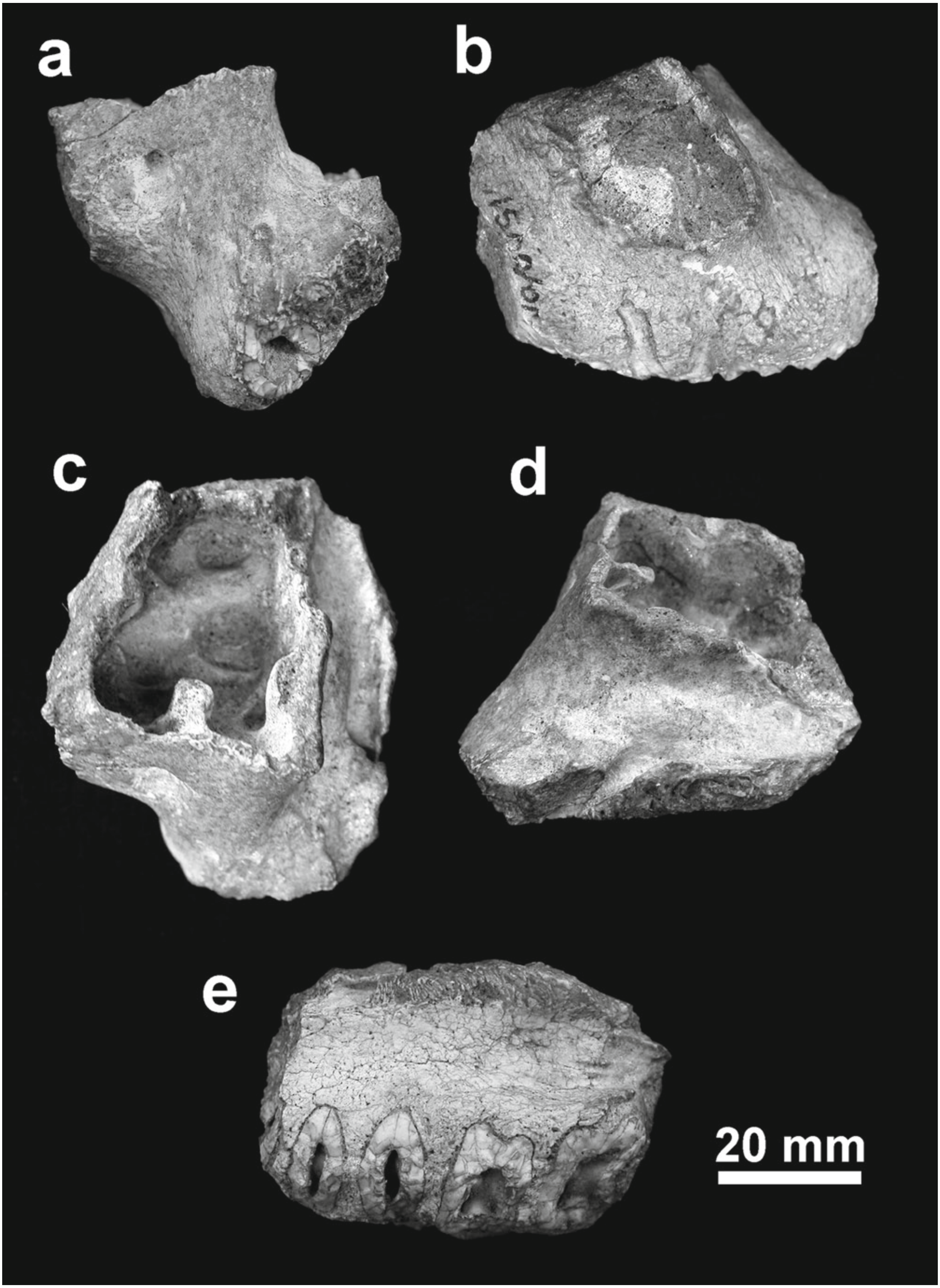
With this discovery, it becomes more likely that the proximal tibia from Loc. 22S belongs to the same species, but the possibility that it represents a second hominin taxon that is not yet identified in the Upper Ndolanya Beds cannot be entirely ruled out. As a consequence, it is left unattributed. In addition, a possible hominin, previously undescribed, was recovered by Mary Leakey’s expeditions in 1975 during excavations in the Upper Ndolanya Beds at Loc. 7E. The specimen consists of a small fragment of the right zygomatic process of the frontal bone of an infant, associated with two other indeterminate cranial fragments. The specimen was originally identified as a cercopithecid, but the size and morphology are consistent with it being a hominin. The specimen is provisionally identified here as cf. Hominini indet.

EP 1500/01

Edentulous right maxilla with the roots for I^2-M^2 (Fig. 7.9).

Location and Stratigraphic Provenance

The author discovered the specimen on July 28, 2001 at the locality of Silal Artum. The specimen was a surface find, partially reburied, but, along with the associated fauna, was unquestionably derived from the Upper Ndolanya Beds.


a
b
c
d
e
20 mm

Detailed information on the locality and hominin find spot are presented in Harrison and Kweka (2011).

Preservation

The specimen consists of a right maxillary fragment comprising a large part of the maxillary corpus. The specimen is edentulous, but preserves the roots of I^2-M^2. The specimen was found partially buried in reworked sediment resting with the roof of the palate facing upwards. There is a sharp change in coloration, from creamy white to orange, across the lateral face of the maxilla that delineates the portion that was buried (orange) from that portion exposed to the elements. The specimen is lightly rolled and abraded.

The anterior part of the maxilla containing the upper canine and incisors is missing. Judging from the sharp break in the bone and the fresher appearance of the exposed surfaces of the roots of the canine and I^2 relative to the cheek teeth, it would appear that this portion was sheared off subsequent to the specimen being weathered out onto the surface, and being rolled and abraded. Given the force needed to cleanly detach the bone fragment, it is likely that the specimen was damaged by trampling. From the orientation of the specimen at the time of discovery and from the color difference of the exposed portion of the maxilla, we know that the subnasal region of the maxilla was projecting above the soil surface and would have been prone to trampling. Nevertheless, the occurrence of adhering matrix to the broken surface of the bone does indicate that some time had elapsed between when the damage was done and when the specimen was collected. The detached piece was not recovered during screening operations following initial discovery of the specimen.

The alveolus for I^1 is matrix filled, indicating that this tooth had been lost before fossilization, but because the alveolar region of the maxilla is missing it is not possible to determine whether the tooth was lost antemortem or postmortem, but the latter seems the most likely scenario. Posteriorly, the palate is preserved as far as the anterior alveolar wall of M^3, but there is no trace of a tooth root. Matrix adhering to the posterior wall of the maxilla at the time of discovery confirms that M^3 was already lost at the time of fossilization. Nevertheless, the contour of the anterior alveolar wall confirms that M^3 was erupted at the time of death. The surface bone of the palate exhibits numerous fine cracks, and these appear to be largely or exclusively the result of postfossilization weathering.

The palate is preserved as far as the midline from opposite the mesial root of P^3 to opposite mid-M^2. Posteriorly the midline region of the palate has been rounded by rolling and abrasion, and most of the horizontal plate of the palatine bone is missing medially and laterally opposite M^3. The lateral margin of the alveolar process of the maxilla has been slightly abraded and smoothed by rolling, especially at the level of the posterior root of M^1 and M^2. This gives the alveolar region and exposed roots a strongly convex contour mediolaterally. The pulp cavity chambers of the cheek teeth have a fine film of calcite covering them, which indicates that some time had elapsed between the teeth being detached from the maxilla and the time of its discovery.

Laterally the root of the zygomatic process is largely missing and the edges of the broken bone are well-rounded, especially inferiorly and posteriorly. On the lateral aspect of the lower face the surface bone is weathered and pitted by weathering. Small flakes of bone have been lost from the alveolar region to expose the lateral aspect of the roots of most of the cheek teeth. This damage most likely occurred prior to fossilization when the bone was still fresh.

Facially, the frontal process of the maxilla is lacking, but the inferolateral margin of the nasal aperture is preserved. No portion of the orbit or orbital wall is preserved. At the time of discovery the maxillary sinus and the inferior meatus of the nasal cavity were filled with sediment. The matrix has since been removed to expose the morphological details of the sinus and nasal passage.

Based on the damage and weathering it is possible to develop a scenario of the series of events that took place in the preservation of the specimen. The maxilla was separated from the rest of the cranium prior to burial and exposed on the Pliocene land surface long enough for weathering to produce some cracking and pitting of the bone surface. During this period, the maxillary fragment was detached from its counterpart on the left side, and the fragile bone covering the lateral roots of the cheek teeth was damaged and flaked away. I^1 and M^3 dropped out of their respective alveoli and were lost. Subsequently, the specimen was buried by ashes of the Upper Ndolanya Beds and fossilized. On weathering out of the sediment, the specimen was exposed to further weathering and experienced some degree of tumbling and transportation that caused rolling and abrasion of the maxilla and loss of the remaining teeth. The subnasal region of the maxilla was detached at a later point in time, probably as a result of trampling, as it lay partially buried upside down in the unconsolidated soil in the location where it was found.

Morphology

The palatal region of the maxilla is preserved to the midline suture from opposite P^3 to mid-M^2. The incisive canal was filled with matrix at the time of discovery, but has since been

Fig. 7.9 EP 1500/01. Right maxillary fragment of *Paranthropus aethiopicus* from Silal Artum. (**a**) anterior view; (**b**) lateral view; (**c**) superior view; (**d**) medial view; (**e**) inferior view cleaned. Just posterior to the anterior broken edge of the maxilla, opposite the posterior margin of the canine root, is a shallow groove that represents the vestibule of the incisive foramen. This groove passes posteriorly for a distance of 11.2 mm, where it disappears beneath the roof of the palate to enter the incisive canal transversely opposite the mesial margin of P^4. The groove deepens as it passes posteriorly, and is angled slightly (~6°) towards the midline. The canal itself forms a bilaterally paired structure, partially separated by a raised keel that passes along the midline of the floor of the nasal canal and the midline of the floor of the inferior surface of the clivus. The dorsal surface or roof of the canal has a low and fine keel that runs posteriorly midway along its length. In section, the palatal aperture of the incisive canal is elliptical in shape with a dorsoventral height of 3.1 mm and a breadth to the midline of 4.1 mm. The vestibule and canal combined have a minimum anteroposterior length of 21.4 mm, measured along the midline of the clivus. In superior view, the canal is funnel shaped, becoming wider as it passes posteriorly, and it eventually opens into a broad and shallow groove running along the floor of the nasal passage. The incisive canal is directed posteriorly at a 30° angle relative to the roof of the palate. In medial view the nasoalveolar clivus overlaps the hard palate (see McCollum 1997).

The palate is relatively wide, with a slight increase in breadth posteriorly. The estimated breadth of the palate at mid-P^3, measured externally to include the alveolar process, is 66.2 mm, whereas at mid-M^2 it is 81.4 mm. The palatal breadth between the roots can be estimated to have been 32.6 mm between the mid-P^3s and 44.6 mm the between mid-M^2s. The depth of the palate is difficult to measure with precision because it is not a simple task to orient the maxilla in the correct mediolateral plane. However, by aligning the alveolar process and the midline axis with the parasagittal plane, it is possible to approximate the correct anatomical position. The palate is flat and relatively shallow, with a depth of only 15 mm in the midline at P^3/P^4 and appears to retain a constant depth posteriorly. The palate is bordered laterally by the sloping internal wall of the alveolar process, which increases in steepness posteriorly.

Beginning anteriorly opposite mid-M^1 is a shallow groove for the greater palatine vessels. Posteriorly opposite M^2 this develops into a pair of grooves, 3.8 mm wide, separated by a low keel. The keel terminates at mid-M^2 to become a shallow single groove after which it begins to ascend more steeply as it approaches the entrance of the greater palatine canal. No portion of the greater palatine foramen is preserved, but it was presumably located opposite M^3. A section of the palatomaxillary suture is visible on the palate originating ~11 mm lateral to the midline opposite anterior M^2. It passes laterally and slightly posteriorly to terminate at the lateral margin of the groove for the greater palatine vessels. The point at which the palatomaxillary suture intercepts the intermaxillary suture in the midline is not preserved.

The sheared-off subnasal clivus exposes the alveolus for I^1 and roots of the right I^2 and upper canine. The alveolus for I^1 is filled with matrix, implying that the tooth was lost perimortem prior to fossilization. Since the clivus and the roots of the canine and incisors were broken obliquely, the cross-sectional area of the roots are greater than they would be if they were broken transversely. Nevertheless, it is possible to compare the size of the roots of the two incisors and to estimate the original diameter of the canine root at the point of breakage. The size of the incisor roots/alveoli indicates that I^1 and I^2 were subequal in size, and relatively small compared to the size of the roots of the cheek teeth. The apico-basal orientation of the roots and the configuration of the subnasal region indicate that the incisors were procumbently implanted in the premaxilla. The intercanine distance is estimated to be ~29 mm, while the external breadth of the palate at the level of the canine roots can be estimated to have been ~50 mm. The I^1 alveolus shows that the root was ovoid in cross-section with a buccolingual diameter much greater than the mesiodistal diameter. A portion of the I^2 root is retained, but it appears to be broken close to the apex of the root. The I^2 and canine root are separated by a distance of only 1.6 mm, indicating that there was no diastema.

The canine root is pyriform in section, narrowing mesiobuccally, and with a concavity on the mesiolingual side. The dimensions of the broken canine root are 11.8 mm (mesiodistal length) and 14.1 (buccolingual breadth), but these are maximal dimensions because of the obliquity of the break. By taking the measurements orthogonal to the long-axis of the root it is possible to estimate that the root was ~10 mm long and ~13 mm wide. This indicates a large canine root, and presumably a large crown, in absolute terms, but one that is relatively small in terms of the overall size of the palate and the roots of the cheek teeth. The lateral margin of the canine root is set medial to the lateral margin of P^3, so the latter tooth forms the anterolateral corner of the rectangular palate. The root of the canine is procumbently implanted at an angle of about 45° to the anteroposterior plane of the palate. The root appears to be relatively straight, with only a slight degree of apicobasal curvature.

None of the crowns of the cheek teeth is preserved, but the roots of P^3-M^2 are exposed in the alveolar process. The roots indicate that the cheek teeth were aligned in relatively straight line that diverged slightly posteriorly. The length of the P^3-M^2 chord, based on the roots alone, is 49.3 mm, although with the reconstructed length of the crowns it can be estimated to have been ~51 mm. This implies that the cheek teeth were absolutely very large.

The premolar roots are extremely broad suggesting that the anterior cheek teeth were massive. The section of the roots for P^4 is slightly larger than that for P^3. The bases of the roots are ovoid in outline with single pulp chambers, but these divide into buccal and lingual canals that enter separate roots. The buccal root of P^3 is prominent, causing the lateral wall of the maxilla to bow outwards slightly, and it curves slightly medially to converge with the canine root. The buccal root in P^4 is partially visible on the lateral side of the maxilla where a small flake of bone has been lost from the lower face. The exposed root is angled slightly anteriorly relative to the midline transverse axis of the pulp cavity. From the external morphology it is likely that the buccal roots of P^3 and P^4 are paired, but this will need to be confirmed with x-ray or CT scanning methods.

The pulp cavities of M^1 and M^2 are relatively large. Each exposes three canals, which lead to separate roots. The lateral roots are partially exposed. The mesiobuccal root penetrates the alveolar process of the maxilla almost vertically, while the distobuccal root is angled posteriorly with a slight distal curvature. The lingual root is single, and judging from the base of the root, the medial face is strongly grooved to produce a bilobate cross-section. Posterior to M^2 is a short section of the lamina of bone that separates it from the alveolus of M^3. The anterior face of the M^3 alveolus has a sharp inferior border, indicating that the last molar was erupted and in place at the time of death. Apart from concluding that the specimen belonged to an adult individual, no other particulars of its age can be given. Judging from the size of the canine root and from the overall robusticity of the maxillary fragment it is possible to infer that the specimen belonged to a male individual.

Anteroposteriorly, the lateral alveolar wall forms a straight line, rather than bowing laterally around the molar row, and diverges slightly posteriorly (5°) relative to the midline axis of the maxilla. This indicates that the palate was rectangular, rather than forming a laterally bowing palate as seen in *A. afarensis*. The lateral surface of the maxilla in the alveolar region of the molars is relatively vertical. There is a slight protuberance of the alveolar region anteriorly to accommodate the buccal root of the P^3. Posterior to this is a small, shallow fossa located above and posterior to the region of P^4. Anterior to the premolars, the alveolar region of the maxilla curves sharply around the root of the canine. There is no distinct anterior pillar or canine jugum associated with the canine root, just a low rounded eminence. There is a very shallow canine fossa (i.e., the maxillary fossula) between the area of the maxilla filled by the canine root and the zygomaticoalveolar crest (Rak 1983, 1985). The curvature of the maxilla around the canine root implies a sharp demarcation between the lateral and anterior regions of the face, and a relatively abbreviated muzzle anteriorly.

The facial region anterior to the zygomatic process and bordering the nasal aperture is very slightly concave mediolaterally, to produce a dished mid-facial region (see Rak 1983, 1985). The lower face slopes steeply down from the infraorbital region, at an angle of 46° to the palatal plane (i.e., the nasocanine angle), to the horizontal level of the middle of the nasal aperture, after which it descends to the incisal region slightly less steeply, at an angle of 38° (i.e., the nasoalveolar angle). Although much of the region inferior to the nasal aperture is not preserved, the configuration of the face lateral to the nasal aperture suggests that subnasal prognathism was pronounced. The minimum dorsoventral thickness of the broken surface of the subnasal alveolar region at I^1 is 12.2 mm in EP 1500/01. A similar thickness occurs at a distance of 10.6 mm posterior to prosthion in KNM-WT 17000, so we can estimate that at least 10 mm is missing from the front of the palate in EP 1500/01. If this is the case, then the anteroposterior length of the subnasal clivus (prosthion-nasospinale) can be estimated to have been ~37 mm.

The root of the zygomatic process is very thick anteroposteriorly, with a broad and smoothly rounded inferior margin. The anterior margin of the zygomatic process is positioned above mid-P^4 and the mid-point of the process is positioned above mid-M^1. It has a minimum height above the alveolar margin of ~15 mm. The anterior face of the zygomatic process is relatively flat to slightly concave mediolaterally, and flares laterally at an angle of 80° to the long-axis of the lateral margin of the alveolar process in inferior view. The low rounded zygomaticoalveolar crest descends the lower face obliquely from the anteroinferior margin of the zygomatic process to terminate just posterior to the P^3 root. This forms the anterior margin of the shallow depression in the maxilla above P^4, and demarcates the lateral face of the maxilla from the anterior face. In anterior view, the zygomaticoalveolar crest is weakly arched.

Superior to the infraorbital foramen the maxilla is slightly mediolaterally concave, but this transitions to a slightly convex surface as it approaches the nasal aperture. This convex surface between the infraorbital foramen and the nasal aperture extends inferiorly to become continuous with the eminence for the canine root, but it does not form a distinct anterior pillar. The center of the infraorbital foramen is located 31.5 mm from the midline in the mediolateral plane and 17.6 mm from the margin of the nasal aperture, opposite the aperture's greatest width. The inferior margin of the foramen is horizontally in line with the anterior nasal spine. It is positioned dorsoventrally above P^4 at a height of 35.9 mm above the alveolar margin. The distance between the center of the foramen and the inferior margin of the zygomatic process is 17.2 mm. The foramen is situated quite low on the face, midway between the nasal aperture and zygomatic process. The infraorbital foramen is circular in outline, with a mediolateral breadth of 4.3 mm. The foramen opens inferiorly and slightly laterally into a distinct teardrop shaped depression.

Unfortunately, no portion of the inferior orbital margin is preserved, so the lower facial height cannot be measured or estimated, but based on the preserved anatomy the lower face was evidently relatively deep. The minimum height of the lower face above P^3 is 48.8 mm to the point where the maxilla is broken superiorly.

Although only a portion of the nasal aperture is preserved, it was clearly pyriform in outline, being broadest inferiorly and narrowing superiorly. The lateral margin of the nasal aperture is smoothly rounded inferiorly, but a low crest is developed about 12.3 mm up from the floor of the nasal aperture about 3.9 mm below the point at which the maxillary fragment is broken superiorly. The greatest breadth of the nasal aperture, at the point where the lateral crest originates, is estimated to be ~28 mm. Laterally, the margin of the nasal aperture is bordered by the canine root, with the root of the lateral incisor situated more medially. The inferior margin of the nasal aperture curves gently medially and inferiorly to reach its most inferior point midway between the greatest lateral extent and the midline, and then it ascends ~3 mm to reach the elevated anterior nasal spine, which is located in the midline and somewhat recessed. A low, rounded crest passes laterally and slightly anteriorly from the anterior nasal spine to demarcate the junction between the clivus and the floor of the nasal cavity. The anterior nasal spine is eroded, but was evidently quite prominent.

The superior margin of the subnasal clivus is damaged. The bone covering the region between the apices of the upper central incisors is largely missing. During removal of the adhering sediment in this region, the cleaning process exposed a small elliptical and smooth-walled pocket of pneumatized bone (15.4 mm × 8.2 mm) that occupied the dorsal surface of the clivus on either side of the anterior nasal spine. Nevertheless, despite this damage, it is possible to infer that the subnasal clivus would have had a slightly convex dorsal margin anteroposteriorly that led smoothly into the floor of the nasal aperture without a distinct nasal sill (Robinson 1953; Ward and Kimbel 1983; McCollum et al. 1993; McCollum 1997). In anterior view, the inferior margin of the nasal aperture is mediolaterally concave, forming a nasoalveolar gutter (Rak 1983, 1985; Strait and Grine 2004).

The floor of the nasal cavity has an elevated and mediolaterally bladelike spine in the mid line. It is clear that the vomer inserted along this crest anteriorly as far as the anterior nasal spine (Robinson 1953; McCollum 1997, 1999). The lateral wall of the cavity, close to the superior break in the maxilla, bears a longitudinal crest that represents the root of the inferior concha. It slopes inferiorly as it passes posteriorly. Anteriorly it is positioned about 15.5 mm above the floor of the nasal canal, just posterior to the internal opening of the incisive canal, whereas posteriorly it is positioned 10.2 mm above the floor of the nasal cavity at the level of M^2 where the posterior break occurs. The lateral wall of the inferior meatus below the line for the attachment of the inferior concha is generally concave, although there is a distinct swelling superior and lateral to the internal opening of the incisive canal. The lateral wall of the nasal cavity separating the inferior meatus from the maxillary sinus is remarkably thick, with a maximum thickness along the broken margin of 6.4 mm, but it does get as thin as 1.6 mm. The palatal process of the maxilla is also very thick (McCollum 1997, 1999), with a maximum dorsoventral thickness of 8.4 mm opposite M^1.

The maxillary sinus is very extensive, extending laterally and anteriorly into the zygomatic process, posteriorly into the alveolar region beyond M^2, and medially to border the nasal aperture. It does not penetrate the maxilla anterior to the zygomatic process in the region of the premolar roots, but it does extend anteromedially as far as the canine root. There is no evidence that it extended into the palatine process of the maxilla medially to form a *recessus palatinus* (Tobias 1967; McCollum 1997). The exposed floor of the sinus has a complex arrangement of buttresses and deep loculations between and around the roots of the molars. The buttresses primarily intersect each other at right angles, and the entire system is arranged so that the buttresses are oriented at ~45° to the mediolateral line of the zygomatic process. Presumably, the network of buttresses criss-crossing the floor of the sinus helps to maintain the structural integrity of the maxilla.

A major buttress, more than 5 mm wide, originates at the medial wall of the sinus opposite the level of M^2, and passes obliquely laterally and anteriorly to meet the lateral wall at a sharp vertically-oriented buttress, which coincide on the external surface of the maxilla with the posterior margin of the zygomatic process. Intersecting this transverse buttress is a longitudinally-oriented buttress that passes anteriorly and medially at an angle of about 90° to the former. It passes towards the base of the pillar of bone that represents the lateral margin of the nasal aperture, where it divides into short medial and lateral arms. This main buttress gives rise to smaller subsidiary buttresses midway along its length that pass medially and laterally. Posterior to the point where the main transverse and longitudinal buttresses intersect, there is a pair of sharp and diverging buttresses that pass to the posterior wall of the sinus. Between the buttresses, the floor of the sinus is excavated to form relatively deep loculi. Centrally, the floor of the sinus bears a very deep loculus bordered laterally and posteriorly by the main longitudinal and transverse buttresses respectively, and medially by the wall of the sinus.

The anterior wall of the sinus bears the remnant of a bony canal that penetrates ~8 mm into the chamber of the sinus. This is the canal leading from the infraorbital foramen into the infraorbital groove that carries the infraorbital nerve and artery. The canal passes superiorly and slightly medially, which corresponds well with the orientation of the infraorbital foramen aperture on the facial aspect of the maxilla. Medial to the canal is a well-developed loculus that penetrates into the pillar that forms the lateral margin of the nasal aperture, just posterior to the canine root.

Comparisons

Comparisons with the crania of other Pliocene hominins indicate that EP 1500/01 exhibits a suite of derived features that it shares uniquely with *Paranthropus* spp. from southern and eastern Africa. These include: relatively small anterior teeth; enlarged premolars and molars; a dished midface; robust and anteriorly placed zygomatic process of the maxilla; zygomaticoalveolar crest weakly arched in anterior view; single infraorbital foramen positioned low on the face and opening inferiorly into a shallow groove; guttered nasoalveolar clivus that grades smoothly into the nasal cavity floor; marked overlap between the nasoalveolar clivus and the anterior margin of the hard palate; anterior vomer insertion that coincides with the anterior nasal spine; recessed anterior nasal spine; and very thick hard palate anteriorly (Rak 1983, 1985; Leakey and Walker 1988; Kimbel et al. 1988; McCollum et al. 1993; Strait et al. 1997; Suwa et al. 1997; McCollum 1997, 1999; Asfaw et al. 1999; Keyser 2000; Strait and Grine 2001, 2004; Steininger et al. 2008).

Further comparisons show that EP 1500/01 is very similar in morphology to KNM-WT 17000 (Walker et al. 1986; Leakey and Walker 1988), and there can be no doubt that the maxilla fragment from the Upper Ndolanya Beds should be attributed to the same species, *Paranthropus aethiopicus*. EP 1500/01 shares the following distinctive (i.e., primitive) features with KNM-WT 17000 that are not found in *P. robustus* or *P. boisei*: larger anterior teeth, relatively flat and shallow palate, and pronounced subnasal prognathism.

EP 1500/01 and KNM-WT 17000 are very similar. The nasal aperture and subnasal region appear to have been very similar in shape and configuration. In both specimens the nasal aperture is pear-shaped in outline, relatively broad low down (although the greatest breadth is somewhat higher in EP 1500/01), with a slightly concave inferior margin mediolaterally (i.e., a guttered nasoalveolar region) and a prominent anterior nasal spine. The maximum breadth of the nasal aperture is estimated to be ~28 mm in EP 1500/01 compared with 27.3 mm in KNM-WT 17000 (Leakey and Walker 1988). The inferolateral margin of the nasal aperture is rounded in both specimens, in contrast to the sharp lateral margin in *A. afarensis*. The crest that forms the lateral margin of the nasal aperture superiorly originates lower in KNM-WT 17000. The estimated depth of the subnasal clivus in EP 1500/01 is comparable to that in KNM-WT 17000, and in both specimens it is sagittally convex and grades smoothly into the nasal passage without a distinct nasal sill. In *A. afarensis* the clivus has a stepped nasal cavity floor with a strongly differentiated nasal sill (Kimbel et al. 2004).

The midface in EP 1500/01 is similar to that of KNM-WT 17000 in lacking an anterior pillar, having a robust zygomatic process that is placed anteriorly relatively to the cheek teeth and being slightly dished. Mediolateral concavity of the midface is relatively slight in EP 1500/01 and more pronounced in KNM-WT 17000. The lateral margin of the nasal aperture is bordered by a low rounded eminence in EP 1500/01, whereas in KNM-WT 17000 this region is relatively flat. Both lack canine juga. The I^2 root in EP 1500/01 and KNM-WT 17000 is positioned medial to the lateral margin of the nasal aperture, as in other species of *Paranthropus* and *A. africanus*, but distinct from *A. afarensis*

In lateral view, the contour of the lower face is very similar in KNM-WT 17000 and EP 1500/00. Both specimens appear to have strong subnasal prognathism. As described above, the lower facial and subnasal angles, relative to the anteroposterior plane of the palate, are 46° and 38° respectively in EP 1500/01, compared with 42° and 30° in KNM-WT 17000. The lower face in *P. aethiopicus* exhibits a similar overall angulation to that of *P. boisei*, except that the subnasal region is much more prognathic. The angulation of the lower face of *A. afarensis* is less steep (i.e., more prognathic), but the degree of facial protrusion is much more pronounced in the subnasal region in *P. aethiopicus* giving the latter taxon a greater degree of prognathism overall (Kimbel et al. 2004).

The zygomatic process of the maxilla originates at approximately the same elevation in both specimens, with its lowest point vertically above mesial M^1. The infraorbital foramina in KNM-WT 17000 are incompletely preserved, but they appear to have been located in a similar position to that in EP 1500/01 (the foramen is positioned slightly higher and more lateral relative to the nasal aperture in KNM-WT 17000). The foramen in KNM-WT 17000 is similar to EP 1500/01 in opening inferiorly into a shallow groove (Leakey and Walker 1988).

The maxillary sinus in KNM-WT 17000 is infilled with matrix, so comparison with the sinus morphology in EP 1500/01 is not possible (Walker et al. 1986; Leakey and Walker 1988). Nevertheless, it is apparent that the sinus extended laterally into the zygomatic process and anteromedially into the lateral rim of the nasal aperture posterior to the canine alveolus (Leakey and Walker 1988). Leakey and Walker (1988) indicate that the sinus in KNM-WT 17000 extends medially into the palatine process of the maxilla, in contrast to EP 1500/01, which lacks a *recessus palatinus*. A portion of the floor of the maxillary sinus is exposed above M^3 in KNM-WT 17000, and this confirms that, as in EP 1500/01, the maxillary sinus had a relatively thick bony floor above the molar roots. This contrasts with the maxillary sinus of *A. afarensis* seen in A.L. 200-1, which has a much thinner sinus floor. In addition, the medial wall of the maxilla separating the maxillary sinus from the nasal passage is relatively thick in *P. aethiopicus*, in contrast to the thin-walled sinus seen in *A. afarensis*.

The palate in both specimens is relatively broad and very shallow (Leakey and Walker 1988; Suwa 1989). The breadth of the palate between the roots of P^4 and M^2 in KNM-WT

17000 is 41.3 and 35.7 respectively. These dimensions compare with estimated values of 38.8 and 39.2 in EP 1500/01. The palate in both specimens is similar in overall dimensions to that of OH 5 (*P. boisei*), but the palate in this latter specimen is much deeper. The palate becomes slightly wider and the tooth rows diverge posteriorly in EP 1500/01, whereas in KNM-WT 17000 the palate narrows slightly posteriorly (although Leakey and Walker (1988) consider that this is likely an artifact of preservation).

The incisive canal has a similar configuration in EP 1500/01 and KNM-WT 17000. The canal exits onto the roof of the palate opposite mid-P^4 and opens anteriorly into a fan-shaped fossa that terminates just posterior to the alveolus of I^1. The structure of the nasal septum and vomeral insertion is nearly identical in both specimens.

The intercanine distance in KNM-WT 17000 is 36.0 mm, whereas the minimum estimated breadth is only 29.0 mm in EP 1500/01, implying that the upper incisors were probably larger in the former. By comparison, the intercanine distance in OH 5 is 31.7, implying that, just as in *P. boisei*, the incisors of *P. aethiopicus* were relatively small in relation to the size of the cheek teeth (Suwa 1989). A similar set of relationships emerges if the mediolateral breadth across the incisor roots is taken into account. In KNM-WT 17000 the breadth is 35.2 mm, compared with only 32.6 mm in OH 5, indicating that *P. aethiopicus* has larger upper incisors than *P. boisei* (see Leakey and Walker 1988; Suwa 1989). However, the same dimension in EP 1500/01 is estimated to be only 30.2 mm, indicating that there was variability in incisor size in *P. aethiopicus*, and that incisor breadth overlapped with that in *P. boisei*.

The alveolus for the upper canine in KNM-WT 17000 measures 7.2 mm (mesiodistally) by 12.7 mm (buccolingually), which is smaller than the estimated dimensions of the canine root in EP 1500/01 (~10.0 mm by ~13.0 mm). Canine root size in KNM-WT 17000 is comparable to that in OH 5, which has a mesiodistal length of only 6.8 mm. The canine root in EP 1500/01 is much larger than in other *Paranthropus* specimens, and, in fact, exceeds the dimensions of the root of the largest canine of *A. afarensis.* A.L. 333x-3, a presumed male individual from Hadar, has basal root dimensions of 8.5 mm by 11.3 mm. Nevertheless, compared to the estimated size of the cheek teeth and the maxilla, the canine in EP 1500/01 would have been relatively smaller than in *A. afarensis*. It would seem that the anterior teeth were somewhat larger on average than in *P. boisei*, but as in the latter species they were small by comparison with the size of the premolars and molars. In addition, the canine roots in *P. aethiopicus* are more procumbently implanted and less apicobasally curved than in *A. afarensis* and *P. boisei*, which have shallower and less prognathic subnasal regions.

Measurements of the P^3-P^4 chord and P^3-M^2 chord of the roots provide an estimation of the relative size of the cheek teeth. In KNM-WT 17000 these dimensions are 20.3 mm and 50.0 mm respectively, compared with 19.0 mm and 49.3 mm in EP 1500/01, indicating that that the teeth might have been slightly smaller in the latter. The same dimensions in OH 5 (*P. boisei*) are 19.6 mm and 50.3 mm respectively. Evidently, the cheek teeth in *P. aethiopicus* were as large (at least in their mesiodistal dimensions) as in *P. boisei*. Based on the roots, the cheek teeth in EP 1500/01 and KNM-WT 17000 formed a relatively straight line, unlike in *A. afarensis* where the cheek tooth rows bow laterally, being widest at the level of M^2.

EP 1000/98

Left proximal tibia (Fig. 7.10).

Location and Stratigraphic Provenance

The specimen was discovered by Chris Robinson on August 19, 1998 at Loc. 22 South. The specimen was found exposed on the surface at the base of Nenguruk Hill, a small hillock on the western side of the Olaitole River valley. The location of the find, as well as the lithology of the adhering matrix and the coloration of the specimen, confirms that it was originally derived from the Upper Ndolanya Beds. Additional details about the locality and provenance are presented by Harrison and Kweka (2011).

Preservation

The specimen consists of a left proximal tibia. Only a short section of the shaft is preserved, with a total proximodistal length of ~58 mm. The proximal articular surface is generally well preserved, but there has been some abrasion and weathering along the anteromedial and posterolateral margins. There are small depressions on the shaft anterior to the medial facet that look superficially like they may have been caused by bite marks from a small carnivore, but closer microscopic examination shows that they are shallow eroded pits caused by weathering. The posterior intercondylar depression, for the attachment of the medial meniscus and the posterior cruciate ligament, has been accentuated by erosion and by loss of the bone surface. The medial and lateral articular surfaces exhibit fine cracks around their perimeters, apparently caused by weathering when the bone was still green. Similarly, the heavy longitudinal cracks along the shaft, and the spiral and angular fractures at the broken end of the shaft, imply that the proximal end of the tibia was detached from the rest of the bone while it was still green and prior to it being buried and fossilized.

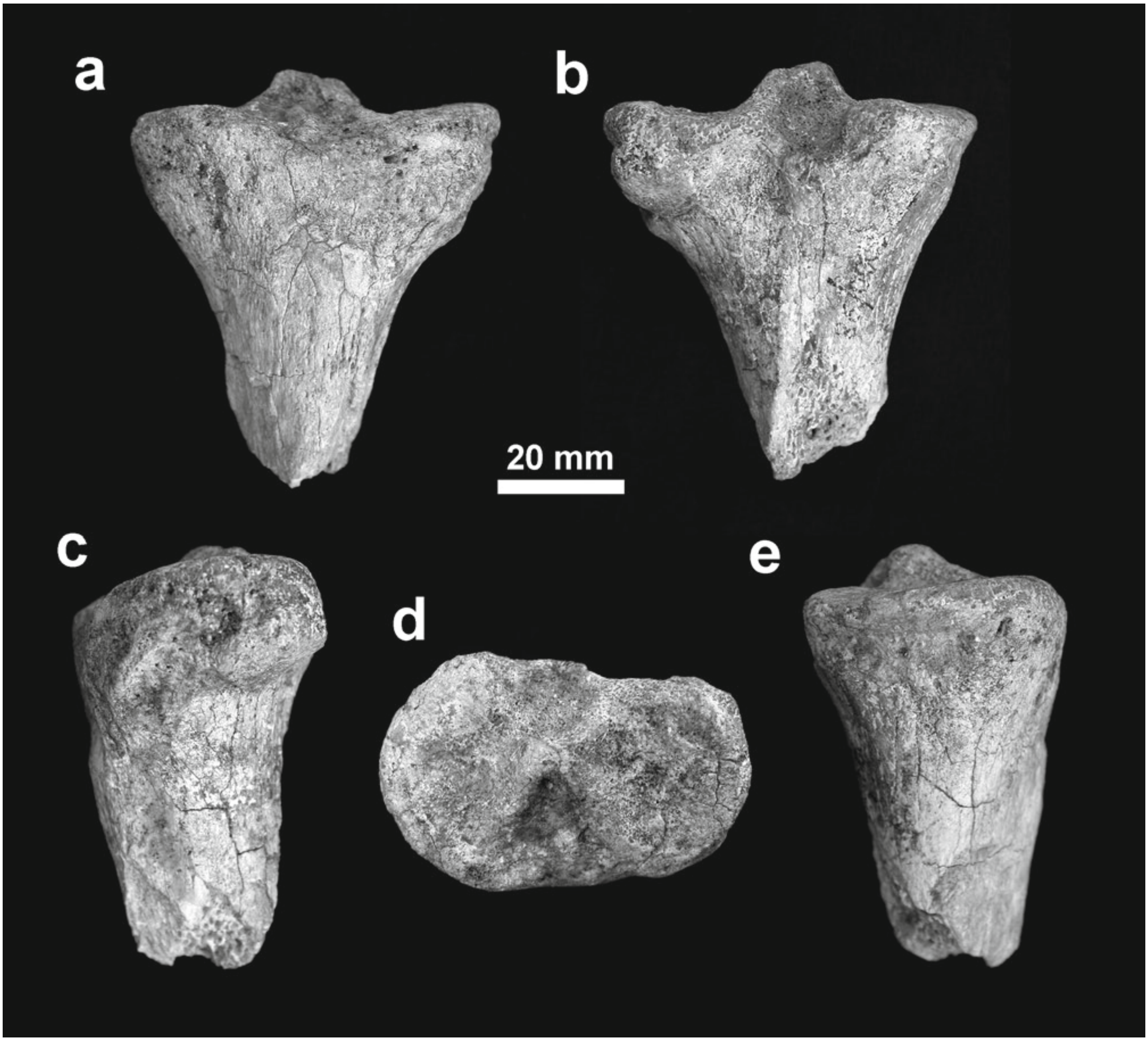


Fig. 7.10 EP 1000/98. Left proximal tibia of cf. *Paranthropus aethiopicus* from Loc. 22S. (**a**) anterior view; (**b**) posterior view; (**c**) lateral view; (**d**) superior view; (**e**) medial view

Morphology

The proximal end of the tibia is broad. The mediolateral breadth is 51.6 and the anteroposterior length is 33.8, with a breadth-length index of 65.5. The condyles are anteroposteriorly short in relation to their breadth. The medial condyle forms a D-shaped facet, with a central depression and a low rounded rim. The lateral condyle is elliptical in shape, with a slightly anteroposteriorly convex lateral surface and a more concave medial surface. The posteromedial margin of the lateral condyle is slightly elevated. Both condyles are mediolaterally concave, but the lateral condyle is more markedly so. The medial condyle is anteroposteriorly longer than the lateral condyle, but mediolaterally narrower. The medial condyle measures 33.0 mm × 20.6 mm; the lateral condyle measures 26.6 mm × 22.1 mm. The surface area of the medial condyle is subequal in size to that of the lateral condyle (375 mm^2 compared with 373 mm^2). The long-axes of the two condyles converge posteriorly.

Between the two condyles is a well developed and elevated intercondylar eminence, with prominent medial and lateral tubercles. The maximum height of the medial tubercle is 5.8 mm. The lateral tubercle is slightly lower. The eminence is located midway across the proximal end of the tibia in the parasagittal plane and slightly posterior of the mid-coronal plane. Laterally, the articular surface of the medial condyle extends almost to the apex of the medial tubercle. In superior view, the medial tubercle forms an oblique crest that continues anteromedially to become the raised lateral margin of the medial condyle. The lateral tubercle forms a robust crescent-shaped ridge that extends anteriorly and posteriorly to form the raised medial margin of the lateral condyle. The two tubercles are united by an elevated transverse crest, directed slightly posterolaterally.

Anterior to the intercondylar eminence is a roughened triangular area, the anterior intercondylar area, bordered by the raised rims of the medial and lateral condyles. Within this area, there is a large triangular region that borders the medial condyle, defined anteriorly by a sharp crest that runs along the anterior margin and laterally by low swellings. This is the area for the anterior cornu of the medial meniscus. Lateral to this is a roughened area, perforated by numerous vascular foramina, that represents the site of the *corpus adiposum infrapatellare* and the attachment for the lateral meniscus. Posterior to these two areas, on the anterior slope of the intercondylar eminence, is a smooth triangular region for the attachment of the anterior cruciate ligament. The posterior intercondylar area has been damaged by erosion, so details of its morphology cannot be discerned. It is not possible, for example, to determine the shape of the posteromedial contour of the lateral condyle or whether or not the lateral meniscus had a posterior attachment. However, the area posterior to the lateral tubercle was evidently quite restricted implying that EP 1000/98 lacked a posterior cornu of the lateral meniscus.

Posterior retroversion of the head is minimal. The articular platform is only very slightly posteriorly tilted in medial view in relation to the long-axis of the shaft. The medial condyle is tilted 4°, whereas the plane of the lateral condyle is tilted only 1°. The lack of retroflexion of the head is structurally associated with a weak overhang of the condyles posteriorly, a steep anterior margin, and a less prominent tibial tuberosity.

Only a short section of the shaft is preserved. It is mediolaterally slightly compressed and triangular in section. The anteroposterior diameter of the shaft at the inferior margin of the tibial tuberosity is at least 21.2 mm, while its mediolateral breadth at this level is 20.2 mm. In anterior view, the shaft below the medial condyle is more robustly built than that below the lateral condyle, which is more hollowed out (Aiello and Dean 1990). This hollowing of the lateral side of the shaft may be more closely tied to the structural and allometric relationships between the size of the tibial plateau and the mediolateral diameter of the shaft, than to the development and disposition of the tibialis posterior muscle (*contra* Aiello and Dean 1990; Berger and Tobias 1996). The mediolateral breadth of the shaft at the level of the inferior margin of the tibial tuberosity is only 39.9% that of the total breadth of the tibial plateau. The remaining portion of the shaft appears to have a long-axis that is approximately in line with the sagittal midline of the articular surface (measurement of the midline of the shaft to the margin of the lateral condyle in the mediolateral plane is 24.3 mm or ~47% of the total breadth of the proximal end of the tibia), and it exhibits no discernable degree of torsion.

The anterior face of the shaft bears a low and domed tuberosity for the attachment of the patella ligament. Its superior margin is situated 22.2 mm inferior to the margin of the anterior intercondylar area. The tuberosity projects anteriorly very little, so that the anterior margin of the tibial shaft descends steeply from the articular platform. Superior to the tuberosity is a slightly rugose tuberosity bordering the anterior margin of the articular surface, which is separated from the tibial tuberosity by a shallow transverse groove. This is bordered by a faint line medially and a stronger crest laterally, marking the extent of the attachment of the capsule. Lateral to the capsular attachment, and immediately anterior and inferior to the lateral condyle, is a raised, elliptical and slightly convex area that marks the site of the iliotibial tract.

On the medial side of the tibial tuberosity the anterior face of the shaft is convex and largely featureless. Numerous vascular foramina are located superiorly, just below to the medial condyle. On the medial side of the shaft, just where the break occurs, there is a small, roughened tuberosity, presumably for the attachment of the tibial collateral ligament. Unfortunately, the site of attachment for the pes anserinus (i.e., the insertion for the sartorius, gracilis and semitendinosus) is not preserved.

On the lateral side of the proximal tibia is a roughened area, which arcs postero-superiorly to antero-inferiorly, for the attachments of the tendon of the biceps femoris and the extensor digitorum longus. Inferior to this area, on the lateral side of the tibial tuberosity is a shallow groove, with a maximum width of 8.6 mm, running proximodistally along the shaft. This is the site of attachment for tibialis anterior. A low rounded crest extending down the middle of the lateral side represents the interosseus border. Posterior to this is the area of attachment for the tibialis posterior. The area for tibialis posterior on the lateral side of the shaft is subequal to that of tibialis anterior.

Just below the posteromedial lip of the medial condyle is a broad and rugose groove, bordered inferiorly by an irregular crest, which terminates medially in a shallow circular depression. The latter marks the insertion for semimembranosus, which appears to have been well developed. The proximal fibular facet is lanceolate, with a long-axis directed antero-laterally. It is relatively large, measuring 16.3 mm by 11.1 mm. It is well-defined, slightly convex anteroposteriorly and mostly flat mediolaterally. The facet faces distally, posteriorly, and slightly laterally. The fibular facet is located 10.1 mm from the posterolateral margin of the lateral condyle. On the posterior surface, immediately medial to the fibular facet is a deep oval depression that extends a short way down the shaft. It is bordered by a raised, convex area medially for the insertion of popliteus, and by a low rounded and ill-defined crest laterally that descends from the fibular facet on the lateral side to at least mid-shaft. The latter crest delimits the posterior border of tibialis posterior and represents the proximal extent of the soleus line.

Comparisons and Functional Implications

Compared with modern humans, EP 1000/98 differs in the following respects: the proximal articular surfaces are anteroposteriorly slightly shorter relative to the breadth (with a breadth-length index of 65.5 in EP 1000/98 compared to a mean value in modern humans of 68.0; see Table 7.12); the articular surface of the medial condyle is more concave; the lateral condyle is slightly convex (generally relatively flat to slightly concave in modern humans, although some humans exhibit a slight degree of convexity) (Tardieu 1982, 1983; Berger and Tobias 1996; Organ and Ward 2006); the intercondylar eminence is more elevated, with a stronger transverse crest linking the medial and lateral tubercles; the tibial tuberosity is much less protuberant; the groove superior to the tibial tuberosity is oblique, rather than transversely oriented; the area for the iliotibial tract has greater relief; the area on the lateral side of the tibial tuberosity for attachment of the tibialis anterior is relatively less extensive, and the interosseus line is more anteriorly located; the proximal fibular facet is relatively larger; the area of attachment for the semimembranosus is better developed and forms a distinct circular depression on the posteromedial margin of the condyle; the depression on the posterior aspect of the shaft medial to the fibular facet is deeper; the lateral meniscus has a single tibial insertion in the anterior intercondylar area (humans are unique among primates in having a double insertion, one for each of the anterior and posterior intercondylar areas respectively) (Senut and Tardieu 1985; Tardieu 1986a, b, 1999; Le Minor 1990; but see Dugan and Holliday 2009); the cross-section of the shaft at the level of the inferior margin of the tibial tuberosity is less compressed mediolaterally (the breadth-length of the cross-section of the shaft at this level is 95.3 in EP 1000/98, compared with a mean value in modern humans of 75.1; see Table 7.12); and the lateral side of the shaft below the lateral condyle is more deeply hollowed.

In addition, EP 1000/98 possesses a weak crest that passes obliquely across the posterior aspect of the shaft, which corresponds to the soleal line in humans. A similar crest is commonly found in the tibiae of chimpanzees, although according to Aiello and Dean (1990) this line does not correspond to the soleal line of humans, because the soleus is normally confined to the fibula in African apes and the crest merely represents the posterior border of the tibialis posterior. However, Gregory (1950) demonstrated that soleus does attach to this crest in *Gorilla*. Given that a similar crest occurs in humans and chimpanzees, it is not possible to determine whether or not there is a soleus attachment in EP 1000/98 or in other fossil tibiae.

Compared with chimpanzees, EP 1000/98 differs in having: a less convex lateral condyle; a relatively more elevated intercondylar eminence; a much less retroverted tibial plateau (in chimpanzees, the average posterior tilt of the medial and lateral condyles relative to the proximodistal long axis of the proximal end of the shaft is 22° and 10° respectively, compared with 4° and 1° in EP 1000/98; see Table 7.12), with less overhang of the condyles posteriorly; the medial and lateral condyles have a similar orientation in the mediolateral plane, whereas in chimpanzees the lateral condyle is more obliquely oriented relative to the transverse plane of the medial condyle; the condyles are proximodistally relatively thicker; the tibial tuberosity is much less protuberant; the area for the iliotibial tract is larger; the proximal fibular facet is relatively smaller; the interosseus line on the lateral side of the shaft is more posteriorly placed;

Table 7.12 Comparison of dimensions (mm) of proximal tibia from Laetoli (EP 1000/98)

	A. africanus[a]		*A. afarensis*		*A. anamensis*	*Pan troglodytes*			*Homo sapiens*		
Dimensions[a]	EP 1000/98	Stw 514a	AL 288–1aq	AL 129–1b	KNM-KP 29285A	N	Mean	Range	N	Mean	Range
AP l prox tibia	33.8	–	32.9	33.3	49.7	10	40.8	39.3–42.6	16	49.4	41.6–53.7
ML br prox tibia	51.6	52.3	50.8	50.6	67.5	10	60.0	55.2–66.2	16	72.6	63.3–80.2
AP l med condyle	33.0	–	31.6	–	43 (e)	10	38.0	36.0–42.6	16	45.6	36.2–51.1
ML br med condyle	20.6	20.5	20.6	–	30 (e)	10	26.6	25.3–28.2	16	31.1	26.0–38.3
AP l lat condyle	26.6	20 (e)	24.8	27.4	–	10	32.6	29.3–37.5	15	38.5	29.2–44.0
ML br lat condyle	22.1	16.8	20.7	22.4	–	10	26.0	23.8–29.3	15	30.7	25.8–33.9
Post slope med condyle	4°	–	9°	14°	17°	10	22°	5–30°	14	9°	3–20°
Post slope lat condyle	1°	–	9°	10°	7°	10	10°	3–20°	14	9°	0–16°
AP l shaft	21.2(–)	–	27.2	28.9	36.2	10	32.4	28.5–35.2	17	38.2	34.8–41.3
ML br shaft	20.2	–	22.3	22.3	29.0	10	21.6	19.6–24.2	17	28.7	24.2–35.2

AP anteroposterior, *br* breadth, *lat* lateral, *l* length, *med* medial, *ML* mediolateral, *post* posterior, *prox* proximal, (–) minimum dimension, (*e*) estimated dimension

[a] Data from Berger and Tobias (1996)

the insertion for semimembranosus is larger and better defined; and the proximal end of the shaft is anteroposteriorly relatively shorter and lacks the marked anterior curvature typical of African apes. However, EP 1000/98 does share a number of features with the tibiae of chimpanzees that distinguish them from those of modern humans. These include: a more convex lateral condyle in the anteroposterior plane; a more elevated crest linking the tubercles of the intercondylar eminence; a relatively small and triangular posterior intercondylar region, presumably lacking a posterior attachment for the lateral meniscus; a less protuberant tibial tuberosity; an oblique groove superior to the tibial tuberosity; and a more pronounced hollowing of the lateral aspect of the shaft below the lateral condyle.

The features that EP 1000/98 shares with modern humans compared with those of African apes, such as the less pronounced retroversion of the proximal tibial plateau (the posterior tilt of the medial and lateral condyles in the fossil falls at the lower end of the range for modern humans; see Hashemi et al. 2008), a more prominent iliotibial tract for insertion of the tensor fascia latae and gluteus maximus, and a more posterior attachment of tibialis posterior, indicate more extended positions of the knee associated with bipedal locomotion (Aiello and Dean 1990; Berger and Tobias 1996). In humans, individuals with a steeper posterior slope of the tibial plateau is associated with an increase in the magnitude of the anteriorly directed component of the compressive forces that act on the tibial articular surface during the intial phase of weight support (Hashemi et al. 2008). This produces greater anterior translation of the tibia and a higher force exerted by the anterior cruciate ligament. The functional shift to fully extended knees at heel strike in hominins, compared with the weight-bearing semiflexed knees in great apes, would favor the development of a less posteriorly tilted tibial plateau.

Nevertheless, a number of primitive features in EP 1000/98 indicate that the knee joint was capable of a greater range of rotation than seen in those of modern humans. These include a more convex lateral condyle in the anteroposterior plane, a relatively larger facet for the proximal fibula, and a single tibial attachment for the lateral meniscus. The hollowing of the lateral side of the shaft below the lateral condyle may imply that the knee was less effective than the modern human knee joint in dissipating high peak loads when the foot made contact with the ground. The relatively well-developed insertion for semimembranosus compared with modern humans, as well as the prominent development of the iliotibial tract, implies well-developed capabilities for extension of the thigh at the hip joint.

Comparisons with the proximal tibiae of other fossil hominins show that EP 1000/98 is very similar to those of *A. afarensis* from Hadar. It is comparable in size and closest in overall morphology to the small tibiae from Hadar, such as A.L. 288-1aq and A.L. 129-1b, which presumably belonged to female individuals (Johanson and Taieb 1976; Johanson and Coppens 1976; Lovejoy et al. 1982; see Table 7.12). The larger proximal tibiae from Hadar (i.e., A.L. 333x-26 and A.L. 333-42) have linear dimensions that are on average ~29% larger than those of EP 1000/98, and they tend to be more robust, but otherwise they exhibit the same suite of distinctive morphological features. Compared with EP 1000/98, AL 288-1aq and AL 129-1b are very slightly smaller in their proximodistal and anteroposterior dimensions, and the shaft is more bilaterally compressed (the breadth-length index of the cross-section of the shaft at the level of the inferior margin of the tibial tuberosity is 77.2 in AL 288-1aq and 82.0 in AL 129-1b, compared with 95.3 in EP 1000/98; see Table 7.12). The different proportions of the shaft in EP 1000/98 are apparently due to the relatively short anteroposterior dimension of the shaft. Just as in EP 1000/98, the lateral side of the shaft has a distinctive hollowing below the lateral condyle.

The morphology of the proximal articular surfaces in the Hadar specimens is identical to that in EP 1000/98, with equal-sized condyles, an anteroposteriorly convex lateral condyle (more marked in the Hadar specimens), similar configuration of the anterior intercondylar area, a relatively restricted posterior intercondylar area lacking a posterior cornu for the lateral meniscus, and a similarly developed intercondylar eminence. On the anterior face of the shaft, the tibiae from Hadar and EP 1000/98 share a relatively low tibial tuberosity (even more weakly expressed in EP 1000/98), an oblique groove on the bursal surface superior to the tibial tuberosity, and a raised surface for a well-developed iliotibial tract. Medially, there is a well-developed depression for the insertion of the semimembranosus. The scar for the pes anserinus, which is very well developed in the proximal tibiae from Hadar, is not preserved in EP 1000/98. In the Hadar specimens, this scar forms a deep groove-like roughened area bordering the raised anterior crest of the shaft. This resembles the condition in African apes more than that in humans, where the attachments for sartorius, gracilis and semitendinosus are placed more laterally and leave a less distinct scar. Laterally, the interosseus line extends down the midline of the shaft, and delimits a relative large area for the attachment of tibialis posterior and a distinctly grooved surface for the tibialis anterior. On the posterior surface of the shaft, there is a pronounced depression below the posteromedial margin of the lateral condyle, bordered laterally by a low rounded crest for the proximal end of the soleal line and medially by a smoothly rounded surface for popliteus. The proximal facet for the fibula is only partially preserved in A.L. 288-1aq, but it does appear to have been relatively smaller than in EP 1000/98. The retroversion of the proximal end is more marked in the Hadar proximal tibiae than in EP 1000/98, and their posterior inclination exceeds or falls within the upper end of the range of modern humans (Table 7.12). This latter feature is structurally associated with the more pronounced development of the tibial tuberosity and greater overhang of the condyles posteriorly in the Hadar specimens. The differences between the proximal tibiae from Hadar and Laetoli are relatively minor, however, and the overall morphology of EP 1000/98 is remarkably similar to the two small proximal tibiae of *Australopithecus afarensis* from Hadar.

The only known proximal tibia of *Australopithecus anamensis* (KNM-KP 29285A from Kanapoi) is much larger than EP 1000/98 (the dimensions of the proximal end are ~39% larger on average, being larger in size than the presumed tibiae of male individuals of *A. afarensis* from Hadar; Table 7.12), but, like those of *A. afarensis*, its overall morphology corresponds closely to that seen in EP 1000/98 (Ward et al. 2001). Other than size, KNM-KP 29285A differs in the following respects: the medial condyle has a slightly more undulating articular surface, being concave anteriorly and slightly convex posteriorly (whereas EP 1000/98 is anteroposteriorly more planar); the lateral rim of the medial condyle is more elevated; the intercondylar eminence is relatively larger and more robust; the anterior intercondylar area is more deeply excavated; retroversion of the proximal tibia is more pronounced, with a posterior slope of the medial condyle of 17° and of the lateral condyle of 7°, and a more strongly developed overhang of the condyles posteriorly; the tibial tuberosity and the area superior to the tuberosity for attachment of the capsule are much more rugose; the anterior margin of the shaft is more strongly keeled; the shaft is more strongly bilaterally compressed (the breadth-length index of the cross-section of the shaft at the level of the inferior margin of the tibial tuberosity is 80.1, compared with 95.3 in EP 1000/98; see Table 7.12); the area on the medial side of the condyle that marks the attachment for semimembranosus is more strongly marked; the raised area for the iliotibial tract is larger and more pronounced; the interosseus line is slightly more posteriorly placed, and the area for tibialis anterior is more concave; the posterior face has a more pronounced soleal line. The majority of these differences simply relate to the larger size, greater robusticity, and more pronounced muscle markings of the Kanapoi tibia, and are probably a function of differences that can be attributed to sexual dimorphism rather than being of taxonomic or behavioral importance. In terms of key anatomical features and functional differences, the proximal tibia of *A. anamensis* is basically indistinguishable from EP 1000/98 and those of *A. afarensis* (Ward et al. 2001).

EP 1000/98 is also similar in size and morphology to the small proximal tibia from Sterkfontein, Stw 514a, belonging to *Australopithecus africanus* (Table 7.12). Although this latter specimen has been described as chimpanzee-like, with possible adaptations for arboreal locomotor behavior (Berger and Tobias 1996), this interpretation may have been somewhat overstated. The combination of ape-like features of this specimen (i.e., anteroposteriorly convex lateral condyle, unnotched posteromedial margin of the lateral condyle associated with the absence of a posterior cornu of the lateral meniscus, hollowing of the lateral side of the shaft below the lateral condyle, oblique groove superior to the tibial tuberosity, insertion for pes anserinus well-developed and represented by a groove on the medial side of the anterior crest, large circular depression for the attachment of semimembranosus; Berger and Tobias 1996) are typically found in other Pliocene hominins, including *Australopithecus anamensis* and *A. afarensis*, as well as EP 1000/98, which all share with modern humans a number of important features of the tibia that are functionally associated with bipedalism. As in EP 1000/98 and other Pliocene hominin tibiae, Stw 514a exhibits a limited degree of retroversion of the tibial plateau, an important feature that it shares with humans in contrast to African great apes.

Finally, a poorly preserved proximal tibia from the Upper Burgi Member (~1.9 Ma) is associated with a partial skeleton (KNM-ER 1500) that includes a mandibular fragment that allows attribution of the specimen to *Paranthropus boisei* (Day et al. 1976; Grausz et al. 1988; Brown and Feibel 1988). The size of the mandible and postcranial elements indicates that the individual was a relatively small female (Grausz et al. 1988). The proximal end of the tibia appears to be slightly larger in overall size than EP 1000/98, although precise measurements are not possible. Although badly weathered and eroded, the anatomical features that are preserved indicate that it was comparable in morphology to EP 1000/98. The key features can be listed as follows: the lateral condyle is convex anteroposteriorly, the posterior intercondylar area is relatively small and lacks a notched posteromedial border of the lateral condyle indicating that there was no posterior cornu for the lateral meniscus, posterior retroversion of the tibial plateau is moderate (about 11° for both the medial and lateral condyles), the remnant of the protuberance for the iliotibial tract is large and well-developed, the site of attachment for the semimembranosus is represented by a large circular depression, the lateral side of the shaft is hollowed below the lateral condyle, and the soleal line is prominent (Day et al. 1976). Few differences separate KNM-ER 1500 from EP 1000/98, with the former having a more retroverted tibial plateau, a more strongly protuberant tibial tuberosity, greater posterior overhang of the medial and lateral condyles (these three features are structurally linked), and a more bilaterally compressed and triangular shaft cross section. KNM-ER 1500 shows the same unique combination of features that are typically found in *Australopithecus* spp., as well as in EP 1000/98.

Comparisons with modern hominoids show that EP 1000/98 can be distinguished from both African great apes and humans. It exhibits a unique combination of features, representing a mosaic of derived specializations associated with bipedalism and a suite of presumably primitive features found in African apes that imply that the knee was capable of a wider range of axial rotation, probably associated with a greater capacity for arboreal climbing. As has been inferred for *A. afarensis* (Senut 1980; Stern and Susman 1983, 1991; Jungers 1982, 1991; Jungers and Stern 1983; Susman et al. 1984; Tardieu 1986a, b, 1999; McHenry 1991, 1994; Duncan et al. 1994; Stern 2000; Ward 2002), the species to which EP 1000/98 belonged was likely to have been an obligate biped on the ground, but quite effective at climbing in trees to exploit arboreal resources.

Comparisons of EP 1000/98 with proximal tibiae belonging to *Australopithecus afarensis, A. anamensis, A. africanus* and *Paranthropus boisei* show that they are all morphological similar, with the same suite of features distinguishing them from extant hominoids. These include: medial and lateral condyles of subequal size; anteroposteriorly relatively short condyles; a lateral condyle that is anteroposteriorly convex; an elevated intercondylar eminence with a well-developed crest linking the medial and lateral tubercles; a small and triangular posterior intercondylar area that lacks a posterior attachment for the lateral meniscus; a relatively low degree of retroversion of the tibial plateau; lateral aspect of the proximal shaft that is hollowed below the lateral condyle; an oblique groove superior to the tibial tuberosity associated with the attachment of the capsule; a distinct scar for the pes anserinus on the medial side of the anterior crest (not preserved in EP 1000/98); a well-developed depression on the medial side of the condyle for the semimembranosus; an interosseus line that divides the lateral side of the shaft into subequal areas for the anterior tibialis and posterior tibialis; a pronounced area for the iliotibial tract; possibly a distinct soleal line (but see comments above); and a shaft that is relatively straight anteroposteriorly, without a pronounced anterior curvature. The minor differences between the fossil proximal tibiae from the Pliocene of Africa are far outweighed by the striking uniformity in the key features that they share, and the anatomical differences certainly do not translate into any apparent functional differences.

Without a direct association of cranio-dental remains with the proximal tibia from the Upper Ndolanya Beds it is not possible to definitively establish the taxonomic identity of EP 1000/98. The fact that EP 1000/98 resembles the tibiae of other Pliocene hominins from East and South Africa means that there are no distinctive features of the proximal tibia that can be used to discriminate early hominin taxa. Potential hominin species that are broadly contemporary with EP 1000/98 include *Paranthropus aethiopicus*, *Australopithecus garhi*, *Australopithecus africanus*, and the earliest representatives of *Homo*. Unfortunately, however, definitive examples of the proximal tibiae of these taxa are unknown, with the exception of *A. africanus*. Given that *Paranthropus aethiopicus* is the only hominin so far represented in the Upper Ndolanya Beds, there is a reasonable likelihood that EP 1000/98 belongs to this species. If so, this would be the first postcranial element attributed to *P. aethiopicus*. The morphology of the proximal tibia is comparable to that of *P. boisei* later in time, as well as to the earlier and more primitive species of *Australopithecus*, so it is possible to deduce that EP 1000/98 is consistent in morphology with what one might anticipate in *P. aethiopicus*. However, given the uncertainties about the taxonomic attribution of EP 1000/98, the specimen is left unassigned as Hominini gen. et sp. indet. The tibia is very similar in morphology to those of *Australopithecus* spp. and *Paranthropus boisei*, and implies that the hominin taxon to which it belonged was comparable to *A. afarensis* in being a terrestrial biped that was adept at arboreal climbing.

EP 1000/98 is comparable in size to the tibiae of female individuals of *A. afarensis* and *P. boisei*. The regression formula for the lengths of the medial and lateral condyles for hominoid primates (including humans) published by Jungers (1988) provides an estimated body mass of 37.7 kg for EP 1000/98, which falls in the lower end of the estimated ranges for *Australopithecus afarensis* (30.4–67.7 kg) and *Paranthropus boisei* (33.0–69.3 kg).

LAET 75-3817

Zygomatic process of the right frontal of an infant. The specimen is associated with a small cranial fragment and an indeterminate bone fragment, but it is uncertain whether these belong to the same individual. The specimen was originally identified as a cercopithecid, but its size and morphology make it much more likely that it belongs to a hominin. It compares favorably with the morphology of juvenile specimens of *Australopithecus*, including the *A. africanus* specimen from Taung, and the *A. afarensis* specimen, A.L. 333-105 from Hadar. LAET 75-3817 is provisionally identified here as cf. Hominini indet.

Location and Stratigraphic Provenance

The specimen was discovered by Mary Leakey's expedition on August 7, 1975, during excavations of the Upper Ndolanya Beds at Loc. 7E. The specimen was recovered from Strip 8.

Preservation

The specimen consists of the zygomatic process of a right frontal preserving a short section of the lateral orbital margin, the lateral orbital plate, the anteriormost portion of the temporal fossa, the lateral recess of the frontal sinus, a portion of the frontal planum and the endocranial surface of the orbital plate of the frontal. The maximum length of the fragment is 26.8 mm and the maximum perpendicular breadth is 15.5 mm. The sutures for the parietal, sphenoid and zygomatic are still patent and unfused, establishing its juvenile status. In addition, the anterior face of the zygomatic process is pitted by tiny vascular canals, typical of juvenile individuals.

Description

The lateral orbital rim of the zygomatic process is mediolaterally slightly convex. The minimum mediolateral breadth between the orbital margin and the lateral margin of the zygomatic process is 7.6 mm (compared with 6.1 mm in Taung and 6.2 mm in A.L. 333-105 from Hadar). Inferiorly it preserves the sutural contact for the zygomatic bone. On the anterior surface, the suture runs mediolaterally and slightly superiorly towards the lateral side. At the junction with the lateral marginal ridge, the suture for the zygomatic bone passes inferiorly.

The lateral marginal ridge, separating the anterior face from the temporal fossa, forms a sharp crest. A short section of the ridge is damaged for about 3 mm of its length, causing a shallow irregular pit (possibly caused by termites or safari ants; Hill 1987). The anterior face and temporal fossa meet opposite the zygomatic suture at an angle that slightly exceeds 90° (as in the infant *Australopithecus* specimens from Taung and Hadar). This indicates a shallow anterior temporal fossa and a limited degree of postorbital constriction (unlike in adult and juvenile cercopithecids, in which the two faces meet at an acute angle greater than 45°). The lateral margin is quite well marked and continues superiorly onto the frontal planum. It was presumably continuous with a relatively pronounced temporal line, but its superior extent is damaged. A large triangular flake of bone has been lost between the suture for the sphenoid and the lateral marginal ridge. This exposes a small area of highly pneumatized bone, infilled with tuffaceous sediment, which probably represents the lateral extent of the frontal sinus. Superiorly the anterior face of the frontal bone exhibits a very slight supero-inferior convexity for the weakly developed superciliary ridge. Superolateral to this ridge the frontal plane is slightly concave to form a shallow sulcus, but otherwise it rises steeply above the orbit. The plane of the frontal just superior to the orbit is angled at 44° relative to the plane of the anterior gutter of the temporal fossa (compared with 45° in the Taung infant), whereas in extant adult cercopithecids the frontal is much more receding (greater than 55°). The configuration of the supraorbital region, with a slight superciliary ridge and steep frontal plane, is closely similar to that seen in Taung and A.L. 333-105.

Superiorly, the frontal fragment is broken at a fresh fracture running mediolaterally. The maximum thickness of bone at the point of breakage is only 2.8 mm, which is slightly thinner than that in Taung. The medial aspect of the frontal planum exposes a triangular section through the lateral recess of the frontal sinus. It is heavily pneumatized and filled with matrix. Frontal sinuses are present bilaterally, but variably developed in adult individuals of *A. afarensis*, *P. boisei* and *P. aethiopicus* (Leakey and Walker 1988; Kimbel et al. 2004). Inferiorly, there is a short section (~4 mm long) of the lateral margin of the orbit. The orbit had a relatively sharp lateral border. The internal surface of the orbit is smoothly concave and featureless, except for some tiny pinprick vascular canals. Inferiorly, the orbital plate ends at the suture for the zygomatic bone and a short section of the suture for the sphenoid. The size of the orbit cannot be estimated, but based on its lateral contour it would have been comparable in size to that in Taung.

Laterally, the anterior margin of the temporal fossa forms a distinct infero-superiorly aligned gutter. This is due to the prominence of the lateral marginal ridge of the orbital rim, but also because the frontal flares strongly towards the posterior break. This implies an inflated neurocranium laterally and a relatively slight degree of postorbital constriction. In this respect, LAET 75-3817 resembles the configuration seen in Taung. The gutter is bordered inferiorly and laterally by sutures for the sphenoid. The endocranial surface is smooth, except for fine vascular foramina and grooves. The surface is infero-superiorly concave, and mediolaterally convex due to low rounded infero-superiorly directed crest.

The two associated bone fragments are much more fragmentary and their precise anatomical location cannot be determined. One piece, a subrectangular plate of bone (29.3 × 16.2 mm), represents a fragment from the neurocranium, probably a piece of the parietal or frontal bone. The preservation matches that of the frontal fragment, and they are similar in thickness, but there appears to be no point of contact between them to confirm that they belong to the same individual. The endocranial surface is smooth and featureless, except for a number of tiny vascular canals. The external surface has a low degree of convexity, implying a relatively large neurocranium. A short section of suture (6.7 mm long) is preserved along its shortest margin. The other piece of bone, measuring 14.6 × 13.1 mm, is too fragmentary to identify anatomically. It is pentagonal in shape. One of the edges preserves a sharp border and the adjacent side preserves a short section of suture.

Comparisons

The general morphology of the frontal fragment and the development of the sutures clearly indicate that LAET 75-3817 belongs to a juvenile individual of a large primate. In terms of its size it is derived from an individual somewhat larger than an infant of *Papio anubis*. It appears to be too large to be attributed to any of the fossil cercopithecids from Laetoli, but does match quite well with the size and morphology of juvenile specimens of *A. africanus* and *A. afarensis*. The following features indicate assignment to a hominin rather that to a cercopithecid: (1) lateral rim of the orbit that meets the temporal fossa at an angle greater than 90°; (2) a narrow temporal fossa gutter with a laterally widely flaring neurocranium posteriorly; (3) relatively weakly develop superciliary ridges; (4) a relatively steep frontal planum; and (5) presence of a lateral recess of a frontal sinus.

Discussion

The discovery of two new specimens of *Australopithecus afarensis* (EP 162/00 and EP 2400/00) from the Upper Laetolil Beds, as well as the attribution of several previously unassigned specimens (L.H. 29 and LAET 79-5447), has increased the sample size of *A. afarensis* from Laetoli from 29 to 33 specimens. The new and previously undescribed specimens include two mandibular corpus fragments and two isolated canines. Although the additional specimens are relatively few, they do help to clarify the extent of morphological and metrical variation in the *A. afarensis* sample from Laetoli, and they provide an opportunity to reassess the taxonomy and evolutionary relationships.

All of the hominins recovered from the Upper Laetolil Beds can be attributed to *Australopithecus afarensis* Johanson, 1978 (see Table 7.1 for nomenclature and synonymy list). Some authorities prefer to include this species in *Praeanthropus*, in conjunction with the growing consensus that the genus *Australopithecus sensu lato* is a paraphyletic taxon (Skelton et al. 1986; Chamberlain and Wood 1987; Wood 1988, 1991; Skelton and McHenry 1992; Strait et al. 1997; Cameron 2003; Strait and Grine 2004; Kimbel et al. 2004, 2006; White et al. 2006). Given that *Australopithecus sensu lato* represents a classic Hennigian comb, with good morphological support to infer that *A. anamensis*, *A. afarensis* and *A. africanus* are successively more closely related to *Homo* or *Homo*+*Paranthropus* (Strait and Grine 2004; Kimbel et al. 2004, 2006), there may be justification to include these species, at least, in different genera. As I have stated previously:

> "[i]n order for the classification to reflect these inferred relationships, *A. africanus*, as the type species of the genus, could be retained in *Australopithecus* or be transferred to *Homo,* while *A. afarensis* would need to be removed from *Australopithecus* and subsequently recognized by the prior name *Praeanthropus africanus* (Weinert 1950). In my view this option may prove to be a necessary and desirable course of action, but I can fully appreciate that the majority of workers might prefer to retain *Australopithecus* as a paraphyletic clustering of stem species (just as I do for the Proconsuloidea), at least until such time as the relationships of the early hominids have been more firmly established" (Harrison 1993: 355–356).

Even though uncertainties still exist about the precise relationships between the constituent taxa traditionally included in *Australopithecus*, there can be little doubt that the genus, as currently construed, is paraphyletic. For the systematic formalist there is only one remedy to this problem – to add new generic names. One solution would be to include all hominin species from *A. anamensis* onwards in the genus *Homo*. Another is to include *afarensis* in the genus *Praeanthropus* and to create a new monospecific genus for *A. anamensis*, and presumably a separate one also for *A. garhi*. Either of these solutions would be perfectly justifiable based on purely phylogenetic grounds, and I am sympathetic to the last of these options, but paleoanthropologists have tended to resist such moves based on our appreciation of early hominin paleobiological diversity. There are good reasons for this resistance, and it stems from the tension that exists between systematic formalism and paleobiology. While many (but not all) paleoanthropologists are willing to accept that *Paranthropus* represents a clade of hominins morphologically and behaviorally distinct enough to be included in a separate genus from *Homo* and *Australopithecus africanus*, the differences between *A. africanus, A. afarensis*, and *A. anamensis* are of the kind and degree that neontologists would readily accommodate within a single genus. The case to separate *A. afarensis* from *A. anamensis* at the genus level would be particularly problematic, considering that they appear to be closely related members of a single lineage (Ward et al. 1999, 2001; Kimbel et al. 2004, 2006; Kimbel and Delezene 2009; Haile-Selassie et al. 2010).

Part of the problem is what I have termed "realized phylogenetic history" (Harrison 1993). Multiple genera are required to accommodate the species included in *Australopithecus* because individual species of *Australopithecus* are the sister taxa of descendant species that are not included in the same genus (i.e., *Homo* and *Paranthropus*). However, during the Pliocene, before the divergence of *Homo* and *Paranthropus*, *Australopithecus* was monophyletic, and its constituent species were similar enough morphologically and behaviorally to be included in a single genus. This means that the constitution and perception of a genus changes through time as its phylogenetic history is realized (see Harrison 1993). *Australopithecus* would have represented a clade in the early

Pliocene, but with the divergence of *Homo* and *Paranthropus* in the late Pliocene it became paraphyletic. It can be seen that taxonomic utility is dependent upon whether one's primary focus is phylogeny or paleobiology. Since most paleoanthropologists are equally concerned with both, the tension between these interests creates a strong motivational force against accepting multiple genera for *Australopithecus sensu lato*. Paleontologists may prefer to include the species of *Australopithecus* in multiple genera because it has a realized phylogenetic history, whereas neontologists would consider *Australopithecus* to be the equivalent of a single extant genus because the constituent species can be inferred to have looked and behaved alike on the Pliocene landscape. There is no easy resolution to this problem, and as a consequence the genus-level nomenclature of *Australopithecus sensu lato* is likely to remain in a state of flux for the foreseeable future. Given these issues, the species from Laetoli is provisionally (and conservatively) retained here in *Australopithecus* (see Table 7.1) rather than included in a monospecific genus, *Praeanthropus* (see Harrison 1993; Strait et al. 1997; Grine et al. 2006).

When *Australopithecus afarensis* was initially described in 1978 (Johanson et al. 1978) the sample of specimens from Laetoli and Hadar were seen as sufficiently close in morphology to be considered conspecific. Although relatively minor differences in the craniodental morphology and metrics were identified between the two samples (Blumberg and Lloyd 1983; White 1985; Kimbel et al. 1985; Cole and Smith 1987), these were considered to be a consequence of sampling (especially due to the relative paucity of specimens from the type locality of Laetoli) and/or a reflection of intraspecific spatio-temporal variation between different populations of the same species. White (1985) argued that some of the morphological and metrical differences between the two samples were due to the skewed representation of the Laetoli sample towards larger-sized individuals, and that if the sample could be enlarged, the range of variation would likely approximate that seen in the much larger Hadar sample. White's contention has been affirmed by the discovery of EP 162/00 and EP 2400/00, which are metrically similar to small (presumably female) individuals of *A. afarensis* from Hadar. These new specimens have helped to close the morphological and metrical gap between the Laetoli and Hadar samples, but a number of differences still remain that appear to consistently distinguish the two samples.

Following detailed comparisons, and taking into account the range of variation in the two samples, the material from Laetoli can be distinguished from the specimens from Hadar in the following features: (1) the I^2 root is medially positioned relative to the lateral margin of the nasal aperture in the Garusi maxilla (as in *A. africanus*), whereas in the maxillae from Hadar and that of *A. anamensis* it is placed lateral to the nasal aperture (Kimbel et al. 2006); (2) the upper canine is more bilaterally compressed (the breadth-length index in the Laetoli sample averages 94.6; $n=4$, range 90.3–98.3) compared with 112.2 in the Hadar sample ($n=12$, range 104.5–124.0; Kimbel et al. 2004) (see also White 1985), but similar in proportions to the upper canines of *A. anamensis* (Ward et al. 2001); (3) P^3 has a more asymmetrical occlusal outline, with a mesiodistally longer buccal moiety and a slightly higher paracone (White 1985; Kimbel and Delezene 2009); (4) P^4 tends to be relatively broader in relation to its mesiodistal length (mean length-breadth index = 68.4, range = 63.8–75.6, $n=4$; compared with the Hadar mean value of 72.4, range = 66.4–81.2, $n=11$, but the difference is not statistically significant, Student's t, $P=0.15$); (5) M^1 and M^2 crowns narrow buccally, with a larger and more distally placed protocone, a smaller hypocone, and a tendency to develop a stronger remnant of the lingual cingulum (Carabelli's trait) on the mesiolingual margin of the protocone (see also White 1985); (6) M^3 is relatively smaller in the Laetoli sample (the area [length x breadth] ranges from 136.5 to 158.5 [$n=4$] compared with 149.3–241.2 [$n=9$] at Hadar; Kimbel et al. 2004), averaging only 85.7% ($n=2$, range = 84.1–87.3) of the area of M^2 in associated upper teeth, compared with 98.6% at Hadar ($n=7$; range = 88.6–108.3), with reduced distal cusps and distal moiety (see also White 1985; Lockwood et al. 2000; Kimbel and Delezene 2009); and (7) P_3 is relatively longer in the Laetoli sample compared with that from Hadar (Lockwood et al. 2000; Kimbel et al. 2006). Although there are difficulties taking standard mesiodistal and buccolingual measurement on P_3 because of variation in the orientation and shape of the crown (see White 1977), the mesiodistal length and maximum length dimensions of the P_3 crowns from Laetoli do appear to be greater than those from Hadar (even with the addition of the small P_3 associated with EP 2400/00). The mesiodistal length of the sample from Laetoli has a mean value of 10.9 mm (range = 9.8–12.2, $n=7$) compared to the mean value at Hadar of 9.2 mm (range = 7.9–11.4, n = 19; Kimbel et al. 2004). This difference is statistically significant (Student's t, $P=0.0001$). Maximum length, regardless of orientation of the tooth, provides a simpler measure of crown length, one that is more easily replicated. In this case, L.H. 3 (13.3 mm), L.H. 14 (left = 13.0 mm; right = 13.3 mm) and L.H. 24 (13.1 mm) fall outside the range for the Hadar sample (9.5–13.0 mm; Kimbel et al. 2004), whereas only EP 2400/00 (11.9 mm), L.H. 2 (10.8 mm), and L.H. 4 (12.6 mm) fall within the range. The mean value for the Laetoli sample is 12.6 compared with 11.4 mm for the Hadar sample, and the difference between the two samples is statistically significant (Student's t, $P=0.0421$). By comparison, the mean maximum length of P_3 in *A. anamensis* is 12.2 mm (Ward et al. 2001), which is smaller than in the Laetoli sample, but not significantly different (Student's t, $P=0.3796$).

A number of other possible morphological differences have been reported in the literature, but these appear to be variable features that do not consistently differentiate the two samples. These are briefly reviewed below.

1. *Configuration of the lateral margin of the nasal aperture*: A number of authors (Puech et al. 1986; Leakey et al. 1995; Ward et al. 2001; Kimbel et al. 2004, 2006) have noted that the Garusi maxilla from Laetoli differs from all of the specimens from Hadar in that the facial aspect of the maxilla grades smoothly into the inferolateral margin of the nasal aperture. In the Hadar maxillae, by contrast, a sharp crest delimits the inferolateral margin of the nasal aperture. In this respect, the Garusi maxilla is similar to the maxilla of *A. anamensis* (KNM-KP 29283) from Kanapoi (Leakey et al. 1995; Ward et al. 2001; Kimbel et al. 2004, 2006). Further comparisons by the author have confirmed the validity of this difference, but unfortunately we do not know enough about the variability of this feature in early hominin populations to assess its taxonomic significance. For example, we only have one example of an adult maxilla at Laetoli and Kanapoi respectively that preserves this region. However, it is important to note that the right maxillary fragment associated with the partial skeleton of an infant from Laetoli, L.H. 21, has a sharp crest forming the lateral margin of the nasal aperture, just as in the adult maxillae from Hadar.
2. *Narrower and shallower palate*: Ward et al. (1999) have suggested that the anterior palate of the Garusi specimen from Laetoli resembles *A. anamensis* in being narrower and shallower than in the Hadar maxillae (see also Puech et al. 1986). However, Kimbel et al. (2004) have shown that the Garusi maxilla is not different from the Hadar maxillae in these respects. The internal palate breadth at P^3 in the Garusi maxilla can be estimated to be 26.2 mm, which corresponds well with comparable dimensions in the maxillae from Hadar.
3. *Inclination and external contour of the mandibular symphysis*: The only mandibular specimen of an adult from Laetoli preserving the symphyseal region is L.H. 4. Kimbel et al. (2004, 2006) have suggested that the Laetoli specimen has a more strongly inclined symphyseal region than in the mandibles from Hadar, and that the external contour of the symphysis is more convex and inferiorly “cut away”, compared to the straighter external surface superiorly with a basal bulge seen in Hadar. However, there is a good deal of variation in the Hadar mandibles. The inclination of the symphysis in L.H. 4 is 127° relative to the alveolar plane of the tooth row, which falls in the upper end of the range of the sample from Hadar (mean = 119°, range 105–134°, $n = 11$), and can be matched or exceeded by several Hadar specimens with more inclined symphyses (i.e., A.L. 333w-12, A.L. 198-1, A.L. 266-1). Comparison of the contour of the external face of the symphysis is more difficult to assess objectively, but, while many of the Hadar mandibles exhibit a steeply inclined superior symphyseal region with a bulging basal aspect, a number of them (i.e., A.L. 207-13, A.L. 315-22, A.L. 330-5 and A.L. 333w-60, A.L. 438-1 g; see Kimbel et al. 2004, fig. 5.29) closely resemble the configuration seen in L.H. 4. Although the symphyseal region of L.H. 4 is not typical of that seen at Hadar, its morphology is certainly encompassed by the range of variation.
4. *Position of the lower canine in relation to the postcanine toothrow*: The larger lower canine roots in *A. anamensis* results in a more laterally expanded canine jugum compared with that in *A. afarensis*. As a result, the mandible has its greatest anterior breadth at the level of the canine in *A. anamensis*, whereas in *A. afarensis* it is greatest at P_3 (Ward et al. 2001). In other words, the lateral aspect of the mandibular corpus curves medially anterior to the lower canine in *A. anamensis*, whereas it curves medially anterior to P_3 in *A. afarensis* from Hadar. Kimbel et al. (2006) contend that the morphology in L.H. 4 is intermediate, with the canine in line with the postcanine long-axis and a medial curvature at C/P_3. However, the P_3 jugum in L.H. 4 is more pronounced than in *A. anamensis* and its configuration closely resembles that in the Hadar sample. A way to quantify the difference between *A. anamensis* and *A. afarensis* in canine position is to measure by how much the long axis of the lower canine deviates medially or laterally from the long axis of the postcanine tooth row. In L.H. 4 the canine deviates medially by a distance of 3.2 mm, which falls within the range of variation of mandibles from Hadar (1.9–4.6 medial deviation, $n = 4$), whereas in *A. anamensis* (KNM-KP 29281A) the canine long-axis deviates *laterally* by 1.0 mm. Although the canine is missing in EP 2400/00, the posterior half of the canine alveolus is preserved, and it is evident that the canine was placed medial to the long-axis of the postcanine tooth row, the P_3 jugum was more pronounced than the canine jugum, and the lateral aspect of the mandible curved medially just anterior to P_3, as in the mandibles from Hadar. In this regard, the Laetoli mandibles do not differ from those from Hadar.
5. *Symmetry of the mesial and distal crown shoulders*: Kimbel et al. (2006) argue that the Hadar upper canines differ from those from Laetoli in having a more asymmetrical crown in lingual view because the mesial shoulder is more apically placed than the distal shoulder, whereas in the upper canines from Laetoli the shoulders are similar in elevation as in *A. anamensis* (Ward et al. 2001). This distinction is valid when the Hadar upper canines are compared with L.H. 3, which appears to be unusual in having mesial and distal shoulders at the same elevation. However, L.H. 5, L.H. 6 and LAET 79-5447

(see Fig. 7.8) are more similar to A.L. 333x-3 in their degree of asymmetry, with a more apically placed mesial shoulder. Besides, the best-preserved upper canine of *A. anamensis* (KNM-KP 35839) (Ward et al. 1999, 2001), which is considered to exhibit the morphology typical of the species (see Ward et al. 2001: 347), has a suite of peculiar features (i.e., strongly developed and basally placed lingual cingulum, a simple lingual face with no pillar, straight mesial and distal crests, a lingually recurved crown, and a slender root) that leaves me unconvinced that this tooth (and the associated "pathological" incisor) is representative of the taxon.

6. *Frequency of occurrence of a prominent metaconid on* P_3: White (1985) noted that there may be a higher frequency of P_3 crowns from Laetoli with a prominent metaconid compared with the sample from Hadar. However, additional data from Laetoli show that the frequency of occurrence of P_3s with a small metaconid is similar to that at Hadar (33.3% at Laetoli [$n=6$] compared with 40% at Hadar [$n=10$]). This contrasts with the more primitive condition in *A. anamensis* in which 100% ($n=5$) of the crowns lack a distinct metaconid (Ward et al. 2001).

A case has been made that the Laetoli specimens are morphologically (and temporally) intermediate between *A. anamensis* and the Hadar samples and that the principal samples of *A. anamensis* (from Kanapoi and Allia Bay) and *A. afarensis* (from Laetoli and Hadar) represent a single anagenetically evolving lineage (or evolutionary species) that extends through time by more than one million years (Ward et al. 1999; Lockwood et al. 2000; Kimbel et al. 2006; White et al. 2006). This has naturally led some authors to question whether *A. anamensis* and *A. afarensis* should be considered separate species, and if so, where to draw the taxonomic line between them (Kimbel et al. 2006; Haile-Selassie et al. 2010). One solution would be to include all of the samples in a single species, *A. afarensis* (Senut 1996; Wolpoff 1999; Kimbel et al. 2006; Haile-Selassie et al. 2010). If one prefers a two-species model, however, the following taxonomic options are conceivable: (1) [Kanapoi = *A. anamensis*] [Allia Bay + Laetoli + Hadar = *A. afarensis*]; (2) [Kanapoi + Allia Bay = *A. anamensis*] [Hadar + Laetoli = *A. afarensis*] – currently the consensus view; and (3) [Kanapoi + Allia Bay + Laetoli = *A. afarensis*] [Hadar = *A. antiquus*] (see also Kimbel et al. 2006).

However, when the evidence is critically scrutinized an entirely different perspective on this problem emerges. While it is justified to conclude that the Laetoli specimens retain a few primitive characteristics that they share with *A. anamensis* not present in the material from Hadar, it is not the case that the Laetoli sample is intermediate in morphology between the samples from Kanapoi + Allia Bay and Hadar when judged in the broader context of their overall morphology. As noted above, there are relatively few features that consistently differentiate the Laetoli and Hadar samples, whereas the morphological divide between *A. afarensis* (Laetoli + Hadar combined) and *A. anamensis* is much more profound. Of the features identified above that consistently differentiate the Laetoli and Hadar samples, only the greater bilateral compression of the upper canines, the relatively longer P_3, the higher frequency of remnants of the lingual cingulum on the upper molars, the asymmetry of the P^3, and possibly the relatively broader P^4 are more primitive features that the Laetoli sample shares with *A. anamensis* (Ward et al. 1999, 2001; Kimbel et al. 2006; White et al. 2006). On the other hand, the position of the I^2 root relative to the lateral margin of the nasal aperture, the higher frequency of a prominent metaconid on P_3, the shape and occlusal morphology of the upper molars, and the relatively small size of M^3 in the Laetoli specimens are either autapomorphies or are more derived features shared with *A. africanus* (in the case of the I^2 root position and the higher frequency of well-developed P_3 metaconids). They cannot be inferred to be intermediate between *A. anamensis* and the Hadar sample.

In contrast, the differences that distinguish *A. anamensis* from *A. afarensis* are much more extensive. These include: articular eminence less well-developed; smaller elliptical external acoustic meatus; larger upper canine roots and more prominent canine juga; palate relatively narrower, with tooth rows almost parallel rather than posteriorly diverging; more strongly inclined mandibular symphysis; longer postincisive planum; mandibular corpus less robust below the molars; lower postcanine tooth rows set close together and more parallel, rather than posteriorly diverging; lower canines more laterally placed relative to the postcanine toothrow, with more prominent juga (in *A. afarensis* the lateral aspect of the corpus turns medially just anterior to P_3); upper canine with a stronger mesiolingual ridge; I_2 is mesiodistally relatively broader; lower canine with pronounced distal heel and basal cingulum; P_3 consistently unicuspid with the metaconid represented by a tiny tubercle on the distolingual crest (in *A. afarensis* more than half of the specimens have a prominent metaconid); mesial fovea of P_3 opens lingually with a notched mesial marginal ridge (i.e., lingual cingulum); P_4 with less expanded distal fovea; molars are lower-crowned, with greater buccolingual flare; lower molars with a higher frequency of a prominent vestige of the buccal cingulum (protostylid) (40% of *A. anamensis* lower molars, compared with only 6.5% in the combined Hadar-Laetoli sample; Hlusko 2004); dP_3 (=dm_1) narrower, with a relatively weakly developed mesial fovea and talonid basin; capitate with laterally facing metacarpal II facet (Leakey et al. 1995, 1998; Ward et al. 1999, 2001; Kimbel et al. 2006; White et al. 2006).

The main point to underscore here is that the morphological and metrical differences between the Laetoli and Hadar

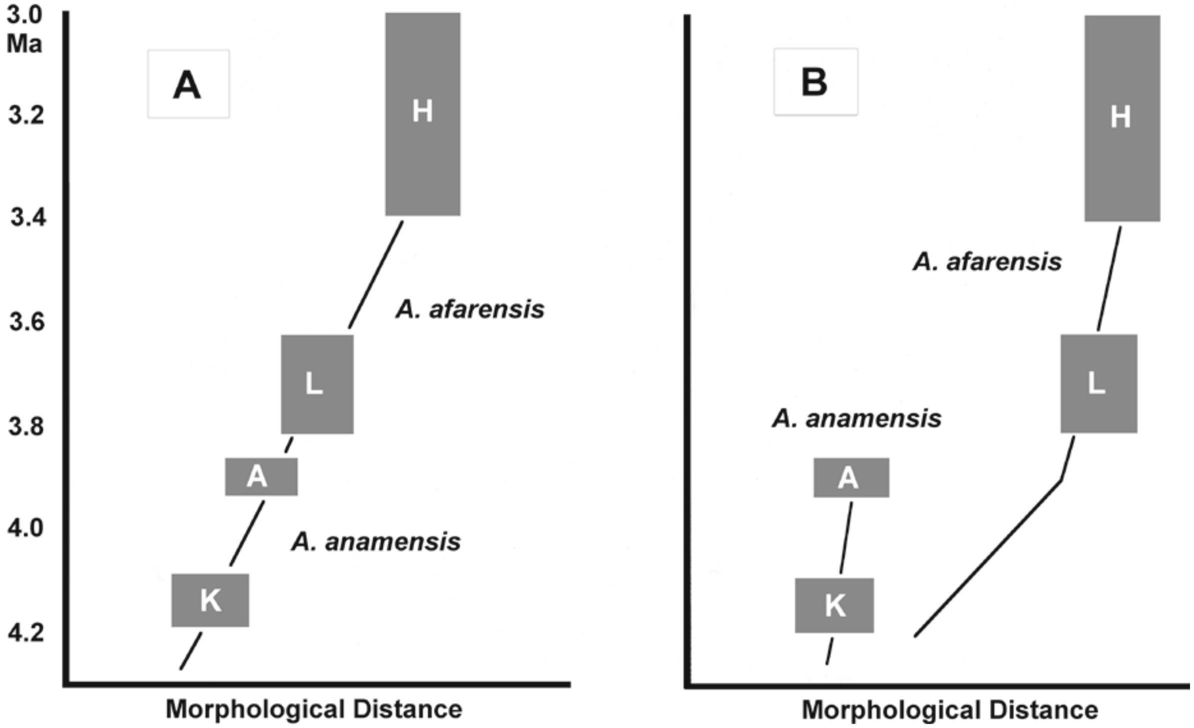


Fig. 7.11 Alternative views of the relationship between the *A. afarensis* samples from Laetoli (L) and Hadar (H), and the *A. anamensis* samples from Kanapoi (K) and Allia Bay (A). The model on the *left*, favored by Kimbel et al. (2006), explains the relationship between *A. anamensis* and *A. afarensis* as the result of anagenesis in a single evolutionary lineage, with each step being separated by small morphological changes through time. The model on the *right*, preferred by the present author, explains the relationship as a cladogenetic event, with minor progressive transformations occurring within the two lineages, but a morphological divide separating *A. anamensis* and *A. afarensis* into distinct sister species

samples are few in number and constitute relatively minor distinctions. Such differences in dental morphology are what one might expect as part of the normal variation seen in populations of a single species of hominoid. Rather than being intermediate in morphology, the evidence indicates that the Laetoli sample represents an earlier population of *A. afarensis*, with almost the full complement of derived features that characterizes the Hadar sample, but, consistent with its greater antiquity, still retaining a small number of more primitive traits. By comparison, the suite of morphological features that distinguishes *A. anamensis* (at least from the type locality of Kanapoi) from *A. afarensis* from Laetoli and Hadar is much more extensive and more substantial in nature, and these clearly provide adequate grounds for the recognition of a species distinction. It is also worth emphasizing here that the temporal gap between the youngest sample of *A. anamensis* from Allia Bay (~3.9 Ma) and the oldest specimens of *A. afarensis* from Laetoli (3.81–3.83 Ma) is probably as little as 70–90 kyrs. A reasonably good case can be made to document temporal trends within both *A. afarensis* and *A. anamensis* and to infer an ancestral-descendant relationship between *A. anamensis* and *A. afarensis* (Ward et al. 1999, 2001; Lockwood et al. 2000; Kimbel et al. 2004, 2006), but the current evidence favors an evolutionary model involving a cladogenetic event rather than a simple anagenetic transformation of a single unbranched lineage through time (see Fig. 7.11).

The recent description of a sample of *Australopithecus* sp. from Woranso-Mille in Ethiopia, contemporaneous (3.57–3.8 Ma) with the sample from Laetoli, adds another level of complexity to unraveling the relationships between *A. anamensis* and *A. afarensis*, by showing that contemporary populations have novel mosaics of cranio-dental features (Haile-Selassie et al. 2010). The material demonstrates how contemporaneous populations of hominins are likely to be characterized by spatial heterogeneity and that one cannot expect that all populations will conform uniformly to simple models of progressive transformation through time. For example, the Woranso-Mille specimens exhibit a less inclined mandibular symphysis and P_3 with a prominent metaconid and a well-developed mesial marginal ridge, features that are typical of *A. afarensis* at Hadar and Laetoli. However, in several features the Woranso-Mille specimens resemble *A. anamensis.* These include greatest anterior breadth of the mandible at the canine rather than P_3 (although the accompanying illustration in Haile-Selassie et al. (2010) appears to show the canine positioned medial to the postcanine tooth row as in *A. afarensis*) and P_4 with a small and elevated trigon basin. Based on the descriptions presented by Haile-Selassie et al. (2010) the Woranso-Mille material seems to be very close in morphology to the contemporary sample from Laetoli, but differs in having a relatively larger M^3. In my view the material is best attributed to *A. afarensis*, but Haile-Selassie et al. (2010) remain undecided about its taxonomic status, so it is best to await more detailed comparisons (and perhaps more material) before making a definitive assignment.

In addition to new specimens from the Upper Laetolil Beds, this report describes the first hominins from the Upper Ndolanya Beds. These are derived from deposits dated to 2.66 Ma (Deino 2011), more than one million years younger than the *A. afarensis* specimens from the Upper Laetolil Beds. Two specimens have been recovered since 1998, a maxilla and a proximal tibia. The maxilla (EP 1500/01) can be definitively attributed to *Paranthropus aethiopicus*, based on its unique combination of features shared with KNM-WT 17000 from the Nachukui Formation, West Turkana, in northern Kenya (Walker et al. 1986; Leakey and Walker 1988; Walker and Leakey 1988; Kimbel et al. 1988; Wood and Constantino 2007). Taxonomic attribution of the tibia is uncertain, because it is not possible to distinguish isolated postcranial elements of Pliocene hominins. Apart from being the first records of hominins from the Upper Ndolanya Beds, these finds are important for several other reasons: (1) the maxilla represents the first definitive record of *P. aethiopicus* outside the Turkana Basin of northern Kenya and southern Ethiopia; (2) it is among the oldest known records of this species; and (3) the proximal tibia is the first postcranial element of an adult individual to be recovered from Laetoli. The broader importance of these specimens is briefly discussed below.

Previously, *Paranthropus aethiopicus* was known only from the Omo Shungura Formation, Ethiopia (including the holotype, Omo 18–18) and the Nachukui Formation, Kenya, on the northern and western side of the Turkana Basin respectively. The new specimens from the Upper Ndolanya Beds thus extend the range of the species from the Turkana Basin to northern Tanzania, almost 800 km to the south. A maxillary specimen of *Paranthropus* from the Pliocene Chiwondo Beds at Malema, Malawi, a locality situated 800 km to the south of Laetoli, could potential represent another specimen of *P. aethiopicus* outside the Turkana Basin (Kullmer et al. 1999). The associated fauna has been estimated to be 2.3–2.5 Ma, which overlaps chronologically with the known time range of *P. aethiopicus* (~2.3–2.7 Ma), although it could be considerably younger (Hill 1999). Nevertheless, the morphology of the specimen indicates that it is best attributed to *P. boisei* rather than *P. aethiopicus* (Kullmer et al. 1999).

Most of the specimens attributed to *P. aethiopicus* from the Turkana Basin, including the cranium KNM-WT 17000, range in age from 2.33 to 2.58 Ma, but a few specimens from the Omo Shungura Formation (i.e., L55-s-33, L 62-17, Omo 18–18, and Omo 84–100) occur in earlier horizons dating to between 2.58 and 2.7 Ma (Feibel et al. 1989; Suwa 1988; Suwa et al. 1996; Wood and Constantino 2007). Omo 18–18 and Omo 84–100 are close in age to 2.6 Ma, while the mandibular fragment L55-s-33 and the isolated molar L 62-17 from Submembers C-6 and C-5 of the Omo Shungura Formation respectively have an estimated age of ~2.70 Ma (Feibel et al. 1989; Suwa et al. 1996; Bobe and Leakey 2009). These latter specimens are attributable to *Paranthropus*, and can be assumed to be *P. aethiopicus*, although they do not preserve any diagnostic features (Suwa et al. 1996). The maxilla from the Upper Ndolanya Beds, dating to 2.66 Ma, is thus the oldest, securely dated specimen definitively attributable to *P. aethiopicus*.

The occurrence of *P. aethiopicus* in the Upper Ndolanya Beds has important implications for understanding and interpreting the biogeography of *Paranthropus*. The evidence suggests that soon after its earliest appearance in East Africa, at about 2.7 Ma, or shortly thereafter, it attained a relatively wide distribution throughout the region occurring from southern Ethiopia to northern Tanzania (Wood and Constantino 2007; Constantino and Wood 2007). Since there is no immediate precursor for *P. aethiopicus* in the Turkana Basin or elsewhere in eastern Africa prior to 2.7 Ma (but see Rak et al. 2007), it might imply that the *Paranthropus* clade originated outside of the geographical province and immigrated into the region. Suwa et al. (1996), however, have tentatively identified a few isolated teeth of relatively large size that might document an earlier occurrence of the *Paranthropus* clade in the Omo Shungura Formation, dating back to ~2.9 Ma. This would push back the age of *Paranthropus* in eastern Africa, but it does not change the overall biogeographic implications. The earlier species, *A. afarensis*, that occupied much of the region until at least 3.0 Ma, is probably morphologically too distinct from *Paranthropus aethiopicus* to have been its immediate ancestor (see Kimbel and Delezene 2009; but see Rak et al. 2007).

The same conclusion might be reached for early *Homo* (Pickford 2004), which also makes an appearance in eastern Africa in the mid-Pliocene (Kimbel et al. 1996; Kimbel, 2009). However, in this case, differences in the timing and distribution might imply that *Homo* and *Paranthropus* do not have coincident biogeographic, ecological and immigration histories. The earliest occurrences of *Homo* are from Member E of the Omo Shungura Formation (2.4 Ma), the Kalochoro Member of the Nachukui Formation (2.3 Ma), the Busidima Formation at Hadar (2.33 Ma), the Chemeron Formation (~2.4 Ma) and the Chiwondo Beds at Uraha (~2.3–2.5 Ma?) (see Kimbel 2009). Contemporaneous with these occurrences and slightly older are archaeological sites with Oldowan stone tools, which extend back to 2.6–2.5 Ma in the Gona region of the Upper Awash (Semaw et al. 1997, 2003).

It is interesting, in this regard, that the Upper Ndolanya Beds at 2.66 Ma only record the presence of *Paranthropus aethiopicus*, with no evidence of early *Homo* or archaeological traces. Lithic artifacts have been reported as surface finds from the Upper Ndolanya Beds at Loc. 18 (Kaiser et al. 1995), but no similar finds have been located *in situ* despite extensive investigations in these horizons by successive teams working at Laetoli, and I am inclined to discount these artifacts as being intrusive from the overlying Ngaloba Beds.

In this case, the evidence indicates that the arrival of *Paranthropus* and *Homo* in different parts of eastern Africa was not synchronous, and that at Laetoli *Paranthropus* colonized the area ahead of *Homo*. A similar pattern is seen in the Turkana Basin, where the paleontological and archaeological record is much more complete. The evidence indicates that *Paranthropus* was present in the Turkana Basin by at least 2.7 Ma, whereas the earliest record of *Homo* and of archaeological sites is at 2.4 Ma (Kibunjia et al. 1992; Prat et al. 2005; Roche et al. 2009; Bobe and Leakey 2009). However, at the other end of the Rift Valley, north of the Turkana Basin, in the Awash region of Ethiopia, archaeological evidence implies that early *Homo* was present by 2.6 Ma, possibly slightly earlier than in the East African Rift to the south, whereas the first record of *Paranthropus* is from Konso at 1.4 Ma. *Homo* and *Paranthropus* may have colonized eastern Africa from different geographic origins, with *Homo* first appearing at the northern end of the Rift Valley and *Paranthropus* first appearing to the south. Detailed comparisons of the faunal, ecological and biogeographical relationships between localities in eastern Africa might yield some valuable clues to understanding the nature and timing of the appearance of *Paranthropus* and *Homo* in the fossil record.

Conclusions

Renewed investigations at Laetoli and at other sites on the Eyasi Plateau since 1998 have led to the recovery of additional fossil hominins. Two specimens, an isolated lower canine (EP 162/00) and a mandibular fragment with P_3–M_1 (EP 2400/00), recovered from the Upper Laetolil Beds at Loc. 16, are referable to *A. afarensis*. In addition, two hominins, a proximal tibia (EP 1000/98) and an edentulous maxilla (EP 1500/01), were recovered from the Upper Ndolanya Beds, and represent the first hominins from this stratigraphic unit. EP 1500/01 represents the only specimen of *P. aethiopicus* recovered from outside the Turkana Basin. A detailed descriptive account of the morphology of these newly collected hominins from Laetoli is presented above. In addition, four specimens from the Kohl-Larsen and Mary Leakey collections are described in detail for the first time. Three of these specimens, L.H. 29, LAET 79-5447 and MB Ma. 8294, are of unknown stratigraphic provenance, but they are almost certainly derived from the Upper Laetolil Beds. All are attributable to *A. afarensis*. Additionally, a specimen (LAET 75-5447) from the Upper Ndolanya Beds collected by Mary Leakey, and originally identified as a cercopithecid, most probably represents a cranial fragment of a hominin infant.

Renewed study of the hominins from Laetoli also provided an opportunity to clarify their chronology and provenance. Fossil hominins have not yet been recovered from the Lower Laetolil Beds (~4.4–3.85 Ma), and they are rare in the younger stratigraphic units that overlie the Upper Laetolil Beds. A single cranium of *Homo sapiens* is known from the Late Pleistocene Upper Ngaloba Beds. The hominins from the Upper Laetolil Beds, dated from 3.63 to 3.85 Ma, are all referable to *Australopithecus afarensis*. Except for a single partial skeleton of an infant (L.H. 21), the sample ($n=33$) consists entirely of cranio-dental specimens (see Su and Harrison 2008). *Australopithecus afarensis* is replaced in the fossil-rich Upper Ndolanya Beds, dated to 2.66 Ma, by *Paranthropus aethiopicus*. The majority of specimens from Laetoli have been recovered as surface finds, and it is important to distinguish between the actual find spot and the stratigraphic horizon from which the fossil originated. The precise stratigraphic provenances listed by Leakey (1987a) are actually the find spots, with the exception of those few specimens recovered from *in situ*. However, the original stratigraphic provenance of most finds can be deduced with a reasonable degree of precision, at least in relation to the designated Upper Laetolil marker tuffs.

Given that *Australopithecus sensu lato* likely represents a paraphyletic group, there may be justification to include the constituent species in multiple genera. For this reason, some authors advocate including *afarensis* in the genus *Praeanthropus*. Although this is a perfectly justifiable move based on purely phylogenetic grounds, and one to which I am sympathetic, I provisionally retain *afarensis* here in *Australopithecus* to reflect its anatomical and paleobiological proximity to the other species of *Australopithecus sensu lato*. In my view, the differences between *A, africanus, A. afarensis* and *A. anamensis* are of the kind and degree that neontologists would easily accommodate within a single genus.

It has been argued that the Laetoli sample of *A. afarensis* is morphologically (and temporally) intermediate between *A. anamensis* and the Hadar sample, and that the principal samples of *A. anamensis* (from Kanapoi and Allia Bay) and *A. afarensis* (from Laetoli and Hadar) represent a single anagenetically evolving lineage (Ward et al. 1999; Lockwood et al. 2000; Kimbel et al. 2006; White et al. 2006). However, the new specimens from the Upper Laetolil Beds have helped to close the morphological and metrical gap between the Laetoli and Hadar samples of *A. afarensis*, and a critical assessment of the morphological variation in the two samples indicates that there are relatively few consistent differences separating them. The Laetoli specimens retain a few primitive characteristics that they share with *A. anamensis* not present in the material from Hadar, but the Laetoli sample cannot be considered to be intermediate in morphology. Only a few features consistently differentiate the Laetoli and Hadar samples, and these are the type of differences that one would expect for intraspecific variation in populations separated in space and time, whereas the morphological divide between *A. afarensis* (Laetoli + Hadar combined) and *A. anamensis* is much greater. Rather than being intermediate in morphology, the Laetoli sample appears to represents an earlier population of *A. afarensis*, with almost the full complement of derived features that characterizes the Hadar sample, but, consistent with its greater antiquity, still retaining a small number of more primitive traits. By comparison, the suite of morphological features that distinguishes *A. anamensis* from *A. afarensis* is much more extensive and more substantial in nature, and these clearly provide adequate grounds for the recognition of a species distinction. The current evidence favors an evolutionary model involving a cladogenetic event rather than a simple anagenetic transformation of a single unbranched lineage through time.

The hominins from the Upper Ndolanya Beds are important because they provide the first record of *P. aethiopicus* outside the Turkana Basin, and the oldest securely dated specimen definitively attributable to this taxon. The occurrence of *P. aethiopicus* at Laetoli also has important implications for understanding and interpreting the biogeography of *Paranthropus*. The evidence suggests that soon after its earliest appearance in East Africa at about 2.7 Ma, it established a relatively wide distribution throughout the region occurring from southern Ethiopia to northern Tanzania. Since there is no immediate precursor for *P. aethiopicus* in eastern Africa prior to 2.7 Ma, the *Paranthropus* clade probably originated outside of the geographical province and immigrated into the region. The earlier species, *A. afarensis*, that occupied much of the region until at least 3.0 Ma, is probably morphologically too distinct from *Paranthropus aethiopicus* to have been its immediate ancestor (but see Rak et al. 2007).

Homo also appears to have been an immigrant into eastern Africa, rather than derived autochthonously from a local ancestral species. However, the timing of its first appearance and its geographic distribution at Pliocene localities suggests that the dispersal events of *Homo* and *Paranthropus* were not coincident or synchronous. The evidence from Laetoli indicates that *Paranthropus* was present locally by at least 2.66 Ma in the absence of any trace, paleontological or archaeological, of early *Homo*. A similar pattern is found in the Turkana Basin where the earliest record of *Paranthropus* at ~2.7 Ma precedes that of *Homo* by about 300 kyrs (Roche et al. 2009; Bobe and Leakey 2009). In contrast, the Awash region of Ethiopia well to the north of the Turkana Basin has archaeological evidence at 2.5–2.6 Ma that implies that early *Homo* was present much earlier than *Paranthropus*. These differences in the timing and mode of immigration into eastern Africa suggests that *Paranthropus* and *Homo* had different biogeographic histories, and that the ancestral species may have had slightly different ecological requirements at the time of their initial influx into the region.

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Chapter 8
Carnivora

Lars Werdelin and Reihaneh Dehghani

Abstract This paper reviews the extensive carnivoran fauna of Laetoli on the basis of collections housed in Berlin, London, Nairobi, and Dar es Salaam. Members of the Carnivora are known from both the Lower and Upper Laetolil Beds, as well as from the Upper Ndolanya Beds. Of these, the Upper Laetolil Beds are best sampled, and the material includes a minimum of 28 species of Carnivora (four Canidae, three Mustelidae, three Viverridae, six Herpestidae, five Hyaenidae, and seven Felidae). Many of the smaller Carnivora species include complete or partial skeletons and whole, undamaged crania, suggesting rapid burial and absence of trampling and other taphonomic processes that severely affected the more fragmentary larger Carnivora. The Upper Ndolanya Beds Carnivora are preserved in a similar fashion. This stratigraphic unit includes nine to ten species (one Mustelidae, two Herpestidae, one or two Hyaenidae, and five Felidae). All of these are also known from the Upper Laetolil Beds. The Lower Laetolil Beds are less well sampled, with only four species of Carnivora (one Mustelidae, one Herpestidae, and two Hyaenidae). Of these, the mustelid and one hyenid are unique to this stratigraphic unit, while one hyenid is shared with the Upper Laetolil Beds and the herpestid with both the Upper Laetolil Beds and the Upper Ndolanya Beds. Three of the Lower Laetolil Beds Carnivora (all except the herpestid) are partial skeletons, suggesting different depositional or taphonomic conditions at that time, while the presence of an otter in the Lower Laetolil Beds indicates the presence of a large, permanent body of water in the vicinity.

Keywords Canidae • Felidae • Herpestidae • Hyaenidae • Mustelidae • Viverridae • Pliocene • Laetoli

Introduction

Carnivorans from the Laetoli deposits have been described several times since their first discovery in the 1930s. The first treatment was by Dietrich (1942). The exact provenance of most of the material described by Dietrich is not known with certainty, but specimens recorded as coming from korongos (gullies) in the Garussi (now spelled "Garusi") region are generally considered to come from the Upper Laetolil Beds. Dietrich described the following taxa from these beds: *Canis (Lupulella) mesomelas* ssp., *Mungos palaeoserengetensis* n. sp., *Mungos palaeogracilis* n. sp., *Crocuta crocuta* subsp., and *Panthera pardus* subsp. (a *Felis* of the "*ocreata* group" is also recorded from Garussi, but these specimens are explicitly stated to be subfossil). Of the Laetolil Beds carnivorans recovered by the German expedition under the direction of Kohl-Larsen (described in Kohl-Larsen [1943]), only a skull and left horizontal mandibular ramus of *M. palaeoserengetensis*, Garussi 2/39, were figured by Dietrich (1942, Plate IV, figs. 31 and 36).

Some 20 years later, Petter (1963) published a study of the "viverrids" (= Viverridae and Herpestidae) of Laetoli. In this work, Petter reassigned *M. palaeoserengetensis* and *M. palaeogracilis* to *Herpestes* and described a new species of herpestid, *Mungos dietrichi*. In Petter's conception, *H. palaeoserengetensis* is based on the skull illustrated by Dietrich (1942, Pl. IV, fig. 31), whereas *M. dietrichi* is based on the mandible that Dietrich associated with the skull and illustrated in his Pl. IV, fig. 36. In addition, Petter (1963) suggested the presence of a second species of *Mungos* on the basis of a skull fragment recovered in 1959 by Louis and Mary Leakey, but she later reassigned this specimen to *M. dietrichi* (Petter 1987). A second new species described by Petter (1963) is the very large viverrid *Viverra leakeyi*, one of a number of extinct viverrids that were considerably larger than any living member of the family.

Collections at Laetoli by teams led by Mary Leakey in 1975–1981 (Leakey and Harris 1987) recovered large quantities of material, including nearly 600 specimens assigned to the Carnivora. These specimens were described by Petter (1987) (Herpestidae, Viverridae, Mustelidae, and two species

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of Canidae) and Barry (1987) (Hyaenidae, Felidae, and remaining Canidae). The study by Petter (1987) constituted a revision of her previous work on the small carnivorans of Laetoli, which had been based almost entirely on the material collected by the Kohl-Larsen expeditions. Amongst the more important revisions in this work was reassigning *Herpestes palaeogracilis* to the genus *Helogale*. The study by Barry (1987) was the first detailed analysis of large carnivorans from Laetoli and one of the first studies of early Pliocene large carnivorans of eastern Africa.

Although no new species-level taxa were described by Petter (1987) or Barry (1987), these studies did add numerous carnivoran taxa to the Laetoli fauna. Since the publications of Petter (1987) and Barry (1987), some minor revisions of the Laetoli carnivorans have taken place. Petter and Howell (1989) redescribed the *Crocuta* n. sp. of Barry (1987) and named it *Crocuta dietrichi*. Turner (1990) reassigned the *Leo* (=*Panthera*) aff. *gombaszoegensis* to *Panthera leo*, and Werdelin and Lewis (2001) reassigned the *Megantereon* sp. material from Laetoli to *Dinofelis petteri*. Recently, Hemmer et al. (2004) suggested that the *Panthera* cf. *pardus* from Laetoli shows affinities with *Puma pardoides* from the Pliocene of Eurasia and was interpreted by them as a primitive cougar rather than as a leopard. Most recently, Werdelin and Lewis (2005), in their review of eastern African Carnivora, implicitly revised the carnivoran faunal list from Laetoli. The justification for this revision is provided herein.

Material and Methods

Laetoli carnivorans are housed in a number of institutions. The material collected by the Kohl-Larsen expeditions in the 1930s is housed in the Museum für Naturkunde, Berlin, Germany. Material collected in the 1950s by occasional expeditions and by the Mary Leakey expeditions of 1975–1982 is housed in the Kenya National Museums, Nairobi, with a very small number housed in the Natural History Museum, London. Material collected by the Eyasi Plateau Research Project directed by Terry Harrison is housed in the National Museum of Tanzania, Dar es Salaam. We have studied all this material in preparation for writing this chapter.

The carnivoran material from Laetoli is extensive and currently stands at 936 numbered specimens (excluding the material housed in Berlin and London). Most of these are fragmentary, rendering species-level identification difficult. A total of 496 of these specimens are cranial and/or dental, and these will form the focus of this contribution. Isolated, fragmentary postcranial bones are difficult to identify, and this will here be attempted only in special cases. Some postcrania are associated with craniodental material, especially in the case of the smaller carnivorans, which in many cases are known from partial skeletons.

Primary identifications have been based on visual inspection in the field and laboratory, complemented whenever possible with quantitative analysis. These analyses have been confined to bivariate methods, as the fragmentary nature of the material makes multivariate analysis impractical.

In the following, material from pre-1975 Leakey expeditions has the prefix "LIT," and material from the 1975–1981 expeditions is prefixed "LAET." In both cases, the first two digits indicate the year of recovery (except as noted). Material from the Eyasi Plateau Research Project has the prefix "EP," and the last two digits indicate the year of recovery. Other catalog number prefixes are "MB" (Museum für Naturkunde, Humboldt Universität, Berlin) and "NHM" (The Natural History Museum, London).

In Tables 8.1–8.8, the following abbreviations are used: L, tooth length; W, tooth width; c, lower canine; p and P, lower and upper premolars, respectively; and m and M, lower and upper molars, respectively. Special measurements are as follows: Lpp4, length of main cusp of p4; Ltm1, length of trigonid of m1; LeP4, buccal length of P4; LiP4, lingual length of P4 (including protocone); WaP4, anterior width of P4; WblP4, width of anterior part of metastyle of P4; LpP4, length of paracone of P4; LmP4, length of metastyle of P4; C-C, width of snout between lateral sides of canines; P-P, width of palate between buccal sides of P4 metastyle; IOB, minimum interorbital width; POC, minimum postorbital constriction width; and ZB, maximum width of zygomatic arch.

Systematic Paleontology

Order Carnivora Bowdich, 1821

Family Canidae Fischer, 1817

The Canidae are the least well known of the larger carnivorans in the fossil record of Africa. They are present in most faunas but are usually represented by a smaller number of specimens than, e.g., Hyaenidae or Felidae. It may be that the favored habitats of the majority of African Canidae are less well represented in the fossil record than those of other carnivoran families. Nevertheless, it is likely Africa holds a key position in the fossil record of Canidae, since the currently oldest published *Canis* is from this continent (Werdelin and Lewis 2000). Metric data for Laetoli Canidae are given in Tables 8.1 and 8.2.

Table 8.1 Measurements of the lower dentition of Laetoli Canidae

Catalog no.	Taxon	Lp1	Wp1	Lp2	Wp2	Lp3	Wp3	Lp4	Wp4	Lm1	Wm1	Ltm1	Lm2	Wm2
LAET 75-3522	?*Nyctereutes barryi*	3.9	2.6	5.9	2.9	7.1	3.1	8.5	3.9	14.2	6.4	9.4	8.1	6.0
EP 1319/98	?*Nyctereutes barryi*									16.0	6.4	11.4		
EP 227/05	?*Nyctereutes barryi*							7.7	4.0	13.7	6.5	9.6		
EP 286/05	?*Nyctereutes barryi*					6.5	2.8							
EP 597/01	?*Nyctereutes barryi*									13.9	6.5	9.4		
EP 892/05	?*Nyctereutes barryi*					7.6	3.6							
LAET 74-249	?*Nyctereutes barryi*									14.4	6.2			
LAET 76-3844	?*Nyctereutes barryi*					6.6	3.2							
EP 2431/03	cf. *Canis* sp. A							11.6	5.3					
EP 2126/00	aff. *Otocyon* sp.	2.4	2.0	5.0	2.8	5.6	2.7	6.1	3.2					

For explanation of abbreviations see Material and Methods

Table 8.2 Measurements of the upper dentition of Laetoli Canidae

Catalog no.	Taxon	LP1	WP1	LP2	WP2	LP3	WP3	LeP4	LiP4	WaP4	WblP4	LpP4	LmP4	LM1	WM1	LM2	WM2
LAET 75-3522	?*Nyctereutes barryi*					7.4	3.2	12.4	12.8	7.0	4.8	6.5	5.1	10.5	11.5	6.4	9.0
EP 1047/98	cf. *Canis* sp. A	4.9	3.3	10.9	5.7												
EP 437a/98	cf. *Canis* sp. A							12.9	13.6	6.6	5.5	7.7	4.9	9.3	13.3		
EP 437c/98	cf. *Canis* sp. A													10.6	14.4	6.8	11.7
EP 437b/98	cf. *Canis* sp. A													10.7	14.9		
EP 1245/01	aff. *Otocyon* sp.													8.2	9.1		
EP 208/01	aff. *Otocyon* sp.					6.3	2.5	9.1	9.6	5.0	4.1	4.6	3.5				

For explanation of abbreviations see Material and Methods

Table 8.3 Measurements of the lower dentition of Herpestidae, Viverridae, and Mustelidae from Laetoli

Catalog number	Taxon	Lp2	Wp2	Lp3	Wp3	Lp4	Wp4	Lm1	Wm1
LAET 78-5346	*Herpestes palaeoserengetensis*	4.4	2.2	4.9	2.1	5.9	2.8		
EP 818/98	*Herpestes palaeoserengetensis*			4.7	2.3	5.4	2.6	6.2	3.6
EP 561/00	*Herpestes palaeoserengetensis*					4.8	2.6	5.3	2.9
EP 270/000	*Herpestes palaeoserengetensis*								
EP 042/04	*Herpestes palaeoserengetensis*			3.3	2.0	4.5	2.5		
EP 890/05	*Herpestes palaeoserengetensis*	4.0	1.9						
LAET 75-2368	*Herpestes ichneumon*							7.6	
LAET 75-1959	*Herpestes ichneumon*					7.3			
LAET 74-289	*Herpestes ichneumon*	4.9	2.5	6.3	3.2		3.6	8.1	4.5
EP 1169/05	*Herpestes ichneumon*	4.4	2.7		2.5	5.3	3.0	7.5	4.2
LAET 77-4570	*Galerella* sp.	3.9	2.0	4.4	2.2		2.6	5.9	3.5
LAET 75-2722	*Galerella* sp.	3.8	2.0	4.5	2.2				
LAET 78-4691	*Galerella* sp.	3.9	2.1						
LAET 78-4955a, b	*Galerella* sp.	3.6	1.9	4.1	2.2		2.7		
LAET 75-3340	*Galerella* sp.							6.2	3.4
LAET 78-5298a, b	*Helogale palaeogracilis*				1.6	3.9	2.0		2.4
LAET 75-2807a, b	*Helogale palaeogracilis*	2.6	1.3	2.8	1.5	3.4	2.0	4.3	2.1
LAET 78-5295	*Helogale palaeogracilis*			3.0	1.6	3.7	2.1		
LAET 78-4980	*Helogale palaeogracilis*	2.6	1.3		1.5				
LAET 78-4736	*Helogale palaeogracilis*					3.7	2.1		
LAET 75-3616	*Helogale palaeogracilis*			3.1	1.4		2.1	4.4	2.5
LIT 59/359	*Helogale palaeogracilis*			2.9	1.6	3.3	2.0	4.1	2.3
LAET 75-3565	*Helogale palaeogracilis*					4.1	2.2	4.5	2.7
LAET 75-940	*Helogale palaeogracilis*								
LAET 75-2997	*Helogale palaeogracilis*		1.4		1.7	3.7	2.1		
LAET 75-3368a	*Helogale palaeogracilis*	2.7	1.2						
LAET 76-3973	*Helogale palaeogracilis*	2.7	1.4	2.9	1.7	3.5	2.1		
EP 015/98	*Helogale palaeogracilis*					3.6	2.1	4.5	2.7
EP 436/98	*Helogale palaeogracilis*	1.9	1.5	3.3	1.7				
EP 1500/98	*Helogale palaeogracilis*					3.8	1.8	4.5	2.8
EP 466/00	*Helogale palaeogracilis*					3.9	2.0	4.7	2.8
EP 531/00	*Helogale palaeogracilis*					3.6	2.0		
EP 1787/00	*Helogale palaeogracilis*	2.8	1.8	3.7	2.1				
EP 1790/00	*Helogale palaeogracilis*			2.9	1.7				
EP 1874/00	*Helogale palaeogracilis*					3.8	1.9	5.1	2.4
EP 2577/00	*Helogale palaeogracilis*	2.4	1.6	2.9	1.6	3.7	2.1		
EP 2887/00	*Helogale palaeogracilis*					3.3	2.0	3.8	2.5
EP 2888/00	*Helogale palaeogracilis*					3.4	2.0		
EP 4167/00	*Helogale palaeogracilis*			3.1	1.7	3.5	2.2		
EP 4168/00	*Helogale palaeogracilis*							3.8	2.5
EP 035/01	*Helogale palaeogracilis*					3.4	2.3	4.0	2.6

(continued)

Table 8.3 (continued)

Catalog number	Taxon	Lp2	Wp2	Lp3	Wp3	Lp4	Wp4	Lm1	Wm1
EP 348/01	*Helogale palaeogracilis*			3.2	2.1	3.3	2.2	4.0	2.7
EP 467/01	*Helogale palaeogracilis*			2.6	1.7				
EP 636/01	*Helogale palaeogracilis*							4.0	2.4
EP 642/01	*Helogale palaeogracilis*					3.4	1.8		
EP 390/03	*Helogale palaeogracilis*			2.9	1.8				
EP 770/03	*Helogale palaeogracilis*			3.9	1.8				
EP 873/03	*Helogale palaeogracilis*	2.7	1.6	3.2	1.8				
EP 985/03	*Helogale palaeogracilis*	2.8	1.6	3.2	1.8	3.6	2.2		
EP 2430/03	*Helogale palaeogracilis*	2.9	1.7	3.1	1.7	3.6	2.3	5.0	2.7
EP 041/04	*Helogale palaeogracilis*			3.0	1.6	3.7	1.9	4.5	2.5
EP 993/04	*Helogale palaeogracilis*	3.2	1.9	3.3	1.7	3.7	2.3	4.2	2.7
EP 1456/04	*Helogale palaeogracilis*			3.6	2.3	3.6	2.1		
EP 1709/04	*Helogale palaeogracilis*	2.9	1.4	3.0	1.6				
EP 118/05	*Helogale palaeogracilis*				1.4	3.3	1.7	3.9	2.6
EP 1224/05	*Helogale palaeogracilis*	2.4	1.5	2.8	1.5	3.5	2.3		
EP 3858a/00	*Helogale palaeogracilis*			2.6	1.5				
EP 3858b/00	*Helogale palaeogracilis*							4.5	2.6
EP 1097/05	*Helogale palaeogracilis*	2.8	1.3						
LAET 75-3334	*Helogale* cf. *palaeogracilis*								
LAET 75-1974	*Helogale* cf. *palaeogracilis*				1.4				
EP 1324/04	*Helogale* cf. *palaeogracilis*					4.2	2.2		
LAET 75-3741	*Mungos dietrichi*								
LAET 75-2769	*Mungos dietrichi*			4.4	2.8		3.6		
LAET 75-3072	*Mungos dietrichi*	3.8	2.3	4.5	2.8	5.5	3.6	5.6	4.0
LAET 77-4571	*Mungos dietrichi*					4.9	3.2	5.3	3.6
EP 1217/03	*Mungos dietrichi*					6.0	3.6	5.7	
LAET 75-1923	*Mungos* sp. nov.?						4.1	5.6	4.2
EP 544/01	*Mungos* sp. nov.?							5.2	4.0
LAET 78-5315	*Genetta* sp.							6.9	4.0
EP 389/03	*Genetta* sp.		1.8	4.7	1.8				
LAET 75-2661	aff. Viverridae								
EP 1140/01	*Propoecilogale bolti*							5.1	2.1
EP 523/04	Mustelidae indet.							6.2	3.0

For explanation of abbreviations see Material and Methods

Table 8.4 Measurements of the upper dentition and cranium of Herpestidae, Viverridae, and Mustelidae from Laetoli

Catalog number	Taxon	LP3	WP3	LP4	WP4	C-C	P-P	IOB	POC	ZB
LAET 78-5435a, b	*Herpestes palaeoserengetensis*	5.2	3.5	7.6	5.3	15.1	25.2	16.4	13.3	44.5
LAET 78-5286	*Herpestes palaeoserengetensis*			7.5	4.9					
LAET 76-3235	*Herpestes palaeoserengetensis*	5.1	3.9	7.6	5.0					
EP 270/00	*Herpestes palaeoserengetensis*	5.2	3.4	7.6	4.8					
LAET 75-2807a, b	*Helogale palaeogracilis*	3.1	2.2	4.4	3.4	9.4	16.7	10.9	10.0	
LAET 75-2994	*Helogale palaeogracilis*	3.5	2.5							
LAET 75-2503	*Helogale palaeogracilis*			4.8	3.7					
LAET 75-3565	*Helogale palaeogracilis*									
LAET 75-940	*Helogale palaeogracilis*	3.2	2.5	4.6	3.9					
LAET 75-3741	*Mungos dietrichi*			5.0	5.9					

For explanation of abbreviations see Material and Methods

Table 8.5 Measurements of the lower dentition of Laetoli Hyaenidae

Catalog no.	Species	Lci	Wci	Lp2	Wp2	Lp3	Wp3	Lp4	Wp4	Lpp4	Lm1	Wm1	Ltm1
LAET 76-3970	*Crocuta dietrichi*					17.9	12.5		12.0	10.9			
LAET 74-149	*Crocuta dietrichi*					17.1	11.3						
LAET 75-2953	*Crocuta dietrichi*					17.8	12.6	20.7	12.4	11.2	26.6	12.2	22.7
LAET 76-3951	*Crocuta dietrichi*			12.2	8.0	17.6	11.0	19.8	11.5	10.4			
LAET 78-5107	*Crocuta dietrichi*			14.4	8.6	17.9	12.3	19.8	12.5				
LAET 77-5370	*Crocuta dietrichi*					17.7	12.3						
EP 1067/04	*Crocuta dietrichi*			12.6	8.7	17.6	11.5						
EP 1390/05	*Crocuta dietrichi*										23.4	10.0	20.7
EP 395/98	*Parahyaena howelli*					19.1	12.5						
EP 463/01	*Parahyaena howelli*	13.8		15.0	8.9								
EP 829/00	*Parahyaena howelli*	13.3	10.7	14.5	9.9	19.7	12.8						
KK 82-58	*Parahyaena howelli*	14.0	12.3	13.4	7.7	18.5	10.7	20.4	10.7	10.2	23.7	9.5	19.4
LAET 75-3338	*Ikelohyaena* cf. *I. abronia*			12.1	6.5		7.9		8.5			8.0	13.9
LAET 75-1849	*Ikelohyaena* cf. *I. abronia*							15.4	8.7				

For explanation of abbreviations see Material and Methods

Table 8.6 Measurements of the upper dentition of Laetoli Hyaenidae

Catalog no.	Species	LCs	WCs	LP1	LP2	WP2	LP3	WP3	LP4	WaP4	WblP4	LpP4	LmP4
LAET 74-185	*Crocuta dietrichi*			5.3	14.1	9.5	18.9	12.9		15.9	9.9	11.4	
EP 1067/04	*Crocuta dietrichi*												
LAET 76-4092	*Parahyaena howelli*						20.7	14.1					
LAET 76-4008	*Parahyaena howelli*				12.6	7.8			29.9	15.7	9.8	10.1	12.9
KK 82-58	*Parahyaena howelli*				15.2	8.8	20.4	12.8	30.2	15.7	9.1	11.1	11.3
LIT 59/465	*Ikelohyaena* cf. *I. abronia*						15.9	9.3		13.5			
EP 1046/98	*Ikelohyaena* cf. *I. abronia*				14.6	9.1	20.6	13.2		18.7	10.6	13.1	
EP 1218/03	*Ikelohyaena* cf. *I. abronia*	11.4	7.9		12.2	7.7							
LAET 75-494	*Lycyaenops* cf. *L. silberbergi*				19.1	11.0							

For explanation of abbreviations see Material and Methods

Table 8.7 Measurements of the lower dentition of Laetoli Felidae

Catalog no.	Taxon	Lp3	Wp3	Lp4	Wp4	Lpp4	Lm1	Wm1	Ltm1
EP 1333/98	*Panthera* sp. aff. *P. leo*						27.6	13.1	27.0
LAET 78-5122	*Panthera* sp. cf. *P. pardus*	12.8	7.2	17.1	8.6				
LAET 75-537	*Panthera* sp. cf. *P. pardus*	10.9	5.6	14.8	7.1	7.8	16.3	7.6	
EP 065/99	*Panthera* sp. cf. *P. pardus*	11.5	5.9						
EP 1622/00	*Panthera* sp. cf. *P. pardus*			16.6	8.6		18.9	8.5	
EP 1621/00	*Acinonyx* sp.						14.4	6.6	13.6
EP 927/01	*Acinonyx* sp.	13.0	7.1	15.8	8.0				
LAET 75-991	*Caracal* sp. or *Leptailurus* sp.	6.5	3.3	8.4	3.8	4.5	10.2	4.3	
EP 093/04	*Caracal* sp. or *Leptailurus* sp.			8.1	3.9				
EP 158/00	*Caracal* sp. or *Leptailurus* sp.	7.3	4.1						
EP 3934/00	*Caracal* sp. or *Leptailurus* sp.	6.6		8.7			9.9		
EP 119/01	*Felis* sp.	5.8	2.3						
EP 120/01	*Felis* sp.			6.8	3.3				

For explanation of abbreviations see Material and Methods

Table 8.8 Measurements of the upper dentition of Laetoli Felidae

Catalog no.	Taxon	LP3	WP3	LP4	WaP4	WM1
N'Garussi 1959	*Panthera* sp. aff. *P. leo*	24.9	13.2	35.5	19.9	12.7

For explanation of abbreviations see Material and Methods

Genus Nyctereutes *Temminck, 1838*

The genus *Nyctereutes*, raccoon dogs, is relatively well known in the Plio-Pleistocene of Eurasia, with a number of identified species (e.g., Tedford and Qiu 1991). In Africa the genus, which is absent from the modern fauna, is much more rare, with the only occurrences apart from the present one being from Ahl al Oughlam in Morocco and Kromdraai and Elandsfontein in South Africa (Ficcarelli et al. 1984; Geraads 1997).

?*Nyctereutes barryi* sp. nov. (Fig. 8.1)

Holotype: LAET 75-3522 (Fig. 8.1; Barry 1987, fig. 7.8 [a, b as LAET 75-3562b]), mandibles and cranial fragment with left i2–m1, m2 alveolus, right i2–p1, p4 alveolus, m1–m2, left I1–C, P1 and P2 alveoli, P3–M1, right M1, right manus (Laetolil Beds, upper unit, Loc. 10W, between Tuff 3 and 3 m below Tuff 1).

Synonymy: cf. *Canis brevirostris* Barry, 1987

Diagnosis: Medium-sized Canidae; premolars set close together, with no diastemata between them; M1 nearly rectangular in occlusal view; paracone and metacone of M1 separated from buccal margin of tooth by a stylar shelf; para- and metacristae of M1 strongly developed; hypocone smaller than protocone and crest-like; postprotocrista strongly developed; m2 relatively large; m1 and m2 nearly equal in width; transverse crest uniting m1 hypoconid and entoconid lacking; small paraconid present on m2.

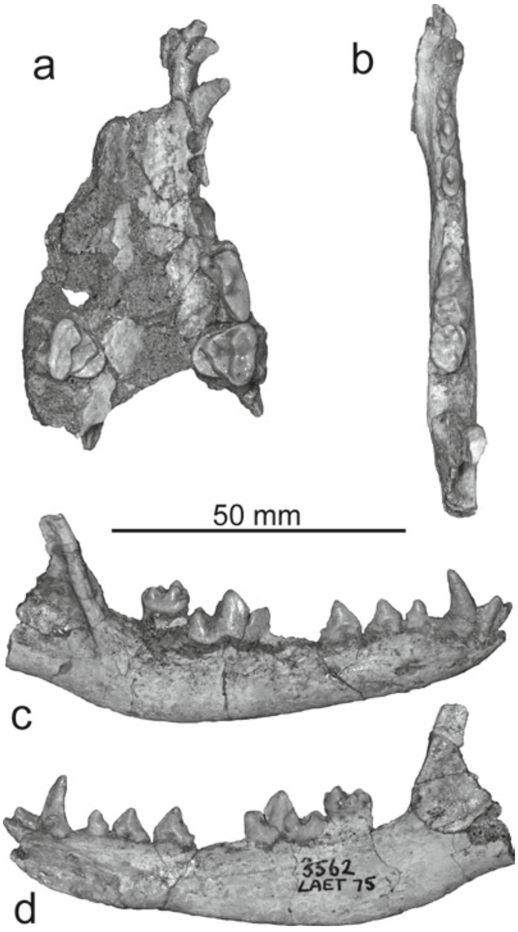

Fig. 8.1 ?*Nyctereutes barryi*, LAET 75-3522 (holotype). (**a**) Cranial fragment in ventral view. (**b**–**d**) Right mandibular ramus (labeled LAET 75-3562) in (**b**) occlusal, (**c**) buccal, and (**d**) lingual view

Derivation of name: After Dr. John Barry in recognition of his major contributions to the study of African carnivores.

Additional specimens: Laetolil Beds, upper unit: LAET 74-249, right mandible fragment with p4–m1, left m1; LAET 76-3844, right mandible fragment with p3 and m1; LAET 75-3108, left edentulous mandible fragment; LAET 78-5251, mandible fragment with c, alveoli for p1–m2; LAET 78-5385, right mandible fragment with roots of p1–p3, broken p4, alveoli of m1–m3; EP 227/05, left mandible fragment with posterior root of p3, p4–m1; EP 597/01, left mandible fragment with m1; EP 1319/98, isolated right m1; ?EP 1765/03, left mandible fragment with roots of p2 and p3, anterior root of p4; EP 286/05, left mandible fragment with broken p2 and p3; EP 892/05, isolated left p2 or p3; ?EP 1049/98, broken right M1; EP 2238/00, left m1 talonid fragment.

Description: This composite description will for the most part be based on LAET 75-3522, just as was the case in Barry (1987). Despite the recovery of a number of new specimens referable to this species, this specimen remains by far the best preserved. In fact, the cranial fragment and upper dentition of this specimen are still the only definite examples of these features, as EP 1049/98 can only tentatively be assigned to this species.

The preserved incisors, I2 and I3, are simple, conical teeth with no caniniform development. Neither has a lingual accessory cusp, but I3 has a small cingulum on its mediolingual corner. The canine, although missing the tip, is short and relatively straight, with distinct mesial and distal crests. There is a short (ca. 4 mm) diastema between I3 and C.

The alveolus for P1 is large and set directly behind the canine. It is followed immediately by the two alveoli for P2, of which the latter is damaged, so their relative sizes cannot be determined accurately. Both of these teeth must have been relatively large. The P3 appears to be of about the same size as P2. It is a simple tooth, lacking mesial and distal accessory cusps. The main cusp is set slightly mesial to the midline, between the mesial and distal roots. The posterior margin of the cusp is somewhat crestlike and distinctly concave. The distal end of the tooth is slightly elongated. The P4 is robust. The mesiobuccal corner is large and rounded. The paracone is tall, with a straight mesial margin. The preparacrista extends to the buccal margin of the small protocone. The postparacrista leads to a shallow carnassial notch, followed by an elongated metastyle. There is a small lingual cingulum at the base of the metastyle.

The M1 is the most distinctive tooth in the upper jaw. The paracone and metacone are both low and separated from the buccal margin of the tooth by a stylar shelf bounded buccally by a strong cingulum. The para- and metacristae are very strongly developed, forming a nearly continuous crest from the mesiobuccal corner of the tooth to the distal-most end. A similar development is seen in the pre- and postprotocristae. The protocone is set mesiolingually and is bordered mesially by a strong cingulum. The hypocone is smaller than the protocone and set distally about halfway between the buccal and lingual margins. Like the other cusps, the hypocone has strong pre- and postcristae. Thus, the center of the tooth between the cusps is surrounded by a nearly continuous crest. Distal to the protocone and lingual to the hypocone there is a broad, flat shelf. Overall, the tooth is relatively rectangular in occlusal view. Barry (1987) describes and figures a right M2 in this specimen. This tooth has subsequently been lost. He describes it as similar in general appearance to M1, but relatively broader and with a less developed buccal cingulum.

The cranium of this specimen is too damaged to provide any useful information on morphological structures, except to note that the anterior margin of the orbit lies above the anterior half of P4.

The lower dentition, with the exception of i2 and m3, is known in its entirety from LAET 75-3522. A number of other specimens, as listed above, provide information on variation.

The mandibular ramus is slender and low with a very weakly developed subangular lobe. The symphyseal rugosity is nearly horizontal and extends distally to the gap between p2 and p3. The masseteric fossa is deep, tall, and short. It extends mesially to about the posterior end of m3. There are two mental foramina: a larger one situated beneath p1 and p2 and a smaller one situated beneath the posterior root of p3. The cheek teeth are set close together with no or only very small diastemata between them.

The incisors are relatively procumbent, though this may in part be a postmortem effect. Both i2 and i3 are similar in general morphology. They are somewhat spatulate and lack distinct medial and lateral accessory cusps. The canine is short, robust, and relatively straight. It has distinct mesial and distal crests.

The p1 is a small, single-rooted tooth with a triangular main cusp that is set slightly anterior to the middle of the tooth. There are no mesial and distal accessory cusps, but there is a very small distal bump indicating an incipient cingulum. The p2 is similar to p1, but it is larger and two rooted. The p3 is similar to p2 and only slightly larger. The p4 is slightly larger than p3 and has a distinct, crestlike distal accessory cusp situated at the middle of the distal face of the main cusp. Posterior to this accessory cusp there is a small cingular cusp.

The lower carnassial is stout. The trigonid constitutes about 3/5 of the total length of the tooth. The paraconid is short and low, and the protoconid is longer and taller. The postprotocristid is strongly developed and meets the metacristid at a shallow notch. The metaconid is low and blunt yet relatively large for a canid. It is about equal in height to the well-developed hypoconid. The latter is connected to the trigonid through a strong cristid obliqua, which runs mesially and slightly lingually from the hypoconid and ends at a shallow postvallid notch. The entoconid is considerably lower and smaller than the hypoconid. There is no transverse crest connecting the two talonid cusps. The m2 is large and nearly equal in width to the m1. There is a small paraconid at the mesial end of the tooth. Mesiobuccal to this, there is a short cingulum shelf. The paraconid and

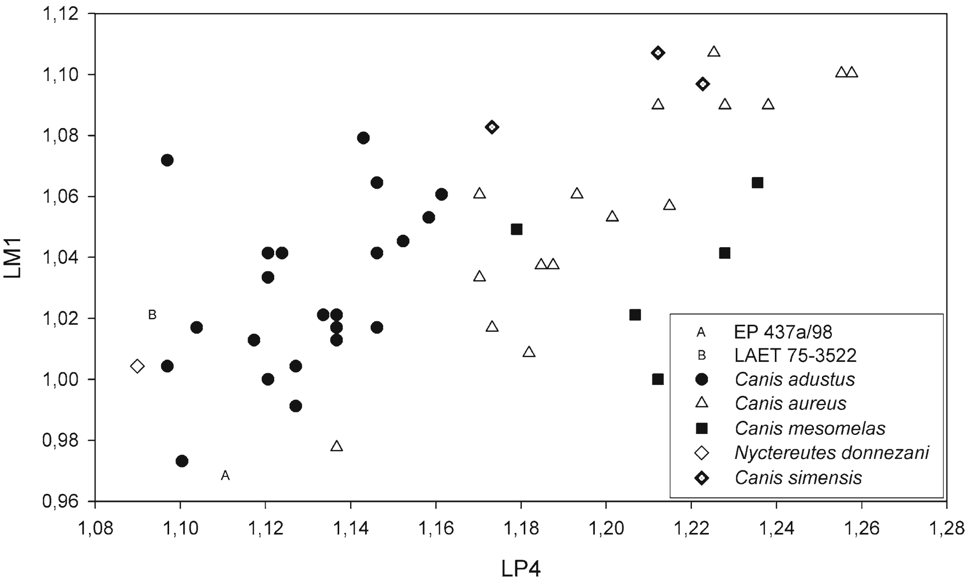

Fig. 8.2 Bivariate diagram of lengths of P4 and M1 in selected Canidae. The relative lengths of these teeth are similar in LAET 75-3522 and *N. donnezani*, a raccoon-dog from the Pliocene of Europe. The proportions of *C. adustus* are also similar, but the morphology is different. EP 437a/98 has a much shorter M1, similar to the situation in *C. aureus* and *C. mesomelas*

protoconid are connected by crests that are interrupted by a shallow notch. The protoconid is robust and triangular in occlusal view. The metaconid is similar in size to the protoconid. The hypoconid is large and connected to the talonid by a distinct prehypocristid. It is set nearly at the distobuccal corner of the tooth. The entoconid is composed of two small cuspids on the lingual margin of the tooth. It is followed distally by a low ridge that runs to the distal-most end of the tooth. The m3 is not present but was a small, single-rooted tooth.

Discussion: This taxon was extensively discussed by Barry (1987). It displays several features of the lower dentition that differentiate it from the *Canis* lineage, including the absence of a transverse crest uniting the hypoconid and entoconid on m1, the closely set premolars, and the relatively broad m1. However, it is in the features of the upper dentition that the differences are clearest. *?Nyctereutes barryi* has a relatively wide P4 with a very small, anteriorly placed protocone and an M1 that is very wide lingually, with a prominent protocone-hypocone crest. Other features that differentiate it from *Canis* are listed in Barry (1987: 240).

In a number of features, *?N. barryi* resembles primitive species of *Nyctereutes*. This is especially true of the upper dentition, which is quite similar in some respects to the primitive *N. tingi* from China (Tedford and Qiu 1991), though the molars of the Laetoli form appear more derived, especially in the subequal paracone and metacone, and are in some respects similar in morphology to the more derived *N. sinensis* (Tedford and Qiu 1991; Fig. 8.2). Like *N. tingii*, *?N. barryi* lacks the subangular lobe of the mandibular ramus characteristic of more derived species of *Nyctereutes*. Barry (1987) also records similarities between the Laetoli form and the European *N. donnezani* (Soria and Aguirre 1976), while noting that the latter is more derived in several features. *N. donnezani* is also more derived than *N. tingi*, and, if the generic attribution is valid, which remains somewhat uncertain, *?N. barryi* is morphologically intermediate between *N. tingi* and *N. donnezani* in the raccoon-dog lineage.

Genus ?Canis

The earliest definite record of *Canis* from Africa, or anywhere, is from South Turkwel at ca. 3.5 Ma (Werdelin and Lewis 2000). Thus, if the Laetoli material is demonstrated to belong to *Canis*, it could be the oldest of the genus on record. The later record of *Canis* in Africa is persistent but spotty, with limited material being found at many sites from the late Pliocene onwards.

cf. *Canis* sp. A (Fig. 8.3)

Specimens: Laetolil Beds, upper unit: LAET 77-4603, left mandible fragment with p3–p4, roots of p2, and anterior root of m1; EP 1047/98, left maxilla fragment with I2–C roots, P1–P2, P3 anterior alveolus; EP 2431/03, left mandible fragment with p4; EP 437a/98, right maxilla with P4–M1; EP 437c/98, left maxilla with M1–M2 (Fig. 8.3); EP 437b/98, right maxilla with P2–M2, cranial fragments.

Description: The mandibular ramus is quite robust and deep, with at least two mental foramina. The larger of the two is situated beneath p1 and the smaller beneath p2. The cheek teeth are set well apart, with distinct diastemata between them. Both p2 and p3 are relatively slender. The p4 appears more robust. The main cusp is set slightly mesial to the middle of the tooth. It is fairly tall, and its distal face has a low but long accessory cusp, followed by a distinct posterior cusplet and cingulum. The P4 is short, with a small, low protocone, a tall paracone, and a short, stout metastyle. The M1 is triangular rather than rectangular in occlusal view. The length/width relationship and its differences from ?*N. barryi* can be seen in Fig. 8.4. It has a low, blunt paracone, which is bounded mesiobuccally by a broad parastyle shelf. The metacone is also low and blunt. On its buccal side there is a broad metastyle shelf, though it is not as broad as the parastyle shelf. These two shelves may (EP 437a/98) or may not (EP 437c/98) be connected. None of the available specimens show the features of the protocone clearly, but it was seemingly robust. The M2 is similar in structure to M1, but smaller and relatively mesiodistally shorter; its metastyle shelf is smaller than in M1 and is connected to the parastyle shelf.

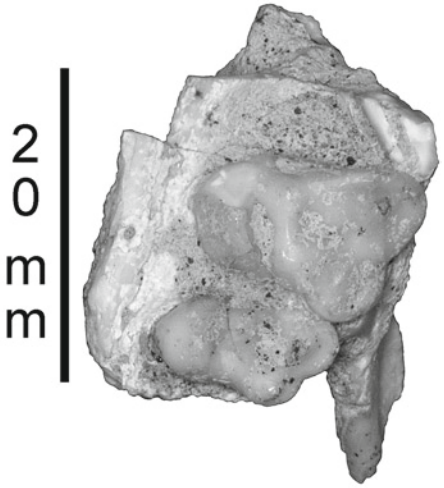

Fig. 8.3 cf. *Canis* sp. A, EP 437c/98. Left maxilla fragment in occlusal view

Discussion: These specimens are united in being roughly the size of a medium-large jackal; in having premolars that are widely spaced as in *Canis*, in contrast to the previous taxon; and in having upper molars that are quite different from those of *?N. barryi* and, again, more *Canis*-like. The p4 of LAET 77-4603 and EP 2431/03 are the size of a large jackal p4. The P4 and upper molars of the three specimens collected under the catalog number EP 437/98, on the other hand, are somewhat smaller (Fig. 8.4), and, if these specimens all belong to the same taxon, it is likely that there is a difference between it and modern jackals in the relative sizes of the premolars and molars. There are clear differences in a number of characters between this material and *?N. barryi*, and, although the fragmentary nature of the material makes it impossible at present to definitely assign it to *Canis*, the few characters available suggest that that is the most plausible generic allocation. There are

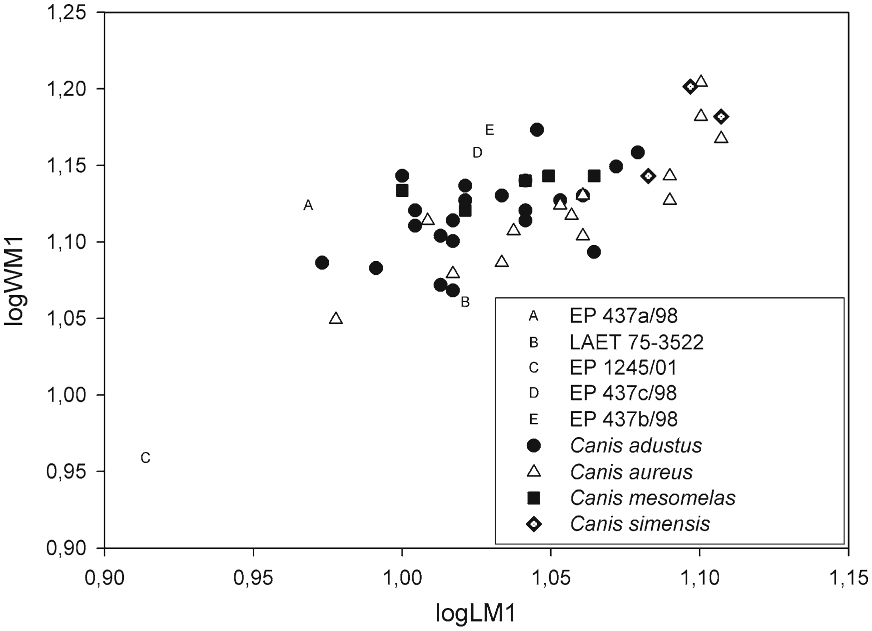

Fig. 8.4 Bivariate diagram of length and width of M1 in selected Canidae. The three specimens numbered EP 437/98 all have a shorter and relatively wider M1 than in modern *Canis* spp., while the M1 of LAET 75-3522 is relatively narrower. The much smaller EP 1245/01 is here referred to aff. *Otocyon* sp.

similarities in size and morphology to undescribed material of Canidae from Hadar (Werdelin and Lewis, unpublished), and a detailed comparison with this material may allow for a more specific determination than is presently possible.

cf. *Canis* sp. B (Fig. 8.5)

Specimens: **Laetolil Beds, upper unit**: LAET 78-4713 (Fig. 8.5; Barry 1987, fig. 7.7), isolated left m1 talonid; EP 2005/00, isolated right m1 talonid.

Description: Both specimens are broken posterior parts of lower carnassials. LAET 78-4713 preserves a larger part of the tooth but is more damaged than EP 2005/00. The protoconid is robust. As is normal in canids, the metaconid is quite low and set slightly distal to the protoconid. The hypoconid is large and has a cristid obliqua that runs mesially to the postvallid notch. The entoconid is very low, hardly more than a bump on the lingual margin of the tooth. It is connected to the hypoconid by a low crest that includes a blunt hypoconulid.

Discussion: Barry (1987) provides an extensive discussion of this taxon based on specimen LAET 78-4713. Specimen EP 2005/00 is nearly identical to LAET 78-4713 but is slightly more worn and preserved quite differently. Barry's (1987) discussion concerns the generic identity of the specimen, based on his belief that the morphology of the talonid, which lacks a true cristid obliqua and transverse crest uniting the hypoconid and entoconid (Barry 1987: 236), precludes allocation to *Canis*. However, canids in which the hypoconid is strongly developed and the entoconid weak seem often to have a cristid obliqua that is directed mesially rather than mesiolingually. Such is the case with the *Canis* sp. from South Turkwel (specimen KNM-ST 22822; Werdelin and Lewis 2000), a site that is roughly contemporaneous with the Upper Laetolil Beds. Since this is the oldest known *Canis*, as attested to by the transverse crest linking the hypoconid and entoconid, the mesially oriented cristid obliqua may perhaps be the primitive condition in this genus. The absence of the transverse crest is a more serious impediment to the assignment of LAET 78-4713 and EP 2005/00 to *Canis*. However, although an entoconid is present in both specimens, it is very low and is more of a distolingual ridge than a proper cusp. This reduction of the entoconid may also have obliterated the transverse crest. Thus, we find the arguments against placing these specimens in *Canis* weakened though still valid. For the time being, we prefer to place them in cf. *Canis* sp. to indicate our opinion of their probable affinities. Barry (1987) suggests that they belong to a form much larger than that represented by the previous taxon. We believe that this size difference is exaggerated, and, although it seems unlikely that *Canis* sp. A and *Canis* sp. B are the same taxon, we cannot definitively rule this out.

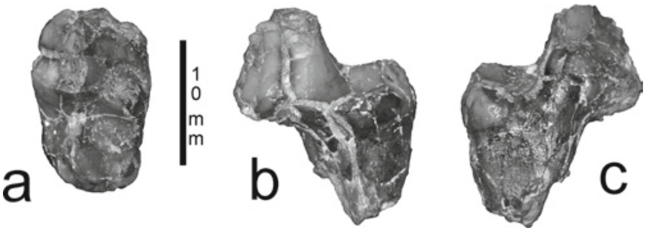

Fig. 8.5 cf. *Canis* sp. B, LAET 78-4713. Left m1 protoconid and talonid in (**a**) occlusal, (**b**) buccal, and (**c**) lingual view

Genus Otocyon *Müller, 1836*

The genus *Otocyon* appears late in the African fossil record, with its only appearance at Lainyamok in Kenya at ca. 300 ka (Potts and Deino 1995). An older record from Olduvai Bed I is referred to the doubtfully distinct genus *Prototocyon* (Petter 1973).

aff. *Otocyon* sp. (Fig. 8.6)

Specimens: Laetolil Beds, upper unit: LAET 75-1419 (Petter 1987: Plate 2, fig. 15), right mandible fragment with alveoli for p1–m3; LAET 75-2812, right distal tibia; LAET 75-3814, right radius lacking proximal end, right distal ulna fragment; LAET 76-3936 (Petter 1987: Plate 1, fig. 9), isolated left m2 or m3; EP 2126/00, right mandible fragment with root of c, p1–p4 (Fig. 8.6); EP 208/01, left maxilla fragment with C, separate fragment with P3–P4; EP 1245/01, isolated right M1; EP 1630/98, right dp4.

Description: The mandibular ramus is very slender. There are at least two mental foramina. The anterior, larger one lies beneath p1, while the posterior, smaller one lies beneath

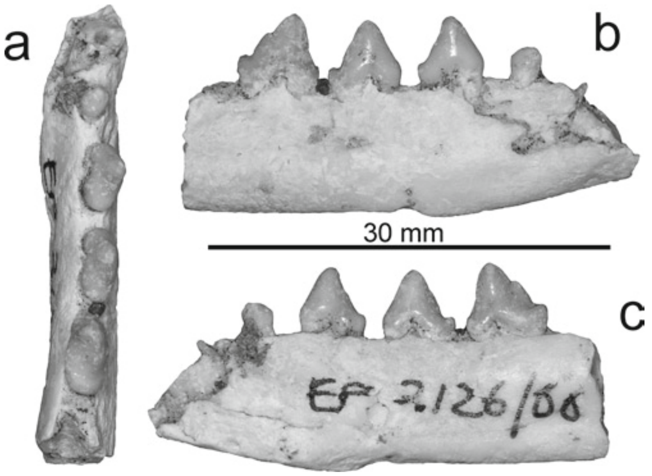

Fig. 8.6 aff. *Otocyon* sp., EP 2126/00. Right mandibular ramus in (**a**) occlusal, (**b**) buccal, and (**c**) lingual view

the posterior end of p3. In EP 2126/00, the latter foramen is double, with the posterior of the pair lying beneath the gap between p3 and p4. The symphysis is short, extending only as far distally as p2. The p1 is a small, single-rooted tooth that is separated from the lower canine by a short diastema. The p2 is a small tooth, triangular in lateral view, that is separated from p1 and p3 by gaps of 1–2 mm. The main and only cusp of p2 is set nearly at the middle of the tooth. The distal end of the tooth is slightly wider than the mesial end. The p3 is similar to p2 but has a small swelling on the distal edge of the main cusp and a distinct distal cusp at the base of the crown. The p4 is similar to the p2 and p3, but the swelling on the distal edge of the main cusp has here developed into a distinct, ridge-like accessory cusp. Distal to this is a cusp that lies at the base of the crown. The P3 is a slender, triangular tooth lacking mesial and distal accessory cusps but with a small cusp at the distal base of the crown. The P4 is short and relatively robust. The parastyle is small, whereas the protocone is relatively large and strong. There is a strong invagination in the middle of the mesial margin of the tooth. The paracone is tall and robust, and the metastyle is short and stout. There is a weak cingulum at the lingual side of the metastyle. The M1 is more or less rectangular in occlusal view, though the metastyle wing extends farther distally than the rest of the distal margin. The paracone is large and blunt. It is separated from the metacone by a distinct notch. The protocone is broad but low, and the center of the tooth is damaged and features are difficult to discern. The stylar shelf is narrow mesially and buccally but broadens considerably distal to the metacone.

Discussion: This material shows the presence at Laetoli of at least one species of small canid the size of a fox. All of the material is smaller than the homologous elements in jackals. The mandible fragment EP 2126/00 is slightly smaller than a jackal and has relatively short and widely spaced premolars, whereas the maxilla fragment EP 208/01 and the M1 EP 1245/01 are considerably smaller than a jackal (Fig. 8.7). These may represent different taxa or simply the sexes of a single species. The morphology of the lower premolars is strongly reminiscent of that of the bat-eared fox, *Otocyon*. The earliest currently known record of this lineage is *Prototocyon recki* from Olduvai Gorge Bed I (Pohle 1928; Petter 1973). At present, there is no reason to believe that more than one taxon is involved, and the Laetoli specimens may represent the earliest known member of the *Otocyon* lineage, which is currently considered the sister group to all other Vulpini (Lindblad-Toh et al. 2005).

Family Mustelidae Fischer, 1817

The fossil record of Mustelidae in Africa is uneven. Some Lutrinae are well represented, especially the lineage of giant bunodont forms referred to the Enhydrini (Morales and Pickford 2005). The *Mellivora* lineage is sporadically represented from the Late Miocene onwards. However, small Mustelidae, especially of the Plio-Pleistocene, are rare, being confined to a handful of records (Werdelin and Lewis 2005). Metric data for Laetoli Mustelidae are given in Tables 8.3 and 8.4.

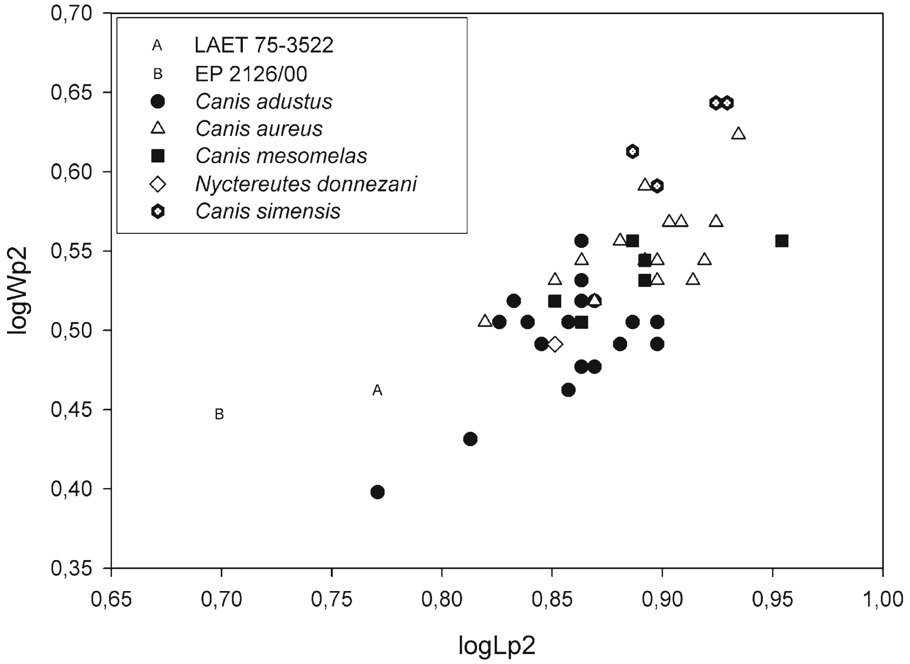

Fig. 8.7 Bivariate diagram of length and width of p2 in selected Canidae. The p2 of EP 2126/00 (aff. *Otocyon* sp.) is shorter and broader than in *Canis* spp. or ?*N. barryi*

Genus Prepoecilogale *Petter, 1987*

This genus is known only from Laetoli and from Bolt's Farm in South Africa. It is closely related to *Poecilogale* and *Ictonyx* (Petter 1987).

Prepoecilogale bolti (Cooke, 1985) (Fig. 8.8)

Specimens: Laetolil Beds, upper unit: LAET 75-1358 (Fig. 8.8; Petter 1987: Plate 1, fig. 3), left maxilla fragment with P3–P4, left premaxilla fragment with incisor, left mandible fragment with p4-m1, left calcaneum, skull fragment, vertebral fragments; LAET 74-248 (Petter 1987: Plate 1, figs. 4–7), maxilla fragment with C, P2–P3, left and right tympanic bullae, right humerus, distal left humerus, proximal right ulna, proximal right femur, distal right femur, proximal and distal right tibia, innominate fragment, left and right astragali, vertebral fragments; EP 634/03, left P4 metastyle; EP 466/01, left calcaneum. Ndolanya Beds, upper unit: EP 789/01, left calcaneum, EP 1140/01, right mandible fragment with m1–m2.

Description: The upper canine is robust and has an oval, nearly round cross-section. It is slightly curved. There is a diastema of just less than 1 mm to the P2, which is small and double-rooted. There is no mesial accessory cusp, and the main cusp is situated nearly at the mesial extremity of the tooth. The posterior shelf is long but lacks a cusp. There is a weak basal cingulum on the lingual side of the tooth. The P3 is a short tooth with small mesial and distal basal cusps. The main cusp is short, nearly symmetrical, and very tall and lies just anterior to the middle of the tooth. The tooth is surrounded by a moderate to weak cingulum. The P4 is slender. The protocone extends far mesial to the parastyle. The paracone is tall and trenchant and continues to the metastyle without a carnassial notch, as is normal in Mustelidae. The p4 is similar to P3 in being short and with a very tall, nearly symmetrical main cusp. This cusp has a very small accessory cusp on its distal face. There are low mesial and distal basal cusps and a strong buccal cingulum. The m1 has a short, low paraconid and a taller, longer protoconid. The metaconid is small and located buccal to the distal end of the protoconid. The talonid is short, with a trenchant hypoconid but no entoconid. The m2 is very small and round in occlusal view.

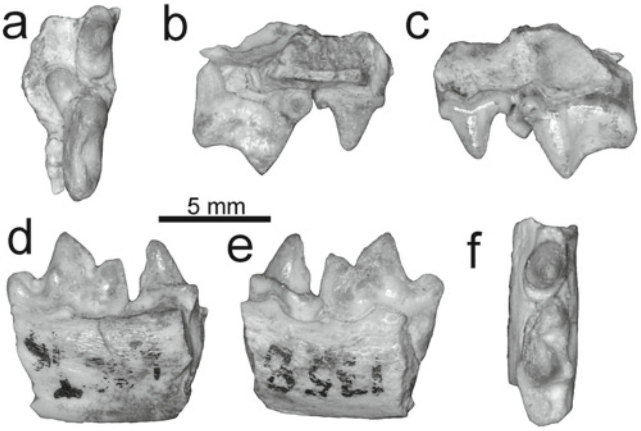

Fig. 8.8 *Prepoecilogale bolti*, LAET 75-1358. (**a–c**) Left maxilla fragment in (**a**) occlusal, (**b**) lingual, and (**c**) buccal view. (**d–f**) Left mandibular fragment in (**d**) lingual, (**e**) buccal, and (**f**) occlusal view

Discussion: This material all clearly represents a mustelid of very small size and is, as noted by Petter (1987), indistinguishable from "*Ictonyx*" *bolti* from Bolt's Farm (Cooke 1985). Small mustelids are exceedingly rare in the African post-Miocene fossil record. Apart from the present material, the only record is from Hadar, where several undescribed taxa of small mustelids have been found.

Prepoecilogale sp.

Specimens: Laetolil Beds, upper unit: EP 2889/00, broken left calcaneum. Ndolanya Beds, upper unit: EP 3324/00, right calcaneum.

Description: The postcranial specimens are typical mustelid in morphology but are not sufficient to definitively identify them as *P. bolti*.

Genus Mellivora *Storr, 1780*

Mellivora probably evolved in the latest Miocene from *Erokomellivora* or a similar form (Werdelin 2003a). The question of the distinction, if any, between *M. benfieldi* from, for example, Langebaanweg (Hendey 1974) and the extant *M. capensis* (Petter 1987) cannot be resolved here.

Mellivora sp.

Specimens: Laetolil Beds, upper unit: LAET 75-530 (Petter 1987: Plate 1, fig. 12 [as LAET 531]; Plate 2, fig. 8), postcranial fragments, including ribs, axis, cervical, thoracic, and lumbar vertebrae, sacrum, proximal and distal phalanges; LAET 78-5078, proximal radius.

Description: This material was described and discussed in detail by Petter, (1987), and this need not be repeated here as no new material of *Mellivora* has been recovered from Laetoli since then.

Tribe Aonyxini Sokolov, 1973

Unlike the Enhydrini, members of which are not present at Laetoli, Aonyxini is poorly represented in the African fossil record. Apart from the Laetoli record, the tribe is known only from some isolated elements from Ethiopia, Kenya, and South Africa.

Aonyxini gen. et sp. nov. (Fig. 8.9)

Specimens: Laetolil Beds, lower unit: KK 82-204, partial juvenile skeleton including maxilla fragment with C root, broken P3-M1, and posterior part of cranium (Fig. 8.9).

Description: The skeleton includes many individual bones but is very poorly preserved. Because the individual is a juvenile, the only diagnostic element is the maxilla fragment, so this description will be restricted to that fragment.

The canine is a rounded oval in occlusal view and lacks mesial and distal ridges or keels. The postcanine diastema is very short, no more than 2 mm. The P3 is very small and only slightly longer than it is wide. Its long axis is set somewhat at an angle to the tooth row. The P4 is rhomboid in occlusal view. The buccal side of the tooth is broken, but the outline remains, showing that the protocone shelf extends farther mesially than the paracone. The protocone itself is low. The distolingual shelf tapers gradually, and there is no distinct hypocone. The M1 has also been broken buccally. Its most prominent features are the strong marginal ridges on the lingual side of the tooth. The tooth is square in occlusal view, whereas other M1 of Lutrinae are, like the M1 of most Carnivora, wider than they are long.

Discussion: These fragments certainly record the presence of a species of lutrine mustelid at Laetoli. However, the exact relationships of the material remain obscure. The referral to Aonyxini is based on the combination of a long lingual shelf on the P4 and the absence of a hypocone. In Lutrini, the shelf normally extends only to the midpoint of the tooth or less, while in the Enhydrini a hypocone is present. However, the presence of only two upper premolars and the nearly square M1 are unique features within the Aonyxini (and, indeed, within the Lutrinae, as far as we are aware). At the very least, a new genus is indicated.

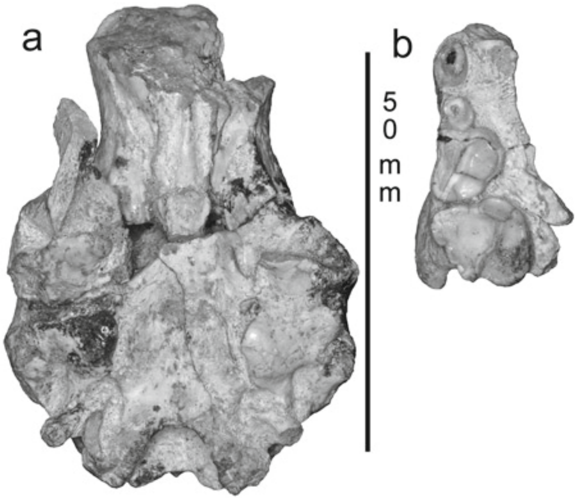

Fig. 8.9 Aonyxini gen. et sp. nov., KK 82-204. (**a**) Posterior cranial fragment in ventral view. (**b**) Right maxilla fragment in occlusal view

Mustelidae indet.

Specimens: Laetolil Beds, upper unit: EP 523/04, left mandible fragment with broken m1, alveolus for m2.

Description: The mandibular ramus is robust and tall, with a deeply excavated but in its preserved part dorsoventrally low masseteric fossa that extends approximately to the distal end of the m2 alveolus. The m1 is a slender tooth. The buccal trigonid cusps are set at a slight angle to the ramus. The presence or absence of a metaconid cannot be determined. The talonid is short, with a low, trenchant hypoconid and a small, distal entoconid. The m2 is single-rooted and slightly longer than it is wide.

Discussion: This specimen is morphologically very similar to *Mellivora* sp. but is smaller than any individual of *Mellivora* known to us. Therefore, we have left it as Mustelidae indet. for the time being.

Family Viverridae Gray, 1821

Viverridae is better known in the fossil record than Herpestidae, though there is considerable confusion regarding the identity of early forms in this family. The Stenoplesictinae, with a fossil record extending back into the European Oligocene, is generally considered the oldest subfamily within the Viverridae (Hunt 1998), although if it associated with the Percrocutidae, as suggested by some authors (Morales et al. 1998; Morales et al. 2003), this would have to be reassessed. In Africa, the genus *Herpestides*, positively identified as being within the Viverridae by Hunt (1991), is known from the early Miocene (Schmidt-Kittler 1987). Many members of the Viverridae from the fossil record of Africa are large forms, in many cases considerably larger than any viverrid alive today [e.g., Hunt (1996)]. Smaller viverrids have a much more restricted fossil record. In eastern Africa, smaller viverrids are known from Lothagam, Middle Awash Adu-Asa Fm., Kanapoi, Allia Bay, Omo Shungura Fm. Mb. B, and the Upper Burgi and Okote Mbs. at Koobi Fora, in addition to Laetoli (Haile-Selassie 2001; Werdelin 2003a, b). Metric data for Laetoli Viverridae are given in Tables 8.3 and 8.4.

Genus Viverra *Linnaeus, 1758*

Viverra is not well represented in the African fossil record. Two taxa are known, the Late Miocene *V. howelli* and the Late Miocene–Early Pliocene *V. leakeyi*, the latter of which is known from several localities in southern and eastern Africa (Petter 1963; Rook and Martinéz-Navarro 2004). Some authors place the latter species in the genus *Megaviverra* (Morales et al. 2005), but we prefer to keep it in the genus *Viverra* for reasons discussed elsewhere (Werdelin 2003a).

Viverra leakeyi Petter, 1963

Specimens: Laetolil Beds, upper unit: LIT 59-466, isolated C, P4, M1, M2 (holotype); LAET 75-2725 (Petter 1987: Plate 2, fig. 5), mandible fragment with p1.

Description: This material was described and discussed in detail by Petter (1963, 1987), and this need not be repeated here, as no new material of this taxon has been recovered from Laetoli.

Genus Genetta *Cuvier, 1817*

Genetta sp. has been recorded from a number of Miocene localities in Africa (e.g., Beni Mellal [Ginsburg 1977]), but in all these cases the referral to *Genetta* is doubtful. The oldest certain record is from Kanapoi, of a species close to the extant *G. genetta* (Werdelin 2003b). The latter is known from the early Pleistocene (Werdelin and Lewis 2005).

Genetta sp. (Fig. 8.10)

Specimens: Laetolil Beds, upper unit: LAET 78-5315, partial right mandible with m1 and alveolus for m2 (Fig. 8.10); EP 389/03, right mandible fragment with p1, broken p2, complete p3.

Description: The mandibular ramus is deep relative to the size of the teeth. There are two mental foramina; the mesial is situated beneath the diastema between p1 and p2, and the distal is situated beneath the distal root of p3. The p1 is a small, single-rooted tooth. It is directed mesially and dorsally and has a distinct distal accessory cusp posterior to the buccolingually compressed main cusp. Although the p2 is broken mesially, it is clear that it is separated from the p1 by a diastema of approximately 1 mm. The p2 has a trenchant accessory cusp on the distal cingulum. The p3 is tall and buccolingually compressed. It has a prominent mesial accessory cusp; a very tall, trenchant main cusp; and a large distal accessory cusp that is appressed to the distal face of the main cusp. Distal to this, the distal cingulum also bears a distinct cusp. The trigonid cusps of the carnassial are well developed and triangular in occlusal view, as is the trigonid itself. The protoconid is situated distobuccal to the paraconid, representing the buccal-most, and hence the widest, part of the tooth. Posterior to the paraconid and somewhat lingual to it is the metaconid. The buccal faces of the para- and protoconid are adapted for shearing, and their shearing blades meet at nearly right angles. The metaconid is lower and more conical than the other trigonid cusps. The talonid is much lower than the trigonid and forms a posterior ridge. The distobuccal portion of the talonid is damaged.

Fig. 8.10 *Genetta* sp., LAET 78-5315, right mandibular ramus in (**a**) buccal, (**b**) lingual, and (**c**) occlusal view

Discussion: The lower carnassial is reduced in size relative to that of *Herpestes*. This reduction is also seen in the modern genet, *G. genetta*, which, together with tooth morphology, supports generic attribution of LAET 78-5315 to *Genetta*. In addition, the m1 of this specimen and specimens of *H. ichneumon* are similar in morphology, but they differ in ramus morphology. The horizontal ramus of LAET 78-5315 is more slender and shallower below m1, as it is in modern genets, in comparison with the more massive ramus of *H. ichneumon*. The anterior premolars in EP 389/03 are comparable to those of modern genets and are likely to belong to the same taxon as LAET 78-5315.

The size and shape of the lower carnassial of LAET 78-5315 are similar to the extant viverrid species *G. genetta* (Fig. 8.11). The metaconid, however, is lower relative to the two other trigonid cusps in *G. genetta* than in LAET 78-5315.

aff. Viverridae

Specimens: Laetolil Beds, upper unit: LAET 75-2661, partial right m1.

Description: This partial right m1 preserves the paraconid, the mesiobuccal part of the protoconid, and the mesial root. The paraconid and buccal part of the protoconid make a shearing facet. The protoconid is taller than the paraconid.

Discussion: This specimen shows general viverrid characters, but the state of preservation does not allow for a more specific determination.

Family Herpestidae Bonaparte, 1845

The Herpestidae is the least-studied carnivoran family in Africa. Although known from records extending back to the early Miocene, the relationships between these earlier forms, such as *Kichechia* and *Legetetia*, and extant herpestids are not known. Laetoli is the source of by far the largest sample of herpestids in eastern Africa and plays a key role in understanding the modern herpestid fauna. Metric data for Laetoli Herpestidae are given in Tables 8.3 and 8.4.

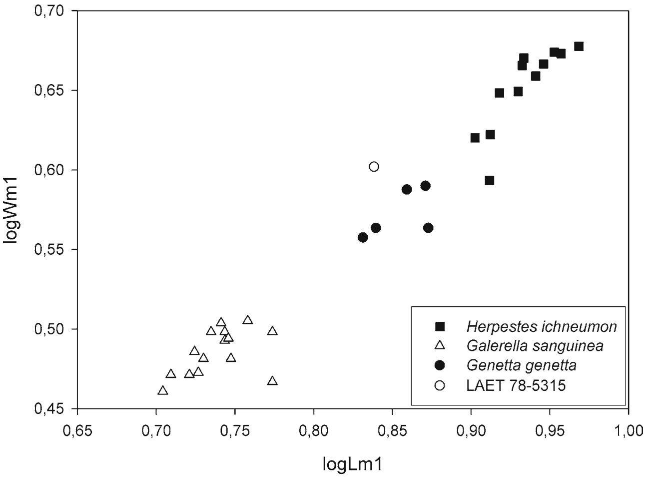

Fig. 8.11 Bivariate diagram of length and width of m1 in selected small Carnivora. The m1 of LAET 78-5315 closely resembles the m1 of *G. genetta* in proportions

Genus Herpestes *Illiger, 1811*

Herpestes has been reported from the Adu-Asa Fm., Middle Awash Valley, Ethiopia, by Haile-Selassie (2001). If this referral is correct, these are the oldest *Herpestes* specimens known. The genus is otherwise rare in the fossil record, being recognized only in the Denen Dora Mb. of the Hadar Fm., Ethiopia, and in Bed I of Olduvai, Tanzania (L.W., personal observation). In the modern African fauna, *Herpestes,* as used herein, is restricted to the Egyptian mongoose or ichneumon, *H. ichneumon*, which has a broad distribution across sub-Saharan Africa, except in the arid regions of southern and southwestern Africa. In the north, it extends along the Nile Valley but does not occur elsewhere in northern Africa (Kingdon 1997).

Herpestes palaeoserengetensis Dietrich, 1942 (Fig. 8.12)

Specimens: Laetolil Beds, upper unit: LAET 76-3235 (Petter 1987: Plate 7.1, fig. 8), partial left maxilla with P3–P4 and a lower tooth fragment in occlusion with P3 and P4;

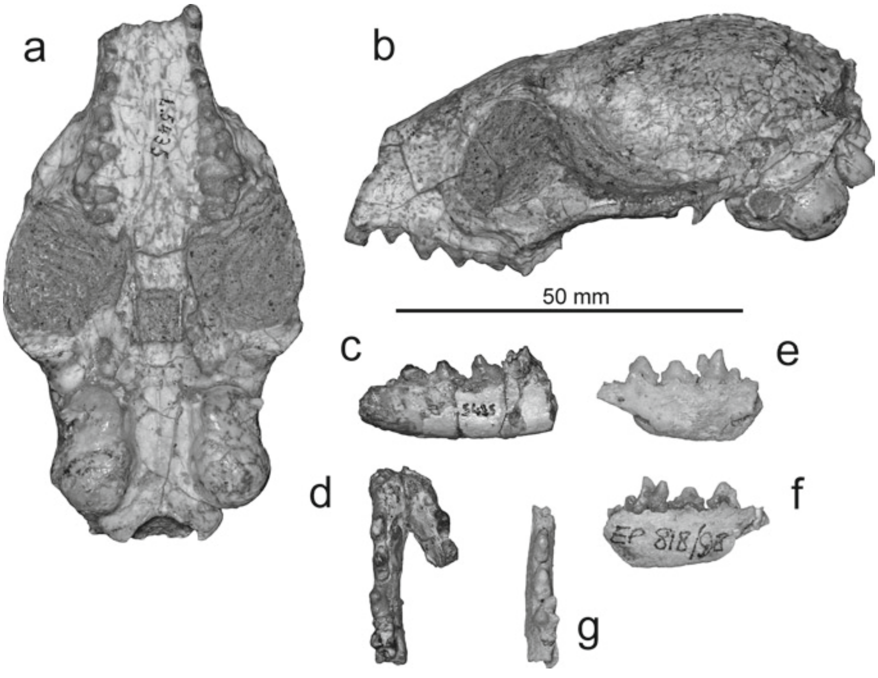

Fig. 8.12 *Herpestes palaeoserengetensis*. (**a-d**) LAET 78-5435; cranium in (**a**) ventral and (**b**) left lateral view; mandible fragment in (**c**) left lateral and (**d**) occlusal view. (**e–g**) EP 818/98; left mandibular ramus in (**e**) buccal, (**f**) lingual, and (**g**) occlusal view

LAET 78-5286, isolated left P4, mesiobuccal root broken; LAET 78-5346, partial left mandible with c, p2–p4 and alveolus for p1, all teeth more or less broken; LAET 78-5435 (Fig. 8.12a–d; Petter 1987: Plate 7.1, fig. 1), cranium (5435a) with right P1–M2 and left C–M2, and mandible fragments (5435b) with left p2–m1, p2 and m1 broken, and right p1–p3, p1 and p3 broken, and an additional mandible fragment with right m1–m2, both teeth in poor condition; EP 890/05, mandible fragments with left c, alveoli of p2–p4, right c–p2, alveoli of p3; EP 818/98 (Fig. 8.12e–g), mandible fragment with p3–m1; EP 561/00, left mandible and maxilla with P2–M1, c–m1 (still in occlusion), right mandible with broken p4–m2, left distal humerus, proximal ulna, radius lacking distal epiphysis, right distal humerus, left proximal humerus; EP 042/04, mandible fragment with p3–p4; EP 270/00, left and right C, left c, right P4 fragment, right mandible fragment with broken p4–m2 (in matrix), right maxilla fragment with P3–M1, right proximal tibia, three innominate fragments, right calcaneum, right astragalus, phalanx, podial, two tibia shaft fragments, distal tibia, left and right distal femora, petrosal, and bone fragments.

Description: The cranium LAET 78-5435a is well preserved but slightly deformed and broken as a result of postmortem damage. The postorbital process is not closed, as is true of the majority of *Herpestes ichneumon* specimens, whereas the orbit is closed in most specimens of *Galerella sanguinea*. The frontal is slightly arched posterior to the postorbital constriction. The braincase is elongated and has its maximum width at the level of the posterior process of the zygomatic arch. The sagittal crest is not well marked or ridgelike, and the posterior part of the parietal slopes downward fairly steeply to the nuchal crest.

The tympanic bullae are well developed and inflated. The ectotympanic is tubular and forms an incomplete circle. The entotympanic chamber is inflated and spherical in shape, forming the deepest part of the bullae. The inflation of the posterior chamber is oriented posteroventrally. The paroccipital is closely appressed to the posterior part of the entotympanic without extending into the paroccipital process. There is no distinct mastoid process. Skull width is intermediate between that of the larger *Herpestes ichneumon* and the smaller *Galerella pulverulenta*. The postorbital constriction is narrower in LAET 78-5435a than in either *H. ichneumon* or *G. pulverulenta*, although only marginally more so than in the latter species. The width of the skull between the buccal margins of P4 and the least width of the skull at the postorbital constriction, relative to the least width between the orbits, are greater in *H. ichneumon* and *G. pulverulenta* than in LAET 78-5435a.

The P1 is single-rooted, whereas P2 has two roots. The apex of the cusp of this latter tooth is located slightly posterior to a position between the two roots. The P3 has three roots, mesial, distal, and lingual. The lingual root is smaller and supports a small cusplet at the middle of the lingual face. There are small basal cingula anteriorly and posteriorly, the latter of which is somewhat ridgelike. The P4 has three roots. The parastyles of both carnassials are worn. The paracone is taller than the protocone. The parastyle is located slightly anterior to the protocone, and the paracone is situated somewhat more buccally than lingually. The metastyle blade is in distal contact with the anterobuccal corner of M1. The M1 is triangular in shape and is mesiodistally short and buccolingually wide. The protocone is the largest of the three cusps. The M2 is small but similar in morphology to the M1.

The p1 is small. The p2 and p3 cusp apices are located between their respective roots. They are both two-rooted and have a posterior accessory cusp and basal cingula mesially and distally. The p4 has the same basic morphology as p2 and p3, but with a more developed posterior accessory cusp and stronger cingulum. The crowns of both m1 and m2 are damaged. An anterior mental foramen is located beneath the anterior edge of p2 and a more posterior one beneath the p2–p3 diastema.

Discussion: The majority of this material was attributed to *Galerella palaeoserengetensis* by Petter (1987) because of the conformity of cranial size and morphology of the tympanic bullae between LAET 78-5435a and the type specimen of *Herpestes palaeoserengetensis*, MB Ma 29566 (Dietrich 1942; Petter 1987). The new material from the Eyasi Plateau project matches that material in every respect. Petter made the distinction between *Herpestes* and *Galerella* on basis of the length of the cranium. In addition, Petter (1973) had described the species *Galerella primitivus* from Bed I at Olduvai, but he later (Petter 1987) synonymized this species with *G. palaeoserengetensis* from Laetoli on the basis of the increased sample of Laetoli material and an expanded comparative base.

The importance of bulla morphology to the generic attribution may be questioned, however. Hunt (1974) showed that the morphology of the auditory region in Carnivora is applicable to systematic problems at the family level but is less useful at lower levels. The dentition of the Laetoli specimens matches that of extant *Herpestes* from Africa most closely in size, whereas the teeth of *Galerella* are generally more reduced. Other features supporting an inclusion in *Herpestes* are the retained first premolar in the lower jaw in the Laetoli specimens, as in extant *Herpestes*, and total skull size. The skull of LAET 78-5435a measures almost 80 mm, despite the frontal breakage, in which feature it resembles larger species of *Herpestes*, whereas *Galerella* is usually smaller.

Herpestes cf. *H. palaeoserengetensis*

Specimens: Laetolil Beds, upper unit: LAET 78-4677, partial right mandible with p1 and broken p2, canine root and anterior p3 alveolus.

Description: The p1 is small and narrow, with the apex anteriorly oriented and a small elevation distally. The p2 has two roots and the crown is broken. There is an anterior mental foramen below p1 and a posterior mental foramen, presumably below the anterior root of p3.

Discussion: This partial mandible is comparable in size to that of *Herpestes palaeoserengetensis* as described above. Features including size and the retained first molar suggest that this specimen belongs in *Herpestes palaeoserengetensis*. Only the state of preservation precludes a positive identification.

Herpestes ichneumon Linnaeus, 1758

Specimens: Laetolil Beds, upper unit: LAET 74-289 (Petter 1987, Plate 7.1, fig. 11), partial right mandible with p2–m1 and alveoli for p1 and m2; LAET 75-1959, partial left mandible with p1–p4 and anterior m1 root, teeth in poor condition; LAET 75-2368, partial left mandible with broken m1 and posterior p4 alveolus; LAET 75-2624, partial left mandible with p1–p3, all teeth broken; EP 1169/05, associated left mandible fragments with p2–p3 and broken p4–m2 (partially in matrix).

Description: The morphology and dental metrics of this material are in general agreement with living *H. ichneumon* (Fig. 8.13). The p1 is a small, single-rooted tooth that is approximately equally long and wide. The p2 has two roots and anterior and posterior cingula. Occasionally, there is an indication of a minute posterior accessory cusp in extant individuals. The p3 is two-rooted and has a small posterior cingulum. There are two accessory cusps, a small mesial one a distal one situated between the main cusp and the cingulum. The p4 has two roots. Its cingulum extends distally below the anterior part of the m1 paraconid. Two accessory cusps are present: a somewhat conical-shaped one mesial to the main cusp and a well-developed one distobuccal to the main cusp. The m1 has two roots. The trigonid is well developed and expands buccally at the level of the protoconid. The metaconid is the smallest trigonid cusp and is somewhat lower than the paraconid and protoconid. The talonid is low, less than half the height of the trigonid, and forms a posterior ridge where the individual talonid cusps are indistinguishable. The labial side of the talonid is more robust in comparison with the lingual side. An anterior mental foramen is located beneath p1, and a more posterior one is located under the distal part of the anterior p3 root.

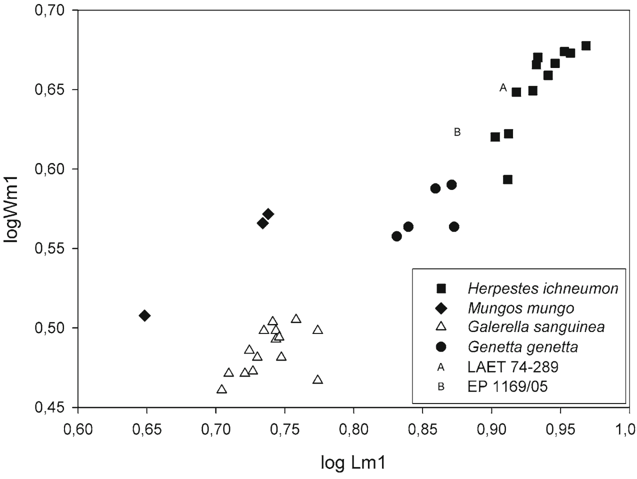

Fig. 8.13 Bivariate diagram of length and width of m1 in selected Herpestidae. The m1 of LAET 74-289 and that of EP 1169/05 are closely similar to those of *H. ichneumon* in size and proportions

Discussion: This material may be separated from specimens of *G. pulverulenta* by its larger size (Fig. 8.13), a somewhat more robust horizontal ramus, and a less rounded inferior border. The dental morphology and metrics are characteristic of the species *H. ichneumon*, and the material may be considered morphologically diagnostic. On the basis of present data, it is not possible to distinguish the Pliocene *H. ichneumon* of Laetoli from the living African *H. ichneumon*.

Genus Galerella *Gray, 1865*

The taxonomy and systematics of Herpestinae are not stable, and this is especially true of the position of the nomen *Galerella* (slender mongooses). A recent study (Veron et al. 2004) came to equivocal conclusions regarding the monophyly of *Galerella*. We retain *Galerella* here for practical reasons because it is used by Wozencraft (2005), in what is the most recent and widely used taxonomic compilation of the Carnivora, and because the material we refer to *Galerella* sp. can be distinguished from material we refer to *Herpestes* spp. This usage does not imply a specific view of the phylogenetic topology within the Herpestinae. The oldest *Galerella* thus far described is from Toros Menalla in Chad (ca. 7–6.5 Ma; Peigné et al. 2005). This material, which consists of fragmentary material of three individuals, has been ascribed to the extant species *G. sanguinea* (Peigné et al. 2005). Today, *Galerella* includes two species of interest to us: *G. sanguinea*, which is distributed throughout sub-Saharan Africa (except the Cape Province and surrounding coast in South Africa), and *G. pulverulenta*, which occupies the southern region where *G. sanguinea* is absent (Kingdon 1997).

Galerella sp.

Specimens: Laetolil Beds, upper unit: LAET 75-2722, partial left mandible with c, p2–p3, and alveoli for p4–m2, c broken; LAET 75-3340 (Petter 1987, Plate 7.2, fig. 10), partial right mandible with p4–m2, p4 broken; LAET 77-4570, partial left mandible with p2–m1 and alveoli for p1 and m2; LAET 78-4691, partial left mandible with p2, broken c, and alveoli for p1 and p3–m1; LAET 78-4955, partial right mandible with i2–c and p2–p3 (LAET 78-4955a) and partial right mandible with p4 and alveoli for m1 (LAET 78-4955b).

Description: The mandibular ramus is slender and straight. There are two mental foramina, the anterior one beneath the p1 alveolus and the posterior one between and ventral to p2 and p3. The p1 was present, as attested to by the presence of its alveolus in some specimens, although this seems variable. The apex of p2 is situated between the two roots. The p2 has two vertically positioned cuspids along the distal edge of the main cusp. The main cusp apex is situated above the anterior half of the tooth. The p3 is somewhat larger than the p2 but has the same basic morphology. The main difference between them is the occurrence of three minute elevations distally along the edge of the main cusp of p3. The distal end of p3 is occupied by a cingulum. The p4 is not well preserved in any specimen. The main cusp is tall, and there is a well developed accessory cusp distobuccal to the main cusp. The trigonid cusps of m1 are well developed and form a nearly equilateral triangle. The distobuccal corner of the paraconid forms a shearing facet together with the mesiobuccal corner of the protoconid. The metaconid is situated distal to the paraconid and slightly lingual to it. The basin-shaped talonid is low and only half the length of the trigonid. It has a posterior, ridgelike development. The proto-, meta-, and entoconid of m2 are all well developed. The protoconid and metaconid form the anterior face of the tooth. The entoconid is located distal to the paraconid. At the posterior end of the talonid there is a ridgelike formation.

Discussion: Specimens LAET 75-2722, LAET 75-3340, LAET 77-4570, and LAET 78-4691 resemble the living members of *Galerella*, and the species *G. pulverulenta* in particular, in features of the lower dentition. Specimen LAET 78-4955, on the other hand, tends to be somewhat closer to *G. sanguinea*. The similarity in dental metrics between these specimens from Laetoli and specimens of living *Galerella* is supported by the morphology of the teeth. Specimen LAET 75-3340, previously considered to belong in the genus *Mungos* (Petter 1987), tends to be closer to *Galerella* with regard to dental metrics. The lower carnassial of this specimen is narrower but longer than the lower carnassial of the extant *Mungos mungo*, as well as specimen LAET 75-3072, a *Mungos dietrichi*. Another feature specific to *M. mungo* and *M. dietrichi* is the increase in mandible depth behind m1 in relation to the length of m1 as compared to other herpestid genera, although there is a slight overlap between *M. mungo* and *G. sanguinea*. This increase in the height of mandible is not present in LAET 75-3340.

Assignment of LAET 75-2722, LAET 75-3340, and LAET 78-4955 to *Galerella* is reasonable with regard to dental metrics of the lower jaw (Fig. 8.14) and is supported by the complete reduction of p1. This is also true of LAET 77-4570 and LAET 78-4691, with the exception of the retained first premolar. The presence of p1 is not diagnostic, however, since a first premolar is present in a small number of individuals of living *Galerella* and may be explained as a primitive retention.

There is no positive evidence that all these specimens belong to a single taxon. In fact, the horizontal ramus of specimen LAET 75-2722 is more massive and taller beneath the tooth row in comparison with the other specimens assigned to *Galerella* sp. With respect to dental metrics, the specimens are intermediate between the smaller *Galerella sanguinea* and the larger *Galerella pulverulenta* or are within the size range of the latter species.

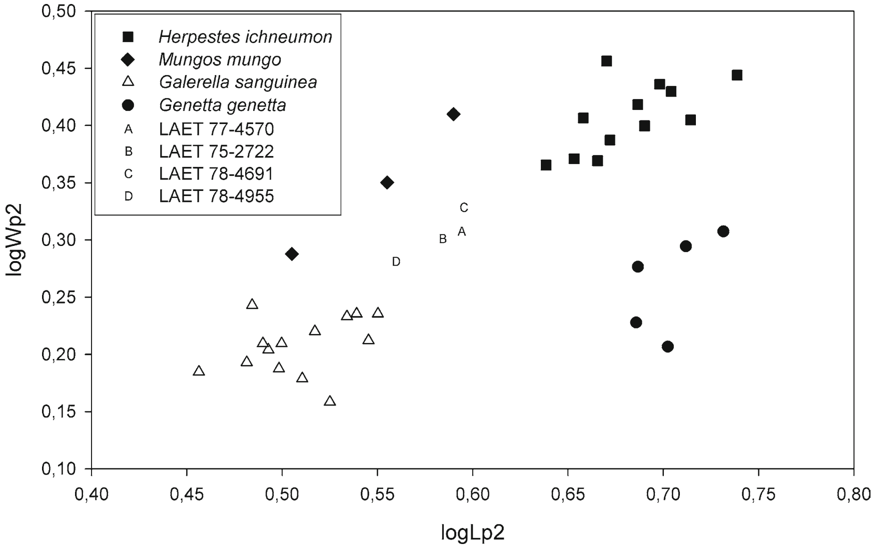

Fig. 8.14 Bivariate diagram of length and width of p2 in selected small Carnivora. The p2 of LAET 77-4570, LAET 75-2722, LAET 78-4691, and LAET 79-4955 all match *G. sanguinea* and *H. ichneumon* in proportions, whereas the p2 of *M. mungo* is broader and that of *G. genetta* is more slender

The identification of *Galerella sanguinea* from Toros Menalla (Peigné et al. 2005) is based on negative evidence – that is, the absence of characters distinguishing the material from the modern species. We are inclined to doubt this for several reasons, not least because the material discussed here, which is intermediate in age between Toros Menalla and the modern fauna, more extensive, and better preserved, shows characters that do distinguish it from both of the extant species. This suggests that if the Toros Menalla sample were larger, this material would also show distinctive characters.

Genus Helogale *Gray, 1862*

The genus *Helogale* (dwarf mongooses) is the most common of the small herpestids in the fossil record, perhaps because of its social habits. Besides Laetoli, the genus is known from Omo, Shungura Fm., Mbs. B, C, E–F, and G, as well as possibly Kanapoi and Hadar, Sidi Hakoma Mb. (Wesselman 1984; Werdelin 2003b). Today, the dwarf mongoose, *H. parvula*, is distributed from Somalia south along the eastern part of Africa to the Transvaal and west to Namibia and Angola, avoiding the Congo Basin. The Somali dwarf mongoose, *H. hirtula*, has a distribution from Somalia down through northern Kenya, as far west as the Turkana Basin (Kingdon 1997).

Helogale palaeogracilis **(Dietrich, 1942)**

Specimens: Laetolil Beds, lower unit: EP 015/98, left mandible fragment with p4–m1. Laetolil Beds, upper unit: LAET 75-2503 (Petter 1987, Plate 7.2, fig. 13), isolated right P4 with broken mesiobuccal and distal root; LAET 75-2807 (Petter 1987, Plate 7.2, figs. 1 and 2), cranium (LAET 75-2807a) with right and left I1–I3, P2–M2, and mandible (LAET 75-2807b) with right p3–m2, left p2–p4 and m2, right c and some incisors attached to the left mandible fragment; LAET 75-2997, partial left mandible with c, p2–m1 and m2 alveolus; LAET 75-2994 (specimen marked 2994, but labeled 2944), partial right mandible with P3 and broken P4; LAET 75-3368, partial right mandible with c, p2–p3, c and p3 broken, and an additional left mandible fragment with alveolus for m2; LAET 75-3565 (Petter 1987, Plate 7.2, fig. 3), partial left mandible with p3–m1 and m2 alveolus, p3 broken; LAET 75-3616 (Petter 1987, Plate 7.2, fig. 4), partial left mandible with p3–m1, alveoli for p2 and m2; LAET 76-3973, partial left mandible with c, p2–p4 and m1 alveoli, c broken; LAET 78-4736, partial left mandible with c and erupting p3–p4; LAET 78-4980, partial right mandible with p2–p4 and anterior m1 alveolus (given as left fragment in Petter 1987); LAET 78-5295, left mandible fragment with canine root, p3–m1, alveoli for p2 and m2, and an additional left mandible fragment with i2–i3 and partial left c alveolus; LAET 78-5298, partial right mandible (LAET 78-5298a) with p3–p4, anterior portion of m1, p2 alveoli, and left mandible (LAET 78-5298b) with p3–m1, all teeth broken (given as p2–p4 in Petter 1987); EP 436/98, left mandible fragment with c–p3; EP 1787/00, right mandible fragment with c, p2, alveoli for p3, p4–m1, proximal right humerus, occipital fragment, indeterminate postcranial fragments; EP 2577/00, right mandible fragment with root of c, p2–p4; EP 873/03, right mandible fragment with p2–p3; EP 985/03, left mandible fragment with p2–p4; EP 2430/03, right mandible fragment with root of c, p2–m1; EP 993/04, left mandible fragment with p2–m2; EP 1709/04, left mandible fragment with c, alveolus for p1, p2–p3; EP 1097/05, left mandible fragment with c–p2, roots of p3-p4, anterior fragment of m1; EP 1224/05, left mandible fragment with c–p4, anterior half of m1; EP 1790/00, left mandible fragment with c, p3; EP 208/00, right mandible fragment with p3; EP 4167/00, right mandible fragment with roots of p2, p3–p4, roots of m1; EP 348/01, left mandible fragment with p3–m1, left maxilla fragment with C–P2, proximal humerus, proximal ulnae, distal radius, proximal radius, tibia shaft, distal femur fragment, five ribs, six vertebrae, three metapodials, terminal phalanx, cranial and postcranial fragments; EP 467/01, left mandible fragment with p3; EP 390/03, left mandible fragment with p3; EP 770/03, right mandible fragment with p3; EP 041/04, right mandible fragment with alveoli for c, p2, p3–m1; EP 1456/04, left mandible fragment with p3–p4; EP 3858a/00, left mandible fragment with p3, broken p4–m1, complete m2; EP 3858b/00, left mandible fragment with m1–m2 (EP 3858/00 also includes a left edentulous mandible fragment, a right maxilla fragment with P2–P3, proximal humerus, distal humerus, proximal ulna, calcaneum, numerous postcranial fragments); EP 118/05, right mandible fragment with broken p2–p3, complete p4–m1; EP 642/01, right mandible fragment with p4; EP 035/01, right mandible fragment with p4–m2; EP 2888/00, right mandible fragment with p4; EP 2887/00, right mandible fragment with p4–m1; EP 1874/00, right mandible fragment with p4–m1; EP 531/00, right mandible fragment with p4; EP 466/00, left mandible fragment with p4–m2; EP 1500/98, right mandible fragment with p4–m1; EP 4168/00, right mandible fragment with m1; EP 636/01, left mandible fragment with m1. Ndolanya Beds, upper unit: LAET 75-940 (Petter 1987: Plate 2, fig. 12), right maxilla fragment with P3 and P4. Unknown stratigraphic level: LIT 59/359, partial right mandible with p3–m1 and alveolus for m2.

Description: The muzzle is short and the braincase relatively elongated. The nasal bones are short, extending ~1.5 mm behind the mid-dorsal part of the frontal-maxillary suture. The sagittal crest consists only of a very short portion merging posteriorly with the nuchal crest. The postorbital processes are well developed but open and short, and they do not extend to the zygomatic arch. The maximum width of the braincase is attained at the posterior part of the zygomatic process. The zygomatic arches are broken on both sides.

The mandibular fossa is present on the right side but broken. The tympanic bulla is well developed, with the caudal entotympanic inflated posteroventrally. The entotympanic is C shaped, with the external auditory meatus located at the lateral center of the C arm. There is a minute elevation posteriorly on the canine crown base.

There is no alveolus for p1. Between the canine and the p2 there is a small diastema. Both p2 and p3 are oval in occlusal view, with the lingual face somewhat more flattened. The height of these two teeth approximately equals their length. Thickenings of the cingulum can be seen mesiolingually and distally. The distal edge of the cusp is concave, which is more evident in p2 than in p3. In p2, the main cusp apex is located above the mesial root, whereas in p3 the main cusp apex is located between the roots. A distal accessory cusp arises from the distal base of the main cusp of p3. The distal width of p4 is greater than the mesial width. The distal accessory cusp of p4 is well developed, separated from the main cusp, and positioned buccally. A cingulum runs from the mesial edge via the lingual face to the distal edge, where it forms a ridge. The cingulum on p4 forms a small mesiolingual cusplet. In m1, the trigonid is slightly longer than the talonid. The trigonid cusps are well developed. The paraconid slopes down distobuccally in the direction of the protoconid. The protoconid, which is the tallest cusp, is located buccally in the middle of the tooth. The protoconid and metaconid apices are oriented slightly backward. The metaconid is located distal to the paraconid and slightly lingually. The talonid forms a distal ridge, where the individual cusps of the talonid are difficult to distinguish. The distal portion of the trigonid represents the widest part of the tooth at the level of the metaconid and protoconid. There are two mental foramina. The anterior one is located below the mesial margin of the mesial root of p2, whereas the posterior one is located below the mesial root of p3. The ventral border of the horizontal ramus is more or less straight.

There is no indication of a P1 alveolus. The upper incisors are small. The buccal surface of the canine is rounded, whereas the lingual surface is flattened. The distal edge is carinate. The P2 is oval in occlusal view, and the cusp is oriented somewhat distally. The apex of the right P2 is located between the two roots, whereas the apex of the left P2 is located closer to the distal root. There are no accessory cusps on P2. The P3 apex is located under the distobuccal root. There is a lingual root on P3 supporting a well-differentiated accessory cusp. The crown of P3 is bordered buccally by a weak cingulum, ending in small cusplets mesially and distally. In both P2 and P3, the height of the tooth approximates the length, and neither tooth has an accessory cusp. All the principal cusps of the upper carnassial are well developed. The protocone is positioned anterolingually. The mesial-most part of the tooth is the base of the parastyle. The paracone is situated on a concave diagonal axis between the protocone and metacone. The distal border of the protocone ends at the midpoint of the lingual face of the paracone. The mesiolingual portion of the metacone forms an open angle with the distal part of the paracone. The M1 is reduced, and the width of the tooth is greater than the length. The protocone is located lingually, with the mesiolingual portion of the tooth slightly more mesial than the mesiobuccal portion, here represented by the paracone. The protocone is buccally elongated into two crests, one mesial and one distal, which are almost equal in height to the protocone. The buccal face of the tooth is taller than the lingual face. The M2 is very reduced and small, with no distinguishable cusps.

Discussion: Helogale palaeogracilis is the smallest herpestid species from Laetoli. The size of the teeth in the specimens here attributed to *H. palaeogracilis* is comparable to that of the living dwarf mongooses, *H. hirtula* and *H. parvula* (Fig. 8.15). The teeth of extinct members of *Helogale* are narrower, however, even though they are of approximately the same length as the teeth of their extant relatives. This relative narrowing gives their teeth a more slender appearance.

The dental ratios of some teeth of the living dwarf mongooses, *H. hirtula* and *H. parvula,* differ from the ratios seen in *H. palaeogracilis*. The length of p3 in *H. hirtula* does not differ from specimens described as *H. palaeogracilis* (Petter 1987). However, p3 in *H. hirtula* is considerably broader in comparison with the Laetoli specimens. This pattern is also seen in the lower carnassial. The lower carnassial of *H. parvula*

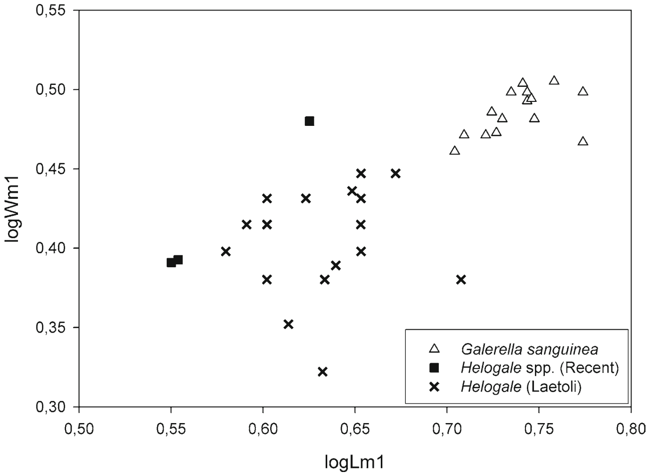

Fig. 8.15 Bivariate diagram of length and width of m1 in selected Herpestidae. Despite the poor sample of extant *Helogale,* it can be seen that the fossil specimens referred to this genus are all in the size range of the extant species. The considerable range of variation in width of the fossil sample may be due to the presence of more than one species-level taxon or (more likely) to measurement error resulting from variable preservation of the material

shows the opposite pattern to that seen in *H. hirtula*. There is a length reduction in the m1 of *H. parvula* in comparison with the material from Laetoli, whereas there is no difference in mean absolute tooth width.

The Laetoli specimen LAET 75-940, referred to *Cynictis* by Petter (1987), has relatively small upper premolars, similar to those of LAET 75-2807 and LAET 75-2994, and is clearly distinct from the yellow mongoose, *Cynictis penicillata*. These bivariate diagrams illustrate the overall smaller size of the P3 in LAET 75-940, LAET 75-2807, and LAET 75-2994 and of the P4 in LAET 75-2503, LAET 75-2867, and LAET 75-940 in comparison with extant *Cynictis* material. The small posterior elevation on the lower canine of specimen LAET 76-3973 is present in specimen NRM VE A583001, an extant *H. parvula*, but is not seen in *Cynictis*.

Laetoli specimen LAET 75-2991 has a relatively small p4, similar to specimens attributed to *H. palaeogracilis* (Petter 1987). The mandible of LAET 75-2991 is also relatively low behind m1, which sets it apart from larger genera, such as *Galerella* and *Herpestes*.

The majority of specimens referred to the taxon *H. palaeogracilis* in the present study were already included in this taxon by Petter (1987). The fossil sample of *Helogale* is indistinguishable from modern *Helogale* spp. in many morphological respects but differs in generally having narrower cheek teeth. Petter (1987) considers *H. palaeogracilis* to be a *Helogale* species with primitive dental characters reminiscent of *Galerella*, although apomorphic cranial characters confirm its assignment to *Helogale*.

Helogale cf. *H. palaeogracilis*

Specimens: Laetolil Beds, upper unit: LAET 75-399 (Petter 1987, Plate 7.2, fig. 9), partial right mandible with c and broken m1, alveoli for p2–p4 and m2; LAET 75-405, partial right mandible with broken p3–p4, alveoli for p2 and m1–m2; LAET 75-1974, partial left mandible with c and broken p2–p3; LAET 75-3334, left mandible fragment with anteriorly damaged p4 and roots of c, p2–p3 and alveoli for m1–m2; EP 1324/04, right mandible fragment with p4–m1.

Description: Specimen LAET 75-1974 is metrically similar to the dwarf mongoose *H. parvula*. The canine and the third premolar in the lower jaw are narrower and shorter in *H. parvula*, LAET 75-1974, LAET 75-2991, and LAET 76-3973 than in the remaining specimens.

Discussion: The complete reduction of p1, the minute posterior elevation (weak in specimens LAET 75-399 and LAET 75-1974 because of preservation) on the canine crown base, and the size of the mandible indicate that this material may be referred to *H. palaeogracilis*, but this attribution must remain tentative given the condition of the material.

Genus Mungos *Geoffroy St.-Hilaire and Cuvier, 1795*

Specimens referred to the genus *Mungos* (banded mongooses) are known from a few eastern African localities apart from Laetoli. The species *M. dietrichi* is tentatively known from the middle and upper parts of the Lomekwi Mb. of the Nachukui Fm., West Turkana, and the extant species *M. mungo* is known from Olduvai, Bed I (Petter 1973, 1987). Today, the genus comprises two species: the banded mongoose, *M. mungo*, which is distributed throughout eastern and central Africa, except in densely forested regions, and the southern margin of the Sahara in western Africa; and the Gambian mongoose, *M. gambianus*, which is known from savannas and woodlands in western Africa from Senegal to the Niger River (Kingdon 1997).

Mungos dietrichi Petter, 1963 (Fig. 8.16)

Specimens: Laetolil Beds, upper unit: LAET 75-2769, partial right mandible with p3–p4, posterior p2 and anterior m1 alveoli (given as left in Petter 1987); LAET 75-3741 (Petter 1987, Plate 7.2, fig. 11), partial left maxilla with P4–M1; LAET 75–548, partial left mandible with broken m1 and posterior p4 alveolus; LAET 77–4571 (Fig. 8.16a–c), partial right mandible with p4–m2. Ndolanya Beds, upper unit: LAET 75-3072 (Petter 1987, Plate 7.1, fig. 2, Plate 7.2, fig. 14), left mandible with c, p2–m2 and alveolus for p1; EP 1217/03, right mandible fragment with p4–m1, alveolus for m2.

Description: The ventral border of the mandible is convex. The angular process is long. The anterior border of the coronoid process slopes posteroventrally immediately behind the second lower molar. High crowns and sharp cusps characterize the teeth, particularly the premolars.

The canine is tall, and the apex points dorsally. The lingual surface of the canine is flattened and the buccal surface convex. There is a small alveolus for p1. The p2 has two roots, and the apex is above the mesial half of the tooth. The basal contour of p2 is oval and slightly broadened posteriorly, with an incipient cingulum formation at the posterolingual angle. There are no accessory cusps on p2. The p3 also has two roots. The apex of the main cusp of p3 is located above the juncture between the two roots. The main cusp is conical, mesially placed, and buccally flanked by a distal accessory cusp. A distal cingulum runs from the distal part of the accessory cusp to the distolingual angle of the tooth. Like p2 and p3, p4 has two roots. The basal contour of this tooth is rectangular, with rounded corners. The main cusp is pointed and conical. There is a well-developed accessory cusp distobuccally and a cingulum distally. The lower carnassial

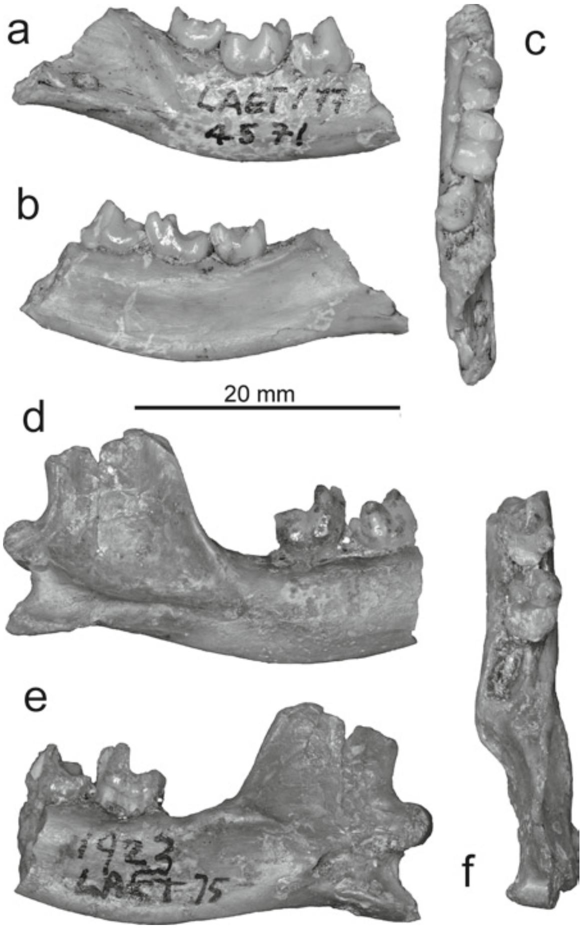

Fig. 8.16 (**a**–**c**) *Mungos dietrichi* LAET 77-4571; right mandibular ramus in (**a**) buccal, (**b**) lingual, and (**c**) occlusal view. (**d**–**f**) *Mungos* sp. nov.?, LAET 75-1923; right mandibular ramus in (**d**) buccal, (**e**) lingual, and (**f**) occlusal view

has two roots and a well-developed trigonid. The trigonid is marginally longer than the talonid. All trigonid cusps are more or less conical in shape and are located close to each other, especially the paraconid and metaconid. The paraconid is located at the mesiolingual corner in front of the metaconid. The protoconid is situated somewhat behind the paraconid and slightly in front of the metaconid on the buccal side. The paraconid and metaconid are joined at their bases, whereas the protoconid is distinct. The talonid of m1 is shorter and lower than the trigonid and square in outline. The hypoconid is large and well developed but worn. The distal border of the talonid forms a ridge surrounding the talonid depression immediately posterior to the trigonid. The m2 somewhat overlaps the distolingual corner of the m1 talonid. All m2 cusps are distinguishable despite being reduced. The proto- and metaconid of m2 are relatively well developed, whereas the paraconid is present as a small bump between the two other cusps. The talonid of m2 is somewhat smaller than the trigonid. The hypoconid is the most readily distinguishable cusp of the m2 talonid, whereas the hypoconulid and entoconid are merged into a posterior crest.

The upper carnassial has three roots and a triangular basal contour with a salient protocone. Unfortunately, the distal part of the P4 metastyle is broken in the only available specimen. In this upper carnassial, the width of the tooth exceeds its length. The salient protocone is well developed, conical, and wide at its base. The parastyle is wide and conical, similar to the protocone but much smaller. The paracone is slightly larger than the protocone. The metastyle blade is somewhat reduced and more buccally oriented in comparison with the parastyle and paracone. The M1 has three roots; the two buccal roots are probably small. The mesiobuccal corner where the paracone is located is damaged. The M1 is wider than it is long. The protocone is well developed and salient. The metacone is somewhat reduced.

Discussion: The teeth of the extant banded mongoose, *Mungos mungo* and specimens herein referred to *M. dietrichi*, are wider relative to length than those of *Helogale*, *Galerella*, and *Herpestes*. The length of the teeth in LAET 75-3072, the best preserved specimen of *M. dietrichi* from Laetoli, is similar to that of a large *Galerella*, whereas the width of the teeth is more like that of the smaller *Herpestes*, making the teeth in LAET 75-3072 relatively wide in relation to their length, as also seen in *M. mungo*. However, the ratios of tooth lengths in LAET 75-3072 and *M. mungo* do not deviate from the pattern seen in the rest of the comparative sample. A feature diagnostic of *Mungos* is the salient protocone on the upper carnassial, sometimes resulting in the width of the carnassial exceeding its length. This feature is seen in extinct as well as extant specimens of the genus. This increase in carnassial tooth width is particularly evident in specimen LAET 75-3741 from Laetoli. The most complete dental series of *M. dietrichi* comes from mandible LAET 75-3072. This specimen approaches and sometimes even exceeds *M. mungo* in size; this is also true of specimen LAET 75-2769. A difference between *M. mungo* and *M. dietrichi* is the presence of p1 in the latter species, as seen in mandible LAET 75-3072 from Laetoli, as well as mandible FLK N 6128 from Olduvai (Petter 1973).

Mungos sp. nov.? (Fig. 8.16)

Specimens: Laetolil Beds, upper unit: LAET 75-1923 (Fig. 8.16d–f), partial right mandible with p4–m1 and alveolus for m2; EP 544/01, left mandible fragment with m1–m2.

Description: The anterior portion of p4 is broken. Distobuccal to the main cusp there is an accessory cusp, of which the uppermost part of the apex is broken. There is a posterior cingulum. The widest part of p4 is probably at the level of the accessory cusp, since it protrudes from the buccal face of the tooth.

The paraconid is slightly the taller of the trigonid cusps on m1, but the protoconid is by far the largest. The mesial and particularly the mesiolingual portions of the trigonid are strongly compressed, making the distance between the paraconid and metaconid apices very short, approximately equal to the total length of the protoconid. The talonid is slightly shorter and much lower than the trigonid. The entoconid is well developed, whereas the hypoconid and hypoconulid are small, low, and set close together.

The m2 is a large, well-developed tooth. The protoconid and metaconid are both well developed and set widely apart. The entoconid is large, as is the hypoconid, which is separated from the metaconid by a deep postvallid notch. The hypoconulid is set posteriorly and is ridgelike.

Discussion: These specimens resemble *M. mungo* and *M. dietrichi* in general features but differ from them in the morphology of m1 and the mandible posterior to the tooth row. They are likely to belong in *Mungos* but may represent a new species within that genus. A larger sample of fossil *Mungos* spp. is required to address this question.

Family Hyaenidae Gray, 1821

The fossil record of Hyaenidae in Africa is extensive (summarized in Werdelin and Turner 1996). All the living species evolved on this continent, which, therefore, is key to understanding the evolution of the extant Hyaenidae. The diversity within the family was greater in the past, and Laetoli exemplifies this, with six species in as many genera. Metric data for Laetoli Hyaenidae are given in Tables 8.5 and 8.6.

Genus Crocuta *Kaup, 1828*

Crocuta is common in the late Pliocene and Pleistocene of Africa. A number of taxa are involved, and the evolution of the genus seems linked to that of the hominin lineage (Lewis and Werdelin 2000). The record of *C. dietrichi* from the Laetolil Beds, upper unit, is the oldest material of the genus, though material from the Kataboi Fm., West Turkana, which belongs to a distinct, undescribed taxon, may be of approximately the same age.

Crocuta dietrichi **Petter and Howell, 1989**

Specimens: Laetolil Beds, upper unit: LAET 75-2953 (holotype, Barry 1987, fig. 7.9a and b; Petter and Howell 1989, fig. 1c and d), left mandible fragment with p2–m1; LAET 76-3970/77-5370, right mandible fragment with p2–p4, isolated left p2, p4; EP 1067/04, left mandible fragment with c root, broken p2–p3, p4 roots; LAET 74-185 (Barry 1987, fig. 7.9c [as LAET 158]; Petter and Howell 1989, fig. 1a and b), left maxilla fragment with P1-P4; LAET 74-149, right mandible fragment with p2–p3. Ndolanya Beds, upper unit: LAET 78-5107 (Barry 1987, fig. 7.9d), right mandible fragment with p2–p4, anterior half of m1; LAET 76-3951 (Barry 1987, fig. 7.11), left mandible fragment with p2–p4; EP 1390/05, right mandible fragment with m1.

Description: Note that although the description of the mandible and lower dentition is a composite, that of the maxilla and upper dentition is based on the single specimen LAET 74-185. The mandibular ramus is robust. The height of the mandibular ramus increases from mesial (moderately tall) to distal (very tall). There is a single mental foramen located beneath the middle of p2. The masseteric fossa extends mesially to about the distal end of m1. The symphysis is large. The rugosity ends just mesial to p2, but the flattened area continues to beneath the middle of p3. The lower canine is known only from the root, which is a rounded oval in cross-section, with its longest diameter at approximately 30° to the cheek tooth row. It is followed by a diastema of a little less than 10 mm. The p2 is robust but low. There is no mesial accessory cusp; the main cusp is low, and the distal accessory cusp is low, somewhat trenchant, and set directly behind the main cusp. The p3 is pyramidal. The tooth is very broad mesially, but there is no mesial accessory cusp. The crest on the mesial face of the main cusp is prominent. The whole tooth has a distalward slant. The distal accessory cusp is small, short, and appressed to the main cusp. It is flanked on either side by narrow shelves. The p4 is robust and wide. The mesial accessory cusp is small and appressed to the main cusp. The main cusp is pyramidal and short. The distal shelf is long but relatively narrow, and its lingual side is formed into a low crest. The m1 is long and low. The paraconid is longer than the protoconid. The metaconid is either very small or simply a bump on the distolingual side of the protoconid. The talonid is short. It has one or two very small cusps. The P1 is a small, single-rooted tooth. The P2 is short and robust. It has a pyramidal crown and a distal (but no mesial) accessory cusp. The P3 is short and wide, with a pyramidal crown. The mesiolingual accessory cusp is small. The crest from it to the apex of the main cusp is strongly developed. The distal accessory cusp is low and appressed to the main cusp. The P4 is long and slender. The parastyle is strong. The protocone is well developed but low. The paracone is broken but must have been tall, whereas the metastyle is long and low, turning buccally at its distal end.

Discussion: *C. dietrichi* was first described as "*Crocuta* new species?" by Barry (1987), then formally described by Petter and Howell (1989). The main characteristic differentiating this species from modern *C. crocuta,* according to these authors, is the reduced size, and especially the small premolars. Barry (1987) lists a number of other characters, some of which are difficult to assess because of the small sample size, some of which fall within the range of variation of the modern species, and yet others whose diagnostic value has been enhanced by the discovery of additional specimens of

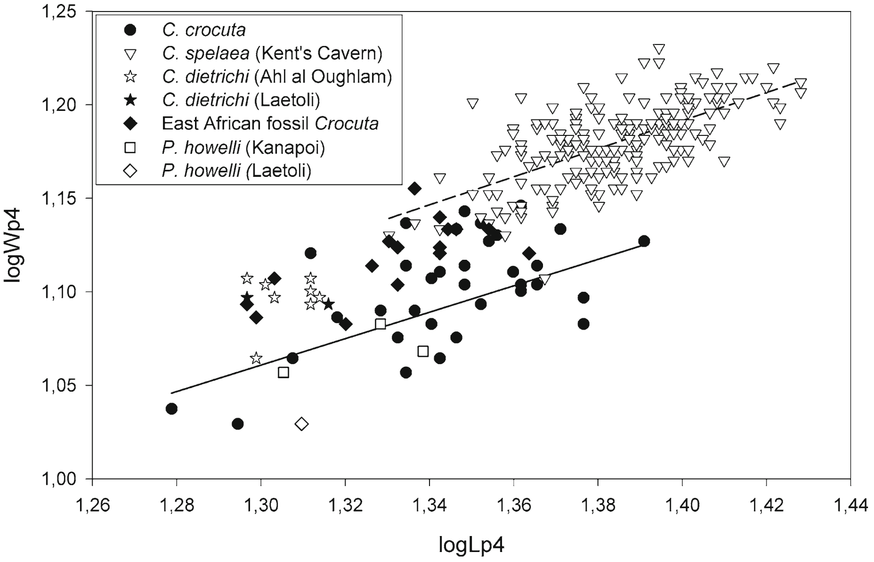

Fig. 8.17 Bivariate diagram of length and width of p4 in selected Hyaenidae. Note the slender p4 of *C. crocuta* compared with those of other *Crocuta*. *C. dietrichi* from Ahl al Oughlam was described as *C. dbaa* by Geraads (1997)

C. dietrichi from Laetoli and other East African sites in the age range of 3.5–2.5 Ma, such as Koobi Fora, West Turkana, and Omo. The youngest record of *C. dietrichi* is from the Upper Burgi Mb. at Koobi Fora – that is, latest Pliocene. Many of these characters are useful in distinguishing *C. dietrichi* from other fossil African *Crocuta*. However, the most significant character distinguishing *C. dietrichi* from modern *Crocuta* has not been mentioned by previous authors. This is the relatively broad p4 (Fig. 8.17), a feature shared with other fossil African *Crocuta*, mainly *C. ultra*, whereas in the modern species, the p4 is quite slender. This, together with the relatively long talonid, provides a stable characterization of the species *C. dietrichi*, *contra* the opinion of Turner (1990), who considered the latter to fall within the range of variation of the modern species.

Genus Parahyaena *(Hendey, 1974)*

Parahyaena was named as a subgenus of *Hyaena* by Hendey (1974) in recognition of differences between the brown and striped hyenas. Although it was originally restricted to the extant brown hyena, Werdelin (2003b) included the fossil *P. howelli* from Kanapoi in the genus. The Laetoli material represents the second known fossil record of this genus.

Parahyaena howelli Werdelin, 2003 (Fig. 8.18)

Specimens: Laetolil Beds, lower unit: KK 82-58 (Fig. 8.18), partial skeleton including cranium, mandibles and nearly complete dentition. Laetolil Beds, upper unit: EP 463/01, left mandible fragment with c, p2-p3 - p4-m1 lost and alveoli resorbed; EP 395/98, isolated right p3; EP 829/00, isolated left c, p2, p3; LAET 76-4008a (Barry 1987, fig. 7.12), right maxilla fragment with P4.

Tentatively assigned specimens: Laetolil Beds, upper unit: LAET 76-4092, isolated right P3; LAET 76-4008b, isolated left P2.

Description: The mandibular ramus is robust and deep, with a distinct ventral angle beneath m1. There is a single mental foramen located beneath p2. The coronoid process is tall, and its dorsal end is squared off. The masseteric fossa is deep and reaches mesially to approximately the m2. The i2 is a small, spatulate tooth without any distinct lingual accessory cusp. The i3 is somewhat larger but still incisiform. It is separated from the lower canine by a diastema of approximately 3 mm. The lower canine is set at approximately 30° to the main axis of the tooth row. It is a flattened oval lacking distinct mesial and distal keels. The postcanine diastema is approximately 10 mm long. The p2 is short. There is no mesial accessory cusp, but a small distal one is set in a short distal shelf. The main cusp is low. The p3 is robust with a squared-off mesial end lacking an accessory cusp. The main cusp is tall and pyramidal, whereas the distal accessory cusp is low and set free of the main cusp. The p4 is long and slender. It has a very low mesial accessory cusp, a low main cusp, and a low, long distal accessory cusp that is set free of the main cusp. The distolingual ridge is short. The m1 is relatively short. The paraconid is somewhat longer than the protoconid, and there is a small metaconid. The talonid is short and has two small cusps that are probably the hypoconid and entoconid. The m2 is a small, single-rooted tooth without

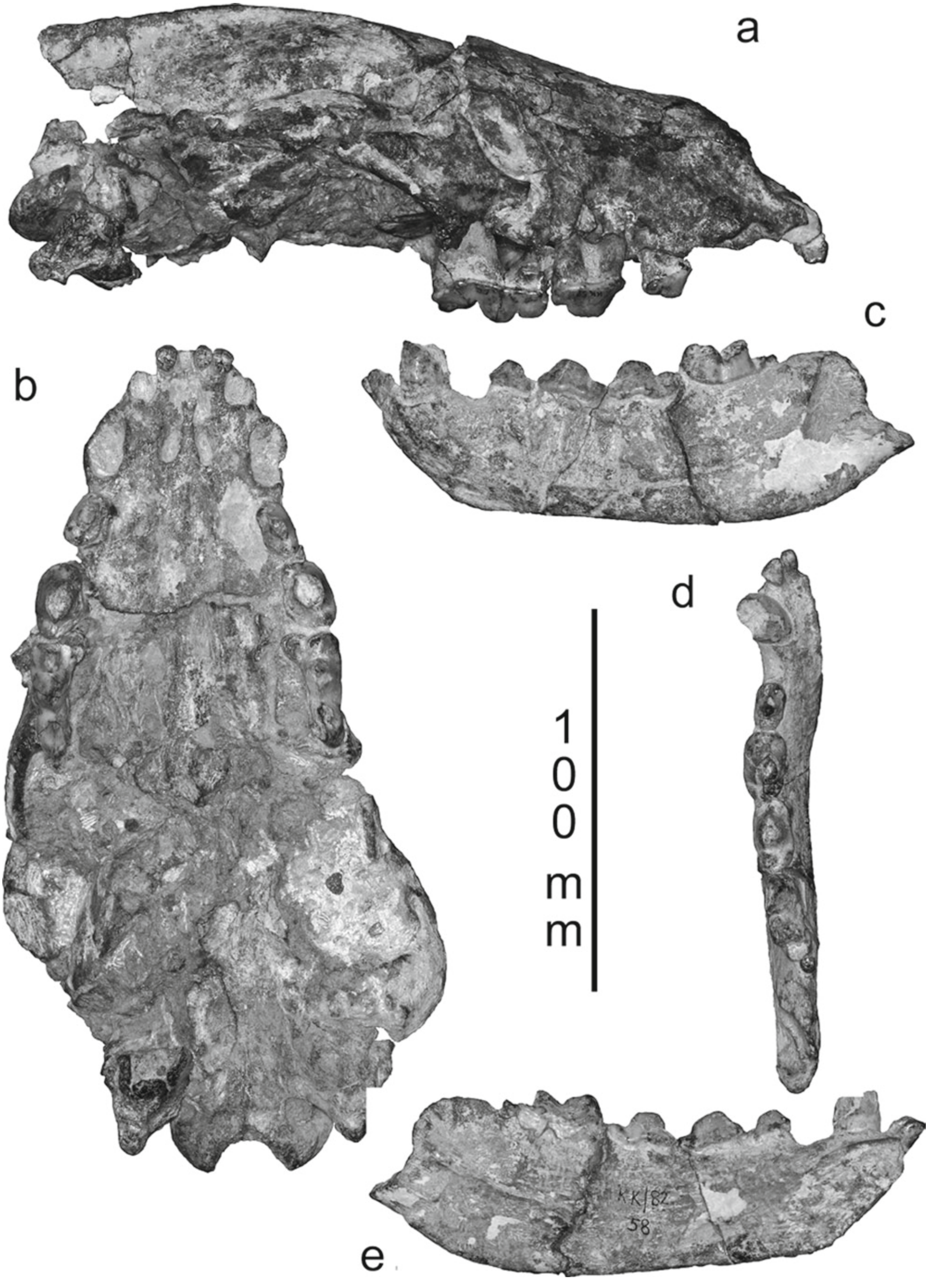

Fig. 8.18 *Parahyaena howelli*, KK 82-58. Skull in (**a**) right lateral and (**b**) ventral view. Left mandibular horizontal ramus in (**c**) buccal, (**d**) occlusal, and (**e**) lingual view

distinct cusps. The upper incisors are set along an arc. The I1 and I2 are small, spatulate teeth, with the I2 very slightly the larger of the two. The I3 is not preserved, but the alveolus indicates that it was about twice the size of I1 and I2. To judge from their alveoli, the upper canines were flattened ovals in occlusal view. There is no P1. The P2 is small and slender. It has no mesial accessory cusp, a low main cusp, and a well-developed distal accessory cusp. The P3 is rounded in occlusal view. Its mesial end is slender, and there is a small accessory cusp set mesial and slightly lingual to the main cusp. The main cusp is pyramidal. There is a distinct cingulum shelf on its lingual side, so that the tooth is widest there. The P4 is long and robust. The parastyle is well developed and slightly larger than the protocone. The latter is set slightly in front of or in line with the parastyle. The paracone is tall and mesiodistally short. The metastyle is longer than the paracone and straight, bending buccally only in its last few millimeters. The M1 is preserved only as a fragment. It was mesiodistally short and buccolingually long.

Discussion: The specimens listed above differ from those assigned to *C. dietrichi* in a number of ways. Most notably, the premolars are considerably more slender, with the p4 approaching *C. crocuta* in this feature (Fig. 8.17). On the other hand, they are closely similar to the hypodigm of *Parahyaena howelli* from Kanapoi (Fig. 8.17; Werdelin 2003b) and they can safely be assigned to this taxon, possibly extending the known temporal range of this species by as much as half a million years.

Genus Ikelohyaena *Werdelin and Solounias, 1991*

Werdelin and Solounias (1991) named *Ikelohyaena* for the *Hyaena abronia* of Hendey (1974), recognizing its distinction from the striped hyenas of the genus *Hyaena*. *Ikelohyaena* is known from a number of sites in Africa, of which Ahl al Oughlam, where "?*Hyaenictitherium barbarum*" was found (Geraads 1997), is the youngest.

***Ikelohyaena* cf. *I. abronia* Hendey, 1974**

Specimens: Laetolil Beds, upper unit: LAET 75-3338 (Barry 1987, fig. 7.10), left mandible fragment with p2–m1; LAET 75-1849, isolated left p4; EP 1046/98, left maxilla fragment with P2–P4. Unknown stratigraphic level: LIT 59/465, left maxilla fragment with P3, anterior part of P4.

Tentatively assigned specimens: Ndolanya Beds, upper unit: EP 1218/03, left maxilla fragment with I3 alveolus, C, P1 root, P2.

Description: The mandibular corpus is robust, with a fairly straight ventral border. There is a single mental foramen situated beneath the middle of p2. The masseteric fossa extends mesially to approximately the level of m2. The p2 has a more or less rectangular occlusal outline. It has no mesial accessory cusp and only a small distal one. The main cusp is robust but relatively low. The p3 is similar to p2 but is much larger. Its main cusp is located toward the mesial end of the tooth, and the mesial accessory cusp is very small. The distal part of the tooth is broken, and the shape and structure of the distal accessory cusp and shelf cannot be determined. Overall, the tooth greatly resembles the p3 of *Hyaena*. The p4 is a relatively short, slender tooth. The mesial accessory cusp is very small, whereas the main cusp is tall and pyramidal. The distal accessory cusp is prominent and set free of the main cusp, not appressed to it. The distolingual shelf has a blunt crest and broadens out on the lingual side. The infraorbital foramen of the maxilla is located above P3. The P2 is similar in structure to p2 but has a prominent cingulum on its lingual side. There are no accessory cusps, and the main cusp is relatively low. The P3 is a robust tooth with a very small mesiolingual accessory cusp; a tall, pyramidal main cusp; and a prominent but low distal accessory cusp appressed to the main cusp. There is a strong lingual cingulum at the base of the tooth. The P4 is short and robust. The parastyle and protocone are both strongly developed and set approximately level with each other. The paracone is tall, whereas the metastyle is broken but was apparently low.

Discussion: This material strongly resembles the topotypic material of *I. abronia* from Langebaanweg (Hendey 1978; Werdelin et al. 1994). This was also noted by Barry (1987) in his comparison between LAET 75-3338 and *Hyaenictis preforfex* (= *I. abronia*). This species has a pivotal role in the evolution of modern hyaenas. Its extensive stratigraphic range, from the late Miocene to the late Pliocene, as well as its intermediate morphological features, indicate that it is either the first species to evolve (on the *Hyaena* lineage) after the split between the striped and brown hyenas (genera *Hyaena* and *Parahyaena,* respectively) or is the last common ancestor of these two. Resolving this issue will greatly assist in understanding the factors leading to the evolution of the modern scavenging hyenas. The Upper Ndolanya Beds material of *Ikelohyaena* is among the last of the species, which has its last known occurrence at Ahl al Oughlam in Morocco (*?Hyaenictitherium barbarum* in Geraads 1997). Laetoli is thus far the only site where *Ikelohyaena* co-occurs with *Parahyaena howelli*, suggesting that the niches of these fossil precursors may have been more different than the niches of their modern descendants, the striped and brown hyenas, which do not have overlapping ranges.

Genus Lycyaenops *Kretzoi, 1938*

The genus *Lycyaenops* was created by Kretzoi (1938) for *L. rhomboideae* from the Pliocene of Hungary. Because of the sketchy nature of Kretzoi's description of and figure illustrating this taxon, doubt remained concerning its validity and phylogenetic position until Werdelin (1999a) showed that it was a member of the "hunting hyena" lineage that also includes *Lycyaena*, *Hyaenictis*, and *Chasmaporthetes* (Werdelin et al. 1994).

Lycyaenops cf. *L. silberbergi* (Broom in Broom and Schepers, 1946) (Fig. 8.19)

Specimens: Laetolil Beds, upper unit: LAET 75-494 (Fig. 8.19), right maxilla fragment with P2–P3. Unknown stratigraphic level: NHM AS 7.VI.35, left P3.

Description: The P2 is slender and rectangular, with its distal end only slightly broader than the mesial end, and the middle of the tooth has a shallow but distinct "waist." There is no distinct mesial accessory cusp. The main cusp is tall and trenchant. The distal accessory cusp is large, somewhat trenchant, and free of the main cusp. It is bordered lingually by a narrow shelf. The P3 has a small mesial accessory cusp set at the mesiolingual corner. The main cusp was tall. There is a basal cingulum distal to the mesial accessory cusp on the lingual side of the tooth. In the isolated P3, the main cusp is very tall and trenchant, and the distal accessory cusp is prominent (Turner 1990, fig. 2).

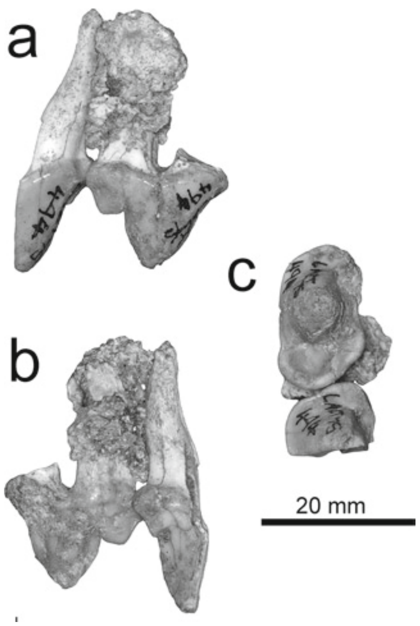

Fig. 8.19 *Lycyaena silberbergi*, LAET 75-494, maxilla fragment in (**a**) buccal, (**b**) lingual, and (**c**) occlusal view

Discussion: Turner (1990) recorded the presence of *Chasmaporthetes silberbergi* from an unknown level at Laetoli, based on a P3 in the collections of the Natural History Museum, London. Subsequently, Werdelin (1999a) transferred this species to the genus *Lycyaenops*, also in the *Lycyaena* lineage of "hunting hyaenas." Specimen LAET 75-494 shows a number of characters indicating that it belongs in this lineage, particularly the relatively slender and long P2 (Fig. 8.19), as noted by Barry (1987). The latter author expressed reservations about assigning the specimen to the *Lycyaena* lineage on the basis of the weak mesial accessory cusps of the P2 and P3. However, these cusps are much less well developed in *Lycyaenops* than in either *Lycyaena* or *Chasmaporthetes*. Therefore, we conclude that this specimen likely represents a species of *Lycyaenops*. Neither this specimen nor the one in the Natural History Museum, London, is adequate to definitively record the presence of the species *L. silberbergi* at Laetoli, however.

Genus ?Pachycrocuta *Kretzoi, 1938*

Pachycrocuta, which is a mainly Eurasian genus (Turner and Antón 1996), has long been known from several finds in South Africa but was not definitely recorded from eastern Africa until material from West Turkana was described by Werdelin (1999b). Some of this material is only slightly younger than the upper unit of the Laetolil Beds.

?Pachycrocuta sp. (Fig. 8.20)

Specimens: Laetolil Beds, upper unit: EP 1370/00 (Fig. 8.20), fragment of p3 or P3.

Description: This specimen is a small fragment of the ?anterobuccal part of a third premolar including an enamel fragment and partial root. The shape of the cingulum, the rounding of the tooth and the texture of the enamel all indicate that it belongs in the Hyaenidae.

Discussion: The specimen is much larger than the third premolars of any of the other hyaenid taxa from Laetoli and only matches *Pachycrocuta* in size. Therefore, we tentatively record the presence of this genus in the Laetolil Beds. This taxon is known from roughly contemporaneous sites in West Turkana (Werdelin 1999b).

Genus Proteles *Geoffroy St.-Hilaire, 1824*

The fossil record of aardwolves has been limited to a few records from the Pleistocene of South Africa (Werdelin and

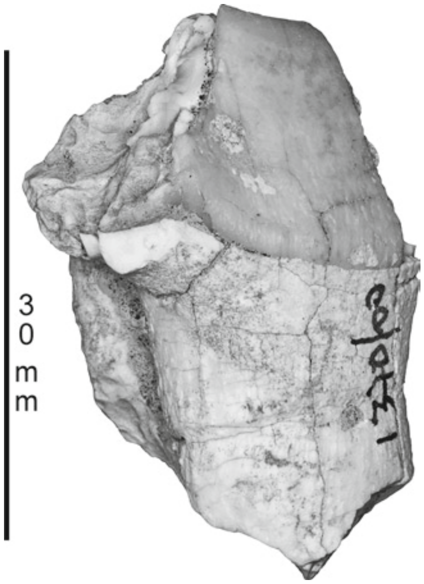

Fig. 8.20 ?*Pachycrocuta* sp., EP 1370/00, dental fragment in buccal? view

Fig. 8.21 aff. *Proteles* sp. (**a**) KK 82-32, proximal right humerus in lateral view. (**b**) KK 82-33, distal right humerus in anterior view

Solounias 1991). The extinct species *P. amplidentus* from the late Pliocene of Swartkrans differs from the extant species in having slightly less reduced cheek teeth, but the specific distinction is debatable.

aff. *Proteles* sp. (Fig. 8.21)

Specimens: Laetolil Beds, lower unit: KK 82-32 (Fig. 8.21a), proximal right humerus fragment; KK 82-33 (Fig. 8.21b), distal right humerus fragment; KK 82-35, distal right radius fragment; KK 82-36, ulna distal shaft fragment; KK 82-37, ulna right shaft fragment; KK 82-38, radius? shaft fragment; KK 82-54, distal humerus shaft fragment. These elements likely belong to a single individual

Description: The proximal humerus is small, approximately 2.5 cm wide transversely and 3 cm long anteroposteriorly. The greater tubercle rises considerably above the head, whereas the lesser tubercle is weak and does not quite rise to the level of the head. The head is approximately equally long and wide. The distal humerus is narrow, indicating cursorial adaptations. The medial and lateral epicondyles are well developed but not prominent.

Discussion: This material is limited and poorly preserved, but the humerus fragments are clearly identifiable as hyaenid on the basis of the size and shape of the greater trochanter and the shape of the medial and lateral distal condyles. All the material matches modern *Proteles* in size. Unfortunately, no craniodental material has been preserved. Though no specific diagnostic features of the humerus of *Proteles* are known, there is no other post-Miocene hyaenid of this size. Hence, we here suggest that the material represents a hyaenid in the *Proteles* lineage, if not *Proteles* itself. If confirmed, this would represent the oldest *Proteles* known, though the lineage itself is far older, at least 10–11 million years (Koepfli et al. 2006).

Family Felidae Fischer, 1817

The Felidae has an extensive fossil record in Africa. However, this record is strongly biased toward the sabertooth forms (Machairodontinae), especially the genera *Dinofelis* and *Homotherium* (Werdelin and Lewis 2001, 2005). Conical-toothed cats are generally much less well represented. However, Laetoli is an exception to this rule, with conical-toothed cats represented by extensive material of five or six species and the sabertooths by limited material of just two. Metric data for Laetoli Felidae are given in Tables 8.7 and 8.8.

Genus Dinofelis *Zdansky, 1924*

The genus *Dinofelis* is the most common cat genus in the Plio-Pleistocene of Africa. It was revised by Werdelin and Lewis (2001).

Dinofelis petteri Werdelin and Lewis, 2001

Specimens: Laetolil Beds, upper unit: LAET 75-448, left P4; LAET 78-4812, left distal radius fragment; LAET 75-868, right i3; LAET 78-5015, left p4 fragment. Ndolanya Beds, upper unit: LAET 78-5045, left distal humerus fragment.

Description: This material was described by Werdelin and Lewis (2001), and no further material has been recovered since. These descriptions therefore need not be reiterated here.

Discussion: A discussion of the status and affinities of this material was provided by Werdelin and Lewis (2001). *Dinofelis petteri* is known from a number of other early Pliocene East African localities, such as Kanapoi, Allia Bay, and Hadar.

Genus Homotherium *Fabrini, 1890*

Homotherium is present in small numbers at most Plio-Pleistocene African sites.

***Homotherium* sp. (Fig. 8.22)**

Specimens: Laetolil Beds, upper unit: LAET 75-2028, anterior fragment of right P4; LAET 74-259, left P4 metastyle fragment; LAET 75-2371, left P4 metastyle; LAET 78-4658, left i3; LAET 75-992, left p3; LAET 78-4977, associated left i1, i2, and i3; EP 1044/98, left proximal MT II; EP 1227/98, proximal MT III; EP 575/00 (Fig. 8.22), left and right C; EP 2545, left astragalus. Ndolanya Beds, upper unit: EP 2197/00, left dc; EP 1216/03, right i3.

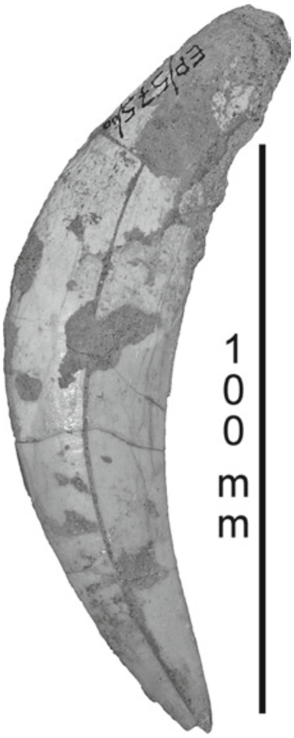

Fig. 8.22 *Homotherium* sp., EP 575/00, left upper canine in lateral view

Description: The incisors all are of typical *Homotherium* morphology, sharply pointed with small medial and larger lateral accessory cusps. The p3 is a small single-rooted tooth with no mesial accessory cusp and only a tiny distal one. The main cusp is low. The upper canines are long, laterally flattened, and strongly curved (Fig. 8.22). The mesial and distal serrations typical of *Homotherium* have been obliterated by wear. The P4 has a prominent parastyle and incipient preparastyle. The protocone is nearly completely reduced. The paracone is relatively low. The metastyle is low and long with a curve in the middle as is typical of *Homotherium*.

Discussion: *Homotherium* can be recognized on the basis of numerous characters of the skull, dentition, and postcranium. All of the characters listed above show features that definitely ally them with this genus. On the other hand, the species-level taxonomy of *Homotherium* in Africa has not been explored in any detail, although several species have been named, such as *H. problematicum* from Makapansgat (Collings 1972) and *H. hadarensis* from Hadar (Petter and Howell 1988). Therefore, it is at present not possible to identify the Laetoli *Homotherium* to the species level.

Genus Panthera *Oken, 1816*

The genus *Panthera* represents a conundrum in the evolution of Felidae. According to molecular studies (Johnson et al. 2006), the genus has a divergence time of >10 Ma, yet the earliest appearance of *Panthera* is from the upper unit of the Laetolil Beds at <3.7 Ma. Be that as it may, perhaps the greatest significance of the Laetolil carnivorans lies in the earliest known appearance of this genus, represented by two species as discussed below.

***Panthera* sp. aff. *P. leo* (Linnaeus, 1758) (Fig. 8.23)**

Specimens: Laetolil Beds, upper unit: LAET 74-330, left mandible fragment with c root; LAET 74-299, left premaxilla fragment with I2, part of I3; LAET 75-2004, I3 fragment; LAET 75-3572, right i3; LAET 75-1567, right i3; LAET 75-983, proximal left radius; LAET 78-5144, right calcaneum; LAET 75-1468, left m1 fragment; LAET 78-4813, left c; LAET 78-4619, right m1 fragment; EP 1333/98 (Fig. 8.23d, e), partial mandible with left c, p3–p4 roots, right i1–i3, p3–p4 roots, broken m1, isolated left i3, right P4 metastyle, premaxilla fragment with C root, cranial fragments. Unknown stratigraphic level: "N'Garussi, 1959" (Fig. 8.23a–c; Barry 1987, fig. 7.13), maxilla fragment with alveolus for P2, complete P3, anterior half of P4, M1.

Description: The lower incisors are small and set in a more or less straight line. They increase in size from i1 to i3. The size difference between i1 and i2 is less than that between

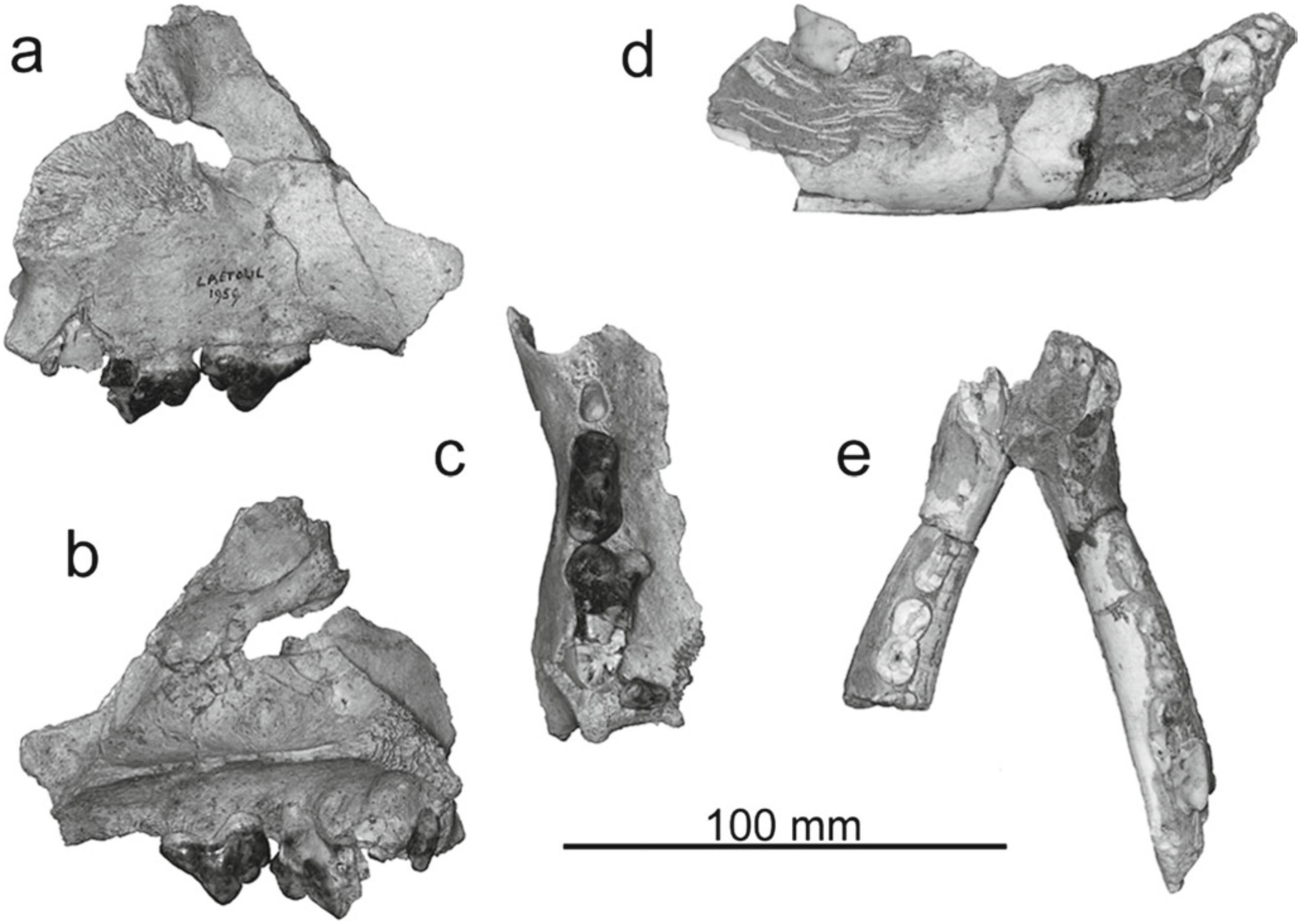

Fig. 8.23 *Panthera* sp. aff. *P. leo*. (**a**–**c**) "N'Garussi, 1959"; right maxilla in (**a**) buccal, (**b**) lingual, and (**c**) occlusal view. (**d**–**e**) EP 1333/98; mandible fragment in (**d**) right lateral and (**e**) occlusal view

i2 and i3. The lower canine is oval in cross-section. The preserved portions provide no indication of mesial or distal crests nor of medial or lateral grooves. The p3 is known only from the root but was apparently substantial. It is two rooted and slender. The p4 is likewise known only from the roots, which are similar to those of p3 but larger. The m1 is long and low. The paraconid is shorter than the protoconid. There is a very small metaconid-talonid complex distal to the protoconid. The infraorbital foramen is located above the distal end of P3. The I2 is a slender, spatulate tooth with a nearly symmetrical mesial cusp. The distal accessory cusp is prominent. The I3 is much larger than I2 and somewhat caniniform. The P2 was a small, single-rooted tooth. A small diastema separates it from the upper canine, and a still smaller one separates it from the P3, which is slender. There is no mesial accessory cusp, but the mesial face of the main cusp slopes very gradually up to its apex. The cusp apex itself is short and is followed distally by a large accessory cusp that is appressed to the main cusp. The tooth broadens out distally, and there is a prominent cusp at the distal end of the tooth. The P4 is robust and relatively short. The parastyle is large, with its anterior end terminated by a small cingulum that extends mesially past the mesial-most point of the protocone. The latter is prominent in occlusal view but very low. The paracone is tall and triangular. The metastyle is broken, but its preserved part indicates that it must have been relatively short, certainly shorter than the paracone. The M1 is small, short mesiodistally, and elongated buccolingually in the typical felid manner.

Discussion: The material assigned to this taxon is quite fragmentary and for the most part poorly preserved. The identification has therefore been controversial. On the basis of the then-available material, Barry (1987) stated that "it is clear that this felid cannot be referred to any of the extant species of *Leo*." Turner (1990), on the other hand, stated that Barry's work gave no "reason to identify the material as anything other than lion." Barry (1987) suggested some possible taxa for comparison, but none of these can be considered of interest here. *Felis crassidens* is a chimera (Turner 1984), and *F. palaeosinensis* is too small to be relevant, as is *P. gombaszoegensis*. However, the important point made by Barry (1987) is that the Laetoli material belongs to an unknown species that is not *P. leo*, whereas Turner (1990) disagrees with this assessment. Most of the discussion at the time centered on a single maxilla fragment from an unknown stratigraphic level at Laetoli (specimen labeled "N'Garussi 1959" in the collections). Because all other material assigned here is from the upper Laetolil Beds, it is likely that this specimen also comes from there, but this cannot be conclusively demonstrated. The specimen is poorly preserved, including a complete P3 and M1 and damaged P4. As such, it can hardly be said to be diagnostic at the species level in the taxa involved. This is especially so as the upper Laetolil Beds are at least 1.5 million years older than the oldest certain record of lion from East Africa (Olduvai, Bed I [Petter 1973]). The specimen does not show any metric characteristics that clearly distinguish it from extant East African *P. leo*, but in view of its age, to blithely say that it "is a lion" may be to take actualism too far.

The new material does not add much to the record of this taxon, except in the case of the partial mandible EP 1333/98. This specimen retains a measurable m1, allowing some consideration of similarities or differences in the lower dentition between it and modern lions. A bivariate diagram of the lower carnassial dimensions (Fig. 8.24) shows that the Laetoli specimen lies outside the range of variation of a small sample of modern East African lions. Although not conclusive evidence, this result at least argues for caution in assigning this material to any modern species of *Panthera*, just as Barry (1987) stated. On the other hand, it is unlikely that the material bears any special relationship to *P. gombaszoegensis*, which is considered by most to be related to the extant jaguar (Hemmer et al. 2003).

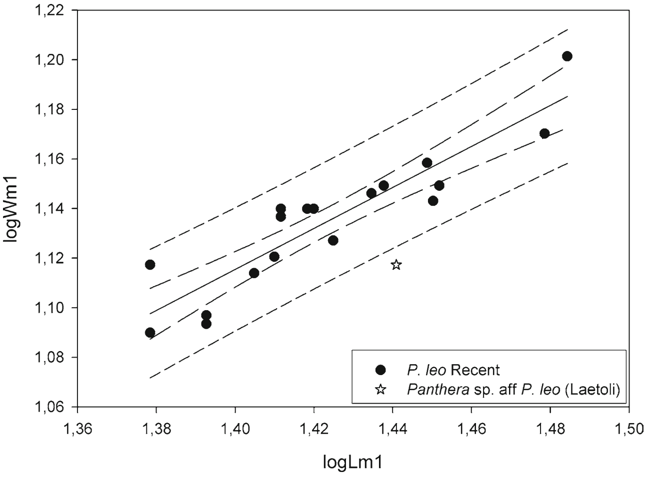

Fig. 8.24 Bivariate diagram of length and width of m1 in large *Panthera*. On the basis of this limited sample, the specimen from Laetoli lies outside the confidence (short dashes) and prediction (long dashes) intervals of modern lions

We add to this argumentation the molecular dates for the splits within the *Panthera* lineage as determined by Johnson et al. (2006). According to these dates, the first split within the genus *Panthera* occurs at ca. 3.7 Ma, and the split between *P. leo* and *P. pardus* occurs at ca. 2.1 Ma. These dates strongly suggest that neither of the Laetoli *Panthera* can be assigned to the extant species. On the other hand, the latter date fits perfectly with the first undoubted *P. leo* and *P. pardus* in the African fossil record (cf. below). Thus, we here assign the larger Laetoli *Panthera* species to *Panthera* sp. aff. *P. leo* with the understanding that this means *a taxon related to but probably different from extant lion*. It may very well be ancestral to extant lions in one way or another, but this is a moot point at present.

***Panthera* sp. cf. *P. pardus* (Linnaeus, 1758) (Fig. 8.25)**

Specimens: Laetolil Beds, upper unit: LAET 75-537 (Fig. 8.25; Barry 1987, fig. 7.14), right mandible fragment with p3–m1; LAET 75-2664, left P3 fragment; LAET 75-2767, right m1 fragment; LAET 74-144, left MT V; LAET 75-2622, right distal humerus; LAET 75-3613, distal left humerus; LAET 75-1912, right MC IV; LAET 75-341, left astragalus; EP 065/99, right p3; EP 1622/00, left mandible fragment with p4–m1; EP 2003/00, left c; EP 4301/00, right I1. Ndolanya Beds, upper unit: LAET 78-5122, partial left mandible with p3–p4, left C; LAET 78-5119, left P3, P4 fragment; LAET 75-931, distal right tibia; EP 1688/03, maxilla fragment with broken P2–P3. Unknown stratigraphic level: LIT 59/105, right m1; LIT 59/106, right p3 fragment; LIT 59/392, right p3 fragment.

Description: The mandibular ramus is robust and moderately deep. It is about equally deep throughout, beneath the tooth

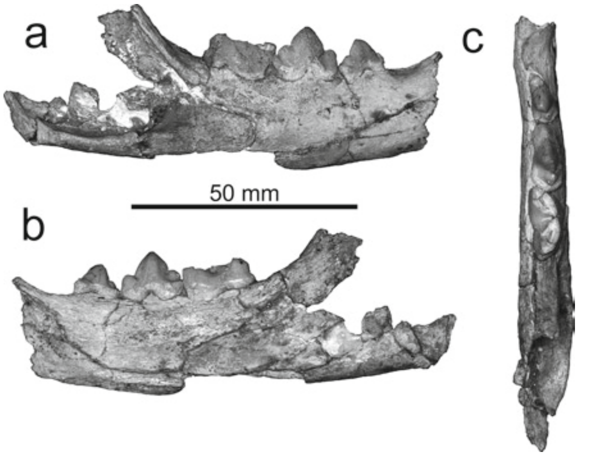

Fig. 8.25 *Panthera* sp. cf. *P. pardus*, LAET 75-537, right mandibular ramus in (**a**) buccal, (**b**) lingual, and (**c**) occlusal view

row. There are two mental foramina. The anterior, smaller foramen is located beneath the middle of the postcanine diastema, and the posterior, larger foramen is located beneath the anterior root of p3. The postcanine diastema is approximately 15 mm in length. The masseteric fossa is deep and ends about level with the distal end of m1. The lower canine is slender and relatively straight. The feline grooves are weakly developed, as are the mesial and distal keels. The p3 is small and slender, broadening out markedly from mesial to distal. There is a small mesial accessory cusp. The main cusp is tall and triangular. The distal accessory cusp is prominent but short and flanked on either side by a narrow cingulum shelf. The p4 is similar to the p3 but larger. The mesial accessory cusp is substantial and set free from the main cusp. The latter is tall and triangular, with a hint of a diamond pattern. The distal end of the tooth broadens out considerably. The distal accessory cusp is prominent and somewhat trenchant. The distal shelf is broader on the lingual side. The m1 is relatively short. The paraconid and protoconid are of about equal length. The metaconid-talonid complex is very small. The upper canine is similar to the lower but is larger and somewhat more curved. The postcanine diastema in the maxilla is only 2–3 mm long. The P2 is long and slender. There is a prominent lingual bulge level with or just posterior to the main cusp. The mesial accessory cusp is very small, whereas the distal one is well developed but short. The P3 has a tall, triangular main cusp. There is no apparent mesial accessory cusp, but the distal cusp is distinct and followed by a larger distal basal cusp.

Discussion: This material, or permutations thereof, has been the subject of considerable taxonomic speculation. Barry (1987) assigned it to *Leo* cf. *pardus*, though he indicated that the main reason to associate it with leopards is size and because the species is well known from Africa. However, he also suggests other taxa with which it should be compared. Of these, *Felis cristata* belongs to *Dinofelis* (Werdelin and Lewis 2001), *F. arvernensis* is probably a synonym of *P. gombaszoegensis* and is clearly distinct from the Laetoli material (Turner 1990), *F. studeri* has been referred to *Miracinonyx* (Van Valkenburgh et al. 1990), *F. palaeosinensis* is too large, and *F. obscura* is a metailurine and quite distinct from the Laetoli material (Turner et al. 1999; Werdelin and Lewis 2005). There remains "*Panthera*" *schaubi* (Viret 1954; Hemmer 1965), which, as shown by Hemmer et al. (2004), has several features in common with the Laetoli taxon. We shall return to this taxon below.

Turner (1990) unhesitatingly referred the Laetoli specimens to *P. pardus* while not noting any features that might differentiate them from extant leopards. Recently, Hemmer et al. (2004) suggested comparisons with the Eurasian "*Puma*" *pardoides*, considered by them to be ancestral to the puma of the New World (cf. also Hemmer 2001). These authors place "*P.*" *schaubi* in synonymy with "*P.*" *pardoides*, which was first described from the Red Crag of England (Owen 1846). The stratigraphic range of the Eurasian species is Lower Villafranchian to early Middle Pleistocene (i.e., ca. 3 to <1 Ma).

Unfortunately, apart from metric features, characters distinguishing *Puma* from *Panthera* that can be studied on the material from Laetoli have not been presented by Hemmer (1965, 2001) or Hemmer et al. (2004). Fig. 8.26 is therefore presented here as a preliminary discussion point. It includes the relevant extant taxa (*Panthera pardus*, *Puma concolor*, and *Acinonyx jubatus*), as well as several Laetoli specimens, the majority of which have been assigned to *Panthera* cf. *pardus* herein. Hemmer et al. (2004) consider the long p3 to be a critical feature distinguishing the Laetoli specimens from *P. pardus* and allying them with "*P.*" *pardoides*. Hence, Fig. 8.26 shows the length relationship between p3 and p4. As Hemmer et al. (2004) have noted, *P. concolor* and *A. jubatus* differ from *P. pardus* in having a relatively long p3. The two relevant specimens from Laetoli, LAET 78-5122 and LAET 75-537 (the latter of which was referred to *Felis* large species by Barry (1987) but suggested to belong in the *P.* cf. *pardus* cluster by Hemmer et al. 2004), both fall between the *Puma/Acinonyx* cluster and the *P. pardus* cluster. This is in contrast to EP 927/01, herein referred to *Acinonyx*, which falls with *Puma/Acinonyx*.

In summary of this brief analysis, the metrics suggest that the Laetoli specimens are different from modern *P. pardus*, *contra* the assignment to that species by Turner (1990), but also that they differ from *Puma/Acinonyx, contra* the suggested assignment to that lineage by Hemmer et al. (2004). For the time being, we retain the taxonomic assignment of Barry (1987) and call the specimens *P.* sp. cf. *P. pardus*, noting, like Barry, that further analysis is required.

Genus Acinonyx *Browokes, 1828*

Cheetahs are morphologically highly distinctive, both postcranially and craniodentally. Despite this, they are not well known in the fossil record. This may be the result of a relatively low abundance, if the mode of life of extinct cheetahs was the same as that of the living species, or it could be the result of sampling bias, if the favored habitats of cheetahs are underrepresented in the African fossil record. The Laetoli record is the oldest of cheetahs.

Acinonyx sp. (Fig. 8.27)

Specimens: Laetolil Beds, upper unit: LAET 75-3569, proximal left ulna fragment; LAET 75-3218, right anterior P4

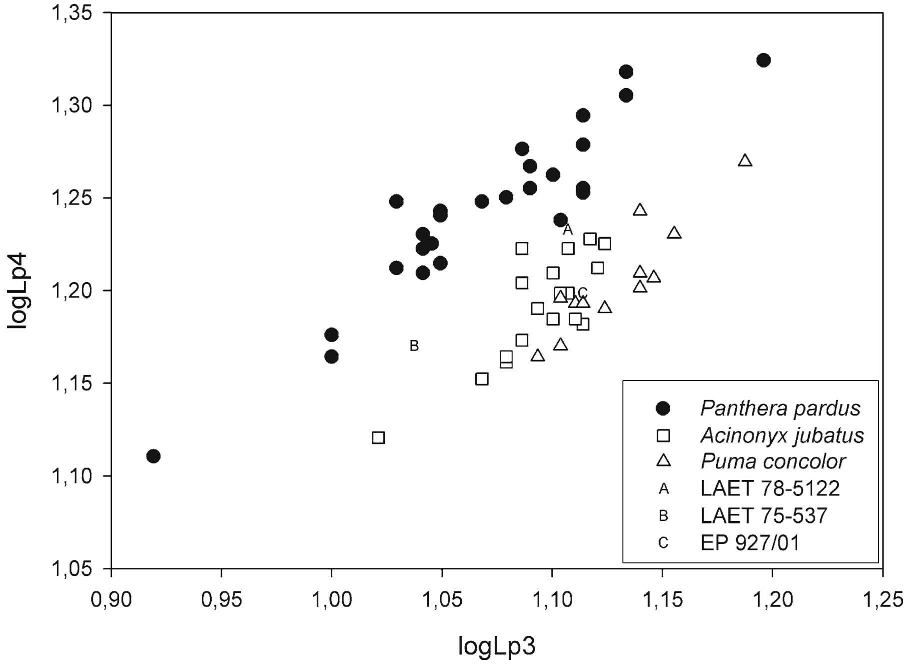

Fig. 8.26 Bivariate diagram showing the relative lengths of p3 and p4 in selected Felidae. *P. pardus* has a short p3 and *A. jubatus* and *P. concolor* a relatively long one. LAET 78-5122 and LAET 75-537, here referred to *Panthera* sp. cf. *P. pardus* are intermediate in p3 length. EP 927/01, here referred to *Acinonyx* sp., has a long p3

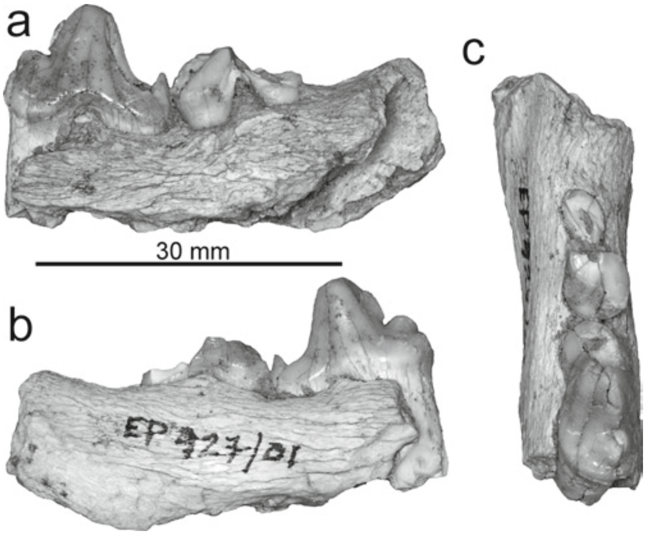

Fig. 8.27 *Acinonyx* sp., EP 927/01, right mandibular ramus in (**a**) buccal, (**b**) lingual, and (**c**) occlusal view

fragment; LAET 74-276, right mandible fragment with broken p4; LAET 75-1904, right astragalus fragment; LAET 75-2236, right proximal radius fragment; EP 1621/00, right m1; EP 927/01 (Fig. 8.27), right mandible fragment with broken p3–p4.

Description: The mandibular ramus is quite robust and deep. There are two mental foramina, a larger one beneath the postcanine diastema and a smaller one beneath the anterior half of p3. The p3 is a slender tooth that widens distally. The p4 is also slender. The mesial part of the main cusp is broken. Judging by the height of the mesial end of the tooth, it is likely that there was a well-developed mesial accessory cusp. The distal edge of the main cusp shows a distinct diamond pattern. The distal accessory cusp is substantial and set well apart from the main cusp. It is followed distally by a narrow cingulum ridge. The m1 is short and tall. The paraconid is somewhat lower than the protoconid and also slightly shorter. There is a distinct distal shelf, but no metaconid-talonid complex is in evidence.

Discussion: Several lines of evidence lead us to associate this material with *Acinonyx*, both qualitative, such as the premolar cusp shapes and sizes, and quantitative, such as the relative premolar size (Fig. 8.26). Nonetheless, this material also shows several traits in premolar and molar shape and size that appear to be more primitive and resemble those of *Puma*. Given that most analyses reconstruct these two genera as closely related (Johnson et al. 2006), these traits may be closer to the ancestral morphotype than their expression in modern cheetahs. However, because these traits also resemble those in *Panthera* and are possibly plesiomorphic for Felinae, it creates some problems in distinguishing the *Acinonyx* sp. material from that here referred to *Panthera* sp. cf. *P. pardus* (medium-sized species), which has features we here consider convergent on *Puma*. Thus, the Laetoli material appears to include a *Puma*-like cheetah (possibly because of close common ancestry) and a *Puma*-like pantherine (possibly because of convergence or plesiomorphy). Interestingly, this very early *Acinonyx* is very similar in size to the living species *A. jubatus*. Other fossil cheetahs, generally grouped together as the Eurasian *A. pardinensis*, are much larger (Kurtén 1968). Hemmer (2001) suggested that there might be a chronocline between the latter and the modern form, but if the earliest known cheetahs were similar in size to the modern species, this scenario might have to be reconsidered.

Genus Caracal *Gray, 1843 or Genus* Leptailurus *Severtzow, 1858*

These two genera are prime examples of the problem of studying felid evolution. They are readily distinguishable on the basis of gross morphological characters in the modern taxa and, although related, have had separate evolutionary histories for at least 5.5 million years (Johnson et al. 2006). Despite this, they are nearly impossible to distinguish in the fossil record because of the uniform morphology of felid cheek teeth and the fragmentary fossil record of the group. Even more importantly, it is not possible at present to state whether fossil representatives assigned to either of these genera belong to the extant species or to extinct forms.

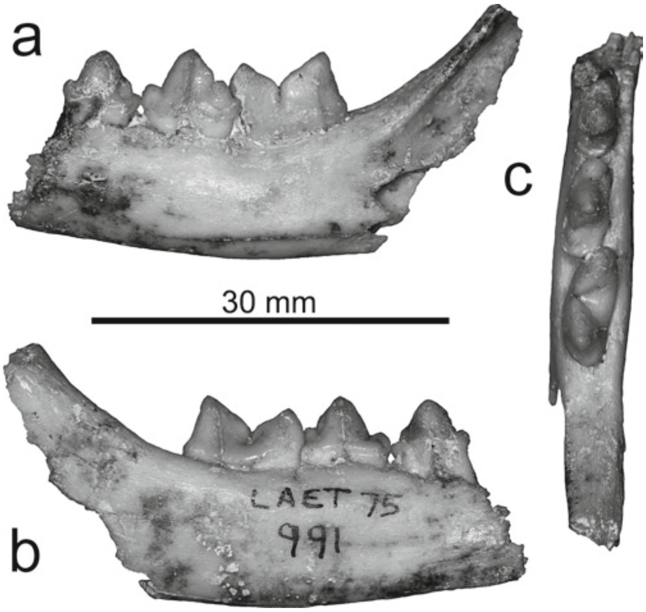

Fig. 8.28 *Caracal* sp. or *Leptailurus* sp., LAET 75-991A, left mandibular ramus in (**a**) buccal, (**b**) lingual, and (**c**) occlusal view

Caracal sp. or *Leptailurus* sp. (Fig. 8.28)

Specimens: Laetolil Beds, upper unit: LAET 78-5140, left mandible fragment with roots of c, p3; LAET 75-3631, left mandible fragment with broken m1; LAET 75-1868, left mandible fragment with broken m1; LAET 75-332, incomplete right innominate; LAET 75-2881, right proximal radius; LAET 75-3328, left proximal MC IV; LAET 75-1395, incomplete right pedal phalanx; LAET 75-991A (Fig. 8.28), left mandible fragment with p3–m1; LAET 75-991B, isolated left p3 and p4; EP 397/98, right proximal ulna fragment; EP 158/00, left mandible fragment with broken p3–p4; EP 1152/00, left mandible fragment with broken p4–m1; EP 3066/00, right proximal radius; EP 3934/00, left mandible fragment with roots of p3–m1; EP 979/01, right mandible fragment with dc, dp3–dp4, emerging m1. Ndolanya Beds, upper unit: EP 093/04, left mandible fragment with p4.

Description: The mandibular ramus is robust and low. There are two mental foramina, a larger one located beneath the middle of the postcanine diastema and a slightly smaller one located beneath the anterior root of p3. The symphysis is rugose and angled approximately 30° from the vertical. The canine is set at an angle of approximately 30° to the main axis of the ramus. It is moderately oval. The postcanine diastema is relatively long, at approximately 10 mm. The masseteric fossa ends near the distal end of the m1. The p3 is short and has a tall crown. There is a distinct but low mesial accessory cusp and a tall main cusp. The main cusp has an incipient distal accessory cusp on the distal edge. The p4 is similar in overall structure to the p3 but is relatively more slender. The mesial accessory cusp is large and angled away from the main cusp. The latter is tall and triangular. The distal accessory cusp is well developed but appressed to the main cusp. There is a prominent distolingual shelf that bears a small distal cusp. The m1 is long and low. The paraconid is somewhat lower and shorter than the main cusp. There is no metaconid-talonid complex but only a minute distal shelf.

Discussion: The available material does not allow the distinction between *Leptailurus* and *Caracal* to be made, although the range of variation in several instances suggests that both are present. Nor can we positively exclude the presence of some other genus of felid in the same size range but extinct today, either locally or globally. For the present, the most parsimonious hypothesis is that the material can be allocated to the extant genera *Leptailurus* and *Caracal*, though not necessarily to their modern-day species, *L. serval* and *C. caracal*, respectively.

Genus Felis *Linnaeus, 1758*

According to recent molecular analyses (Johnson et al. 2006) the leopard cat and domestic cat lineages were the last to split off in the evolution of Felidae, sometime around 6.2 Ma. The oldest currently known *Felis* is from Kanapoi, which is slightly older than the Laetoli specimens discussed below.

***Felis* sp. (Fig. 8.29)**

Specimens: Laetolil Beds, upper unit: LAET 75-3098, distal right humerus fragment; EP 119/01 (Fig. 8.29), left mandible fragment with p4; EP 980/01, left astragalus; EP 120/01, mandible fragments.

Description: EP 119/01 and 120/01 are likely to belong to the same individual because they were found near each other, are the same size, and present no overlapping elements, one being a right and the other a left mandible fragment. The p4 is of typical *Felis* spp. morphology. It is long and slender and has a tall main cusp. The distal accessory cusp is well developed and sharp and is situated near the base of the distal face of the main cusp and somewhat to its buccal side. The mesial and distal margins of the tooth are damaged, so the presence and size of cingulum cusps cannot be determined. The postcranial fragments are typically felid in morphology and very small.

Discussion: These few specimens clearly represent a felid that is considerably smaller than *Leptailurus* or *Caracal* (Fig. 8.28). The only African genus that is available for such small felids is *Felis*, though this identification is based on the assumption that no extinct genus of small felids existed in the African early Pliocene, as none of the available specimens displays any diagnostic characters apart from size.

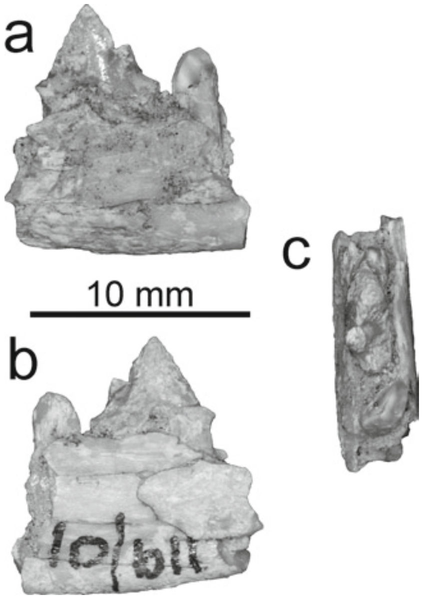

Fig. 8.29 *Felis* sp., EP 119/01, left mandibular ramus in (**a**) buccal, (**b**) lingual, and (**c**) occlusal view

Discussion

This discussion of the Laetoli carnivorans will proceed family by family, discussing the contribution of Laetoli to our knowledge of the African and global evolution of each family. We will then end with a discussion of the significance of the Laetoli Carnivora as a whole.

Canidae

Canids are uncommon in the African Pliocene fossil record. This may be a result of the preference of most canids for open habitats, whereas the African pre-Pleistocene fossil record appears to mostly sample closed to semi-closed habitats. Despite this relative scarcity, African canids may have played a crucial role in the evolution of Plio-Pleistocene canids worldwide and, therefore, deciphering the fossil record of the group in Africa takes on particular significance.

The oldest records of canids in Africa are from Chad, where a small fox (Vulpini) has recently been described from Toros Menalla (de Bonis et al. 2007), and Kenya, where scarce remains of *Eucyon intrepidus* have been found in the Lukeino Fm. (Morales et al. 2005). The former record is ca. 7–6 Ma and the latter 6.1–5.6 Ma. Prior to these recent finds, the oldest canid in Africa was *Eucyon* sp. from Langebaanweg, South Africa (dated ca. 5.3–5 Ma). A few additional finds of canids exist from the time interval 5–4 Ma (L.W., personal observations), but the Upper Laetolil Beds are the first record in Africa of multiple species of canid from a single locality.

Because of their age and the state of preservation of the material, the canids from Laetoli are difficult to interpret. If the *Canis* spp. should be correctly interpreted, this may be the oldest described *Canis* in the world, rivaled only by the *Canis* sp. from South Turkwel, Kenya (Werdelin and Lewis 2000). The aff. *Otocyon* sp. nearly doubles the age of the oldest known member of its lineage. ?*Nyctereutes barryi* is the oldest *Nyctereutes* in Africa. Although not globally the oldest, it does provide a minimum date for the first dispersal of the genus into Africa. Whether the younger *N. terblanchei* (Ficcarelli et al. 1984) is descended from the Laetoli form or is the result of a dispersal of a more derived *Nyctereutes* into Africa is not known at present, though the latter seems indicated, as the alternative scenario would require extensive parallel evolution of key features of derived *Nyctereutes*.

Mustelidae

Like the Viverridae, the Mustelidae are poorly represented at Laetoli. Ironically, the Mustelidae present are among the largest and smallest of all mustelids, *Mellivora* and *Prepoecilogale*. The former is known from several other localities in Africa, whereas the latter is known from only one, Bolt's Farm in South Africa (Cooke 1985). Mustelids are, in general, rare in African Plio-Pleistocene localities and are, of course, not particularly common or diverse in extant faunas, either. The known record, including that from Laetoli, suggests that mustelids have always had a limited diversity in post-Miocene Africa. The presence of a new genus of Aonyxini from the Lower Laetolil Beds is, of course, of the greatest importance, not least to reconstructions of the paleoecology of those beds.

Viverridae

Viverridae are poorly represented at Laetoli compared with Herpestidae. This is likely to reflect a difference in preferred habitat relative to those available at Laetoli, although that would be difficult to demonstrate with certainty. However, it can hardly be coincidence that the arboreal genets are rare at Laetoli while the terrestrial small herpestids are common. The viverrids of the Plio-Pleistocene show marked differences in adaptations from those of today. This is most clearly manifested in the presence at many sites, including Laetoli, of viverrids of considerably larger size than any in the modern fauna. *Viverra leakeyi*, first described from Laetoli (Petter 1963) but known from several other sites (Werdelin and Lewis 2005), is one example.

Herpestidae

Most of what we know of the evolutionary history of modern Herpestidae in Africa comes from Laetoli. Although herpestids referred to extant genera and even extant species have been reported from Miocene African localities (Peigné et al. 2005), it is not until the Laetolil Beds that a diverse fauna of small carnivores of modern aspect is known. Indeed, *H. palaeogracilis* is by far the most common carnivore at Laetoli. Herpestids continue to be reported infrequently in sites younger than the Laetolil Beds, but only at Olduvai is there a diverse assemblage (Petter 1973). This temporal distribution clearly has to do with taphonomic and collecting biases, and the record of Herpestidae and small carnivores in general in Africa is far more biased than that of the larger carnivores. Nonetheless, it is probably significant to note that all the Herpestidae of Laetoli have been referred to extant genera. There is no record within this family of adaptations beyond the range of what is seen in its African members today. Judging by the frequency and state of preservation of the Laetoli finds, it is likely that *Helogale* and possibly some of the other herpestids were social and lived in burrows, just like today, setting a minimum age for the evolution of sociality in Herpestidae (cf. Veron et al. 2004).

Hyaenidae

Knowledge of fossil Hyaenidae, not least in Africa, has improved greatly since Barry (1987) published his review of the Laetoli carnivores (Werdelin and Solounias 1991; Werdelin et al. 1994; Werdelin and Turner 1996b; Werdelin 1999b, 2003b). Thus, it is now possible to address the problems of identification that Barry (1987) pointed out and put names on the Laetoli hyenas.

In the case of *C. dietrichi*, this has already been done by Petter and Howell (1989) and their and Barry's (1987) identification of the Laetoli hyena as a species distinct from the extant *C. crocuta* is corroborated herein. In addition, LAET 76-3951, discussed separately by Barry (1987), has been assigned to this taxon.

Barry's (1987) Hyaenidae, *incerta sedis* (specimens LAET 75-3338 and 75-1849) are now assigned to *I.* cf. *I. abronia* and are very likely to represent a late form of this species. The same is true of specimen LIT 59/465, discussed separately by Barry (1987). The species *P. howelli* had not been described when Barry wrote his review, and only one specimen was known at the time. The recovery of additional material from Kanapoi has allowed recognition of this species (Werdelin 2003b) and the referral of LAET 76-4008, discussed separately by Barry (1987), to this taxon. It is interesting that the partial skeleton from the Lower Laetolil beds can be assigned to this taxon, as they are approximately coeval with the Kanapoi deposits. Also of great interest is the identification of LAET 75-494 (another specimen discussed separately by Barry (1987)) as *Lycyaenops* cf. *L. silberbergi*, corroborating Turner's (1990) identification of a member of this lineage at Laetoli. The identification of *Pachycrocuta* from Laetoli is less secure, but not unexpected, given its presence at other, similarly aged deposits in eastern Africa (Werdelin 1999b).

Our understanding of the Hyaenidae of Laetoli has thus changed, from one identifiable taxon and a number of individual specimens of uncertain affinities to five taxa, all known from other African sites of similar age to the Laetolil Beds.

Felidae

The Felidae is the most complex family present at Laetoli, both because of its great diversity and because of the difficulty in assigning the material to a particular species or species group. There are two species assigned to *Panthera*, one approximately lion-sized and one approximately leopard-sized. Both show clear differences from the modern species in size range and both have been the subject of taxonomic controversy. There is also a taxon similar to but different from the extant cheetah, along with two or three smaller felid taxa. Add to this two machairodont taxa, and the total diversity of Felidae represented at Laetoli is 7–8 species-level taxa. Part of the problem in definitely assigning the material to genera, let alone species, is that these are the earliest records for several of these taxa. For the large *Panthera* in particular this is a problem, as the first record of such a form in eastern Africa is from Olduvai, Bed I, where material indistinguishable from modern lion is present. The relationship between the Laetoli and Olduvai large *Panthera* cannot be determined at present, though the most parsimonious assumption must surely be that they represent two members of the same lineage. A similar gap in the temporal distribution of the leopard-like form is bridged in part by material from the Omo sequence of Ethiopia (Howell and Petter 1976), though this material also is fragmentary and consists mainly of isolated teeth, thus not solving the attribution problems discussed here. *Panthera* indistinguishable from the modern leopard is present in the KBS Mb. of the Koobi Fora Fm., at about the same time as the modern lion appears at Olduvai. Material from South Africa must be reanalyzed for comparison with the eastern African material for a better understanding of the history of these taxa, but this is beyond the scope of the present contribution.

The *Acinonyx* sp. from Laetoli has similar issues. It is the first record of the genus and shows characters distinguishing it from the modern species, but the exact relationships between them cannot be determined. The smaller felids are difficult to assess because of the lack of clear autapomorphic traits distinguishing different genera and species, coupled with the very small samples available, which preclude true statistical assessment of the material.

Ironically, it is the extinct felid species that present the fewest problems, though the lack of an analysis of *Homotherium* in Africa makes it impossible to assign the Laetoli material to a species or to evaluate its position relative to other *Homotherium*, in Africa and elsewhere.

Table 8.9 Presence (X) of carnivoran faunal elements in the major stratigraphic subdivisions of the Laetoli site

Family	Taxon	Lower unit	Upper unit	Ndolanya Beds
Canidae				
	?*Nyctereutes barryi*		X	
	cf. *Canis* sp. A		X	
	cf. *Canis* sp. B		X	
	aff. *Otocyon* sp.		X	
Mustelidae				
	Prepoecilogale bolti		X	X
	Mellivora sp.		X	
	Aonyxini gen. et sp. nov.	X		
	Mustelidae indet.		X	
Viverridae				
	Viverra leakeyi		X	
	Genetta sp.		X	
	aff. Viverridae		X	
Herpestidae				
	Herpestes palaeoserengetensis		X	
	Herpestes ichneumon		X	
	Galerella sp.		X	
	Helogale palaeogracilis	X	X	X
	Mungos dietrichi		X	X
	Mungos sp. nov.?		X	
Hyaenidae				
	Crocuta dietrichi		X	X
	Parahyaena howelli	X	X	
	Ikelohyaena cf. *I. abronia*		X	?
	Lycyaenops cf. *L. silberbergi*		X	
	?*Pachycrocuta* sp.		X	
	aff. *Proteles* sp.	X		
Felidae				
	Dinofelis petteri		X	X
	Homotherium sp.		X	X
	Panthera sp. aff. *P. leo*		X	
	Panthera sp. cf. *P. pardus*		X	X
	Acinonyx sp.		X	
	Caracal sp. or *Leptailurus* sp.		X	X
	Felis sp.		X	X

Summary

In summary, compared with other Pliocene eastern African carnivore faunas, Laetoli shows several unique features: the diversity of Canidae, the diversity of small carnivores, the possible presence of *Proteles*, and the presence of the earliest *Panthera* (two species) and *Acinonyx*.

One interesting aspect of the Laetoli carnivoran fauna is the differences (or lack thereof) between the major stratigraphic units (Table 8.9). Of course, the material from the Laetolil Beds (upper unit) overshadows the material from the lower unit and from the Ndolanya Beds. This notwithstanding, the similarity between the upper unit and the Ndolanya Beds faunas is striking. The latter has no taxa that are not present in the former, and the additional taxa present in the upper unit can most likely be ascribed to a sampling effect, given the discrepancy in the number of specimens available between the two units. It might be thought that the absence of taxa unique to the Ndolanya Beds is also due to sampling, but this is to some extent negated by the lower unit fauna. Despite the fact that there is very little material available from the lower unit, two of four taxa found there are unique to that unit.

This pattern of similarities and differences in carnivoran representations mirrors that of eastern Africa as a whole. Werdelin and Lewis (2005) showed that the time between 3.4 and 2.5 Ma is one of reduced turnover in eastern African carnivoran faunas, and the Laetoli sequence is no exception. By contrast, there is considerable turnover between 4.0 and 3.4 Ma. It is not until about 2.4 Ma that turnover increases again, with the influx of a number of new taxa. It should be noted that the lower unit and Ndolanya Beds material was not included in these calculations. Thus, from a carnivore's perspective, the environment in eastern Africa in the time span from the Upper Laetolil Beds to the Upper Ndolanya Beds was apparently highly stable, regardless of the particular environment at any given site.

Leaving the small carnivores aside, as their presence in the collections is clearly a result of sampling effort, we interpret the presence of the other taxa as indicating some differences in the environmental mosaic that is Laetoli from the environments sampled at other localities of similar age (4–2.5 Ma). Though carnivores in general are poor environmental indicators, there is one aspect of habitat that they do record, and that is the open/closed habitat spectrum, especially if viewed in a comparative context. Thus, all or nearly all of the taxa present at Laetoli and absent from similarly aged localities are taxa that are indicative of open grassland or woodland, rather than forested, habitats. This is true of Canidae, which, as a group, is probably the most open-habitat–adapted carnivore family; it is true of *Proteles*, which is dependent on open-habitat–dwelling termites for its subsistence; and it is true of species of *Panthera* and *Acinonyx*, especially if compared with the relatively closed-habitat–adapted machairodonts (though *Homotherium* apparently inhabited a broad spectrum of habitats).

Further, the taxa listed above, with the exception of *Proteles* and *Acinonyx,* are also generalist species relative to those present at other sites. Perhaps we are seeing in the carnivore fauna of Laetoli the first manifestation of the modern-day situation in eastern Africa, with much of the environment dominated by open-habitat, generalist carnivores. Regardless, Laetoli has a carnivore guild that is unique among Pliocene African localities, and further studies of this assemblage should shed considerable light on the origin of modern African carnivore guilds.

Note

During the time this paper has been in press, some additional papers on fossil carnivores of Africa have been published, that directly impact on statements made herein. Tedford et al. (2009) have definitively identified *Canis ferox* from North America as the oldest *Canis*. Geraads et al. (2010) have described a new species of *Nyctereutes*, *N. lockwoodi*, from Dikika. This species is also found at Hadar and is considerably more derived than ?*Nyctereutes barryi*, described herein. Finally, the new species of *Crocuta* from the Kataboi Mb. alluded to herein has been described as *C. eturono* (Werdelin and Lewis, 2008).

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Chapter 9
Proboscidea

William J. Sanders

Abstract Paleontological fieldwork between 1998–2005 by the Eyasi Plateau Expedition at Laetoli and nearby sites produced a large collection of proboscidean fossils from the early to mid Pliocene Lower and Upper Laetolil Beds and late Pliocene Upper Ndolanya Beds, and possibly older sediments at Endolele, that substantially enlarges the sample of proboscidean material recovered earlier by Louis Leakey in 1935, Kohl-Larsen in 1938–1939, and Mary Leakey in the 1970s and early 1980s. The present study of the combined proboscidean sample confirms the presence of deinotheres and loxodont elephants, and provides the first description of anancine gomphotheres from the area. In addition, the first stegodont from the Eyasi Plateau is identified. The study also suggests that gomphotheres and loxodont elephants evolved locally in the Eyasi Plateau during the early Pliocene. Inference from stratigraphic distribution of proboscidean taxa, isotopic analyses, and dental morphology corresponds with paleoecological reconstruction depicting the Eyasi Plateau during the early-mid Pliocene as covered with abundant shrub- and grassland, with more restricted gallery forest, and as drier during the late Pliocene. Age-grade mortality profiles of elephants and deinotheres from the Laetolil and Upper Ndolanya Beds indicate a chronic lack of standing water or cyclical incidences of drought in the region for a sustained interval of time.

Keywords Laetoli • Endolele • Pliocene • Tanzania • Deinotheres • Loxodont elephants • Anancine gomphotheres

Introduction

Pliocene fossil proboscidean remains from the Eyasi Plateau comprise an integral segment of the temporally successive record of the order from northern Tanzania, interpolated between Mio-Pliocene localities of the Manonga Valley that have yielded fossils of the archaic elephants *Primelephas korotorensis* and *Stegotetrabelodon orbus* and the primitive anancine gomphothere *Anancus kenyensis* (Sanders 1997) and Pleistocene horizons at Olduvai dominated by the more advanced elephant *Elephas recki* (Maglio 1973; Coppens et al. 1978; Beden 1980, 1985). The most productive sites of the Eyasi Plateau for proboscidean fossils are Kakesio and Laetoli, which have yielded important collections from the Lower Laetolil Beds, Upper Laetolil Beds and Upper Ndolanya Beds, respectively. Of these sites, the greatest number of proboscidean fossils derives from Laetoli. The discovery of hominin fossils at Laetoli, including the holotype specimen of *Australopithecus afarensis*, several series of bipedal trackways attributed to *A. afarensis*, possibly the oldest specimen of *Paranthropus aethiopicus*, and an archaic *Homo sapiens* cranium (Johanson et al. 1978; Leakey and Hay 1979; Day and Wickens 1980; Day et al. 1980; Leakey 1987a, b; Harrison 2002, 2011) have made it one of the most famous paleontological sites in East Africa. Although less celebrated than the hominins, the proboscideans from Laetoli and other Eyasi Plateau sites are nonetheless important for establishing a reliable chronological framework for the region, and for paleoecological reconstruction. Moreover, they provide evidence of environmental changes that may have impacted on regional succession of early hominins.

The East African Archaeological Expedition of 1934–1935, led by Louis Leakey, undertook the first paleontological collecting in the Eyasi Plateau area, and recovered a small number of proboscidean fossils from Laetoli and Endolele (or Endulele = Esere?). The Laetoli ("Vogel River") material was briefly mentioned by Hopwood in Kent (1941), who recognized the occurrence of two elephant species and *Deinotherium bozasi*, after initially placing the elephant fossils into one species (Hopwood 1936). It is less clear whether Hopwood's (Kent 1941: 179) "*Mastodon* from the basal beds" refers to gomphothere specimens from Endolele. Slightly later, in 1938–1939, Kohl-Larsen made a larger collection of deinotheres and elephants at Laetoli, which was subsequently described by Dietrich (1941, 1942). Given what is now understood about the elephant sample from

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the site, it is notable that Dietrich grouped the elephant specimens from the Laetolil Beds into a single species, "*Archidiskodon exoptatus*." It was not until much later, however, that Coppens (1965) first recognized that this elephant belonged in *Loxodonta*. A return to a two-species taxonomic scheme was made by Maglio (1969, 1973), who identified *Elephas recki* and *Loxodonta adaurora* in the combined Louis Leakey and Kohl-Larsen collections. More recently, however, with the addition of a much larger proboscidean collection from the Mary Leakey expeditions to Laetoli in the 1970s and early 1980s, Beden (1987a) organized all of the Laetolil Beds elephant material again into one species, *Loxodonta exoptata*. This work was supplemented by Harris' (1987a) detailed description of the deinothere specimens. Although Mary Leakey's group collected at the nearby site of Kakesio, at which the Lower Laetolil Beds is exposed, the proboscidean fossils recovered there were not described, nor was a gomphothere molar from the Upper Laetolil Beds.

Between 1998–2005, paleontological survey and collecting were resumed at Laetoli and nearby sites by the Eyasi Plateau Expedition, under the direction of Terry Harrison, in collaboration with the Tanzanian National Museums. A substantial number of proboscidean fossils with well-controlled chronostratigraphic proveniences were recovered, increasing size of the overall sample and taxonomic diversity. In addition to supporting the identification and validity of *Loxodonta exoptata* from the Laetolil Beds (and overlying Upper Ndolanya Beds), study of this material also confirms the presence of *Deinotherium bozasi*, adds the first formal record of the rare (in the eastern rift) *Stegodon* from Tanzania, and provides the first description and taxonomic interpretation of anancine gomphotheres from Endolele, Kakesio, and Laetoli. The proboscidean sample shows signs of regional evolution of the anancine gomphotheres and elephants, is consistent with early-late Pliocene dating of the Lower and Upper Units of the Laetolil Beds and Upper Ndolanya Beds, and suggests that the enigmatic site of Endolele may be older than Lower Laetolil Beds localities (particularly Kakesio) dated to ca. 4.4–3.85 Ma (Deino 2011). Furthermore, by inference from dental morphology, isotopic analyses, and stratigraphic occurrence of taxa, the proboscidean sample supports paleoecological reconstruction depicting Laetoli and the surrounding area during the mid-Pliocene as primarily covered with abundant grassland and shrubland, with more restricted patches of gallery forest, and becoming drier in the late Pliocene. In addition, the age-grade mortality profile of the proboscidean sample, particularly the elephants, indicates the periodic occurrence of drought or chronic lack of standing water. This view of ancient Laetoli is critical for understanding the ecological dynamics associated with the evolution of early hominins, including our own precursors.

Abbreviations

Geological: Loc., locality; Ma, Mega annum (10^6 years); Mb., member; Fm., formation. Skeletal: dP/dp, upper/lower deciduous premolar; ET, enamel thickness; H, height; HI, hypsodonty index (H x 100/W); l., left; L, length; LF, lamellar frequency (number of plates per 100 mm); M/m, upper/lower molar; mc, metacarpal; mm, millimeters; mt, metatarsal; P/p, upper/lower premolar; r., right; W, width; x, anterior or posterior cingulum(id). Institutional: BM(NH), The Natural History Museum, London (formerly the British Museum [Natural History]); -AT, Aterir, Kenya; -BC, Chemeron Formation, Baringo Basin, Kenya; EP, specimens collected by the Eyasi Plateau Expedition; KK, Kakesio, Tanzania; KNM, Kenya National Museums; -KP, Kanapoi, Kenya; L followed by a number series, Middle Awash, Ethiopia; LAET, specimens from Laetoli collected by Mary Leakey; -LT, Lothagam, Kenya; NK, Kaiso-Nkondo Area, Nyawiega, Uganda; WM, Wembere-Manonga Formation, Manonga, Tanzania.

Systematic Paleontology

Order PROBOSCIDEA Illiger, 1811
Suborder INCERTAE SEDIS
Superfamily DEINOTHERIOIDEA Bonaparte, 1845
Family DEINOTHERIIDAE Bonaparte, 1845
Subfamily DEINOTHERIINAE Bonaparte, 1845
Genus *DEINOTHERIUM* Kaup, 1829
DEINOTHERIUM BOZASI Arambourg, 1934

Eyasi Plateau Occurrence: Upper Laetolil Beds: Loc. 2, 5–10, 10NE, 10W, and 22; Upper Ndolanya Beds: surface below Loc. 7E.

Diagnosis: Readily distinguished from elephantoid proboscideans by its low-slung cranium, absence of upper tusks, downturned mandibular symphysis and lower tusks, molar bilophodonty (except for trilophodont dP4/dp4 and M1/m1), and simultaneous presence of all cheek teeth in adult animals (no horizontal tooth replacement) (Harris 1978). Differentiated from *Chilgatherium* and *Prodeinotherium* by larger teeth, from *Prodeinotherium* by simplification of postmetaloph ornamentation of second and third molars, more retracted nasal aperture, and a shorter, narrower cranial roof, and from *D. giganteum* by narrower external nares and rostral trough (Harris 1978; Sanders et al. 2004).

Description: *Deinotherium bozasi* is represented at Laetoli by a small number of mostly isolated teeth. While there are five teeth (P3-M3) in each adult jaw quadrant, as opposed to three deciduous teeth (dP2-4) in infant and juvenile jaw quadrants, the proportion of deciduous premolars in the combined deinothere cheek tooth collection from Laetoli (13/39) indicates a substantial percentage of pre-adult individuals in the sample, especially as at least four adult teeth are from one individual.

The majority of the best specimens from the Mary Leakey expeditions have been previously well described and figured, and include LAET 75-541, r. dp2, LAET 78-5221, r. dp2, LAET 79-5452, l. dp3, LAET 81-16, r. dp4, LAET 81-77, l. dp4, LAET 75-2032, l. p3-4 and m2-3, and LAET 78-4973, l. P3 (Table 9.1; Harris 1987a).

A tooth from the Mary Leakey collection previously not described is a heavily worn left dP2, LAET 81-10 (Fig. 9.1a), from Loc. 2. This deciduous premolar is missing most of its lingual edge, and enamel is spalled off of its buccal and distal margins. The protocone and hypocone have been worn into large dentine ovals that are transversely connected to the ectoloph by ridges forming the proto-and metalophs, respectively. These lophs tightly enclose a central fovea. There is a remnant of a low mesial cingulum. Though dP2 is otherwise poorly known for *D. bozasi*, the preserved length of LAET 81-10 (Table 9.1) is typical in size for other species of *Deinotherium*.

Earlier (1938–1939), Kohl-Larsen collected a small number of deinothere fossils from the Laetoli area, including 12 teeth and a third metacarpal, apparently from the Upper Laetolil Beds. The dental sample is composed of four dp3s, a p4, two P3s, a P4, two M1s, an M2, and an M3, and was briefly described by Dietrich (1942). Dimensions for these teeth are provided in Table 9.1, and fall within the range for *Deinotherium* (Fig. 9.2a). The metacarpal has a greatest length of 210 mm and mid-shaft breadth of 65 mm (Dietrich 1942: 92).

Louis Leakey (together with G.T. Bell, Stanhope White, and Peter Kent, part of the East African Archaeological Expedition of 1934–1935) collected the first deinothere fossils from the Laetoli area in 1935. These include two dP2s and part of a permanent molar. Each dP2 preserves enough morphology to show that the ectoloph merged with the transverse proto-and metalophs in wear (Fig. 9.1b), and that when unworn these lophs were ornamented apically by mammelons. Dimensions for these few specimens are listed in Table 9.1.

More recent collecting by the Eyasi Plateau Expedition has produced eight deinothere dental specimens, from Loc. 2, 8, 9, and 10. All of these derive from the Upper Laetolil Beds. Several of these are complete enough to warrant description: EP 412/98 is a dp3 with the mesial cingulid and protolophid intact, and a remnant of the anterior cristid of the hypolophid showing. The protolophid exhibits typical deinothere chisel-like wear along its distal margin, and has a height of 38.5 mm. The exposed enamel ranges from 1.5–1.7 mm in thickness. EP 4231/00, from Loc. 2, is a moderately worn right dP3, nearly complete (Fig. 9.1c). It has low mesial and distal cingula closely appressed to the main lophs, which are separated by a transverse valley. The proto-and metalophs form continuous transverse crests that expand into large dentine ovals lingually; prominent cristae project distally from the buccal margins of each crest. EP 1410/03 is a more heavily worn, left dP3

Table 9.1 Inventory and dimensions of identifiable deinothere cheek teeth from Laetoli (Eyasi Plateau region), in mm. Specimens lacking accession numbers were collected by Kohl-Larsen and measured by Dietrich (1942)

Taxon/Accession #/ Specimen	Locality	Plates/Loph(id)s	L	W	H	ET	HI
Deinotherium bozasi							
No# dp3		–	53.0	37.0	–	–	–
No# p4		–	82.0	64.0	–	–	–
No# P3		–	91.0	–	–	–	–
No# P4		–	90.0	–	–	–	–
No# M1		3	102.0	80.0	–	–	–
No# M2		2	98.0	–	–	–	–
No# M3		2	100.0	98.0	–	–	–
BM(NH) 14946 Permanent molar		–	–	–	–	–	–
BM(NH) 14946 dP2		2	40.7	36.7	–	–	–
LIT.AS 7-VI-35 ?dP2		Loph	–	40.7	–	–	–

(continued)

Table 9.1 (continued)

Taxon/Accession #/ Specimen	Locality	Plates/Loph(id)s	L	W	H	ET	HI
LAET 75-541 dp2	10	–	34.0	21.3	32.0	–	150
LAET 78-5221 dp2	7	–	32.5	23.0	31.0	1.5	135
LAET 79-5452 dp3	6	2	55.5	40.8	–	–	–
LAET 81-16 dp4	2	3	73.5	50.5	–	–	–
LAET 81-77 dp4	10	3	76.4	49.0	–	–	–
LAET 75-2032 p3	10	–	77.6	57.9	–	–	–
LAET 75-2032 p4	10	2	81.5	67.5	53.0	–	78
LAET 75-2032[a] m2	10	2	92.3e	81.1	–	–	–
LAET 75-2032[a] m3	10	2	109.2e	91.7+	–	–	–
LAET 81-10 dP2	2	2	41.7+	35.5+	–	–	–
LAET 78-4973[a]	2	2	94.5e	93.5e	–	–	–
LAET 75-621 Molar fragments	5	–	–	–	–	–	–
LAET 81-80 Parts of two loph(id)s	7 east	–	–	–	–	–	–
LAET 75-813 Protolophid of m2 or m3	7	–	–	–	–	–	–
LAET 75-156B Tooth chip	9	–	–	–	–	–	–
LAET 75-1411 Small molar fragment	9	–	–	–	–	–	–
LAET 75-2554 Molar fragment	10 northeast	–	–	–	–	–	–
LAET 75-2314 Molar fragment	10	–	–	–	–	–	–
LAET 75-635 Molar fragment	22	–	–	–	–	–	–
EP 412/98 dp3	10	2	46.9+	–	38.5	1.5–1.7	–
EP 4231/00 dP3	2	2	54.9	49.3	–	–	–
EP 1410/03 dP3	8	2	56.7	53.4	–	–	–
EP 697/00 Molar fragment	2	–	–	–	–	–	–
EP 4126/00 DP fragment	8	–	–	–	–	–	–
EP 1082/98 Adult molar fragment	9	–	–	–	–	–	–
EP 3200/00 Molar fragment	10 west	–	–	–	–	–	–
EP 3199/00 adult lower molar fragments	10 west	–	–	–	–	–	–

BM(NH) and LIT.AS specimens are from the 1935 collection of Louis Leakey. LAET specimens are from the Mary Leakey collections. EP specimens are from the collection of Eyasi Plateau expeditions

e estimated, *ET* enamel thickness, *H* height, *HI* hypsodonty index, Hx100/W, *L* length, *W* width, + indicates a missing portion of a specimen, and that the dimension was greater when complete

[a] Marks specimens with dimensions from Harris (1987a)

(Fig. 9.1d), from Loc. 8. It is similar in shape and occlusal construction to EP 4231/00, with a prominent ento-and ectoflexus demarcating the two lophs. This gives the crown a figure eight shape in occlusal view. A strong crista extends posteriorly from the buccal margin of the protoloph to connect with a nearly indistinct, low crista extending anteriorly from the buccal margin of the metaloph. Because of the high degree of wear, the lophs converge nearly across the transverse valley in the midline. Upper deciduous third premolars are poorly known for *D. bozasi*; however, the dimensions of the Laetoli specimens (Table 9.1) are similar to those of dP3s of *D. giganteum*, and exceed the range for *Prodeinotherium* (Fig. 9.2b).

Remarks: At Laetoli, deinotheres are known for certainty from the Upper Laetolil Beds. A fragment of an upper permanent molar (LAET 81-80, not 80-81 as is listed in Harris 1987a) was thought to be of unknown provenience because it was a surface find (Harris 1987a: 295), but its collection below Loc. 7E indicates that it derives from the Upper Ndolanya Beds. Because they are very useful in distinguishing African *Deinotherium* from *Prodeinotherium*, it is unfortunate that no deinothere crania or dentaries were recovered from Laetoli. Tusk fragments associated with LAET 75-2032 in the collection are too large to belong to a deinothere and are clearly those of an elephant. Nonetheless, the cheek teeth in the sample are large (Fig. 9.2a, b) and distally simple enough to indicate assignment to *Deinotherium*. As pointed out by Harris (1987a), the only deinothere identified from late Miocene-early Pleistocene sites in Africa is *D. bozasi*, so it is likely that this is the species present at Laetoli.

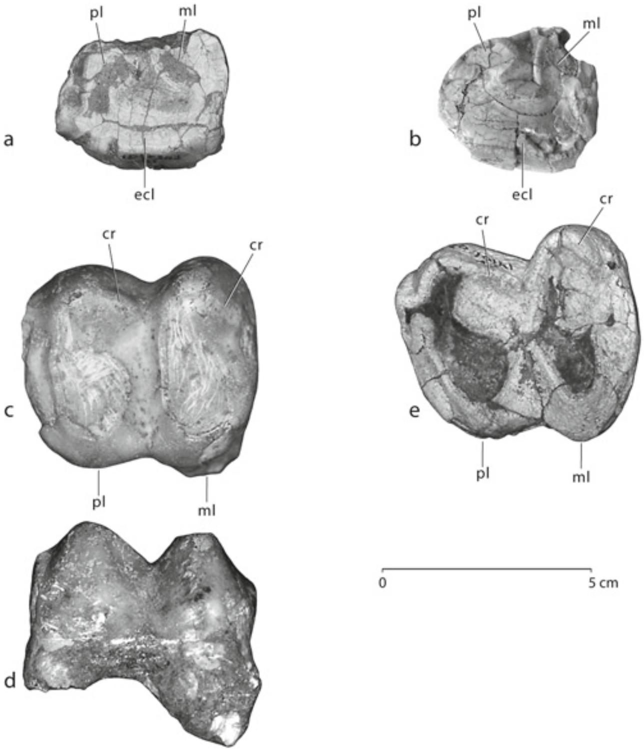


Fig. 9.1 Dental specimens of *Deinotherium bozasi* from Laetoli (*cr* crista, *ecl* ectoloph, *ml* metaloph, *pl* protoloph). Anterior is to the left in each specimen. (**a**) Occlusal view, left dP2 specimen LAET 81-10 (*reversed*). (**b**) Occlusal view, right dP2 specimen BM(NH) 14946. (**c**) Occlusal view, right dP3 specimen EP 4231/00 (*reversed*). (**d**) Lateral view, right dP3 specimen EP 4231/00 (*reversed*). (**e**) Occlusal view, left dP3 specimen EP 1410/03

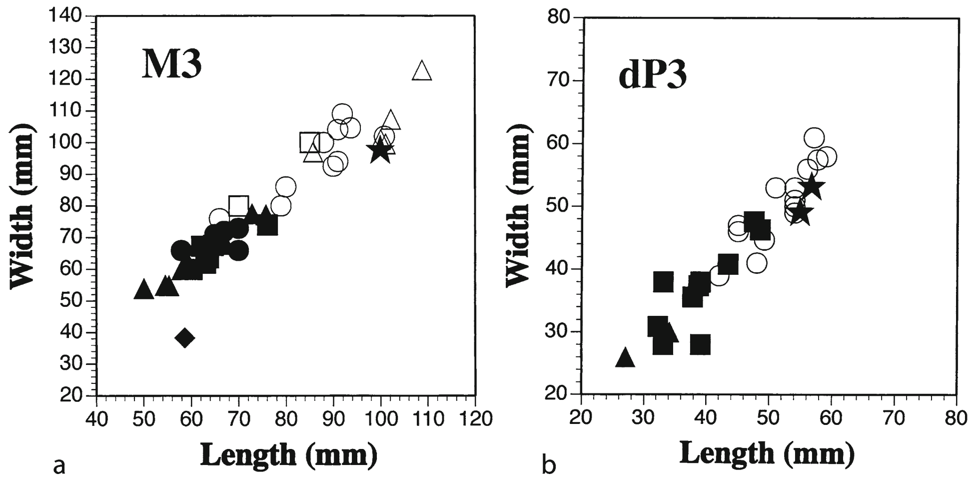


Fig. 9.2 Bivariate plots of M3 and dP3 crown length versus width in deinotheres. Comparative dimensions supplementing original measurements are from Bachmann (1875), Weinsheimer (1883), Roger (1886), Andrews (1911), Cooper (1922), Palmer (1924), Éhik (1930), MacInnes (1942), Gräf (1957), Sahni and Tripathi (1957), Symeonidis (1970), Harris (1973, 1977, 1983, 1987a), Gaziry (1976), Tobien (1988), Tsoukala and Melentis (1994), Huttunen (2000), Sach and Heizmann (2001), Sanders (2003), and Sanders et al. (2004). Symbols: ♦, *Chilgatherium harrisi*; ▲, *Prodeinotherium hobleyi*; ■, *P. bavaricum* (including "*P. hungaricum*"); ●, *P. pentapotamiae*; Δ, *Deinotherium bozasi*; ○, *D. giganteum* (including "*D. levius*"); □, *D. indicum*; ★, deinothere specimens from Laetoli. (**a**) M3. (**b**) dP3

Deinotherium bozasi is the terminal species of a specialized proboscidean family that first appeared in the late Oligocene of Africa (Sanders et al. 2004) and persisted on the continent until the end of the early Pleistocene (Beden 1985; Behrensmeyer et al. 1995). Although possibly the largest terrestrial animal of the African Neogene (Christiansen 2004), it is poorly represented in the fossil record (Harris 1987a), usually by pieces of isolated teeth. The structure of its brachyodont, lophodont molars and results of dental isotopic analyses indicate that it was a dedicated browser (Harris 1975; Cerling et al. 2005). Harris (1978) interpreted its craniodental features to suggest that it occupied densely vegetated gallery forests, which has important implications for reconstructing the paleoecology of mid Pliocene Laetoli. If *D. bozasi* was as rare in the Upper Ndolanya Beds as evidence indicates (only one specimen recovered), this may signal a shift to drier conditions locally during the late Pliocene. Although deinotheres are thought to have had shorter trunks and less ability to reach the ground than elephants (Harris 1975), δ^{18}O enamel composition for deinotheres and elephants at Laetoli are equally depleted (Kingston and Harrison 2007), suggesting that they both relied on drinking meteoric water and therefore presumably were not drought resistant. This might be an important consideration for determining the cause of high pre-adult mortality of deinotheres at Laetoli.

Suborder ELEPHANTIFORMES Tassy, 1988
Superfamily ELEPHANTOIDEA Gray, 1821
Family GOMPHOTHERIIDAE Hay, 1922
Subfamily ANANCINAE Hay, 1922
Genus *ANANCUS* Aymard, 1855
ANANCUS KENYENSIS (MacInnes, 1942)

Eyasi Plateau Occurrence: ?Lower Laetolil Beds: Endolele (Endulele) = Esere?.

Diagnosis: African anancine gomphotheres have short, broad crania with elevated vaults and raised bases. Upper tusks are straight and lack enamel. Mandibles are brevirostrine and lack incisors. Intermediate molars (dP4/dp4-M2/m2) of *A. kenyensis* are tetralophodont. Third molars have five or six loph(id)s. Dental enamel is very thick (5.0–7.0 mm in third molars), and usually unfolded. Crown morphology is simple, with posttrite posterior accessory conules restricted to the mesial moiety of m3, and usually M3, as well. Loph(id)s are constructed of massive, low conelets. In upper molars, pretrite half-lophs are offset anteriorly, relative to their posttrite half-lophs (anancoidy), and the reverse condition occurs in lower molars; anancoidy may be weakly expressed.

Description: No crania or mandibles of this species have been recovered from the Eyasi Plateau region. Nonetheless, two molars from Endolele document the presence of *A. kenyensis* at the site. These specimens are distinctly different from anancine gomphothere molars from the Lower and Upper Laetolil Beds at Kakesio and Laetoli. BM(NH) 32958 is a nearly complete right M3 in wear, collected in 1935 by Louis Leakey, missing only its posterior cingulum, with five lophs, accessory conules to mid-crown, moderately well-expressed anancoidy, and a trace of cementum in the transverse valleys (Fig. 9.3a). Enamel is very thick, and coarsely folded in the first loph. The lamellar frequency is 3.75, reflecting the anteroposterior massivity of the lophs.

The second specimen (Endo: LS BKE 35 is its field catalogue reference) confirms the presence of *A. kenyensis* at the site. It is a very worn, tetralophodont right M1 or M2 (Fig. 9.3b). Despite the wear, anancoid arrangement of half-lophs is perceptible. This tooth was also collected by Louis Leakey in 1935. Dimensions for these specimens are provided in Table 9.2. Comparative assessment of these specimens (Table 9.3) confirms the opinion of V. J. Maglio, in a note accessioned with them, that the specimens are "not *A. osiris*. Looks like good *kenyensis*."

A fragmentary astragalus from Esere 1 (=Endolele?) (EP 1671/98) has a more saddle-shaped tibial articular surface than is typical for elephants, and might also belong to *A. kenyensis*. Although African anancine gomphotheres are well-represented craniodentally, little is known of their postcranials.

Remarks: *Anancus kenyensis* is the best-known anancine gomphothere species of East and Central Africa, and is also the oldest representative of the subfamily in Africa. Abundant evidence exists showing that the species underwent progressive evolution, with increases over time in occlusal complexity, crown size, loph(id) number, and degree of anancoidy (Mebrate and Kalb 1985; Kalb and Mebrate 1993; Kalb and Froehlich 1995). The East-Central African anancine lineage was subdivided into time-successive stages by Mebrate and Kalb (1985), and into primitive "*kenyensis*"- and advanced "*petrocchii*"-morphs by Tassy (1986). The use of the term "*petrocchii*-morph," however, was unfortunate because it confused an advanced *stage* with a North African anancine *species* (*A. petrocchii*) that originally was depicted as having a simple crown morphology and weak anancoidy (Petrocchi 1943, 1954; Coppens 1965; Sanders 2008). Examination of unnumbered anancine gomphothere molars collected more recently at Sahabi (Boaz et al. 1979) reveals a more complex occlusal pattern than reported by Petrocchi or Coppens (Sanders 2008). This calls into question whether Petrocchi's original descriptions and figure (1943, 1954: Fig. 20b) were inaccurate or, alternatively, a precise depiction of a sample from a different geological unit than the specimens more recently studied. There is some evidence that the proboscidean collections from Sahabi are representative of two time-successive intervals of late Miocene and early Pliocene age (Sanders 2008). If so, the older material may belong in *A. petrocchii*, and the younger material may be identifiable with the

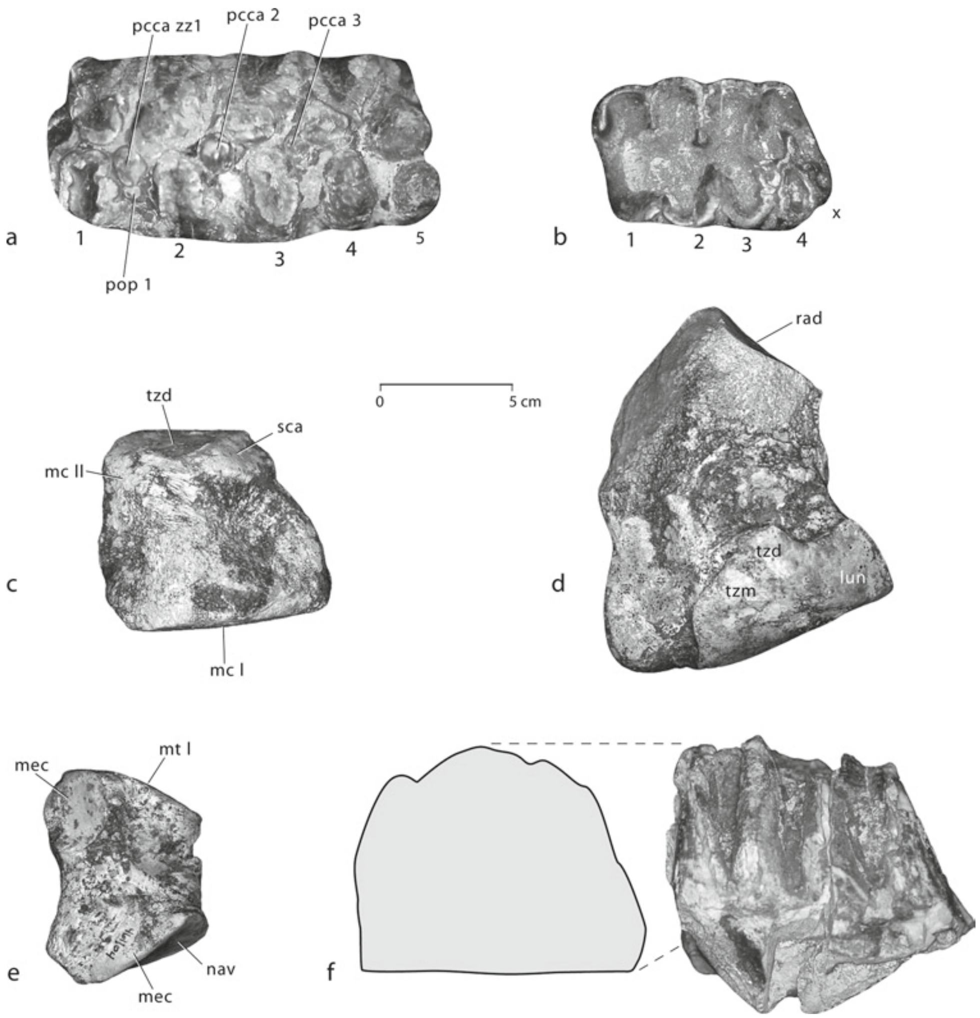


Fig. 9.3 Elephantoid dental and postcranial specimens from Endolele and Noiti 3 (*lun* lunate, *mc* metacarpal, *mec* mesocuneiform, *mt* metatarsal, *nav* navicular, *pcca*, posterior pretrite accessory conule, *pop* posterior posttrite accessory conule, *rad*, radius, *sca* scaphoid, *tzd*, trapezoid, *tzm* trapezium, *x* cingulum(id)). Anterior is to the left in each tooth. (**a**) Occlusal view, right M3 specimen BM(NH) 32958, *Anancus kenyensis*, from Endolele. (**b**) Occlusal view, right M1 or M2 specimen Endo: LS BKE 35, *A. kenyensis*, from Endolele. (**c**) Lateral view, trapezium EP 461/04, *Loxodonta exoptata*, from Noiti 3. (**d**) Lateral view, scaphoid EP 461/04, *L. exoptata*, from Noiti 3. (**e**) Lateral view, entocuneiform EP 461/04, *L. exoptata*, from Noiti 3. (**f**) Lateral view and anterior cross-section, third molar specimen Endo: LS BKE 35, *Loxodonta* sp. *cf. Loxodonta cookei*, from Endolele

advanced morph of *A. kenyensis*. In any case, differences between the primitive and advanced anancine gomphothere morphs of East and Central Africa are substantial enough to merit formal taxonomic division. Here, the primitive morph of the lineage is retained in *A. kenyensis* with the type from Kanam, Kenya (MacInnes 1942), and the advanced morph is placed in its own species (see below).

Anancus kenyensis (as newly defined above) is a late Miocene-early Pliocene species, with an established age range of ca. 7.4–4.3 Ma (Sanders et al. 2010), occurring in the Lower and Upper Mbs. of the Nawata Fm. at Lothagam, Kenya (Tassy 2003), at Toros Menalla, Chad (Vignaud et al. 2002; Hautier et al. 2009), the Mpesida Beds and Lukeino Fm. in the Tugen Hills, Kenya (Hill et al. 1985, 1986; Tassy 1986; Hill 2002), the Adu Asa Fm. and Kuseralee and Haradaso Mbs. of the Sagantole Fm., Middle Awash, Ethiopia (Kalb and Mebrate 1993; Haile-Selassie 2001; Haile-Selassie et al. 2004), Lemundong'o, Kenya (Ambrose et al. 2003; Saegusa and Hlusko 2007), the Ibole Mb. of the Wembere-Manonga Fm., Manonga Valley, Tanzania (Sanders 1997), Kanam East and West, Kenya (MacInnes 1942; Tassy 1986), Nkondo, Uganda (Tassy 1985), Lasdanan Mb., Galili, Ethiopia (Kullmer et al. 2008), and at Kossom Bougoudi, Chad (Brunet et al. 2000; Brunet 2001). A note written by Louis Leakey in 1935 locates Endolele in the "general Laetolil area... near the 'springs' some 8 miles away [from the Laetoli type site] in a different formation." The lower age assessment of 4.4 Ma for the Lower Laetolil Beds exposed at

Table 9.2 Dimensions of anancine gomphothere cheek teeth from the Eyasi Plateau region, in mm

Taxon/Accession #/Locality	Specimen	Plates/Loph(id)s	L	W	H	ET	HI
Anancus kenyensis							
No # (Endo: LS BK 35) (Endolele)	M2	x4x	99.1	60.9 (4)	–	3.0–3.9	–
BM(NH) 32958 (Endolele)	M3	x5+	160.0+	76.0	66.0 (4)	4.9–5.5	87
Anancus ultimus sp. nov.							
EP 157/00 Loc. 16, Upper Unit	dP2	x3	25.7	18.5	–	–	–
EP 1149/00 Loc. 8, Upper Unit	dp2	*x*2	25.1	14.4	–	–	–
EP 080/98 (Kakesio 6)	dp3	x3x	50.2	30.9 (3)	–	–	–
EP 1514/04 (Loc. 22 East, Upper Unit)	dp3	x3x	47.0	28.2 (3)	–	–	–
KK 82-57 (Kakesio)	dp3	x3x	58.1	37.4	–	1.5	–
	dp4	5x	102.5	52.2	–	–	–
LAET 81-75 (?Laetoli ?Upper Unit)	Distal molar frag.	+3x	+87.3	+76.3	–	5.7–6.0	–
KK 82-49 (Kakesio)	Molar frag.	+3+	+56.1+	56.0+	–	3.9–4.8	–
EP 073/98 (Kakesio 6)	Molar frag.	x3+	109.0+	69.8+	–	4.3–4.6	–
EP 861/04 (Kakesio 8)	Distal molar frag.	+1x	+41.0	63.5	57.0	3.3	90
KK 82-248 (Kakesio)	m1	x5x	123.6	64.0 (4)	–	5.0	–
EP 073/98 (Kakesio 6)	M2 or M3	x3+	102.0+	67.9+	–	2.7–3.5	–
KK 82-69 (Kakesio)	M3	7x	220.0	80.8 (6)	–	5.0–5.2	–
KK 82-292 (Kakesio)	M3	x7x	205.0	90.0 (3)	–	4.8–5.5	–
EP 197/05 (type) (Loc. 16, Upper Unit)	m3	x7x	160.0	79.6 (2)	–	–	–

e estimated, *ET* enamel thickness, *H* height, *HI* hypsodonty index, H x 100/W, *L* length, *W* width, + indicates a missing portion of a specimen, and that the dimension was greater when complete. Numbers in parentheses indicate loph(id)s of greatest width and height

Table 9.3 Comparative distribution of traits in African anancine gomphothere molars

Taxon	Intermediate molars	Third molars	Anancoidy	Crown complexity	Enamel folding	Other
Anancus kenyensis	Tetralophodont	5–6 loph(id)s	Weak	Simple	None-coarse	
A. ultimus sp. nov.	Pentalophodont	6–7 loph(id)s	Moderate-pronounced	Complex	Moderate-strong	
A. capensis	Tetralophodont	6–7 loph(id)s	Pronounced	Complex	Moderate-strong	
A. petrocchii (type series of Petrocchi, 1943, 1954)	Pentalophodont	6 lophids (only m3 known)	Weak	Simple	Unknown	m3 very large, relatively narrow
A. osiris	Tetralophodont	5–6 loph(id)s	Weak-pronounced	Very simple	None-coarse	

Kakesio (Drake and Curtis 1987; Harris 1987b; Hay 1987; Deino 2011), with its more derived anancine than at Endolele, indicates that Endolele is even older, supporting Louis Leakey's assertion about the stratigraphy of the site.

ANANCUS ULTIMUS SP. NOV.

Partial Synonymy: *Trilophodon angustidens cf. kisumuensis* (in part), Hooijer, 1963; *Anancus osiris*, Coppens, 1965; *A. osiris*, Servant-Vildary, 1973; *A. kenyensis* (in part), Coppens et al., 1978; *A. kenyensis* (in part; *A. kenyensis* "*petrocchii*-morph"), Tassy, 1986; *Anancus* sp. (Sagantole-type), Kalb and Mebrate, 1993; *Anancus cf. Anancus* sp. (Sagantole-type), Sanders, 1997; *A. kenyensis*, Harris and Leakey, 2003; *A. kenyensis* (in part), Tassy, 2003; *A. kenyensis*, Mackaye et al., 2005; *A. osiris*, Mackaye et al., 2005; *A. kenyensis*, Kingston and Harrison, 2007.

Etymology: *Ultim'us* (L., masc.), meaning "most extreme in time or sequence," in reference to the final phase of the anancine gomphothere lineage in East-Central Africa.

Holotype: Tanzanian National Museums, Dar es Salaam, EP 197/05, l. m3 (Fig. 9.4a).

Paratypes: Laetoli, EP 157/00, ?r. dP2; EP 1149/00, l. dp2; EP 1514/04, r. dp3; LAET 81-75, molar fragment.

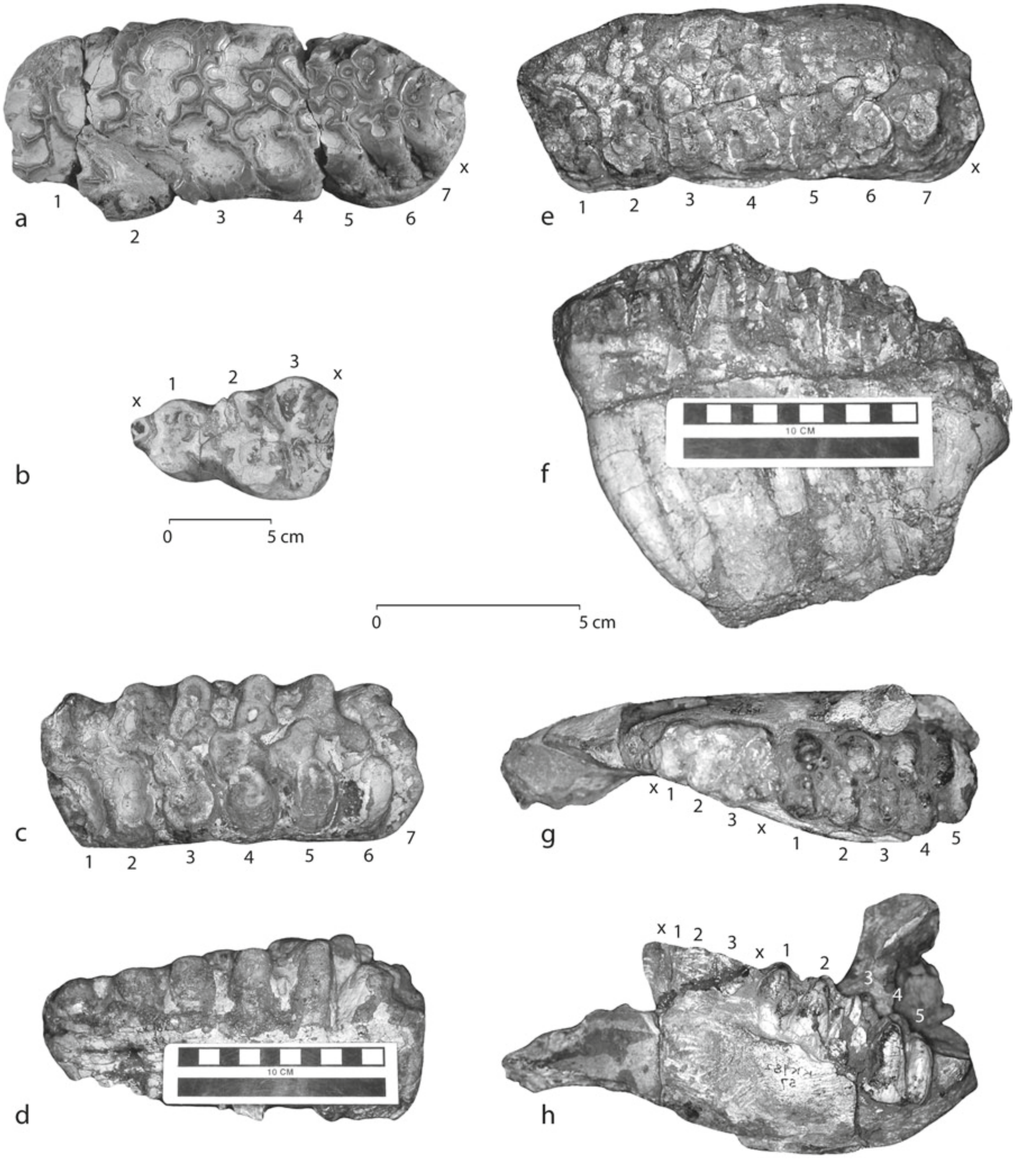


Fig. 9.4 Dental specimens of *Anancus ultimus* sp. nov. from Kakesio and Laetoli (*x* cingulum(id)). (**a**) Occlusal view, left m3 specimen EP 197/05, holotype. (**b**) Occlusal view, left dp3 specimen EP 080/98. (**c**) Occlusal view, M3 specimen KK 82-292. (**d**) Lateral view, M3 specimen KK 82-292. (**e**) Occlusal view, M3 specimen KK 82-69. (**f**) Lateral view, M3 specimen KK 82-69. (**g**) Occlusal view, right partial dentary with worn dp3 and emergent dp4 KK 82-57. (**h**) Lateral view, right partial dentary with worn dp3 and emergent dp4 KK 82-57

Type Locality: Loc. 16, Upper Laetolil Beds, Laetoli, Tanzania, ca. 3.6 Ma.

Age and Occurrence: Early-mid Pliocene, eastern, central, and ?North Africa.

Eyasi Plateau Occurrence: Lower Laetolil Beds: Kakesio 6 and 8, Kakesio South; Upper Laetolil Beds: Loc. 16 and 22E.

Referred Specimens: Kanapoi, Kenya: KNM-KP 384, l. m2; KNM-KP 410, associated l. and r. m2, l. m3. Chemeron Fm., Tugen Hills, Kenya: KNM-BC 33, l. M3; KNM-BC 380, r. dentary fragment with partial m3; KNM-BC 1627, l. M2 or M3 fragment; KNM-BC 1628, r. M1 or M2 fragment; KNM-BC 1655, l. dentary fragment with m3; KNM-TH 15591, l. M3. Aterir, Kenya: KNM-AT 20, l. M3; EP 197/05, l. m3. Lothagam, Kenya: KNM-LT 341, associated r. and l. partial m3 and l. partial M3; KNM-LT 361, r. partial m1; KNM-LT 383, r. partial M1; KNM-LT 23790, l. partial M1 or M2; KNM-LT 28567, l. partial P4. Kiloleli, Tanzania: WM 927/92, r. partial ?M3. Ngofila 1, 2, Tanzania: WM 493/94, molar fragment; WM 791/94, molar fragment. Beredi South 3, Tanzania: WM 1706/92, molar fragment. Kakesio, Tanzania: KK 82-292, r. M3 (Fig. 9.4c, d); KK 82-49, molar fragment; KK 82-57, r. dentary with dp3-dp4 (Fig. 9.4g, h); KK 82-69, l. m3 (Fig. 9.4e, f); KK 82-248, r. dentary fragment with m1 or m2; EP 073/98, l. M2 or M3 fragment; EP 080/98, l. dp3; EP 861/04, molar fragment. Middle Awash, Ethiopia: L124-1, r. partial M3; L227-1, r. M2; L337-3, l. M3; L140-1, r. partial m3; L150-1, r. m3; (Dhidnley and Shabeley Laag Mbs., Galili, Ethiopia) GAL-VP 1/002, l. M2; GLL-242, l. m1 or m2. As Duma, Gona, Ethiopia: WMS 6 P1, r. m3; WM 9 P346, r. dp4 or m1. Nkondo-Kaiso Area, Nyawiega, Uganda: NK 438’86, maxillary fragment with r. M2-M3 and pieces of a left molar; NK 2580’89, molar fragment; BM(NH) 25159, l. partial m1; BM(NH) 25166, molar fragment. Sinda River, Democratic Republic of Congo: Sinda nº 2, r. partial M3.

Diagnosis: Intermediate molars (dP4/dp4-M2/m2) pentalophodont; third molars with six or seven loph(id)s. Lower third molars smaller and relatively wider than those of *A. petrocchii*. Anancoidy well expressed. Occlusal morphology usually complex; posttrite and pretrite accessory conules often extend to the posterior moiety of molar crowns. Accessory conules may be doubled. Talonids may be crowded with many conelets. Moderately worn half-loph(id)s with coarsely to finely folded enamel. This combination of features is unique among African species of *Anancus* (Table 9.3).

Description: The type m3, from Laetoli, Tanzania is worn and some pieces are missing along its edges, but exhibits its important diagnostic features. This molar has very derived anancine morphology, with seven lophids, strong anancoidy, and a complex occlusal pattern of anterior and posterior central accessory conules throughout nearly the entire extent of both the pre-and posttrite sides (Fig. 9.4a). The complexity of the crown characteristic of *A. ultimus* sp. nov. is also exhibited by a partial upper molar that may have been derived from the Upper Laetolil Beds, LAET 81-75. If so, this is the first anancine gomphothere specimen recovered from the Upper Unit, unreported until now. The presence of anancine gomphotheres in the Upper Laetolil Beds is also marked by EP 1514/04, an extremely worn right dp3 from Loc. 22E. Even in this state of wear, the offset of pre-and posttrite half-lophids is apparent. In occlusal view, this specimen has an elongate triangular shape, and exhibits a small anterior cingulid and three lophids.

EP 1514/04 closely resembles EP 080/98, a left dp3 from an older horizon at nearby Kakesio. EP 080/98 is heavily worn, and has a diminutive anterior cingulid, three lophids, and a compressed posterior cingulid with obvious transverse offset of half-lophids (Fig. 9.4b).

In addition, two other deciduous teeth from Laetoli may also belong to *A. ultimus* sp. nov. The first is a small, narrow, sub-triangulate dp2 (EP 1149/00) with a diminutive anterior cingulid formed of a single conelet, a first lophid composed of two slightly offset conelets, and a posterior lophid formed of one stout conelet. The second is a more robust, worn dP2 (EP 157/00) that is rounder in occlusal aspect. This tooth is relatively broader, and has three lophs, each formed of two conelets. The conelets in lophs 2 and 3 are slightly offset. Low anterior and posterior cingulae are apparent, though heavily worn and closely appressed to lophs. Dimensions for these specimens are given in Table 9.2. The offset of half-loph(id) conelets suggests they are from anancine gomphotheres.

Anancine gomphothere fossils are far more common in the Lower than Upper Laetolil Beds, particularly at Kakesio, and unmistakably document the presence of *Anancus ultimus* sp. nov. in the lower part of the Laetolil Beds sequence. Molars from Kanapoi, Kenya (Harris et al. 2003), dated to 4.2–4.1 Ma (Feibel 2003), are morphologically similar to those from Kakesio, helping to corroborate its age at ca. 4.4–3.85 Ma (Drake and Curtis 1987; Deino 2011). An M3 from Kakesio (KK/82 292) is strongly anancoid, with thick (4.8–5.5 mm), coarsely folded enamel, seven lophs, posterior accessory conules fused to worn pretrite half-lophs 1–5, and doubled posterior accessory conules associated with posttrite half-lophs 1–4 (Fig. 9.4c, d). Cementum is thinly distributed on loph walls and in the transverse valleys. Similarly, although crown details are not as easy to see in M3 specimen KK 82-69, it is evident that it has seven lophs and posttrite accessory conules (Fig. 9.4e, f). EP 073/98 is an incomplete M2 or M3 from Kakesio that exhibits the strong anancoidy and doubled posttrite accessory conules typical of the species.

Among the features distinguishing *A. ultimus* sp. nov. from *A. kenyensis* is pentalophodonty of intermediate molars, present in several specimens from Kakesio. Specimen KK 82-248 is a right dentary fragment with a complete, worn m1 or m2 that has five lophids and pretrite accessory conules associated with lophids 1–3. KK 82-57 is a partial right dentary with a worn dp3 and emergent dp4. The dentary is brevirostrine, with a corpus height of 76.5 mm and width of 68.2 mm at the anterior end of dp4. The dp3 has a lophid formula of x3x, and is larger and less triangulate in occlusal shape than EP 080/98 or EP 1514/04. The dp4 has five lophids and a low posterior cingulid tightly appressed to the last lophid, distinct anancoidy, traces of cementum, and accessory conules associated with pre-and posttrite half-lophids to the middle of the crown (Fig. 9.4g, h). It is possible that Kakesio is the source area of the "*Mastodon*" from the "basal beds" mentioned by Hopwood in Kent (1941: 178–179).

Remarks: *Anancus ultimus* sp. nov. is primarily composed of specimens of the "advanced morph" of the *A. kenyensis* lineage. The species is present in the Chemeron Fm., Tugen Hills, Kenya (Hill et al. 1985, 1986), the Apak Mb. of the Nachukui Fm. at Lothagam, Kenya (Tassy 2003), at Kollé, Chad (Brunet 2001), Nyawiega, Uganda (Tassy 1995), Aterir, Kenya (Hill 1994), in the Kilolei Mb. of the Wembere-Manonga Fm., Manonga Valley, Tanzania (Sanders 1997), at Kanapoi, Kenya (Harris et al. 2003), at Ekora, Kenya (Kalb and Mebrate 1993), in the Aramis, Beidareem, and Adgantole Mbs. of the Sagantole Fm., Middle Awash, Ethiopia (Kalb and Mebrate 1993; Kalb and Froehlich 1995; Renne et al. 1999), in the Dhidnley and Shabeley Laag Mbs. of the Mount Galili Fm., Galili, Ethiopia (Kullmer et al. 2008), at As Duma, Gona, Ethiopia (Semaw et al. 2005), and in the Sinda Beds, Democratic Republic of Congo (Hooijer 1963; Yasui et al. 1992; Boaz 1994). The age of these sites suggests that evolution of tetralophodont into pentalophodont anancine gomphotheres in East-Central Africa occurred in the 5.0–4.5 Ma interval, and that tetralophodont and pentalophodont forms coexisted for at least 500,000 years. The last known occurrence of *A. ultimus* sp. nov. is at Laetoli, marking a mid-Pliocene termination of anancines in East-Central Africa. In northern and southern Africa, however, the subfamily persisted until the end of the late Pliocene (Depéret et al. 1925; Arambourg 1945, 1970; Fournet 1971; Hendey 1978, 1981; Cooke 1993; Geraads and Amani 1998; Geraads and Metz-Muller 1999; Geraads 2002; Sahnouni et al. 2002).

Considerable intra-site variation and morphological and metric overlap among temporally successive site samples complicate attempts to subdivide the *A. kenyensis*-*A. ultimus* sp. nov. lineage, particularly at sites where fossil teeth are fragmentary and intermediate molars are absent. Further taxonomic challenges may arise due to progressive changes in the morphology of early to late forms of *A. ultimus* sp. nov. For example, molars of the species from the lower Chemeron Fm., Tugen Hills, Kenya have little or no folding of enamel wear figures, thick enamel, and a maximum of six loph(id)s in third molars. Third molar specimens from the Aramis and Beidareem Mbs. of the Sagantole Fm., Middle Awash, Ethiopia that are probably geologically younger, on the other hand, have a more complex occlusal morphology, with pre-and posttrite accessory conules distributed throughout the length of the crown, thinner enamel, greater enamel folding, and thicker cementum. Despite these complications, differences in molar occlusal organization, particularly between end members of this lineage, are more than sufficient to reliably distinguish *A. kenyensis* and *A. ultimus* sp. nov. at the species level.

Anancine gomphotheres may have differentiated regionally over time in Africa, based on different combinations of cheek tooth features (Table 9.3). For example, while the *A. kenyensis*-*A. ultimus* sp. nov. lineage of East and Central Africa evolved molars with more complex distribution of accessory conules, more folded enamel, stronger anancoidy, pentalophodonty of intermediate molars, and a greater number of third molar loph(id)s (Mebrate and Kalb 1985; Kalb and Mebrate 1993), in South Africa progressive molar crown features in *A. capensis* are accompanied by primitive retention of tetralophdonty of intermediate molars (Sanders 2006, 2007), and in North Africa, *A. osiris* primitively retained simple molar crowns with heavy, pyramidal loph(id)s, and tetralophodont intermediate molars, right to the end of the Pliocene (Arambourg 1945; Coppens 1965; Coppens et al. 1978; Tassy 1986). *Anancus petrocchii*, known only from the latest Miocene or early Pliocene of Sahabi, Libya (Coppens 1965; Coppens et al. 1978), was depicted as uniquely having massive, pyramidal molar loph(id)s, simple occlusal morphology, and weak anancoidy coupled with the more advanced trait of intermediate molar pentalophodonty (Petrocchi 1943, 1954). Examination of more recently collected anancine molars from Sahabi reveals occlusal morphology that is more complex than previously described, with small pre-and posttrite accessory conules distributed throughout molar crowns, and coarsely-folded enamel in some worn specimens (Sanders 2008). This sample is much closer morphologically to *A. ultimus* sp. nov. than to *A. osiris*, differentiated from the former primarily by larger size and relative narrowness of its third molars (Sanders 2008). Assessing whether this implies a biogeographic connection between anancine populations in East-Central and northeast Africa, or is due to convergence, will require further investigation. *Anancus ultimus* sp. nov. clearly differs morphometrically from *A. petrocchii* as described by Petrocchi (1943, 1954) and Coppens (1965). If the original diagnoses and illustration of *A. petrocchii* are incorrect, and the entire anancine sample from Sahabi is as derived as *A. ultimus*, a good argument could be made for invalidating *A. petrocchii* and placing the sample in *A. ultimus*.

Because of the low-crowned, bunodont condition of their molars, anancine gomphotheres were considered to have been browsers that inhabited forests (Smart 1976). However, stable isotope analyses on tooth enamel from a number of

East and Central African sites, including Kakesio, indicate that anancines had predominantly C_4-plant based diets (Cerling et al. 1999, 2003; Zazzo et al. 2000; Harris et al. 2003; Semaw et al. 2005; Kingston and Harrison 2007), except at Langebaanweg, South Africa, where C_3 grasses are inferred to have been prevalent (Franz-Odendaal et al. 2002). Preference for graze and the need to feed close to the ground, and possibly greater reliance on the trunk for food acquisition, might be correlated with the loss of lower tusks in this gomphothere subfamily.

Family STEGODONTIDAE Osborn, 1918
Genus *STEGODON* Falconer and Cautley, 1847
STEGODON SP. *CF*. *STEGODON KAISENSIS* Hopwood, 1939

Eyasi Plateau Occurrence: Upper Laetolil Beds: Loc. 22.

Diagnosis: Convergent on elephants in having molars constructed of enamel plates, high, antero-posteriorly compressed crania with elevated parietals and occipital, and mandibles with brevirostrine symphyses and no lower tusks (Osborn 1942; Saegusa 1987, 1996; Kalb et al. 1996). Molars are very brachyodont, with plates separated by Y-shaped transverse valleys in lateral cross-section, and formed of numerous bi-laterally compressed conelets, or “mammellons” (Osborn 1942; Coppens et al. 1978; Kalb et al. 1996; Saegusa 1996).

Description: Only one stegodont specimen has been recovered from the Laetoli area, EP 1197/98, a fragment of a left upper fourth deciduous premolar (Fig. 9.5a, b). The specimen preserves one full plate, and parts of two other plates. Its length is +30.8+ mm, width is 44.6 mm, slightly worn height is 34.6 mm, and enamel thickness is 1.8 mm. The greater width than height of the tooth shows that it was low crowned. It has abundant cementum coating the anteriormost transverse valley, and infilling the posteriormost transverse valley. There are no accessory conules. The complete plate is formed of 11 laterally compressed conelets, and is transversely straight. The first two plates are apically divergent, indicating that this is an upper tooth, and the width of the specimen suggests it is a dP4.

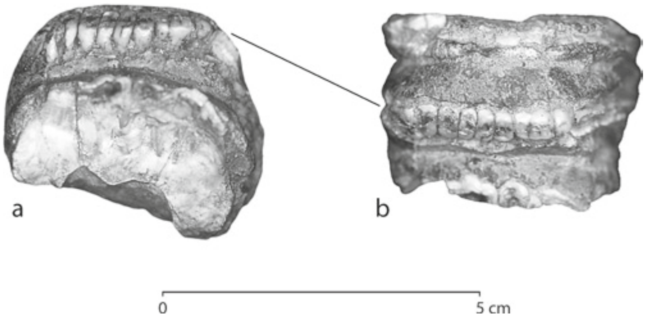


Fig. 9.5 Dental specimen of *Stegodon* sp. *cf*. *Stegodon kaisensis* from Laetoli. (**a**) Anterior oblique view, partial dP4 specimen EP 1197/98. (**b**) Occlusal view, partial dP4 specimen EP 1197/98. Note the transversely straight array of numerous, laterally compressed conelets, typical of stegodonts

Remarks: Elephants and stegodonts both have molars constructed of plates, rather than loph(id)s, and in both, plates of deciduous premolars may be formed of numerous conelets. The identification of EP 1197/98 as a stegodont is based on the lateral compression of the conelets, so that each has a greater mesio-distal than transverse dimension.

Stegodonts are best known in Africa from latest Miocene-mid Pliocene sites in Central Africa (Brunet et al. 1998, 2000; Zazzo et al. 2000; Brunet 2001; Fara et al. 2005) and the Western Rift (Hopwood 1939; MacInnes 1942; Cooke and Coryndon 1970; Coppens et al. 1978; Sanders 1990; Yasui et al. 1992; Pickford et al. 1993; Tassy 1995). By comparison, in East Africa stegodont occurrences are extremely rare, known only from a handful of specimens from the Tugen Hills, Kenya (Sanders 1999), Manonga Valley, Tanzania, and the Omo, Ethiopia (Beden 1975, 1976), of late Miocene to late Pliocene age (Harrison and Baker 1997; Kingston et al. 2002; Alemseged 2003). Thus, it is not surprising that only a single specimen has been recovered from the Laetoli area. Together with the Manonga specimens, the Laetoli tooth represents the southernmost extent of stegodonts in Africa.

Only one species of stegodont, *Stegodon kaisensis*, is currently recognized in Africa (Sanders et al. 2010). Tassy (1995) has divided this species into a primitive “Nkondo stage” and more derived “Warwire stage,” separated by slight differences in crown height, plate number, conelet compression, and development of cementum. Based on Tassy’s criteria, EP 1197/98 is most similar to “Warwire stage” molars from the Western Rift, Koro Toro, Chad, and the Omo, Ethiopia, of mid to late Pliocene age.

Based on their extreme brachyodonty, upper tusk morphology, body proportions, and isotopic analysis of South Asian molar specimens, stegodonts have been depicted as forest-dwelling browsers (Osborn 1921, 1942; Cerling et al. 1999). Isotopic analysis of Central African stegodonts, however, shows that during the mid to late Pliocene, their feedings habits in that region shifted from browsing to grazing (Zazzo et al. 2000). Because the East African stegodont sample, including EP 1197/98, has not been similarly isotopically sampled, it is not known if they followed the same trend.

Family ELEPHANTIDAE Gray, 1821
Subfamily ELEPHANTINAE Gray, 1821
Genus *LOXODONTA* Cuvier, 1825 (anonymous emendation 1827)
LOXODONTA SP. *CF*. *LOXODONTA COOKEI* Sanders, 2007

Eyasi Plateau Occurrence: ?Lower Laetolil Beds: Endolele (Endulele) = Esere 1.

Diagnosis: *Loxodonta cookei* is a primitive loxodont elephant that retained permanent third and fourth premolars. It is further distinguished from other species of *Loxodonta* by having fewer molar plates and lower hypsodonty indices, usually less than 100 (third molar width exceeds height; Sanders 2007). Plate formulae: dp2 = 3x; dp3 = x4x; dp4 = x6x; p3 = x3x − x4x; p4 = x4x; m1 = x5x; m2 = x7x; m3 = x7x − x8x; dP3 = x4; dP4 = x5x or x6; P3 = x3x − x4; M1 = 5x − x6; M2 = x5x − x6x; M3 = 7 − 8.

Description: A partial third molar with four preserved plates from Endolele (Endo: LS BKE 35) is wider (93.6 mm) than high (79.0 mm), with each plate composed of between four-six conelets. Lamellar frequency is 4.0. In anterior view, the plates are broadest basally and taper gradually inward toward the crown (Fig. 9.3f). In lateral view, the plates are parallel-sided and separated by U-shaped transverse valleys that are antero-posteriorly compressed and filled with cementum (Fig. 9.3f). Distribution of accessory conules suggests that they would have been incorporated into loxodont sinuses, or "< >" figures, with wear of enamel.

Other fragmentary molar specimens, collected more recently from Esere 1, may also belong to this taxon. The most substantial of these specimens is EP 117/99, a partial third molar with a greatest width of 89.4 mm, and enamel thickness reaching 3.3 mm.

Remarks: The morphology of the elephant molar from Endolele is more primitive than that of *L. exoptata* molars in anterior cross-sectional shape (Fig. 9.3f compared with Fig. 9.8) and crown height. Its closest resemblance is to molars of *L. cookei*, which are best documented at the latest Miocene-early Pliocene site of Langebaanweg, South Africa and that have also been recovered from the Chemeron Fm. (5.3–4.0 Ma; Hill et al. 1985, 1986; Deino et al. 2002) and possibly from the Lukeino Fm. (6.2–5.6 Ma; Hill et al. 1985, 1986; Tassy 1986; Hill 2002) in the Tugen Hills, Kenya, as well as from the Nkondo Fm. in the Nkondo-Kaiso region, Uganda (ca. 5.0 Ma; Pickford et al. 1993; [=*Loxodonta* sp]. "Lukeino stage" of Tassy, 1995) (see Sanders 2007). In third molars of this species, lamellar frequencies are low (3.4–4.2), and crown height rarely exceeds width (hypsodonty indices range from 81–102). Molars are also primitive in having fewer plates than all other crown elephant species (*Mammuthus* spp., *Elephas* spp., *Loxodonta* spp.); for example, third molars have only seven-eight plates. As in molars from the *L. exoptata-L. africana* + *L. cyclotis* lineage, in *L. cookei* molars accessory conules are lower than plate conelets and with wear form loxodont sinuses that may touch in the midline. *Loxodonta cookei* is contrasted with the contemporaneous *L. adaurora* by the development of more prominent loxodont sinuses, and appears to have been a late Miocene-early Pliocene precursor of the *L. exoptata-L. africana* + *L. cyclotis* clade. The presence of a primitive loxodont elephant at Endolele supports the inference made from its anancine fossils that it is older than Kakesio and other localities in the Eyasi Plateau that have exposures of the Lower Laetolil Beds.

LOXODONTA EXOPTATA (Dietrich, 1941)

Eyasi Plateau Occurrence: Lower Laetolil Beds: Kakesio, Kakesio 2, 6, 8, Noiti 3, and Emboremony; Upper Laetolil Beds: Loc. 1–9, 9S, 10, 10E, 10W, 10NE, 11–17, 19–22, 22E, and Garusi River southwest of Norsigidok; Upper Ndolanya Beds: Loc. 7E (=10West in Beden 1987a), 14 (=18 in Beden 1987a), 18, 22S (Nenguruk Hill), 22E, and Silal Artum.

Diagnosis: Molars slightly hypsodont with moderately thick enamel (third molar ET = 2.0–4.0 mm), and plates closer spaced than in archaic elephants (third molar LF = 4.1–5.5). With occlusal wear, anterior and posterior accessory central conules contribute to formation of loxodont median sinuses that occur throughout the length of molar crowns; when wear is light, sinuses may not be apparent or enamel figures may form "propeller" shapes, with the center of the figure prominently rounded and the lateral segments of the figure antero-posteriorly compressed (Kalb and Mebrate 1993; Sanders 1997). Notably, the main criterion used by Dietrich (1941) for creating the species "*exoptatus*" from Laetoli was the similarity of its occlusal enamel figures in the anterior molars to those in *Loxodonta africana*. Compared with *L. cookei*, molars of *L. exoptata* have more plates, are higher crowned, have their widest point higher on the crown, and have higher lamellar frequencies, and permanent premolars were apparently lost (Sanders 2007). Distinguished from contemporaneous *L. adaurora* by molars with narrower plates, more delicate plate construction, and more pronounced development of median sinuses.

Plate formulae: dp2 − x3x − x4x; dp3 = x6x; dp4 = ?7; m1 = x7x − x8 (?9); m2 = 8 − 9x; m3 = 11 − 12; dP2 = x3x = x4; dP3 = x5x = 6x; dP4 = ?x6 − x7x; M2 = 8x − 9x; M3 = 11 − 12 (Beden 1983, 1987b; Harris et al. 2003; Sanders et al. 2010).

Description: Fossil remains of *Loxodonta exoptata* numerically dominate the proboscidean sample from the Eyasi Plateau. Specimens attributable to this species were first recovered by Louis Leakey and party in 1935, and later were added to by more significant collections made by Kohl-Larsen in 1938–1939, Mary Leakey in the 1970s and early 1980s, and the Eyasi Plateau Expedition between 1998–2005. These remains derive primarily from the Upper Laetolil Beds, and a few are also known from the Lower Laetolil Beds and the Upper Ndolanya Beds (Table 9.4). There are no crania of *L. exoptata* known from Laetoli or elsewhere, and the only parts of mandibles that exist for the species are a right dentary fragment with an m2 and crypt for m3 from Kanapoi, Kenya (KNM-KP 30611) and right dentary fragment with an m3 from the Kohl-Larsen collection from Laetoli (lectotype GADJ 2/39 = IPUB 24). The Kanapoi dentary is 111.0 mm high and 102.0 mm wide at the mid-crown of m2.

Table 9.4 Inventory and dimensions of identifiable *Loxodonta exoptata* cheek teeth from the Eyasi Plateau, in mm. All specimens are from the Upper Laetolil Beds, Laetoli, unless otherwise specified

Specimen	Locality	Plates	L	W	H	ET	HI
dP2							
LAET 75-3025	9 south	x3x	26.0	21.1	10.5+	–	–
LAET 74-212	5	x4 or x3X	26.0	21.0	–	–	–
IPUB (18)		x3x	27.0	19.0	13.0	–	68
IPUB (20)		x3	25.0	22.0	–	–	–
IPUB (21)		x3x	26.0	22.0	17.0	–	77
IPUB (22)		x3+	23.0+	22.0	–	–	–
EP 268/03	16	x3x or x4	22.6	16.6	12.0+	–	–
EP 895/98	9 south	x4	22.0	18.3	11.6	–	64
		x3x	21.9	17.8	–	–	–
EP 2652/00	2	x3x	20.3	15.4	–	–	–
EP 209/99	9	x3+	17.0+	14.0	10.7+	–	–
EP 207/01	3	x4x	28.7	21.2	–	–	–
EP 265/99	9 south	x3x	–	–	–	–	–
EP 255/01	5	+2x	+15.3	18.8	14.9	–	79
EP 268/03	16	3x	22.6	16.6	+12.0	–	–
EP 878/98	10	2 plates	–	15.2	12.0	–	79
EP 3696/00	21	–	–	–	–	–	–
EP 4127/00	8	–	–	–	–	–	–
EP 280/04[a]	18	x3+	17.4+	11/6+	–	–	–
dp2							
LAET 75-500	11	x3x	19.8	14.3	10.5	–	73
LAET 74-312	6	x3x	18.8	15.2	–	–	–
IPUB (17)		x3x	22.0	15.0	15.0	–	100
IPUB (23)		3x	20.0	16.0	13.0	–	81
EP 517/98	10	x3x	22.3	16.3	–	–	–
EP 301/00	8	+3x	21.3	17.2	17.0	–	99
EP 112/01	6	x3+	25.0	18.5	–	–	–
EP 753/00	2	x3+	28.8	20.7	14.0	–	68
EP 499/01	2	x3x	25.0	–	–	–	–
EP 792/00	10 east	x3 or 4	27.9	21.9	–	–	–
EP 1150/00	8	–	–	–	–	–	–
EP 1479/00	7 east[a]	x4 or x3X	21.0	17.0	18.0	–	106
dP3							
LAET 75-3451	21	6	55.1	38.3	33.0	1.5	86
LAET 78-4996	2	6	e 55.8	34.1	21.6+	–	–
LAET 75-3044	17	6 or x5	58.8	37.9	–	1.0–1.4	–
LAET 74-114	1	+3+	+31.3+	–	–	1.1–1.3	–
LAET 74-106	x	+4	+50.0	–	–	1.3–1.6	–
LAET 75-1249	8	+3+	–	–	–	1.3–1.5	–
LAET 75-3311	19	+4	+45.0	41.0	–	1.5	–
LAET 76-3950	18[a]	7	53.0	50.0	36.0	1.4–1.5	90
BM(NH) 14941		x6x	59.8	31.0	–	1.2	–
BM(NH) (9)		+4x	+41.0	40.0	–	1.3–1.7	–
LIT.AS 10-VI-35		x6+	61.4+	37.2	–	–	–
IPUB (12)		6	54.0	40.0	–	1.5	–
IPUB (16)		6x	71.0	43.0	–	1.5–1.8	–
EP 1323/04	5	6x	56.2	33.4	–	–	–
EP 121/04	22	+3+	+24.5+	33.9	–	1.3	–
EP 113/01	6	+2x	+27.8	33.8	–	1.0–1.5	–
EP 681/03	2 west	–	–	–	–	–	–
EP 3695/00	8	–	–	–	–	–	–
EP 3349/00	15	x3+	–	–	–	–	–
EP 693/00	2	–	–	–	–	–	–
EP 692/00	2	–	–	–	–	–	–

(continued)

Table 9.4 (continued)

Specimen	Locality	Plates	L	W	H	ET	HI
EP 1148/00	8	–	–	–	–	–	–
EP 612/98	10 west	–	–	–	–	–	–
EP 807/98	10 west	–	–	–	–	–	–
EP 733/98	10 west	–	–	–	–	–	–
EP 734/98	10 west	–	–	–	–	–	–
EP 1081/98	9	–	–	–	–	–	–
EP 1619/98	10 west	–	–	–	–	–	–
dp3							
LAET 76-3963	9 north	6	66.8	35.8	–	1.2	–
LAET 78-5364	21	+4x	+38.3	32.0	–	1.6–1.8	–
LAET 78-5125	4	+5	e 61.5	37.1	–	–	–
LAET 75-1090	6	6x	62.3	34.1	–	1.0–1.5	–
LAET 78-4635	3	4+	41.2+	28.6+	–	–	–
LAET 75-1711	2	x6x	69.3	40.7	–	1.4–2.0	–
LAET 75-1366	12 south	x5+	45.1+	33.1+	26.0+	–	–
LAET 75-822	7	x3+	27.0+	28.4+	–	–	–
LAET 74-280	9	+4x	+38.6	33.1	–	–	–
LAET 78-5164	9	x6	82.7	38.0	32.0	–	84
LAET 75-1503	9	*x*2+	19.0+	–	22.0	–	–
LAET 75-1930	2	+3	+26.0	–	–	1.5	–
LAET 75-2823	6	–	–	–	–	–	–
LAET 74-236	8	–	–	–	–	–	–
BM(NH) 14942		x6x	73.3	36.2	–	1.2	–
BM(NH) (8)		?6	+62.0	38.0	–	1.6	–
BM(NH) (16)		x7	59.0+	34.0	–	1.4–1.6	–
LM.AS 7-VI-35		+5x	+55.5	33.1	–	0.8–1.0	–
IPUB (9)		+4x	+40.0	35.0	–	1.4–1.7	–
IPUB (10)		x3+	30.0+	–	–	1.2–1.5	–
IPUB (11)		6	55.0	36.0	–	1.5	–
IPUB (13)		7x	70.0	38.0	33.0	1.2–1.5	87
IPUB (14)		+4	+42.0	36.0	–	1.2–1.6	–
EP 2201/03	7	x5x or x6	66.0	–	–	–	–
EP 896/98	9 south	+4x	+43.2	34.6	–	1.6–1.9	–
EP 911/04	21	*x*2+ or 3+	22.0+	28.0	–	1.8	–
EP 910/04	21	x3+ or 4+	41.2+	31.2	–	–	–
EP 370/01	2	x3+	41.5+	30.2	–	–	–
EP 269/03	16	+4	56.3+	40.4	–	–	–
EP 815/01	18	–	–	–	–	–	–
EP 2362/03	13 east	–	–	–	–	–	–
EP 270/03	16	–	–	–	–	–	–
EP 1619/98	10 west	–	–	–	–	–	–
dP4							
LAET 75-2248	10 east	+4x	+63.6	47.1+	–	2.0–2.2	–
LAET 75-2180	4	x3+	46.7+	47.0	–	2.5	–
LAET 75-3043	12	3+	27.0+	–	47.0	1.8–2.0	–
LAET 74-196	5	5+	49.8+	47.1	–	–	–
LAET 75-2267	10	+1x	–	–	–	2.0	–
LAET 75-2930	4	5+	47.0+	53.0	–	1.8–2.2	–
LAET 74-212	5	–	–	–	–	–	–
BM(NH) (4)		4+	45.0+	–	–	2.0	–
BM(NH) (7)		3+	32.0+	–	–	1.8	–
LIT.AS 10-VI-35		+3x	+43.4	58.7	47.0	–	80
LIT.AS 6-VI-35		x3+	52.0+	41.0+	–	–	–
IPUB (6)		+4	+45.0	61.0	–	2.0	–
IPUB (25)		+4	–	–	–	1.8	–
EP 1887/03	1	+4x	+65.5	48.2	–	1.9–2.2	–
EP 1698/00	5	+6+	+73.8+	39.8+	–	2.2–2.5	–

(continued)

Table 9.4 (continued)

Specimen	Locality	Plates	L	W	H	ET	HI
EP 691/00	2	x3+	46.7+	50.8	45.0	2.7	89
EP 633/98	10 west	+5+	+58.5+	47.5	45.0	1.6–2.8	95
EP 808/98	10 west	x6+ (originally x7x)	76.5+	45.4	–	–	–
EP 3065/00	5	–	–	–	–	–	–
EP 516/98	10	–	–	–	–	–	–
EP 767/03	9	–	–	–	–	–	–
EP 496/05	1	–	–	–	–	–	–
EP 068/03	2 west	–	–	–	–	–	–
dp4							
LAET 76-3919	1	x4+	67.5+	47.1	–	1.2–1.6	–
LAET 78-4923	5	6+	72.5+	46.1	–	1.8–2.5	–
LAET 75-2027	10	+3x	+54.0	44.0	–	2.3–2.8	–
LAET 75-2553	10	+3x	+45.3	39.5+	–	1.8–2.2	–
LAET 75-2552	10 northeast	7+	85.8+	46.8	48.0	1.4–2.0	103
LAET 75-519	1	–	–	–	–	–	–
LAET 75-1452	9 south	Plate	–	–	–	–	–
LAET 78-5164	9	–	–	–	–	–	–
LAET 75-2240	10 east	–	–	–	–	–	–
LAET 75-3102	12	–	–	–	–	–	–
LAET 75-1969	14[a]	9	113.0	–	–	1.8–2.2	–
?dp4?							
LIT.AS 10-VI-35		+4x	+41.1	38.9	–	1.3	–
BM(NH) no #		x3+	52.0+	41.0+	–	–	–
BM(NH) (1)		4+	35.0+	–	–	1.8	–
BM(NH) (6)		+4x	+72.0	59.0	–	2.0–2.5	–
BM(NH) (10)		4+	45.0+	–	–	1.8–2.1	–
IPUB (2)		5+	55.0+	–	–	1.8–2.0	–
IPUB (15)		5+	53.0+	–	–	1.5–1.8	–
EP 1147/00	8	+4x	+46.4	36.2	–	1.2	–
EP 2201/03	7	–	–	–	–	–	–
EP 269/03	16	–	–	–	–	–	–
EP 2995/00	–	–	–	–	–	–	–
EP 016/98	Kakesio 2[b]	+4+	+71.7+	50.0+	–	2.5–2.7	–
EP 556/04	Silal Artum[a]	–	–	–	–	–	–
M1							
LAET 75-488	10 west	+3+	+50.0+	59.5	78.5	2.3–2.7	132
LAET 75-3101	12	6+	92.4+	–	–	3.3	–
LAET 74-302	6	+3x	+59.0	–	–	2.0–2.2	–
LOL:AS 12-VI-35		+4+	+64.1+	72.7	–	3.2–3.7	–
EP 559/00	22	+3+	44.8+	57.0	–	2.4–3.0	–
EP 695/00		–	–	–	–	–	–
EP 1617/00		–	–	–	–	–	–
EP 1957/00		–	–	–	–	–	–
m1							
LAET 75-522	4	+6x	+125.0	60.0	–	2.2–3.1	–
LAET 74-194	5	+5	+90.2	63.6	–	2.6–3.9	–
LAET 78-4829	18[a]	+4	+67.0	+63.0	–	2.5–2.8	–
LAET 75-277	18[a]	+2+	–	–	–	2.0–2.4	–
BM(NH) (5) = LIT.AS 6-VI-35		x4+	60.0+	–	–	2.4–2.8	–
LIT.AS 6-VI-35		+4x	+74.2	54.0	–	–	–
IPUB (5)		+5	+113.0	–	–	2.4–2.8	–
IPUB (31)		+3x	+58.0	–	–	2.5	–
IPUB (35)		+5x	+91.0	56.0	–	2.5–2.8	–
IPUB (36)		+4+	+107.0+	63.0	–	2.3–2.7	–
EP 1270/01	9 south	x7x or x8	120.5	–	–	2.4–2.6	–

(continued)

Table 9.4 (continued)

Specimen	Locality	Plates	L	W	H	ET	HI
EP 560/00	22	+3+	+77.4+	–	–	2.8–3.5	–
EP 2406/00	16	+4x	+122.2	64.6	–	3.0–3.3	–
EP 1196/98	22	+6	+118.7	67.0	–	3.0–4.0	–
EP 1605/04	11	+3+	+44.4+	60.7	–	2.2	–
KK 82-249	Kakesio[b]	7	133.7	+64.0	–	3.0	–
M2							
LAET 75-3818A	7 east (10 west in Beden, 1987a)	+6	+140.0	–	–	3.0–3.5	–
LAET 75-3818B	7 east (10 west in Beden, 1987a)	+6	+145.0	67.9	–	3.0–3.5	–
LAET 75-521	2	+5+	+107.1+	76.1	–	3.0–3.5	–
LAET 76-4117	12	+4+	+65.6+	+56.7	–	2.3–3.1	–
LAET 75-428		9x	162.0	78.0	80.0	3.0–3.6	103
LAET 75-2574B	15	–	–	–	–	–	–
LAET 75-1684	14[a]	7+	–	–	–	–	–
LOL.AS 12-VI-35		+3+	+71.9+	+78.0	–	2.7–3.7	–
LOL.AS 12-VI-35		+3+	+88.7+	77.7+	–	2.5–3.0	–
BM(NH) 15416		+7x (x9 in Beden, 1987a)	+195.0	86.0	–	3.4–3.7	–
IPUB (7)		+4	+73.0	80.0	–	3.0–3.2	–
IPUB (28)		7+	160.0+	–	–	3.2	–
IPUB (33)		+6x	+103.0	80.0	–	3.0–3.4	–
EP 320/03	3	x2+	58.8+	73.6	–	3.0–3.2	–
EP 694/00	2	+7	+122.7	75.7	–	3.0–4.0	–
EP 519/98	10	8x or 9	+190.0	64.9	72.0	3.4–3.8	111
EP 017/98	Kakesio 2[b]	+3x	+62.7	68.2	+61.0	2.9–3.5	–
EP 029/99	Kakesio 6[b]	5+	107.5+	–	–	2.5–2.7	–
m2							
LAET 75-2791	5	+5	+90.0	69.8	86.0	2.4–2.6	123
LAET 75-1365	12	+4	+108.0	–	–	3.1–3.3	–
LAET 75-3361	21	–	–	–	–	–	–
IPUB (3)		+6	+109.0	75.0	–	–	–
IPUB (4)		+7	+155.0	81.0	–	3.2–3.5	–
IPUB (27)		+4x	+88.0	79.0	–	3.1	–
EP 3173/00	10 west	+3x or +4	+59.8	64.6+	–	2.4–3.6	–
EP 3559/00	12	+4x	+105.1	78.0	84.0	–	108
KK 82-290B	Kakesio[b]	x4+	87.5+	72.5+	–	3.0–3.4	–
M3							
LAET 75-3370	21	+6x	+135.0	85.0	–	3.0–3.7	–
LAET 74-325	7	3+	74.2+	88.8	99.0	3.5–3.7	111
LAET 75-2135	2	x7+	153.0+	84.0	–	3.1–3.5	–
LAET 75-3310	19	x7+	150.0+	77.1	87.0+	3.0–3.3	–
LAET 76-4558	14[a]	11x (13 in Beden, 1987a)	250.0	93.2	100.0	3.0–4.0	107
IPUB (30)		+4x	+103.0	79.0	–	3.4–3.8	–
IPUB (32)		+5x	+118.0	84.0	–	3.5	–
EP 321/03	3	+6+	+128.7	75.4+	–	3.6–3.7	–
EP 1023/00	16	+4+	+59.0+	79.2	111.5	3.2–3.4	141
EP 1618/00	3	+12x	290.0	97.5	140.0	3.5	144
KK 82-no #	Kakesio[b]	+10x	+210.0	76.0+	55.0+	3.0–3.3	–
m3							
LAET 75-489	10 west	+3+	+40.0+	87.6	–	2.5–4.0	–
LAET 79-5458	14[a]	+4+	+85.5+	+75.3	–	3.5–4.0	–
LAET 80-6403	18[a]	11	260.0	82.0	–	3.0–3.5	–
IPUB (8)		+5+	+137.0+	–	–	3.2–3.5	–

(continued)

Table 9.4 (continued)

Specimen	Locality	Plates	L	W	H	ET	HI
IPUB (24) Lectotype		+7x	+205.0	84.0	97.0	3.0–3.3	115
IPUB (26)		+3+	+73.0+	–	–	3.0–3.3	–
IPUB (29)		+4+	+85.0+	84.0	+80.0	3.5	–
IPUB (34)		+7x	+165.0	93.0	–	3.4–3.7	–
IPUB (37)		+8	+184.0	82.0	–	3.2–3.6	–
EP 2295/00	7	+5+	+98.5+	85.7	–	3.0–4.0	–
EP 696/00	2	–	–	–	–	–	–
EP 1650/04	4	–	–	–	–	–	–
EP 029/99	Kakesio 6[b]	–	–	–	–	–	–

BM(NH), LIT.AS, and LM.AS specimens are from the 1935 collection of Louis Leakey. IPUB specimens are from the Kohl-Larsen collection and their measurements are from Beden (1987a). KK and LAET specimens are from the Mary Leakey collection. EP specimens are from the collection of Eyasi Plateau expeditions

e estimated, *ET* enamel thickness, *H* height, *HI* hypsodonty index, H x100/width, *L* length, *W* width, *x* indicates an anterior or posterior cingulum (id), *X* indicates a very large cingulum (id), or incipient plate, + indicates a missing portion of a specimen, and that the dimension was greater when complete

[a] specimen from the Upper Ndolanya Beds, Laetoli

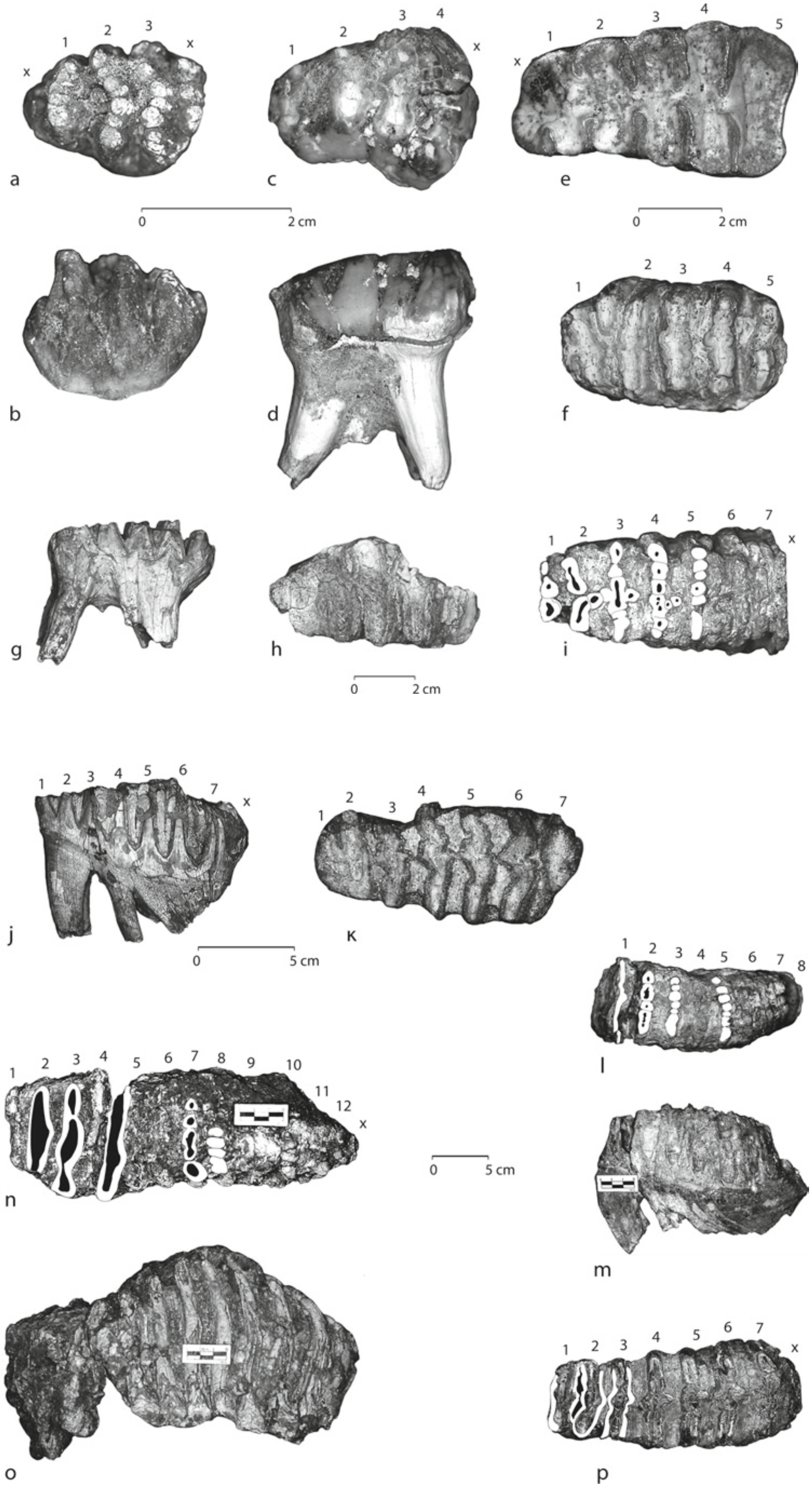
[b] specimen from the Lower Member of the Laetolil Beds

Most of the Eyasi Plateau specimens consist of isolated teeth and tusk fragments. Dietrich (1942: 73) reported a total of 108 elephant teeth from Laetoli, of which 42, or 39%, are deciduous, and the remainder permanent molars. Beden (1987a: 263) sorted these into categories of “very young” (dP2/dp2-dP3/dp3), 24%; “young” (dP4/dp4-M1/m1), 34%; and “adult” (M2/m2-M3/m3), 42%. Unfortunately, many of these teeth did not survive the ravages of World War II. From the combined Louis Leakey, Kohl-Larsen, and Mary Leakey collections, Beden (1987a) estimated that more than 100 individuals were represented, and that more than half of these individuals were infants or young juveniles at death. The recovery of a substantial number of teeth by the Eyasi Plateau Expedition skews the distribution towards infants and young juveniles even more (Table 9.4): 65% (138/213) of identifiable specimens are deciduous teeth (deciduous second premolars, 14%; deciduous third premolars, 29%; and deciduous fourth premolars 22%), and 35% (75/213) are permanent molars (first molars, 11%; second molars, 13%, and third molars 11%). Extant African elephants with only deciduous teeth in occlusion are calves and juveniles; puberty is reached as the first molar starts to emerge, and animals become mature coincident with the first molar being completely in place and well worn (Laws 1966; Sikes 1967). The small percentage of second and third molars in the Eyasi Plateau collections indicates that few prime adults or senior elephants are represented. The increased ratio of deciduous-to-adult teeth in the sample between 1935 and 2005 can be explained as a collecting phenomenon, that is, larger, adult teeth were easily discovered early on, leaving smaller, deciduous teeth to be recovered by more recent intensive collecting episodes, with little fossil “turnover” from erosion in the interim. Because of the large number of fragmentary, unidentifiable specimens (not listed in Table 9.4), and because proveniences are poorly known for most of the Kohl-Larsen and Louis Leakey specimens, however, it is impossible to precisely calculate the minimum number of individuals for the combined *L. exoptata* sample.

Deciduous second premolars are relatively very small and sub-triangulate in shape in occlusal view, with the narrower end anterior (Fig. 9.6a–d). They usually have three plates and anterior and posterior cingulae(id)s, or more rarely four plates. dP2 tends to be much broader posteriorly than dp2. Plates exhibit five or six apical digitations, but are not accompanied by accessory central conules.

Deciduous third premolars are approximately twice the size of the diminutive dP2/dp2s, and vary in occlusal shape from rectangular to sub-triangular, with the narrowest end anterior (Fig. 9.6e–g). Uppers are relatively broader and shorter than lowers. Small anterior and posterior swellings may project from moderately worn plates in the midline, but true loxodont sinuses are not generally formed. Depending on how anterior and posterior cingulae(id)s are counted, these teeth appear to

Fig. 9.6 Cheek tooth specimens of *Loxodonta exoptata* from Kanapoi, Kenya and the Eyasi Plateau, Tanzania. Anterior is to the left (x cingulum(id)). (**a**) Occlusal view, dp2 specimen EP 1479/00. (**b**) Lateral view, dp2 specimen EP 1479/00. (**c**) Occlusal view, dP2 specimen EP 207/01. (**d**) Lateral view, dP2 specimen EP 207/01. (**e**) Occlusal view, dp3 specimen LAET 76-3963. (**f**) Occlusal view, dP3 specimen EP 1323/04. (**g**) Lateral view, dP3 specimen EP 1323/04. (**h**) Occlusal view, dP4 specimen EP 1698/00. (**i**) Occlusal view, dp4 specimen LAET 75-2552. (**j**) Lateral view, m1 specimen EP 1270/01 (reversed). (**k**) Occlusal view, m1 specimen KK 82-249. (**l**) Occlusal view, M2 specimen EP 519/98 (reversed). (**m**) Lateral view, M2 specimen EP 519/98 (*reversed*). (**n**) Occlusal view, M3 specimen EP 1618/00 (*reversed*). (**o**) Lateral view, M3 specimen EP 1618/00 (*reversed*). (**p**) Occlusal view m2 specimen KNM-KP 30611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0 2 cm
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have six-seven plates (or a lamellar formula as low as x4x), each formed of numerous (eight-nine) rounded conelets.

Deciduous fourth premolars tend to have at least six-seven plates, formed of stouter, rounded conelets. In each plate, the central conelet is larger than the lateral ones. As with all other cheek teeth, uppers are relatively wider and shorter than lowers. In occlusal view, these teeth are rectangular (Fig. 9.6h, i). Accessory central conules, particularly posterior ones, are more prominent than in other deciduous premolars, and with moderate wear enamel figures are propeller-shaped. With additional wear, loxodont sinuses may be formed, but when heavily worn enamel figures are rectilinear. LAET 75-1969, from the Upper Ndolanya Beds, has nine plates, but its length (113.0 mm) and enamel thickness (1.8–2.2) are undersized for a permanent molar, and consequently it has been interpreted as a dp4 (Beden 1987a). If so, it is the only complete deciduous fourth premolar known for the species, and indicates that either an estimate of six-seven plates for dP4/dp4 is too low, or that later demes of *L. exoptata* are more progressive in plate number. However, the resemblance of LAET 75-1969 to m1 specimen EP 1270/01 in length, plate number, and overall structure suggests that it is more likely to be a delicate m1 than a dp4.

Permanent molars from M1/m1 to M3/m3 (Figs. 9.6j–p and 9.7a–e) are similar in occlusal morphology, but increase serially in length, width, height, enamel thickness, and number of plates (see above; Table 9.4). Plates are formed of a modest number of conelets (usually five-seven, with the central conelet the most prominent), are moderately spaced, and in lateral view are parallel-sided and separated by U-shaped transverse valleys that are filled with cementum. Cementum covers plates in unworn specimens. Enamel is coarsely to moderately folded in worn specimens. Greatest width of plates is usually slightly above their bases (Fig. 9.8), and in transverse view plates taper gently towards their apices. Anterior and larger posterior accessory central conules are present throughout the crown, and are lower than plates. In unworn specimens or sections of molars, accessory conules may not be visible, and molars may appear to lack these structures and loxodont sinuses in light wear stages (Figs. 9.7a and 9.9a, b). Accessory conules are intimately attached to plates (Fig. 9.9d) and have their greatest girth at their mid-height (Fig. 9.9c), so it is only with moderate

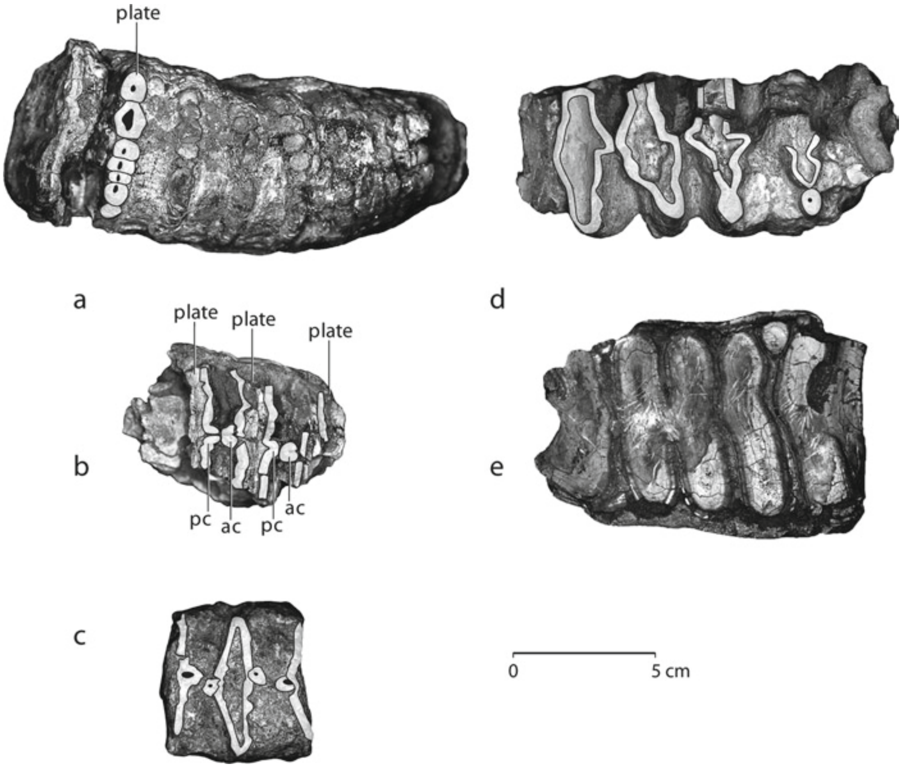

Fig. 9.7 Occlusal view, molar specimens of *Loxodonta exoptata* in different stages of wear (*ac* anterior accessory conule, *pc* posterior accessory conule). (**a**) Occlusal view, M2 specimen EP 519/98, with little or no wear on plates 3–8. No accessory conules are evident in association with plates 3–8, as they are still covered over with cementum. A small accessory conule is present posterior to and fused with plate 2. (**b**) Occlusal view, partial m1 specimen EP 560/00, in moderate wear. Accessory conules are evident anterior and posterior to plates, and were in the process of being incorporated into the enamel wear figures. (**c**) Occlusal view, partial M1 specimen LAET 75-488, in medium wear. Angulation of plate arms and position of accessory conules contribute to the formation of antero-posterior "loxodont sinus" enamel wear figures. (**d**) Occlusal view, M2 specimen LAET 75-3818B, in medium-heavy wear. Accessory conules are completely incorporated into *L. africana*-like loxodont sinus enamel wear figures. (**e**) Occlusal view, ?M2 specimen EP 694/00, in heavy wear. The crown has been worn nearly to the level of the cervix, and the accessory conules and loxodont sinuses have been obliterated (see Fig. 9.9)

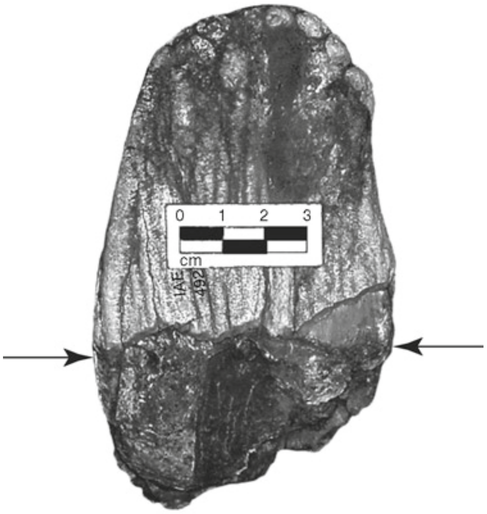

Fig. 9.8 Anterior view, molar plate, LAET 78-4927, *Loxodonta exoptata*. Note that the plate is higher than wide, gently tapered towards the apex, and the greatest width occurs about one-third of the total height of the specimen above its base (which is partially broken). Superficial apical digitations ("conelets") are evident superiorly

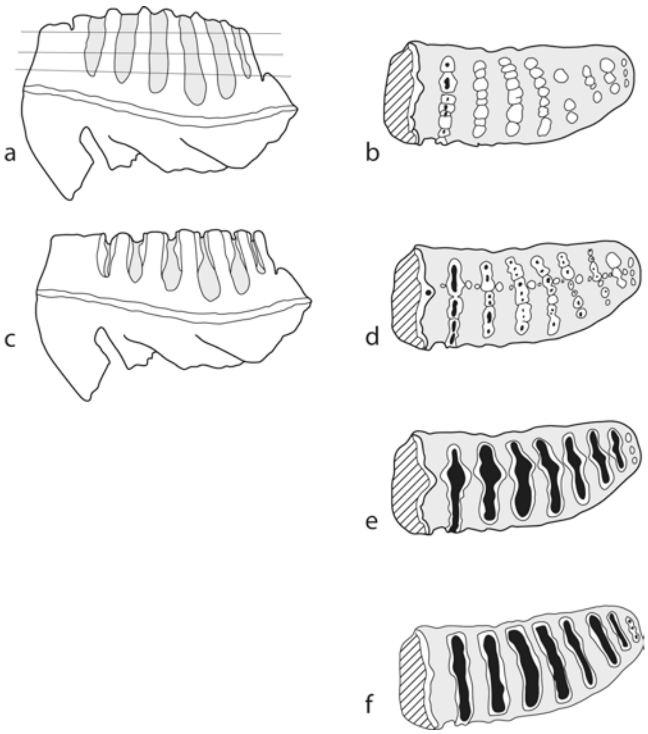

Fig. 9.9 Stages of molar wear and associated patterns of occlusal enamel wear figures, based on M2 specimen EP 519/98, *Loxodonta exoptata*. (**a**) Lateral view, unworn or lightly worn from plates 3–8. Note the tall, U-shaped transverse valleys, filled with cementum, and the parallel arrangement of the plates. Lines placed over the specimen indicate hypothetical areas of transverse cross-sectioning, reflected in occlusal diagrams c-f. (**b**) Occlusal view, plates 3–8 unworn or lightly worn. In this stage, individual apical digitations, or conelets, can be seen, but accessory conules are not evident, and plates are approximately rectilinear in shape transversely. (**c**) Lateral view, in light wear (*uppermost line*). Cementum is cut away, and the anterior and posterior accessory conules can be seen. Note that the greatest diameter of the accessory conules is at their mid-height or slightly below, occlusally producing the greatest development of loxodont sinuses throughout the crown. (**d**) Occlusal view, light wear on the plates (*uppermost line*). Conelets have not worn together to form enamel loops yet, but accessory conules are evident anterior and posterior to the plates. (**e**) Occlusal view, medium wear on the plates (*middle line*). Conelets have combined to form complete enamel loops, which incorporate anterior and posterior accessory conules to form "loxodont sinuses" that may touch in the midline. (**f**) Occlusal view, heavy wear on the plates (*lowermost line*). Accessory conuules and loxodont sinues are obliterated, and enamel wear figures are transversely rectilinear in shape

wear that they begin to contribute to the formation of propeller shapes and loxodont sinuses, or "< >" enamel wear figures (Figs. 9.7b–d and 9.9e). In heavy wear, accessory conules taper away, and plates assume more rectilinear occlusal shapes with the obliteration of the midline sinuses (Figs. 9.7e and 9.9f). For this reason, molars of *L. exoptata* exhibit a high degree of variation in occlusal morphology, which has almost certainly contributed to the contentious taxonomic history of this taxon (see below). Even individual molars have plates worn differentially to a variety of different occlusal shapes, as, for example, in KNM-KP 30611, a complete right m2 from Kanapoi, Kenya (Fig. 9.6p).

There are also a number of largely isolated postcranial elements in the combined *L. exoptata* sample, primarily dense, compact podials that survive weathering well. Many of these are from the Upper Ndolanya Beds. The most complete elements are described here, and include LAET 75-1017 (Fig. 9.10a), a right astragalus from Loc. 7E that was listed by Beden (1987a) as a juvenile left astragalus. The dimensions of this podial are L = 109.1 mm, W = 127.1 mm, and H = 80.2 mm. As noted by Beden, it differs from astragali of *Elephas* and is similar to those of *Loxodonta africana* in having a medial tuberosity that does not extend posterior to the tibial articular surface, and by the absence of a tuberosity on its neck. Another podial from the Upper Ndolanya Beds is LAET 76-18-263 (listed as 74-263 in Beden 1987a, but not described), a right navicular from Loc. 18. This podial is anteroposteriorly flattened and arcuate in anterior view (Fig. 9.10b), and measures 120.0 mm in width and 79.0 mm in height. Its dimensions make it a good fit for an astragalus the size of LAET 75-1017. Proximally, its astragalar surface is modestly concave, and distally it presents flattened facets for ento-, meso-, and ectocuneiforms and cuboid. A third podial from the Upper Ndolanya Beds is LAET 75-1033, a right ectocuneiform from Loc. 7E. This small bone is subtriangular in shape (Fig. 9.10c), and is 79.4 mm in its longest dimension and 46.7 mm in width. Also from Loc. 18 in the Upper Ndolanya Beds is a left unciform, LAET 76-18-308 (listed as 74–308 by Beden 1987a, but not described). This blocky, trapezoidal-shaped element has a greatest length of 133.7 mm, width of 112.4 mm, and thickness of 102.7 mm. Distally, it has distinct, confluent facets for metacarpals III–V,

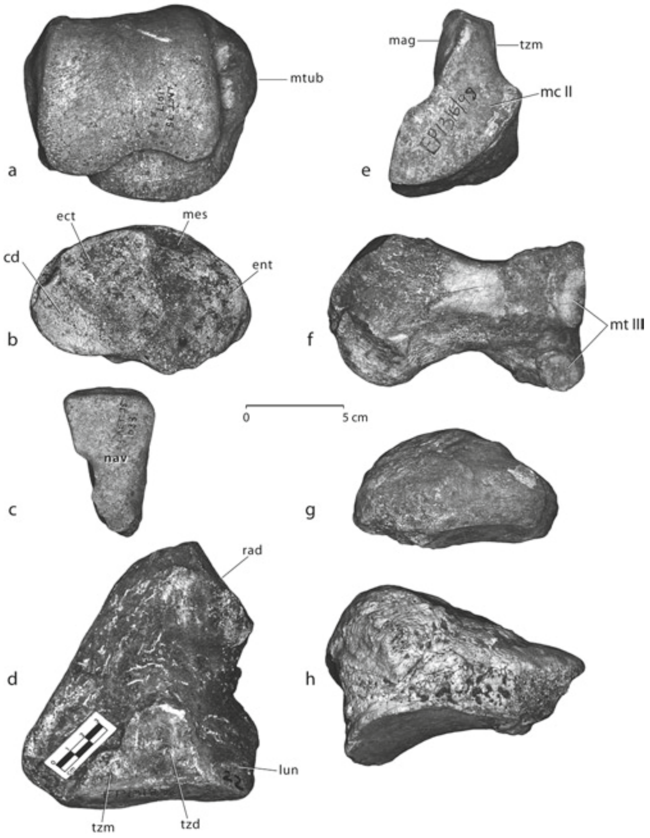

Fig. 9.10 Postcranial specimens of *Loxodonta exoptata* from Laetoli (*cd* cuboid, *ect* ectocuneiform, *ent* entocuneiform, *lun* lunate, *mag* magnum, *mc II* metacarpal II, *mes* mesocuneiform, *mt III* metatarsal III, *mtub* medial tuberosity, *nav* navicular, *rad*, radius, *tzd*, trapezoid, *tzm* trapezium). (**a**) Superior view, right astragalus LAET 75-1017. (**b**) Distal view, right navicular LAET 76-18-263. (**c**) Proximal view, right ectocuneiform LAET 75-1033. (**d**) Lateral view, right scaphoid EP 1318/98. (**e**) Distal view, left trapezoid EP 1316/98. (**f**) Lateral view, left mt IV LAET 78-4909. (**g**) Lateral view, patella EP 1422/04. (**h**) Lateral view, patella EP 402/04

two elongate articular facets for the os magnum medially, and a large squared surface proximally for articulation with the triquetrum (cuneiform). The elephant postcranial collection of Mary Leakey from the Upper Ndolanya Beds is supplemented by the more fragmentary LAET 75-1068, distal radius, LAET 76-18-177 (74-177 in Beden 1987a), femoral head, and LAET 75-2981, vertebral fragments.

Collecting by Eyasi Plateau expeditions have contributed to the elephant postcranial sample from the Upper Ndolanya Beds. EP 4023/00, from Loc. 7E, is a manual sesamoid that measures 63.8 mm in height, 37.8 mm in width, and has a thickness of 36.1 mm. A thoracic vertebral body, EP 3031/00, was recovered from Loc. 1. A fragmentary os magnum, EP 1227/00, was also collected from Loc. 22 S. EP 1317/98, from Loc. 22 S, is a mostly complete sacrum missing its caudalmost extreme; its dimensions are L = 210.0+ mm, W = 280.0 mm, and thickness = 100.0 mm. The discrete nature of the bone scatter at Loc. 22 S makes it possible that several other elephant postcranials from the locality are from the same individual. EP 1318/98 is a right scaphoid in good preservation, and closely resembles the scaphoid from Noiti 3 (EP 461/04) (Fig. 9.10d; compare with Fig. 9.3d). EP1318/98 measures 142.7 in length and 116.0 mm in width. The manus is further represented at Loc. 22S by EP 1316/98, a left trapezoid. This element laterally has two curved facets for the os magnum, a large curved facet medially for the os trapezium, and flattened, keyhole shaped articular surfaces proximally and distally for the os lunate and mc II, respectively (Fig. 9.10e). Dimensions of the facet for mc II are L = 86.2 and W = 78.5; dimensions of the facet for the os lunate are L = 78.0 mm and W = 56.3 mm; and overall length of the specimen is 105.6 mm.

Postcranials from the Upper Laetolil Beds include LAET 75-1250, probably a proximal phalanx for mt II, which measures 50.7 mm in length and is 52.2 mm wide at the base and 42.8 mm wide distally. A right patella, EP 1422/04 (Fig. 9.10g), derives from Loc. 6, and may be from a female individual, with its small dimensions of L = 118.0 mm, W = 86.3 mm, and thickness = 68.2 mm. A larger, presumably male left patella, EP 402/04 (Fig. 9.10h), from Loc. 16, measures 137.6 mm in length, 99.3 mm in width, and has a thickness of 95.7 mm, due in large part to its robust proximal end. Earlier, Mary Leakey collected LAET 78-4909, a left mt IV (Fig. 9.10f), from Loc. 22 south. This metapodial is robust, with a length of 131.3 mm and basal, midshaft, and head widths of 72.8 mm, 53.5 mm, and 77.5 mm, respectively. This is an important specimen because it exhibits a number of loxodont elephant features, enumerated by Beden (1987a), such as double facets for mt III that do not touch the cuboid articulation.

Other proboscidean postcranials were collected from the Lower Laetolil Beds. These include an abraded left mc II, EP 210/03, from Kakesio 8, with a length of 140 mm and width across the base of 54.6 mm and across the head of 65.0 mm. In size and morphology, it appears to belong in the elephant sample. Collecting in 2004 at Noiti 3 yielded an elephant maxillary fragment with alveoli for M2-3 associated with postcranial specimens. Each postcranial element carries the same accession number, EP 461/04. Among these are a first cervical vertebra fragment, two thoracic vertebrae, right trapezium, right scaphoid, and a left entocuneiform, most likely from the same individual. The trapezium is a blocky, trapezoidal-shaped specimen (Fig. 9.3c), with a distal articular surface for the first metacarpal (mc I) that is broader (86.0 mm) than its proximal end (61.6 mm) and greater than overall length (85.1 mm). Three distinct articular surfaces are confluent at the proximal end: a large, flat articulation for the adjacent trapezoid, a smaller articulation for the scaphoid, and a diminutive surface for mc II.

The scaphoid measures 136.7 mm in greatest length, and is 110.4 mm in distal width and 85.0 mm across its midsection. Part of its medio-proximal surface is missing, but otherwise the specimen retains its original elongate trapezoidal shape (Fig. 9.3d). At the proximal end, the articular surface for the radius is flattened and acutely angled relative to the long axis of the bone. The articulation for the lunate at the proximal end of the scaphoid is broken away, but the distal articular surface for the lunate is preserved and is confluent with the small trapezoid articulation and larger, more distally facing surface for the trapezium. Together, the articular surfaces for the trapezoid and lunate are 85.3 mm long. A large tuberosity is located along the disto-lateral portion of the scaphoid.

The third podial from Noiti 3 is a left medial, or ento-, cuneiform (Fig. 9.3e), measuring 86.6 mm in length, 66.5 mm in proximal width, and 62.9 mm across its distal end. Proximally, the articular surface for the navicular is slightly concave and is continuous at a right angle to a smaller, flat surface for the middle, or meso-, cuneiform. A round, flat additional articulation for the mesocuneiform is located at the distal end of the specimen, set at a right angle to the large, distally facing articulation for the first metatarsal. Both the navicular and metatarsal articular surfaces slope toward each other at their ventral extents.

Remarks: *Loxodonta exoptata* is best documented at Laetoli in the Upper Laetolil Beds, and is also known from a few specimens in the Lower Laetolil Beds and Upper Ndolanya Beds. Along with its Eyasi Plateau occurrences (Beden 1987a; Harris 1987b; Sanders 2005), *L. exoptata* has also been documented in the Kiloleli Mb. of the Wembere-Manonga Fm. in the Manonga Valley, Tanzania (Sanders 1997), at Kanapoi, Kenya (Harris et al. 2003), in the Chiwondo Beds, Malawi (Bromage et al. 1995), at Allia Bay, Kenya (Beden 1983), Koro Toro, Chad (Brunet et al. 1995; Brunet 2001), in the Nachukui Fm. at West Turkana, Kenya (Harris et al. 1988), the Warwire and Nyakabingo Fms., Nkondo and Nyabusosi Areas, Uganda (Tassy 1995), Mb. A of the Shungura Fm., Omo, Ethiopia (Beden 1987b), the Denen Dora Mb. of the Hadar Fm., Hadar, Ethiopia (White et al. 1984), and apparently in the Matabaietu Fm. of the Middle Awash, Ethiopia (Kalb and Mebrate 1993; Kalb 1995), giving it an estimated temporal range of ca. 4.5 to 2.0 Ma (de Heinzelin 1983; Drake and Curtis 1987; Hay 1987; Brown 1994; Harrison and Baker 1997; Harrison 2002; Alemseged 2003; Feibel 2003; Bonnefille et al. 2004).

The elephant fossils from the Laetolil and Ndolanya Beds have a long and colorful taxonomic history, which has been recounted in detail by Beden (1983, 1987a). The material recovered by the Leakey expedition in 1935 was initially placed by Hopwood (1936) in *Palaeoloxodon antiquus recki*, though he soon (in Kent 1941) transferred these fossils into two species, *Elephas recki* and *E.* aff. *planifrons*. The interpretation of multiple elephant species at Laetoli was followed in a number of subsequent studies, including those of Dietrich (1941, 1942), who had a larger sample at hand with the addition of the Kohl-Larsen 1938–1939 fossils and identified, from different levels, *Archidiskodon exoptatus*, *Palaeoloxodon antiquus*, and a subspecies of *Loxodonta africana*. Most importantly, however, Dietrich (1941, 1942) placed all of the elephant remains from the Laetolil Beds in a single species (his "*A.*" *exoptatus*), hence providing the species nomen used today for this material. Nonetheless, for most of the interval since their first discovery, the Laetoli fossils have been placed in various lineages or species of *Elephas* (e.g., Arambourg 1943, 1947; Cooke 1960), and it was not until 1965 that Coppens finally recognized the presence of true loxodont elephants in the Laetolil Beds ("*Loxodonta africanavus exoptata*"). Cooke's (1960) identification of some elephant teeth from Laetoli with *Archidiskodon subplanifrons* from the Vaal River, South Africa inadvertently proved prescient, because the Vaal River specimens in fact belong in *Loxodonta* (Sanders 2007; Sanders et al. 2010).

Subsequently, Maglio (1969) undertook taxonomic revision of the Louis Leakey and Kohl-Larsen elephant collections, and also assigned the specimens to two species. After designating IPUB 24, a right dentary fragment with its m3, as the lectotype of *Archidiskodon exoptatus* Dietrich, 1941, he sank the taxon into *Elephas recki*, and placed other specimens into *Loxodonta* sp. Largely on the basis of differential preservation, he believed that the occurrences of these taxa at Laetoli were separated stratigraphically and temporally, with the loxodont elephant being older. In subsequent publications (e.g., Maglio 1970, 1973; Cooke and Maglio 1972), he refined his identifications and assigned the Laetoli elephants to *Elephas recki* stage 2 and *Loxodonta adaurora*, using morphometric criteria such as degree of enamel folding, hypsodonty indices, expression of accessory conules, and enamel thickness to distinguish them.

More recently, Beden (1987a) restudied these fossils, and with the advantage of having a much larger elephant sample from the Mary Leakey collections, reached the very different conclusion that all of the elephant specimens from the Laetolil Beds belong in a single loxodont species which can be distinguished from both *E. recki* and *L. adaurora*. In doing so, Beden (1987a) resurrected Dietrich's (1941) species, giving it the more proper nomen "*Loxodonta exoptata*." In addition, he also recognized the affinity of the few elephant fossils from the Ndolanya Beds to *Loxodonta exoptata*.

The addition of a wealth of fossil elephant teeth to the sample by the Eyasi Plateau Expedition helps to confirm that the morphometric variation of the combined dental sample can be accommodated within a single loxodont species of elephant. While there is evidence for *Elephas recki* from younger horizons at Laetoli, such as LAET-87-L16-1, an incomplete right m1 collected by the IHO 1987 Expedition that probably derives from the Olpiro Beds, and a broken right M1 (S 88) illustrated by Dietrich (1942: fig. VI, 60) that is likely also from the Olpiro Beds, the rest of the elephant sample, from the Laetolil and Ndolanya Beds, belongs in *L. exoptata*. Metric variation for the combined sample is normal for a species (Table 9.4), and, taking into account wear (Figs. 9.7 and 9.9) and weathering, the morphology for each tooth type (e.g., m1, m2) is consistent within its set. Thus, the present study supports Beden's (1987a) assessment and is in agreement with his explanation that the incomplete condition of many of the molars, and varying states of occlusal wear, particularly as it impacted on expression of loxodont sinuses, complicated previous taxonomic efforts. *Loxodonta exoptata* is distinguishable from the penecontemporaneous *L. adaurora*, and appears from its more pronounced development of loxodont molar sinuses to be phylogenetically closer (and possibly ancestral) to the extant *Loxodonta africana* (Beden 1983; Kalb and Mebrate 1993; Kalb et al. 1996; Tassy 2003; Sanders et al. 2010).

Beden (1987a) reasoned that the presumed displacement of loxodont elephants by *Elephas recki* throughout East Africa for much of the Pleistocene was due to preference of loxodonts for humid or wet wooded savannas and disappearance of those habitats at the end of the Pliocene. Based in part on that assumption, he used the absence of *Elephas recki* (which was otherwise widely prevelant throughout East Africa during the time of deposition of the Laetolil and Ndolanya Beds [Maglio 1973; Sanders et al. 2010]) at Laetoli to reconstruct the Pliocene environment of the area as a wet wooded savanna (Beden 1987a: 276). However, carbon isotope analysis of elephant tooth enamel from Eyasi Plateau sites indicates that these animals were mixed feeders or grazers; their $\delta^{13}C_{\text{enamel}}$ signal does not reveal any evidence of being specialists for a unique dietary niche (Kingston and Harrison 2007). Moreover, paleoecological reconstruction of the Upper Laetolil Beds using diverse ecovariables (including faunal composition) reveals an ecosystem with a mosaic of habitat types that remained stable over the entire interval of deposition (3.8–3.5 Ma), with grassland, savanna, and open woodland, but not specifically humid savanna, as important components of that ecosystem (Su and Harrison 2007). In addition, faunal analysis of the suprajacent Ndolanya Beds indicates the dominance of semi-arid scrub or bushland, but certainly not wet wooded savanna, at Laetoli around 2.7–2.6 Ma (Kovarovic et al. 2002). Perhaps, as speculated by Beden (1987a), the absence of *E. recki* at Pliocene Laetoli had more to do with the availability of drinking water.

The most interesting aspect of the *L. exoptata* collection from the Eyasi Plateau is its large number of deciduous premolars, suggesting a disproportionate representation of calves and juveniles in the sample. Although the anancine gomphothere sample, particularly from the Upper Laetolil Beds, is too small to similarly assess its mortality profile, juveniles are also well represented in the modest deinothere sample. Dietrich (1942) believed that this ratio of elephant juveniles to adults was possibly due to a catastrophic volcanic explosion, but the stratigraphic distribution of these specimens shows that the die off was not a singular event (Beden 1987a).

A more likely explanation is that the age-grade mortality profile of Eyasi Plateau elephants indicates attritional mortality due to repeated drought conditions, in which young individuals too small to reach into holes dug into the lower water table are far more vulnerable to die offs than mature elephants (Dudley et al. 2001; Wittemeyer et al. 2005; Woolley et al. 2008). The oxygen isotope data for elephants from the Laetolil and Ndolanya Beds indicates that these animals relied on meteoric water for hydration (Kingston and Harrison 2007). African elephants are weaned around the age of 4–5 years (Moss 1992), by which time they have shed their deciduous second premolars (at about two years of age) and their deciduous fourth premolars are fully erupted (Sikes 1967). Nursing calves hydrating from milk have more protection from arid conditions than older juveniles, particularly if their mothers are experienced (Dudley et al. 2001; Foley et al. 2008; Woolley et al. 2008), which is consistent with the higher percentage of third and fourth than second deciduous premolars in the Eyasi Plateau elephant sample (see above).

A more even representation of all age groups would indicate time-averaged, cumulative single mortalities (Niven 2005), and die off due to disease would also cause mortality in all age classes (Lindeque and Turnbull 1994). An alternative explanation for the high occurrence of juvenile mortality in the Eyasi Plateau elephants is cumulative predation by lions, especially of weaned juveniles whose maternal bonds are weaker than those of nursing calves (Woolley et al. 2008 and references therein); attritional mortality of ungulate populations caused by carnivores usually yields high numbers of juveniles in death assemblages (Palmqvist et al. 1996). Lion predation on elephant calves is documented to increase during times of drought (Loveridge et al. 2006). However, predation of modern elephant populations accounts for only a small percentage of total juvenile mortality (e.g., Wittemeyer et al. 2005). It is also possible that the ratio of deciduous-to-adult teeth in the elephant sample is, at least in part, a taphonomic effect: small deciduous molars that accumulated on the surface at Laetoli are far more compact than adult molars and probably better survived weathering and trampling. Indeed, few complete permanent molars from Laetoli have been recovered, and approximately 75 unidentifiable dental specimens (from the Mary Leakey and Eyasi Plateau Expedition collections, but not included in Table 9.4) may be fragments of adult teeth. Even if these specimens were accounted for in the calculation of deciduous-to-adult tooth ratio, however, deciduous premolars would still comprise nearly half of all teeth in the sample, continuing to indicate a disproportionate mortality of calves and older juveniles in successive populations of *L. exoptata* (and possibly other proboscideans) from the Eyasi Plateau. Thus, drought (or at least seasonally inadequate supply of standing water) cannot be ruled out as a factor contributing to the skewed mortality profile of fossil elephants from this region.

Discussion

The proboscidean sample from the Eyasi Plateau region derives from the Lower and Upper Laetolil Beds (ca. 4.4–3.85 Ma and 3.85–3.6 Ma, respectively; Deino 2011) and the Upper Ndolanya Beds (2.66 Ma; Deino 2011), principally exposed at Kakesio and Laetoli. In addition, proboscidean remains that have been recovered from Endolele (=Esere?) may be from older deposits. The taxa represented are taxonomically diverse and include deinotheres, a stegodont, anancine gomphotheres, and elephants. They are stratigraphically distributed as follows: from Endolele, *Anancus kenyensis* and *Loxodonta* sp. *cf. L. cookei*; from the Lower Laetolil Beds, *Anancus ultimus* sp. nov. and *Loxodonta exoptata*; from the Upper Laetolil Beds, *Deinotherium bozasi*, *A. ultimus* sp. nov. (including the holotype), *Stegodon* sp. *cf. S. kaisensis*, and *L. exoptata* (including the lectotype); and from the Upper Ndolanya Beds, *L. exoptata* and a single specimen of *D. bozasi*. Also, several elephant molars attributable to *Elephas recki*, but not detailed in the present study, appear to be from the Olpiro Beds (ca. 1.2 Ma, Hay 1987; 2.1–2.0 Ma, Deino 2011).

The Eyasi Plateau sample is important for the study of proboscidean evolution because anancine gomphotheres made their last East African appearance in the Upper Laetolil Beds at Laetoli; the elephant fossils were the first recovered of *Loxodonta exoptata* and constitute the most substantial collection of the species; and it documents regional evolution of anancine gomphotheres and elephants over much of the Pliocene. In Africa, the early-mid Pliocene interval was a particularly dynamic one for proboscidean evolution, as archaic elephant genera such as *Stegotetrabelodon*, *Stegodibelodon*, and *Primelephas* disappeared and were replaced by an adaptive radiation of cranio-dentally more advanced crown elephant species (*Loxodonta adaurora*, *L. cookei, L. exoptata, Elephas ekorensis, E. recki, M. africanavus*). As all Mio-Pliocene elephants and most anancine gomphotheres relied heavily on C_4 plants in their diets (Cerling et al. 1999, 2003; Zazzo et al. 2000; Harris et al. 2003; Semaw et al. 2005), it can be inferred that progressive changes in molar crown morphology that occurred independently within the *Anancus kenyensis*-*A. ultimus* sp. nov. succession and among crown elephant lineages, such as increased hypsodonty and number of plates (or loph(id)s), were associated with ecological changes that favored enhanced efficiency in grazing adaptations during the early-mid Pliocene. The paleoenvironment of mid Pliocene Laetoli has been reconstructed as including open woodland, shrubland, grassland, and more limited gallery forest (Andrews and Bamford 2008; Su and Harrison 2007, 2008), and may have become considerably drier during the late Pliocene time of deposition of the Upper Ndolanya Beds (Kovarovic et al. 2002). This fits well with the ecologically diverse presence of grazers, such as *L. exoptata* and *A. ultimus* alongside committed browsers, such as *Deinotherium bozasi* (which may not have been ultimately sustainable locally during the time of deposition of the Upper Ndolanya Beds). The absence from Laetoli of *Elephas recki* and the large elephant *Loxodonta adaurora*, which contemporaneously occurred elsewhere in East Africa, and the high proportion of calves and juveniles in the proboscidean assemblage from the site indicate that these habitats may have periodically been subject to drought, seasonally low rainfall, a poor supply of standing water, or some combination of these factors.

Taxonomically, the identification of deinotheres and a stegodont at Laetoli is straightforward, because their dental morphology is so distinct. As well, there is little question that the anancine gomphothere specimens from Endolele, and Kakesio and Laetoli respectively belong to what has been considered primitive and advanced morphs, or different stages, of the East-Central African species *Anancus kenyensis* (Tassy 1986; Kalb and Mebrate 1993; Kalb 1995). Because the differences between these morphs are consistent, especially in the number of loph(id)s in intermediate molars and complexity of distribution of accessory conules throughout molar crowns, and are typical for paleo-sister species, these morphs or stages are elevated here to species level, with the primitive forms (including the type from Kanam, Kenya [MacInnes 1942]) retained in the original species, *A. kenyensis*, and the advanced forms in a new species, *A. ultimus* sp. nov. The molar chosen for the type of *A. ultimus* sp nov., m3 specimen EP 197/05, was selected because of its extreme occlusal complexity, high number of lophids, and because it is the youngest known anancine gomphothere specimen of the lineage (ca. 3.5 Ma). Anancine gomphotheres in this lineage paralleled elephants in their commitment to a C_4-plant based diet (Cerling et al. 1999, 2003; Zazzo et al. 2000; Harris et al. 2003; Semaw et al. 2005; Kingston and Harrison 2007), and associated evolutionary progression of molar hypsodonty and addition of loph(id)s to cheek teeth (Kalb and Mebrate 1993; Kalb 1995). It appears, however, that they were outcompeted for grazing resources, or ecologically swamped by expanding adaptive radiations to C_4 diets of other large-bodied mammals, including elephants, bovids, rhinos, equids, suids, and hippos (see Cerling et al. 2003), likely contributing to their mid Pliocene demise in East Africa.

By contrast, the elephant fossils from the region, particularly the most substantive sub-sample from the Upper Laetolil Beds, escaped proper taxonomic assignment for so long because of several confounding factors: first, the nomenclature initially chosen for the Louis Leakey collection (and later for the Kohl-Larsen assemblage) followed a now-outdated systematic scheme based heavily on ideas of Eurasian elephant phylogeny, and was evidently typological in approach, given the low amount of occlusal variation among those few molars; second, and rather surprisingly, it was not until relatively late that paleontologists recognized the presence of fossil *Loxodonta* in African Plio-Pleistocene deposits (e.g., Coppens 1965); third, early representatives of the African *Elephas* lineage have molars with accessory conules throughout much of their crowns, particularly on the posterior side of plates (but do not develop loxodont sinuses), and, depending on wear stage, this can make it difficult to differentiate partial molars of *Loxodonta* and early *Elephas*; and last, with a much more comprehensive sample of teeth of *L. exoptata* now available, it is evident that molars of the species underwent substantial morphological transformation as they wore down (Figs. 9.7 and 9.9).

The identification by Beden (1987a) of a single, loxodont elephant species, *L. exoptata*, at Laetoli, supported here, has implications for the reconstruction of African elephant phylogeny. *Loxodonta exoptata* is documented at other sites by only a handful of specimens, and its existence might be questionable if not for the evidence from Laetoli. The development of true loxodont sinuses throughout the molar crowns of this species is shared morphologically by older, more primitive, Mio-Pliocene loxodont elephants (*L. cookei*; see Sanders 2006, 2007), and by the extant African savanna and forest elephants *L. africana* and *L. cyclotis*. Thus, *L. exoptata* appears to provide an important link that extends the phylogeny of modern African elephants back into the late Miocene, consistent with genomic estimates of elephant lineage divergence dates (Rohland et al. 2007). Conversely, the loxodont contemporary of *L. exoptata*, *L. adaurora*, which existed from the earliest Pliocene until the start of the Pleistocene in East Africa (Sanders et al. 2010; Maglio 1973), has little development of median sinuses in its molars, and is therefore less likely to have been ancestral to modern African elephants.

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Chapter 10
Orycteropodidae

Terry Harrison

Abstract The small sample of fossil orycteropodids ($n=27$) available from the Laetolil Beds at Laetoli consists of isolated postcranials and a few cranio-dental specimens. The material can all be attributed to a single species of the genus *Orycteropus*. The Laetoli aardvark is generally similar in morphology to the extant *O. afer*, but differs in being smaller and in having a more gracile postcranial skeleton. The material is also distinguishable from *O. abundulafus* and *O. djourabensis* from the late Miocene and early Pliocene of Chad. Given its unique combination of features, the orycteropodid from Laetoli very likely represents a distinct species, but the material is not adequate to designate a new taxon. However, the evidence indicates that there was a greater diversity of aardvarks in the Pliocene of East Africa than is currently recognized.

Keywords Aardvarks • *Orycteropus* • Tubulidentata • Pliocene • Laetolil Beds • Laetoli

Introduction

Twenty seven specimens attributable to *Orycteropus* sp. have been recovered from Laetoli. All of the specimens are from the Upper Laetolil Beds, dated from 3.6 to 3.85 Ma, except for a single terminal phalanx from the Lower Laetolil Beds at Emboremony 1, dated to 3.85–4.4 Ma. The material consists of three cranio-dental specimens and a number of isolated postcranial elements. Two of the specimens, a mandibular fragment with M_3 and a metacarpal V were discovered during Kohl-Larsen's 1938–1939 expedition (Dietrich 1942). An additional specimen from the Kohl-Larsen collection, MB Ma. 30868, referred to by Leakey (1987) as coming from Laetoli, is actually from the Pleistocene locality of Eyasi (Njarasa of Reck and Kohl-Larsen 1936). Teams led by Mary Leakey recovered an additional 11 specimens, which were briefly described by Meave Leakey (Leakey 1987). Recent paleontological collections at Laetoli (1998–2005) have yielded 14 additional aardvark specimens, all isolated postcranial specimens. The material can be attributed to a single species of the genus *Orycteropus*.

There is only a single living species of aardvark, *Orycteropus afer*, but a number of fossil taxa have been described from the Miocene and Plio-Pleistocene of Africa. At least three genera and seven species of orycteropodids are known from the late Miocene and Pliocene of Africa (Lehmann 2009a). *Orycteropus chemeldoi* is known from the Ngorora Formation in Kenya (~9–12 Ma), and possibly from the late Miocene of Kakara (~10 Ma) in Uganda, and *Amphiorycteropus mauritanicus* is known from similarly aged deposits at Bou Hanifia 1 (~11 Ma) in Algeria (Arambourg 1959; Pickford 1975, 1994; Lehmann 2009a). *Leptorycteropus guilielmi*, from the Lower Nawata Formation at Lothagam in Kenya (~6–7 Ma), differs from modern *O. afer* in being only about half the size, with a shorter face and more gracile limbs (Patterson 1975, 1978; Milledge 2003). Some larger postcranials from the Lower and Upper Nawata Formation (5–7 Ma) are referred to *Orycteropus* sp., but these are still only about 75% of the size of *O. afer* (Milledge 2003). Two postcranial specimens from the Lukeino Formation in Kenya indicate the presence of two distinct species of *Orycteropus* that differ considerably in size (Pickford 1975). Two species of aardvarks have recently been named from the late Miocene and early Pliocene of Chad – *Orycteropus djourabensis* from Kollé (~4–5 Ma) and *O. abundulafus* from Kossom Bougoudi and Toros-Menalla (~5–7 Ma) – both of which are smaller than *O. afer* (Lehmann et al. 2004, 2005, 2006). Recently, Lehmann (2008) has provisionally referred additional material to *O. djourabensis* from the early Pliocene of Asa Issie, Ethiopia (~4.1–4.2 Ma) and the Plio-Pleistocene Koobi Fora Formation, Kenya (~1.5–2.4 Ma). Lehmann (2009a) also suggested that the late Miocene orycteropodids from Lothagam and Lukeino might have their closest affinities

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with *O. djourabensis*. A few isolated postcranials of *Amphiorycteropus* sp. and *Orycteropus* sp. have been recorded from the late Miocene Asa Koma Member in the Middle Awash (5.54–5.77 ma), Ethiopia (Lehmann 2009a, b). Lehmann (2008) makes reference to *Orycteropus* sp. from Area 250 in East Turkana, based on a partial skeleton (KNM-ER 18855), which may be 3.4–4.0 Ma in age, and therefore of similar age to the Upper Laetolil Beds. The earliest occurrence of *O. afer* is possibly at Langebaanweg in South Africa (~5 Ma), and similar forms occur in later Pliocene localities in South Africa, including Makapansgat (~3.0–3.3 Ma), Swartkrans (~1.5–1.8 Ma) and Baard's Quarry (1.8 Ma) (Kitching 1963; Hendey 1973; Pickford 1975, 2005; Lehmann 2004, 2008, 2009a). During the late Pleistocene, a large and robust aardvark, *O. crassidens*, is represented in East Africa by several partial skeletons from Rusinga Island, Kanjera, and possibly East Turkana in Kenya (MacInnes 1956; Pickford 1975).

The current evidence indicates that two species of orycteropodids – *O. afer* and *O. djourabensis* – are found at localities in Africa that are broadly contemporaneous with the Upper Laetolil Beds. As noted by Leakey (1987) and Lehmann (2009a) the Laetoli aardvark is morphologically comparable to the extant *O. afer*, but differs primarily in being smaller and in having a more gracile postcranial skeleton. The material can also be distinguished on the basis of size and morphological features from *O. djourabensis* (Lehmann 2009a). Given the unique combination of features exhibited by the Laetoli material, it very likely represents a distinct taxon, but, unfortunately, the material is not adequate to designate a new species. Nevertheless, the Laetoli aardvark does provide new evidence concerning the diversity and paleobiology of orycteropodids in the Pliocene of East Africa. The material is briefly described below and compared with other orycteropodids from the Pliocene of Africa.

Material

The author studied the original fossils from Laetoli at the National Museum of Tanzania in Dar es Salaam (EP, Eyasi Plateau expedition; 1998–2005 Harrison collection), the National Museums of Kenya in Nairobi (LAET, 1974–1979 Leakey collections on loan from Tanzania) and the Humboldt-Universität Museum für Naturkunde in Berlin (MB Ma., 1938–1939 Kohl-Larsen collection) (see Table 10.1). Comparisons were made with other East African fossil aardvarks at the National Museums of Kenya. Skeletal material of extant *Orycteropus afer* were studied at the National Museums of Kenya, the Natural History Museum in London and the American Museum of Natural History in New York.

Table 10.1 List of *Orycteropus* sp. material from Laetoli

Specimen	Locality	Element
MB Ma. 30867	Garusi	Right mandibular fragment with M_3
MB Ma. 30869	Vogelfluss	Right metacarpal V
LAET 75-1418	Loc. 9	Left mandibular fragment with distal M_1, M_2 and mesial M_3
LAET 75-1812	Loc. 10W	Left proximal phalanx of pedal ray I
LAET 75-1813	Loc. 10W	Left radius
LAET 75-2711	Loc. 3	Right middle phalanx of pedal digit V
LAET 75-2737	Loc. 3	Middle phalanx of pedal digits II–IV
LAET 75-3010	Loc. 10	Left distal fibula
LAET 75-3234	Loc. 11	Left astragalus
LAET 75-3469	Loc. 3	Middle phalanx of pedal digits II–IV
LAET 75-3625	Loc. 22	Left proximal ulna
LAET 78-4891	Loc. 22	Right distal tibia
LAET 78-4937	Loc. 5	Left M_2
EP 219/98	Loc.10E	Right metacarpal III
EP 616/98	Loc. 10W	Distal end of right metatarsal II
EP 992/98	Loc. 9S	Middle phalanx of pedal digits II–IV
EP 1064/98	Loc. 9S	Left distal fibula
EP 1226/98	Loc. 22	Left metatarsal IV
EP 2654/00	Loc. 2	Left proximal ulna
EP 3525/00	Loc. 12E	Middle phalanx of pedal digits II–IV
EP 3612/00	Loc. 21	Left proximal radius
EP 114/01	Loc. 6	Left middle phalanx of manual digit V
EP 1356/01	Emboremony 1	Terminal phalanx of pedal digits II–IV
EP 387/03	Loc. 5	Left astragalus
EP 1634/03	Loc. 13	Middle phalanx of manual digits II–IV
EP 1950/03	Loc. 7	Distal end of proximal phalanx of pedal digits II–IV
EP 2415/03	Loc. 9S	Right middle phalanx from manual digit V

Description

Cranio-Dental Specimens

LAET 75-1418 consists of a left mandibular fragment with M_2 and the partial crowns of M_1 and M_3 (Fig. 10.1). The mandibular corpus has an incomplete inferior margin, except for a small section below M_2. The corpus is quite shallow, with a height at M_2 of 17.7 mm, and a mediolateral breadth of 12.0 mm. The breadth of the corpus at M_3 is 11.9. The corpus is similar in breadth to that of modern *O. afer*, but relatively slightly shallower. The lateral aspect of the corpus is strongly convex inferosuperiorly. Midway down the corpus below M_2 there are five vascular openings that all open

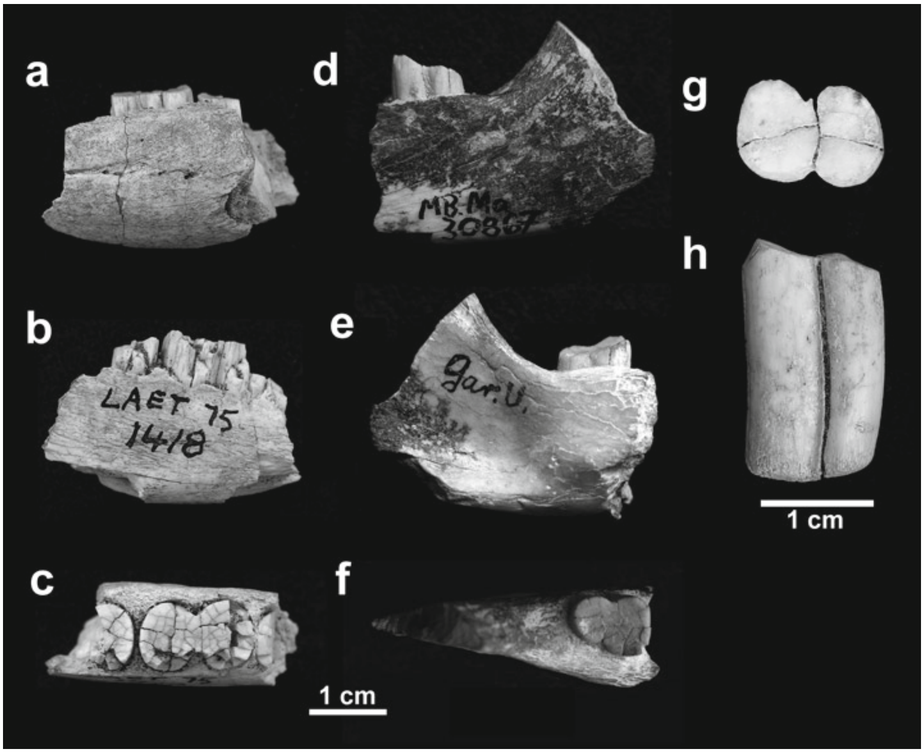

Fig. 10.1 Cranio-dental specimens of *Orycteropus* sp. from Laetoli. (**a**–**c**) LAET 75-1418, left mandibular fragment with distal M_1, M_2 and mesial M_3; (**a**) medial view, (**b**) lateral view, (**c**) occlusal view. (**d**–**f**) MB Ma. 30867, right mandibular fragment with M_3, (**d**) medial view, (**e**) lateral view; (**f**) occlusal view. (**g**–**h**) LAET 78-4937, left M_2; (**g**) occlusal view, (**h**) buccal view. Scale bar on left refers to (**a–f**); scale bar of right refers to (**g–h**)

posteriorly. A shallow, but distinct groove connects the four larger foramina in a straight line across the corpus. The medial side of the corpus is flat or slightly convex infero-superiorly. The inferior border of the corpus is robust and rounded.

Only a small fragment of the distal margin of M_1 is preserved. It has a strongly convex distal margin with a minimum breadth of 6.7 mm. In M_2 the mesial end of the tooth has been lost and the lingual and distobuccal faces are chipped. Despite the damage, it is possible to reconstruct the shape and dimensions of the crown. The crown has a symmetrical figure of 8 shape in which the distal lobe is more or less the same size and shape as the mesial lobe. In *O. afer* the mesial lobe on M_2 tends to be shorter, more rectangular mesially, and slightly narrower than the distal lobe. The fossil also differs in having a relatively narrower crown, and a stronger degree of waisting between the lobes. The M_2 crown is worn obliquely, sloping down towards the buccal and slightly towards the distal aspect. It is worn down to within 1.2 mm of the distobuccal alveolar margin. A similar wear pattern is found in *O. afer*, except that the mesial lobe tends to have flatter wear than the distal lobe. M_3 consists of the greater part of the mesial lobe only. It is relatively narrower than in *O. afer*. The breadth of the crown suggests that M_3 was smaller than M_2. As in M_2, the mesial lobe of M_3 is more elongated than in the corresponding tooth in *O. afer*, and the crown appears to have been more strongly waisted (maximum waist breadth of 6.2 mm). Wear on the mesial lobe produces a buccally sloping occlusal face, not flattened as in *O. afer.*

LAET 78-4937 consists of an isolated M_2 (Fig. 10.1). The height of the crown is 21.0 mm, which implies that the tooth came from an individual with a deeper mandibular corpus than LAET 75-1418, more like extant *O. afer.* The crown exhibits the same relatively symmetrical figure of 8 pattern as seen in the corresponding tooth in LAET 75-1418, with a similarly narrow crown and strong buccolingual waisting. Like LAET 75-1418, it differs from M_2 in *O. afer* in having a relatively narrower crown, stronger waisting and subequal mesial and distal lobes. Wear produces a flat surface over most of the occlusal area, and this slopes buccally and distally. A short facet occurs mesially, and this slopes towards the mesial margin.

MB Ma. 30867 is a right mandibular fragment retaining the crown of M_3 (Fig. 10.1). The mandibular corpus is broken just anterior to the posterior margin of the alveolus for M_2, but does extend posteriorly beyond M_3 to preserve a short section of the ramus. The corpus is quite shallow, with a height at M_3 of 19.6 mm and a mediolateral breadth of 11.9 mm. It is comparable in size to the mandibular corpus in LAET 75-1418. The lateral aspect of the corpus below the

Table 10.2 Dimensions (mm) of lower molars of *Orycteropus* sp. from Laetoli

	Lower M2			Lower M3		
Specimen	MD	BL mes	BL dist	MD	BL mes	BL dist
LAET 75-1418	13.2	8.0	7.8	–	7.4	–
LAET 78-4937	12.2	7.7	8.0			
MB Ma. 30867				9.2	7.3	5.5

BL dist buccolingual breadth of distal lobe, *BL mes* buccolingual breadth of mesial lobe, *MD* mesiodistal length

posterior molar is strongly convex inferosuperiorly, with a distinct swelling at the base of the M_3 root. Posteriorly, the ramus has a concave lateral surface. The medial side of the corpus is flat or slightly convex infero-superiorly.

The M_3 narrows distally with marked buccolingual waisting (the minimum buccolingual breadth is 5.2 compared with the maximum breadth of 7.3). The mesial lobe is buccolingually broader and mesiodistally longer than the reduced distal lobe. The crown is relatively short compared with the length of M_2, as in LAET 75-1418, confirming that M_3 in this species is much smaller than M_2. Dimensions of the lower molars from Laetoli are presented in Table 10.2.

Postcranials

LAET 75-1813 consists of an entire radius (Fig. 10.2; Table 10.3). The radius is very similar in morphology to *O. afer*, but differs in having linear dimensions only 80% of the average of *O. afer* ($n=8$) and in being more gracile. The articular surface of the head slopes anteriorly and slightly medially. It has a well-developed and sharply raised rim, especially posterolaterally, but it is not as well developed as in *O. afer*. This lip helps to stabilize the elbow joint in flexed positions. The central depression of the proximal articular facet is quite deep (1.6 mm), but shallower than in *O. afer*. The head is elliptical in outline, with its long-axis directed distomedially, although the breadth-length proportions of the head are less than in *O. afer* (Table 10.3). The medial facet for the proximal ulna is represented by a very small lunate facet (10.2 mm long and 3.2 mm wide), as in *O. afer*. The elliptical head and the small proximal ulnar facet would accommodate a limited range of pronation–supination. As in *O. afer*, there is a distinct, rounded tubercle on the margin of the head anterior to the ulnar facet that acts as a guide for the trochlear groove of the distal humerus in full flexion. The bicipital tuberosity is very well-developed, forming an oval and rugose protuberance that faces antero-medially. It is 11.1 × 6.0 mm in diameter. As in *O. afer*, the neck of the radius is extremely short, and the bicipital tuberosity approaches to within 2.1 mm of the proximal ulnar facet. The shaft of the radius is relatively more slender than in *O. afer*. The muscle markings on the shaft are well developed, and are identical in configuration to those of *O. afer*. The distal articulation for the ulna consists of a small elliptical facet, which is posteromedially positioned. As in the proximal articular facet, the range of pronation-supination is limited. The distal articular facet has the same specialized hinge joint for the carpus as in *O. afer*, but it has a lower anterior rim, a shallower mediolateral groove, a narrower anteroposterior diameter, and a more convex posterior lip.

Table 10.3 Dimensions (mm) of radius of *Orycteropus* sp. from Laetoli

	EP 3612/00	LAET 75-1813
Maximum length of radius	–	95.0
Anteroposterior diameter of radial head	15.5	14.2
Perpendicular breadth of radial head	12.1	12.1
Proximodistal length of bicipital tuberosity	11.0	11.1
Anteroposterior breadth of midshaft	–	12.8
Mediolateral breadth of midshaft	–	8.1
Anteroposterior breadth of distal end	–	18.7
Mediolateral breadth of distal end	–	25.2

EP 3612/00 consists of the proximal end of a left radius (Fig. 10.2). The fragment is weathered, and there is evidence of rodent gnawing on the radial head, bicipital tuberosity and shaft. It is very similar to LAET 75-1813, but somewhat larger (its linear dimensions are 85% the average size of *O. afer* radii [$n=8$]) (Table 10.3). The head is elliptical in outline, with a deep capitular depression and a raised lip, especially posteriorly. The head has a strong antero-posterior tilt, being more elevated posteriorly. The neck is very short. The ulnar facet is represented by a narrow articular strip with a maximum diameter of 11.5 mm. The bicipital tuberosity is well-developed and forms an elliptical protuberance. The shaft is more robust than in LAET 75-1813, but more gracile than in *O. afer*.

LAET 75-3625 comprises a proximal ulna lacking the olecranon process (Fig. 10.2; Table 10.4). It is slightly smaller than extant *O. afer*, with its average linear dimensions being only 78% of that of *O. afer* ($n=6$). The articular facet for the humeral trochlear is morphologically similar to that of *O. afer*, but it is mediolaterally narrower, especially the coronoid portion. The edges of the articular surface on the lateral side have been slightly eroded and abraded, but this has not significantly impacted on the morphology (*contra* Leakey 1987). The articular surface for the radial head is represented by a small lunate facet, as in *O. afer*. The anterior margin of the ulna shaft below the coronoid is not as robust as in *O. afer*,

Fig. 10.2 Forelimb specimens of *Orycteropus* sp. from Laetoli. (**a–c**) LAET 75-1813, left radius. (**a**) anterior view; (**b**) medial view; (**c**) posterior view. (**d–e**) EP 3612/00, left proximal radius. (**d**) posterior view; (**e**) anterior view. (**f–g**) EP 2654/00, left proximal ulna. (**f**) lateral view; (**g**) medial view. (**h–i**) LAET 75-3625, left proximal ulna. (**h**) lateral view; (**i**) medial view. (**j–l**) EP 219/98, right metacarpal III. (**j**) lateral view; (**k**) ventral view; (**l**) dorsal view. (**m–o**) MB Ma. 30869, right metacarpal V. (**m**) dorsal view; (**n**) ventral view; (**o**) lateral view. All to the same scale

Table 10.4 Dimensions (mm) of ulnae of *Orycteropus* sp. from Laetoli

	LAET 75-3625	EP 2654/00
Proximodistal height of olecranon process	–	25.4
Proximodistal height of trochlear notch	22.0	20.4
Anteroposterior length at olecranon beak	25.0	26.1
Anteroposterior length at trochlear notch	15.2	15.7
Anteroposterior length at coronoid process	27.4	27.5
Mediolateral breadth at olecranon beak	14.6	17.0
Minimum mediolateral breadth of trochlear notch	14.2	11.6

and the muscle markings and the pit for the interosseus ligament just below the coronoid process is not as well developed.

EP 2654/00 is a left proximal ulna missing the tip of the olecranon process and most of the shaft inferior to the coronoid process (Fig. 10.2; Table 10.4). The preserved fragment has a transverse fracture across the trochlear notch, with a thin wedge of bone missing from the medial side, and a fracture just inferior to the coronoid process. The margins of the coronoid process are abraded. The fossil closely resembles the morphology seen in *O. afer*, but it is smaller (79% of its average linear dimensions, $n = 6$). The olecranon process was long and well developed as in *O afer*, with strong muscle markings for the triceps brachii (Thewissen and Badoux 1986). The height of the anterior margin of the olecranon relative to the height of the trochlear notch is 124.5%, which falls within the range of variation for *O. afer*. The olecranon process diverges medially at a marked angle relative to the long axis of the shaft. The anterior margin of the olecranon process tilts posteriorly, while the posterior margin is relatively straight. As a result, the olecranon process tapers proximally. The posterior border of the olecranon process has well-developed markings for anconeus. This scar is continuous with a roughed ridge posterolaterally for the extensor and flexor carpi ulnaris, which then runs the length of the preserved fragment (see Thewissen and Badoux 1986). There is a well-developed roughened depression on the medial side of the olecranon, just proximal to the olecranon beak, for the humero-ulna ligament. The trochlear notch is similar in contour to that in *O. afer*, but relatively narrower. There is a small lunate facet for articulation with the radius. The coronoid process projects anteriorly slightly more than the olecranon beak. The specimen differs from *O. afer* primarily in being smaller and having a narrower trochlear notch.

EP 219/98 consists of an almost complete metacarpal III (Fig. 10.2; Table 10.5). The specimen is weathered, there is evidence of rodent gnawing on the superolateral surface and the distal articular surface, and the superior portion of the proximal articular facet is missing. It is smaller than the corresponding bone in *O. afer* (the maximum length is only 80% of the average length of the corresponding metacarpal in *O. afer* [*n*=6]), but it is morphologically very similar. It differs from *O. afer* in the following regards: the distal articular surface is narrower and has a sharper median keel; the median keel has a slightly stronger spiral, such that its superior extent is slightly more laterally placed; the shaft is more slender; the inferior portion of the proximal facet is slightly less mediolaterally concave; and the medial facets for metacarpal II are relatively smaller.

MB Ma. 30869 consists of a complete and well-preserved right metacarpal V (Fig. 10.2; Table 10.5). This specimen was described and figured by Dietrich (1942; Tafel III, 15–16). It is similar in morphology to the corresponding bone in *O. afer*, but differs in being smaller (the length is only 89% of the average dimension of the corresponding metacarpal in *O. afer* [*n*=6]).

EP 1634/03 represents a middle phalanx from digit II to IV of the manus (Fig. 10.3; Table 10.5). It is complete except for the dorsal margin of the proximal articular surface. It is much smaller and more gracile than the corresponding bone in *O. afer*, and differs in the following regards: the distal articulation is dorsoventrally higher and narrower; the distal articular facet does not continue as far dorsally; the shaft tapers more strongly distally; the proximal facet is narrower, and it tapers dorsally; and the dorsal tubercle of the proximal end is damaged, but was probably not as prominent.

EP 114/01 and EP 2415/03 are middle phalanges from digit V of the manus (Fig. 10.3; Table 10.5). EP 114/01 is complete except for the dorsal tubercle of the proximal articular facet. EP 2415/03 has slight damage to the proximal facet ventrally, and possibly comes from an immature individual. Both specimens are much smaller and more gracile than those of *O. afer*, and they differ in the following morphological features: the distal articulation is dorsoventrally shallower; the distal articular facet does not extend as far dorsally, and has a shallower trochlear groove; the shaft is dorsoventrally more compressed, and tapers more strongly distally; and the proximal articulation is dorsoventrally lower.

Table 10.5 Dimensions (mm) of metapodials and phalanges of *Orycteropus* sp. from Laetoli

Specimen	Element	ML dist	DV dist	ML shaft	DV shaft	ML prox	DV prox	PD L
EP 219/98	Metacarpal III	–	13.5	8.2	9.0	9.1	12.6	49.5
MB Ma. 30869	Metacarpal V	9.3	11.7	9.1	7.0	9.2	10.5	22.0
EP 1634/03	Mid Ph Manus II–IV	5.7	7.4	6.4	5.7	8.6	9.4	16.9
EP 114/01	Mid Ph Manus V	8.0	8.7	8.6	7.5	10.6	–	16.6
EP 2415/03	Mid Ph Manus V	5.6	5.7	5.4	5.2	6.5	6.6	10.7
EP 616/98	Metatarsal II	13.8	11.4	11.2	10.0	–	–	–
EP 1226/98	Metatarsal IV	15.1	12.8	13.2	10.8	17.5	20.7	62.9
LAET 75-1812	Prox Ph Pes I	8.5	6.8	7.0	6.6	11.1	8.8	32.3
LAET 75-3469	Mid Ph Pes II–IV	9.7	7.3	8.3	6.2	10.9	10.0	18.0
LAET 75-2737	Mid Ph Pes II–IV	8.6	7.4	7.5	6.0	9.8	9.4	17.5
EP 992/98	Mid Ph Pes II–IV	9.6	7.4	9.7	6.9	12.7	11.1	19.6
EP 3525/00	Mid Ph Pes II–IV	9.1	7.6	8.8	6.7	11.5	11.1	19.8
LAET 75-2711	Mid Ph Pes V	6.2	5.4	6.1	4.5	7.6	6.7	11.4
EP 1356/01	Term Ph Pes II–IV	10.3	5.3	8.7	6.9	9.4	9.3	21.3

ML dist mediolateral breadth of distal end, *DV dist* dorsoventral height of distal end, *ML shaft* mediolateral breadth of mid-shaft, *DV shaft* dorsoventral height of mid-shaft, *ML prox* mediolateral breadth of proximal end, *DV prox* dorsoventral height of proximal end, *PD L* total proximodistal length of bone, *Mid Ph*, Middle phalanx, *Prox Ph* Proximal phalanx, *Term Ph* Terminal phalanx

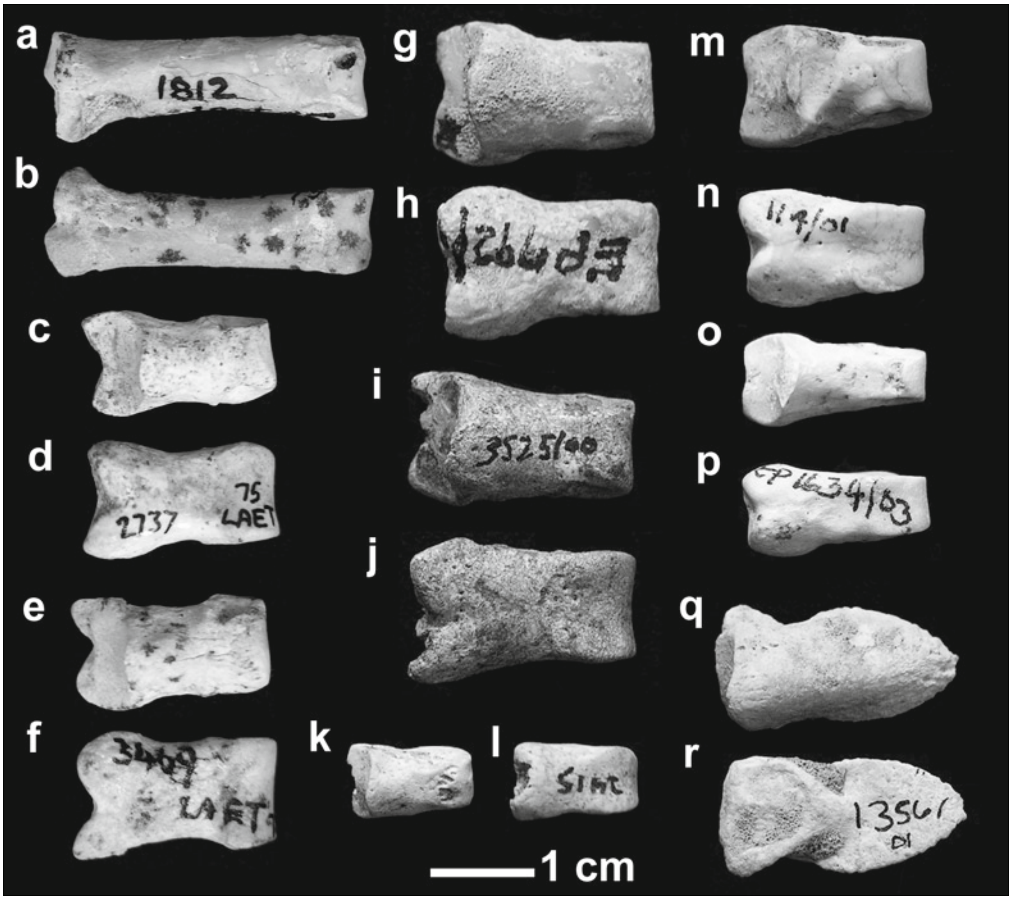

Fig. 10.3 Phalanges of *Orycteropus* sp. from Laetoli. Alternating dorsal (*top*) and ventral views (*bottom*) of the same phalanx, except k–l with dorsal (*left*) and ventral (*right*). (**a**–**b**) LAET 75-1812, left proximal phalanx of pedal ray I; (**c**–**d**) LAET 75-2737, middle phalanx of pedal digits II–IV; (**e**–**f**) LAET 75-3469, middle phalanx of pedal digits II–IV; (**g**–**h**) EP 992/98, middle phalanx of pedal digits II–IV; (**i**–**j**) EP 3525/00, middle phalanx of pedal digits II–IV; (**k**–**l**) EP 2415/03, right middle phalanx from manual digit V; (**m**–**n**) EP 114/01, left middle phalanx of manual digit V; (**o**–**p**) EP 1634/03, middle phalanx of manual digits II–IV; (**q**–**r**) EP1356/01, terminal phalanx of pedal digits II–IV. All to the same scale

LAET 78-4891 is a right distal tibia lacking the medial malleolus. The total length of the fragment is about 45 mm. It is very similar in morphology to the corresponding bone in *O. afer*, but is smaller (the linear dimensions average 84% of those of *O. afer* [$n=7$]). The distal articular surface for the astragalus has a deep and well-defined rectangular groove for articulation with the medial ridge of the trochlea of the astragalus. The facet for the lateral ridge is shallower and laterally sloping. These two grooves are separated by a strong keel that articulates with the trochlear groove of the astragalus. The posterior margin of the distal articular facet has a well developed rim. The medial malleolus is missing, but judging from its base it was a substantial tuberosity. The anterior tubercle on the anterior margin of the distal tibia is prominent, but not as bulky as is typically seen in *O. afer*. The anterior tubercle has two distinct facets, both of which are slightly weathered. There is a flattened surface on the tip of the anterior tuberosity that articulates with the distal margin of the astragalar trochlear, and this acts as a bony stop in full dorsiflexion. A rectangular facet is present on the anterior face of the anterior tubercle, which makes contact with the distal marginal tubercle of the calcaneus in full dorsiflexion of the foot. A similar configuration of these facets is found in *O. afer*. The distal facet for the fibula is eroded, but it is evident that it was a substantial lunate facet as in *O. afer*. There is a broad and shallow groove for the tendon of the tibialis posterior on the posterior face of the medial aspect of the bone. Anterolaterally there is a roughened triangular area for attachment of the tibiofibular ligament. Clearly, the distal fibula was strongly bound to the distal tibia by ligamentous attachment, just as in *O. afer*. Given the size of the distal end of the fibula, the preserved portion of the shaft appears to be relatively stout. Apart from its slightly smaller size, the relatively smaller anterior tubercle, and possibly the robusticity of the shaft, the distal tibia is very similar in morphology to that of *O. afer*.

LAET 75-3010 is a left distal fibula lacking the lateral malleolus (Fig. 10.4). EP 1064/98 is a left distal fibula, better preserved and more complete than LAET 75-3010. Both specimens are only 80% of the average size of the corresponding element in *O. afer* ($n=7$), with a more gracile shaft. The distal articular facets and scars for ligamentous attachments match those of *O. afer*. Medially, there is a large D-shaped facet for articulation with the lateral wall of the astragalus. Inferior to this is a small U-shaped facet that articulates with the fibula flange on the astragalus in full dorsiflexion. Superior to the astragalar facets is a large and roughened lunate facet for contact with the distal tibia. The attachment for the tibio-fibular ligament is strongly developed, and is associated with the development of a prominent bony spicule on the anterior margin of the shaft (which is better developed than in *O. afer*). The distal margin of the fibula has a pit for the astragalo-fibular ligament, but this is shallower than in *O. afer*. The lateral malleolus is strongly projecting.

LAET 75-3234 is an entire astragalus, lacking only the medial tuberosity proximally (Fig. 10.4; Table 10.6). It has the same general morphology as *O. afer*, but its linear dimensions are on average only 87% of those of *O. afer* ($n=7$). The astragalar body is relatively broad, with a deep trochlear groove for articulation with the distal tibia. Distally, the trochlear facet has a deep concavity to accommodate the prominent anterior tuberosity of the distal tibia in full dorsiflexion.

Table 10.6 Dimensions (mm) of astragali of *Orycteropus* sp. from Laetoli

	LAET 75-3234	EP 387/03
Proximo-distal length of astragalus	33.3	31.7
Mediolateral breadth of talus (excluding head and neck)	29.0	–
Mediolateral breadth of head	14.7	–
Mediolateral breadth of neck	13.0	11.6
Length of the lateral side of the talar body	22.5	20.4
Dorso-ventral height of lateral side of talar body	17.4	16.5
Angle of neck relative to long axis of tibial facet	18°	28°
Length of body in midline of tibial facet	19.0	17.5
Length of anterior calcaneal facet	14.7	14.7
Length of anterior calcaneal facet	16.0	15.3

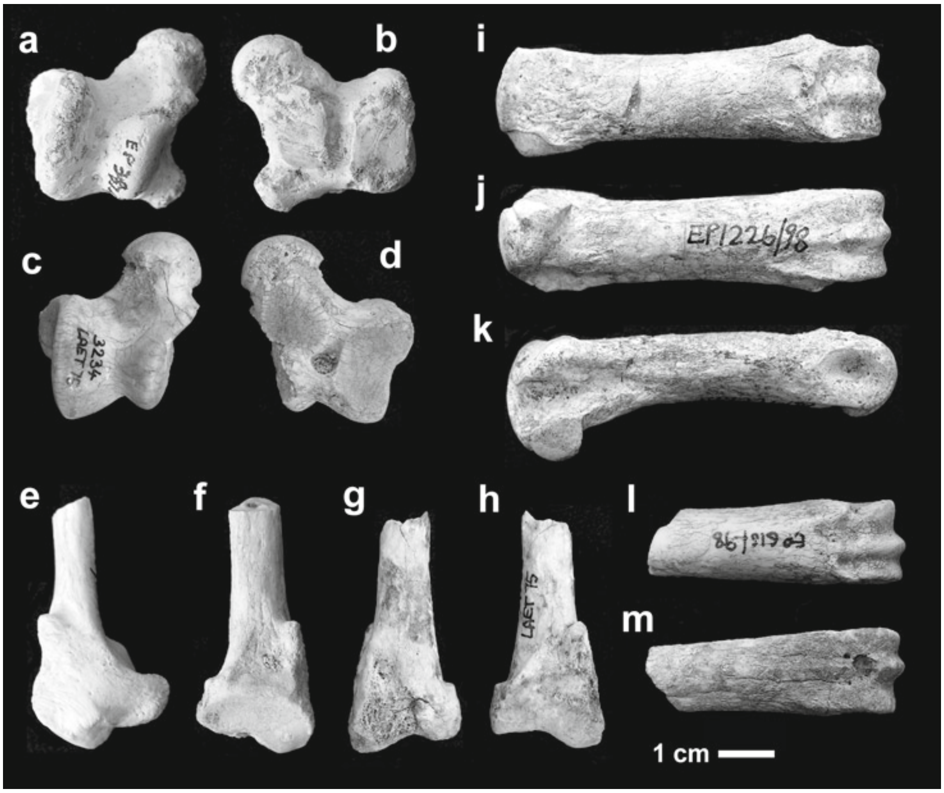

Fig. 10.4 Hindlimb specimens of *Orycteropus* sp. from Laetoli. (**a**, **b**) EP 387/03, left astragalus. (**a**) dorsal view; (**b**) ventral view. (**c**, **d**) LAET 75-3234, left astragalus. (**c**) dorsal view; (**d**) ventral view. (**e**, **f**) EP 1064/98, left distal fibula. (**e**) anterior view; (**f**) medial view. (**g**, **h**) LAET 75-3010, left distal fibula. (**g**) lateral view; (**h**) medial view. (**i–k**) EP 1226/98, left metatarsal IV. (**i**) dorsal view; (**j**) ventral view; (**k**) lateral view. (**l**, **m**) EP 616/98, distal end of right metatarsal III. (**l**) ventral view; (**m**) dorsal view. All to the same scale

This concavity tends to be shallower in *O. afer*. The lateral and medial margins of the trochlear facet are elevated to form sharp and steep sided margins. Distally, there is a small triangular facet where the lateral trochlear ridge meets the neck. This is a contact facet for the anterior tuberosity of the distal tibia. Similarly, there is small facet on the infero-medial side of the head for contact with the anteromedial margin of the distal tibia. The facet is weathered and eroded, so only a remnant is visible. This facet provides increased stabilization of the astragalo-tibial joint during dorsiflexion. Leakey (1987) argued that the fossil astragalus was less derived than that of *O. afer* in lacking this facet, and concluded on this basis that the Laetoli aardvark may have been less specialized for fossorial behaviors. However, this observation is not supported on closer examination, and the contact facets for the distal tibia appear to be identical to those of *O. afer*. The astragalar body is relatively lower in *O. afer*, and the lateral ridge is more rounded. Laterally, the fibula flange is relatively short. The medial malleolar facet is sharply delineated. The neck is relatively short, but slightly longer and more medially directed than the neck in *O. afer*. The head is relatively narrower than in *O. afer*, and it narrows distally. Proximally there is no lateral tubercle and the medial tubercle is broken. The anterior and posterior calcaneal facets on the inferior surface of the astragalus have their long-axes sub-parallel and are separated by a shallow sinus tarsi with a small astragalar foramen. The anterior facet has a convex distal face and a grooved proximal face, which helps to create a locking mechanism with the sustentaculum of the calcaneus in dorsiflexion. The anterior facet appears to be less specialized than in *O. afer*, with a lower topography and a shallower proximal groove.

EP 387/03 represents a complete right astragalus, except for the tip of the fibular flange laterally (Fig. 10.4; Table 10.6). It is slightly weathered, and there is evidence of rodent gnawing, especially on the head. It is similar in size and morphology to LAET 75-3234, but differs in having a slightly shorter neck and a more rounded lateral trochlear keel as in *O. afer*. The medial process is preserved in EP 387/03, unlike in LAET 75-3234. It is very well-developed, being much larger than in *O. afer*. The linear dimensions of the astragalus are on average only 79% of those of *O. afer* ($n=8$) (Table 10.6).

EP 616/98 represents the distal half of metatarsal II (Fig. 10.4; Table 10.5). The bone is weathered and cracked, and the inferior beak of the median keel is abraded. The specimen is smaller than the corresponding element in *O. afer*, but is otherwise very similar in morphology. The distal end is mediolaterally broad and relatively low. The distal keel is placed slightly laterally relative to the midline and terminates inferiorly at a shallow vascular pit. Dorsally, the shaft has a pair of depressions just proximal to the head as in *O. afer*. The shaft is dorsoventrally compressed, with a flattened ventral surface except for an indistinct keel that passes along the shaft from the vascular pit as in *O. afer*. In addition to its smaller size, the fossil differs from *O. afer* in having a more slender and dorsoventrally compressed shaft, and a dorsoventrally shallower distal end.

EP 1226/98 is an entire left metatarsal IV, which is slightly weathered (Fig. 10.4; Table 10.5). It is similar in size and morphology to specimens of *O. afer*, rather than smaller as seen in most of the postcranial specimens from Laetoli (its length is 95% of the average length of the corresponding metatarsal in *O. afer*). The proximal facet is slightly convex mediolaterally and strongly convex dorsoventrally. Medially, the distal end has two elliptical facets for metatarsal III. There is a large U-shaped facet on the lateral side for articulation with metatarsal V. There are deeply excavated ligamentous pits on the medial and lateral side of the distal end of the shaft. The shaft is quite stout, being more robust than in male specimens of *O. afer*, but it is slightly shorter. The distal articular surface is similar to that in *O. afer*, with a well-developed central keel. The medial condyle of the distal articulation is dorsoventrally higher than the lateral condyle and it has a sharper marginal keel. A prominent plantar tubercle is present just proximal to the distal articulation on the inferior surface of the shaft. On the dorsal surface, just proximal to the distal articular surface, is a pair of deep pits. These are bordered proximally by bony exostoses running mediolaterally, presumably a pathological feature related to extreme dorsiflexion at the metatarso-phalangeal joint.

LAET 75-1812 is a proximal phalanx of pedal ray I (Fig. 10.3; Table 10.5). Some weathering of the bone and rodent gnawing is evident. A large opening on the medial side of the shaft, close to the proximal end, and a smaller perforation on the dorsal aspect of the distal aspect of the distal articulation are caused by rodent gnawing (not a carnivore bite mark as inferred by Leakey 1987). The fossil is slightly smaller than *O. afer*, with linear dimensions that are on average only 93% of that of the extant taxon ($n=6$), but the morphology is very similar. The distal articulation has a shallow trochlear groove and narrows dorsally. The distal end is dorsoventrally flatter than in *O. afer*. Well-developed pits are present on the medial and lateral side of the distal end for the interphalangeal collateral ligaments. The shaft is somewhat more slender than in *O. afer* and slightly dorsoventrally flatter. It exhibits the same medial curvatures as seen in *O. afer*, but in the fossil it is less pronounced. The proximal articulation is dorsoventrally concave, with a slight groove on its inferior margin. Proportionally, it is dorsoventrally lower than in *O. afer*.

LAET 75-2711 is a middle phalanx of pedal digit V (Table 10.5). It is a very small phalanx, with linear dimensions that are on average only 71% of the linear dimensions of *O. afer* ($n=6$), but it does appear to be from an adult individual. The distal articular surface narrows dorsally and has a very shallow trochlear groove. There are well-developed pits on the medial and lateral side of the distal end for strong collateral ligaments. The shaft is short and quite stout. The proximal facet is deeply concave, with an extended inferior lip. The phalanx is generally similar to that in *O. afer*, but differs in the following respects: the distal articular surface is dorsoventrally lower, has only a faint trochlear groove and does not extend as far onto the dorsal aspect of the shaft, the shaft is shorter and relatively much more gracile, and the proximal articular facet is narrower and tapers dorsally.

LAET 75-2737 and LAET 75-3469 are middle phalanges of digits II–IV of the pes (Fig. 10.3; Table 10.5). It is not possible to confidently attribute isolated phalanges from digits II, III or IV to particular rays. The distal articular facet narrows dorsally, extends only a short distance onto the dorsal aspect of the shaft, and has a shallow trochlear groove. The shaft is relatively long and slender. The proximal end is relatively narrow, and tapers dorsally. The proximal articular surface is strongly concave, with a deep notch inferiorly and a well-developed inferior lip. The shaft of LAET 75-3469 is broader than in LAET 75-2737, but is otherwise very similar in morphology. It is conceivable that they belong to the same individual.

EP 992/98, EP 3525/00 and EP 1950/03 are recently recovered middle phalanges of digit II–IV of the pes (Fig. 10.3; Table 10.5). They are very similar to the specimens described above, but are larger and more robust. These phalanges differ from the corresponding elements in *O. afer* in having a narrower distal end that tapers more strongly dorsally, the distal articular surface does not extend as far onto the dorsal side of the shaft and is less concave in the mediolateral plane, the shaft is relatively more slender, the proximal facet is much narrower and tapers dorsally more strongly, and the inferior lip of the proximal articulation is less robust.

EP 1356/01 is a complete and well-preserved terminal phalanx of digit II-IV of the pes. It is morphologically similar to the corresponding phalanges in *O. afer*, but it is somewhat smaller (the linear dimensions average only 81% of those of the extant species, *n* = 4). The distal end is of the phalanx is expanded mediolaterally, but tapers dorsoventrally to support a broad ungula. The dorsal surface of the phalanx is mediolaterally convex. Ventrally, the distal pad is slightly concave, and it is bordered by sharp margins laterally, medially and apically. The distal pad occupies about 60% of the total length of the phalanx. The proximal articular surface is U-shaped, with a relatively straight inferior margin. The facet is strongly convex dorsoventrally, with prominent superior and inferior lips, and is slightly convex mediolaterally. A large flattened triangular plateau, for attachment of the digital flexor, is present on the ventral surface of the phalanx proximally. A small triangular flange extends from the flexor pad out to one side of the shaft.

Comparisons

The lower molars and mandible fragments from Laetoli are morphologically similar to those of *O. afer*, except that the mandibular corpus is relatively shallower, the M_2 is narrower with a greater degree of waisting and subequal mesial and distal lobes, and M_3 is much smaller in relation to the size of M_2. In addition, the teeth are slightly smaller on average, with the linear dimensions of M_2 only 95% of the dimensions of the corresponding tooth of *O. afer*. The limb bones are morphologically very similar to modern *O. afer*, but differ in being smaller and relatively more slender. The linear dimensions of the postcranial elements are on average only 83% of those of the average values for *O. afer* (range = 71–95%). From a functional perspective, the forelimb bones clearly show that the fossil aardvark from Laetoli had the same suite of features associated with the specialized fossorial behavior of *O. afer*. However, the detailed morphology of the articular surfaces of the phalanges indicate that the manus was not quite as specialized for digging as in the modern species. The phalanges are longer and dorsoventrally more compressed (i.e., less able to resist dorsoventral bending stresses), with more stable interphalangeal joints in semiflexed postures rather than in full extension. In general the hindlimb and foot bones from Laetoli correspond morphologically to those of the extant *O. afer*, but differ primarily in being smaller and more gracile. However, a few anatomical features indicate that the pes of fossil aardvark from Laetoli was not as specialized as that in *O. afer*. For example, the astragalus from Laetoli differs from that of the modern species in having a deeper body, a shorter fibular flange, a more prominent medial process, a narrower head, and a shallower anterior calcaneal facet with a less pronounced proximal groove. In addition, the metatarsals and pedal phalanges have more slender and more dorsoventrally compressed shafts than in *O. afer*. The pedal phalanges, like those of the manus, differ from those of *O. afer* in having distal articular surfaces that narrow dorsally, do not extend superiorly as far onto the dorsal surface, and have shallower trochlear grooves. These differences imply that the toes were less well adapted for resisting bending stresses and for maintaining joint stability during full extension of the digits.

When compared with orycteropodids from other Plio-Pleistocene localities in Africa, the fossil aardvark from Laetoli can be distinguished metrically and morphologically from all of the currently named taxa, and very likely represents an unnamed species. The lower molars are smaller and relatively narrower than those of *O. afer* and O. *crassidens*, and are intermediate in size between those of *O. abundulafus* and *O. djourabensis* (Lehmann 2009a). In addition, the aardvark from Laetoli appears to be distinctive in having a relatively much smaller M_3 compared to the size of M_2. Compared to *O. chemeldoi* from the middle to late Miocene of Kenya, the lower molars of the Laetoli orycteropodid are slightly shorter, but much broader, and the M_3 is less reduced in overall size (Pickford 1975). The postcranials provide further confirmation that the Laetoli aardvark is intermediate in size between *O. abundulafus* and *O. djourabensis*. They are on average only 85% of the size of the corresponding elements in *O. adundulafus* and 108% of those of *O. djourabensis*. In addition, the postcranials from Laetoli differ morphologically from those of *O. djourabensis* in the orientation of the trochlear notch of the ulna, the quadrate shape of the astragalus and the more rounded astragalar head (Lehmann 2009a).

In conclusion, the material from Laetoli appears to belong to a single species of orycteropodid, morphologically similar enough to extant and Plio-Pleistocene aardvarks from Africa to be attributed to the genus *Orycteropus*. However, its smaller size and morphological differences distinguish it from extant *O. afer*, and preclude it from being referred to this species. Compared with extinct representatives of *Orycteropus*, the Laetoli species is significantly smaller than *O. crassidens* and *O. djourabensis*, but larger than *O. adundulafus* from the late Miocene-early Pliocene of Chad (Lehmann 2008, 2009a). It cannot be easily accommodated in any of these taxa, and it likely represents a distinct species. An undescribed partial skeleton (KNM-KP 30390) of *Orycteropus* sp. from Kanapoi (4.1–4.2 Ma), with corresponding bones similar in morphology to the isolated postcranials from Laetoli but slightly smaller, could belong to the same species. However, until better material is obtained to allow a more definitive determination of its taxonomic status, the specimens from Laetoli are referred to *Orycteropus* sp. (following Leakey 1987; Lehmann 2009a). The evidence does suggest that the diversity of aardvarks in the Pliocene of Africa was greater than that indicated by the currently recognized species.

Conclusions

The small sample of fossil orycteropodids from the Laetolil Beds (3.6–4.4 Ma) has doubled during the course of recent paleontological investigation at Laetoli. There are now 27 specimens, consisting mostly of isolated postcranials and a few cranio-dental specimens. The material can all be attributed to a single species of *Orycteropus*. However, the Laetoli aardvark differs morphologically and metrically from the orycteropodids from other Plio-Pleistocene localities in Africa. It is morphologically similar to the extant *O. afer*, but differs primarily in being smaller and in having a more gracile postcranial skeleton. The material can also be distinguished on the basis of size and morphological features from *O. djourabensis* and *O. abundulafus* from the late Miocene and early Pliocene of Chad. Given the unique combination of features exhibited by the Laetoli specimens, they very likely belong to a distinct species, but the material is not adequate enough to make a more precise taxonomic determination or designate a new species. Nevertheless, the evidence does indicate that the diversity of aardvarks in the Pliocene of East Africa was greater than currently indicated by the recognized species.

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Chapter 11
Rhinocerotidae

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Abstract The remains of fossil rhinoceroses from Laetoli represent at least three taxa: *Ceratotherium efficax*, *Ceratotherium* cf. *simum*, and *Diceros* sp. The great majority of the material from the Pliocene Laetolil Beds belongs to *C. efficax*, for which we provide a revised diagnosis. This taxon has been frequently misidentified and inaccurately referred to as *C. praecox*, *C. germanoafricanum*, or *C. mauritanicum*. A cranium from the Upper Ndolanya Beds shows more derived dental features, but a precise assignment to *C. germanoafricanum* or *C. simum* is presently not possible. The occurrence of true *Diceros* in the Laetolil Beds is demonstrated by a partial cranium with incomplete dentition, but very few other specimens can be potentially attributed to this genus. Analysis of occlusal wear patterns suggests that *C. efficax* was a grazer or possibly a graze-dominated mixed feeder; in either case it probably included a variable component of browse in its diet. The transition from a *Diceros*-like ectolophodont dentition to the full-fledged plagiolophodonty seen in extant *Ceratotherium simum* included a substantial period of stasis, spanning at least the interval represented by the Laetolil Beds. A shift in the dietary regime towards increased grazing had occurred by the Upper Ndolanya time, and this trend continued from the early Pleistocene to the Recent. Based on the available fossil record, the split of the two lineages leading to the extant species must have taken place in Africa during the Miocene.

Keywords Rhinocerotidae • *Ceratotherium* • *Diceros* • Taxonomy • Evolution • Nomenclature • Paleoecology • Paleodiet

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Introduction

Since the first systematic description by the German paleontologist W. O. Dietrich during the Second World War (Dietrich 1942, 1945), fossil remains of rhinoceroses from Laetoli have been described and discussed under a variety of names (Arambourg 1947, 1959; Hooijer 1969, 1972; Groves 1975; Guérin 1979, 1980a, 1987a; Geraads 2005). The Laetoli rhinoceroses are of particular interest for understanding the early evolution of the *Ceratotherium* lineage during the Plio-Pleistocene, as well as for interpreting the paleoecological setting of the locality. In particular, the transition from a generalized ancestral morphology to the specialized grazing condition of the extant white rhinoceros, *Ceratotherium simum*, has been long regarded as a case study for evolutionary research (Osborn 1903; Dietrich 1942; Thenius 1969; Stanley 1979).

Our aim is simple: to revise the taxonomy of the rhinoceros material from Laetoli housed in the collections of the National Museums of Tanzania and Kenya, and in the collections of the Natural History Museum, London. Furthermore, we describe it with emphasis on functional aspects, particularly the dental functional morphology and wear patterns. We consider the implications of our findings for the paleoecology of the Laetoli sequence and the evolutionary history of the taxa, including the origins of *Ceratotherium simum*. We also discuss in detail the complicated taxonomic history of *C. efficax* (Dietrich, 1942), and *Ceratotherium praecox* Hooijer and Patterson, 1972.

Materials and Methods

Institutional Abbreviations

AMPG: Athens Museum of Paleontology and Geology, University of Athens; BMNH: British Museum of Natural History (=Natural History Museum), London; BSPG: Bayerische Staatssammlung für Paläontologie und Geologie,

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München; FSL: Faculté des Sciences, University of Lyon; GSN: Geological Survey of Namibia, Windhoek; IPUW: Institut für Paläontologie der Universität, Wien; KMMA: Koninklijk Museum voor Midden-Afrika, Tervuren; KNM: National Museums of Kenya, Nairobi; LGPUT: Laboratory of Geology and Palaeontology, University of Thessaloniki; MNHB: Museum der Naturkunde für Humboldt Universität zu Berlin; MNHN: Muséum National d'Histoire Naturelle, Paris; NHMW: Naturhistorisches Museum, Wien; NME: National Museum of Ethiopia, Addis Ababa; NMT: National Museum of Tanzania, Dar es Salaam; RMNH: Rijkmuseum van Natuurlijke Historie (Naturalis), Leiden; SAM: South African Museum, Cape Town; SMF: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main; SMNK: Staatliches Museum für Naturkunde, Karlsruhe; SMNS: Staatliches Museum für Naturkunde, Stuttgart; ZMA: Zoological Museum, Amsterdam.

Material

The material of fossil rhinoceroses from Laetoli is housed at the National Museum of Tanzania in Dar es Salaam, the National Museums of Kenya in Nairobi, the Museum der Naturkunde für Humboldt Universität in Berlin, and the Natural History Museum of London. Detailed information about the excavation and research history of the locality, as well as of the geological and stratigraphical setting is provided by Harrison (2011), Ditchfield and Harrison (2011), and Harrison and Kweka (2011).

The Laetoli material was compared with selected fossils from the Aterir Beds (Hooijer 1973), Chemeron Formation (Hooijer 1969), Kanapoi (Hooijer and Patterson 1972), and Koobi Fora and West Turkana (Harris 1976, 1983) at the collections of KNM. Additional comparative studies with material from the Plio-Pleistocene localities of Hadar (Guérin 1980b; Geraads 2005) and Dikika (Geraads 2005) were carried out at the NME; from the Omo Valley (Arambourg 1947; Hooijer 1969, 1972, 1973, 1975; Guérin 1985) at NME, RMNH and MNHN. Pleistocene material from Olduvai Gorge, Kanjera, Kanam West, and Rawi (Hooijer 1969; Groves 1975) was studied at BMNH. The Kohl-Larsen fossil collection from East Africa (Dietrich 1942, 1945) was studied at MNHB. Specimens from Bou Hanifia (Arambourg 1959; Geraads 1986), Ternifine (Pomel 1895) and several Plio-Pleistocene North African localities (Arambourg 1970) were examined at MNHN. Materials of "*Diceros*" *neumayri* from Greece (Pikermi, Samos, Axios Valley: Gaudry 1862–1867; Geraads 1988; Geraads and Koufos 1990; Giaourtsakis et al. 2006; Giaourtsakis 2009) were studied at AMPG, LGPUT, MNHN, BMNH, NHMW, IPUW, SMNS, BSPG, SMF and HLMD; those from Turkey (Various localities: Heissig 1975, 1996; Geraads 1994; Fortelius et al. 2003) were studied at BSPG, SMNK, and MNHN; and those from Iran (Maragheh: Osborn 1900; Thenius 1955) were examined at NHMW and MNHN. Casts of specimens from Fort Ternan (Hooijer 1968) and Langebaanweg (Hooijer 1972) were examined at BMNH and BSPG, respectively. Cranial material of *Diceros douariensis* from Douaria (Guérin 1966) was kindly shown to MF by C. Guérin and digital images of the specimens were provided by C. Guérin and A. Prieur. The rhinoceros material from the following localities was studied based on the referred publications: Arrisdrift, Namibia (Guérin 2000, 2003); Ekora Formation, Kenya (Hooijer and Patterson 1972); Lothagam, Kenya (Hooijer and Patterson 1972; Harris and Leakey 2003); Ahl al Oughlam and Oulad Hamida, Morocco (Geraads 2005). Comparative studies with the extant species *Ceratotherium simum* and *Diceros bicornis* have been also carried out at the zoological collections of the aforementioned institutions.

Stratigraphy

For temporal resolution of the Laetoli Sequence, we used the stratigraphic position of the localities relative to the marker tuffs to create semi-arbitrary Tuff Groups (Harrison and Kweka 2011). The following groups were created: 1-LLB = Lower Laetolil Beds, 2-BT3 = below Tuff 3, 3-T3-5 = between Tuffs 3 and 5, 4-T5-7 = between Tuffs 5 and 7, 5-STRT7 = straddles Tuff 7, 6-AT7 = above Tuff 7, 7-UND = Upper Ndolanya Beds.

Mesowear

We applied the original mesowear scoring system and analytical techniques introduced by Fortelius and Solounias (2000) for the upper dentition. We also extended the methodology to the cusp sharpness of the buccal enamel band of the lower teeth. We did this by a subjective judgment of equivalences according to the following guideline: distinct phase I facets with sharp boundaries = sharp; distinct phase I facets with fuzzy boundaries = rounded; no phase I facets = blunt. Relief was not scored for lower teeth and, apart from hierarchic clustering, we have limited our comparisons to cusp sharpness only. All teeth that were sufficiently well preserved were scored for mesowear, but only the first and second molars were included in the final analyses, and only the uppers in the hierarchic clustering analysis. Results generally remain similar even if premolars and deciduous teeth are included. We used polysiloxane putty (Provil Novo Putty regular set, Heraeus Kulzer GmbH, Hanau, Germany) to make partial molds of the teeth and synthetic dental stone

(Fujirock by GC Europe n.v., Leuwen, Belgium) to make replicas.

The curvature of the facets and enamel were further examined by high-resolution 3D scanning techniques. We used this methodology to study the enamel edges of the upper and lower teeth of *C. efficax,* the derived *Ceratotherium* from latest Pliocene and early Pleistocene, extant *C. simum*, Pliocene *Diceros* and extant *D. bicornis*. An area of at least 2×3 mm around the enamel edge and the facet was scanned using a Nextec Hawk 3D laser scanner at 30×30 µm resolution. The scanned area extended from the vertical buccal side of enamel, over the worn enamel surface, to the dentine on the occlusal surface. Point clouds were realigned using Rhinoceros 3.0 (McNeel, Seattle, WA, USA). They were then imported into Surfer for Windows v. 8 (Golden Software, Colorado, USA) and a 30 × 30 µm resolution grid was generated using Kriging interpolation. Surface curvature was calculated according to Evans (2005): the surface was smoothed three times using a 9×9 kernel with central weighting of 4 to reduce surface noise, and then directional curvature was calculated at 10° intervals for 180°. The maximum curvature at each x, y point for all directions was determined. Radius of curvature (inverse of curvature) plots were overlain on the smoothed surface plot to visualize flat and curved areas (Evans 2005).

Statistical calculations were carried out using the statistics package JMP 6.0 (SAS Institute, Inc., Cary, NC, USA), except for the polar clustering diagrams (Fig. R.4.1), which were produced in Systat 11.0 (Systat Software, Inc., San Jose, CA, USA).

Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Perissodactyla Owen, 1848
Suborder Ceratomorpha Wood, 1937
Superfamily Rhinocerotoidea Owen, 1845
Family Rhinocerotidae Owen, 1845
Subfamily Rhinocerotinae Owen, 1845
Tribe Dicerotini Ringström, 1924
Genus *Ceratotherium* Gray, 1868
Ceratotherium efficax (Dietrich, 1942)

Synonymy

1907. non *Opsiceros simplicidens* sp. nov. – Scott: pp. 257–259, pl. 17, Figs. 3–5.
1926. pro parte sub *Rhinoceros scotti* sp. nov. – Hopwood: pp. 216–217, Fig. 3; (Kaiso).
1942. *Serengeticeros efficax* gen. et sp. nov. – Dietrich: pp. 297–300, Fig. 2; (Laetoli).
1945. *Serengeticeros efficax* Dietrich, 1942. – Dietrich: pp. 56–67; pl. 13, Figs. 1, 3, 4, 6; pl. 14, Figs. 8, 10; pl. 15, Figs. 11–15, 18–20; pl. 16, Figs. 21–23; pl. 17, Fig. 28; pl. 18, Fig. 36; pl. 19, Fig. 42; (Laetoli).
1947. pro parte *Atelodus germanoafricanus* (Hilzheimer, 1925). – Arambourg: pp. 299–301. (Laetoli).
1969. pro parte *Ceratotherium simum germanoafricanum* (Hilzheimer, 1925). – Hooijer: pp. 74–75, 85–86, pl. 3; (Laetoli).
1972. pro parte *Ceratotherium simum germanoafricanum* (Hilzheimer, 1925). – Hooijer: p. 153; (Laetoli).
1976. *Ceratotherium* sp. – Leakey et al.: p. 464; (Laetoli).
1979. *Ceratotherium* sp. – Leakey and Hay: p. 4; (Laetoli).
1980b. pro parte *Ceratotherium praecox* Hooijer and Patterson, 1972. – Guérin: p. 61; (Hadar).
1987a. pro parte *Ceratotherium praecox* Hooijer and Patterson 1972. – Guérin: pp. 321–326, pl. 9.4, Figs. A-C; (Laetoli, Hadar).
2005. pro parte *Ceratotherium mauritanicum* (Pomel, 1888). – Geraads: pp. 452–455, Figs. 1a–b; (Hadar, Dikika, Koobi Fora, Laetoli).

Holotype. Maxillary fragments with left and right M1-M3 of the same individual (MNHB: MB.Ma.42009), illustrated by Dietrich (1945: taf. 13, Fig. 1, 6).

Type Locality. Vogelflussgebiet near the Garrusi River of the Southern Serengeti, known today as Laetoli, Tanzania.

Stratigraphical level. Grey volcanic tuff of the Serengeti Beds (Dietrich 1945), corresponding to the Upper Laetolil Beds of current usage (Hay 1987; Ditchfield and Harrison, 2011).

Age. Pliocene.

Geographical distribution. Presently known from East Africa: Tanzania, Kenya, Ethiopia, Uganda, and perhaps Chad. Fossil evidence from other African countries is presently insufficient.

Revised descriptive diagnosis. Ceratotherium of large size; nasal and frontal horns present, nasal bones rostrally rounded with abrupt and broad termination; premaxillary bones reduced; lower border of orbita sloping laterally downwards; supraorbital process very strong, postorbital process absent; average position of the anterior orbital border at the level between the distal half of M2 and the mesial half of M3; dorsal cranial profile gently concave; strong nuchal crest with concave occipital notch, extending posteriorly over the level of the occipital condyles; occipital plane posterodorsally inclined; postglenoid and posttympanic processes without contact. Upper and lower incisors absent or vestigial. High crowned, functionally hypsodont maxillary dentition with relatively flattened occlusal surface, rather constant enamel thickness, and significant cement coating. D1 not persisting in adulthood. Upper premolars with: protocone markedly larger than hypocone after moderate stage of wear; protocone constricted only by a mesial groove; distal protocone groove and antecrochet absent; hypocone not constricted; medisinus basin lingually open, protoloph and metaloph fusing only during late to latest stages of wear; lingual cingulum present, moderately expressed, and frequently continuous; crochet always present and well developed; crista mostly present, usually weak; medifossette rarely formed and only after moderate to late stages of wear; paracone fold faint to weak; metacone fold absent. Upper molars (M1, M2) with: protoloph bending markedly distolingually; metaloph shorter and relatively less oblique, particularly on M1; mesial protocone groove present, deep and marked; distal protocone groove absent; lingual protocone groove generally present and well marked; crochet strong; expression of crista variable; formation of closed medifossettes frequent after early to moderate stages of wear; buccal profile of ectoloph in molars slightly undulated; paracone fold present but weak to faint; mesostyle bulge prominent, but not acute and not markedly stronger than the paracone fold; metacone fold absent. M3 with predominately continuous ectometaloph and without postfossette. Lower premolars with lingually open trigonid and talonid basins, forming occasionally closed fossetids; lower molars with buccal wall of the trigonid frequently flattened. Appendicular skeleton with markedly long and relatively slender metapodials.

Differential diagnosis. *Ceratotherium efficax* is distinguished from *C. mauritanicum*, *C. germanoafricanum* and *C. simum* by its more primitive dentition, as well as from the latter two species by the different size and proportions of its appendicular skeleton, in particular of the metapodials. Based on the available evidence, *C. mauritanicum* differs from *C. efficax* by showing population variants with frequent expression of a shallow buccal depression slightly demarcating the continuity of the ectolometaloph on M3, upper premolars with earlier fusion of protoloph and metaloph, upper premolars with weaker and frequently discontinuous lingual cingulum, and lower premolars forming more frequently closed fossetids during moderate stages of occlusal wear. *C. germanoafricanum* and *C. simum* differ from *C. efficax* and *C. mauritanicum* by the following dental features: the ectoloph and metaloph on M3 are always markedly separated forming a postfossette; the lingual protocone groove on the molars is absent or only faintly expressed; the metaloph on the molars and premolars is longer and bends more markedly distolingually. Extant *C. simum* differs additionally by at least the following dental features: the teeth are absolutely and relatively more high crowned; the protoloph and metaloph of the premolars fuse after early stages of occlusal wear closing the entrance of the medisinus; the lingual cingulum on the premolars is virtually absent; the paracone fold on the buccal wall of the premolars and particularly of the molars is completely suppressed by a deep parastyle groove; the mesostyle bulge is more acute and always developed as the most prominent fold on the buccal wall of the ectoloph; the metaloph of the molars and the premolars bends more markedly distolingually; a closed medifossette is very frequently formed on the premolars during early to moderate stages of occlusal wear, and it is almost always formed on the molars during the earliest stages of occlusal wear. *C. efficax* differs from *C. simum* by its absolutely longer and relatively more slender appendicular skeleton. *C. germanoafricanum* differs from *C. efficax* and *C. simum* by its absolutely larger and relatively more robust appendicular skeleton.

Material

Lower Laetolil Beds (NMT)

Mandibles: EP 062/98, KK 82/294, KK 82/71
Deciduous teeth: Rt DP2 EP 098/98, lt DP4 EP 066/98
Permanent teeth: lt P3/4 EP 062/98, rt P3/4 EP 3927/00, rt P/M EP 1343/03, rt M1/2 EP 103/98, lt M2 EP 100/98, M frgt EP 221/03, lt m3 KK 82/213, m frgt EP 522/03

Upper Laetolil Beds (NMT)

Crania: LAET 74-323, LAET 78-4979
Mandibles: LAET 74-188, LAET 75-2836
Deciduous teeth: lt DP1 EP 122/98, LAET 75-2617, EP 458/04, EP 3824/00, LAET 75-1182, LAET 75-1275; rt DP2 EP 1318/04, EP 1358/00a, EP 038/01, EP 1006/04; lt DP2 EP 458/04, LAET 75-3434, EP 1493/04, LAET 78-4714; rt. DP3 EP 458/04, EP 038/01; lt DP3 EP 1240/01; rt DP4 LAET 75-3118, EP 038/01; lt DP4 EP 458/04, LAET 74-215, LAET 75-618; rt dp2 LAET 75-1782; EP 2323/03, EP 512/00; lt dp2 EP 4120/00; rt dp3 EP 1421/00, EP 1506/03, EP 308/00, EP 331/04, EP 410/00, EP 432/04, EP 673/00, EP 721/04; lt dp3 EP 1365/98, EP 2879/00, EP 2998/00, LAET 74-214, LAET 75-1855, LAET 75-2209, LAET 75-3531, LAET 78-4884; dp3/4 LAET 74.100, LAET 74-145; rt dp4 EP 1179/98, EP 2198/03, EP 457/00, LAET 75-3747, LAET 75-456; lt dp4 EP 1297/03, EP 1759/00, EP 2455/00, EP 2646/00, EP 3609/00, EP 418/98, LAET 78-5137, LAET 78-5335

Permanent teeth: rt P2 EP 1218/98, EP 1237/01, EP 1843/00, EP 2574/00, LAET 75-1378, LAET 75-3649, LAET 75-630; lt P2 EP 1132/04, EP 1358/00c, EP 1366/98, EP 4224/00, EP 660/98, LAET 74-50, LAET 75-1992, LAET 75-2115, LAET 75-2544, LAET 75-3582, LAET 78-5009; rt P3/4 EP 120B/98, EP 454/03, EP 088/00, EP 118/98, EP 121/98, EP 154/00, EP 155/00, EP 366a/98, EP 3927/00, LAET 74-250, LAET 75-3091, LAET 75-3371, LAET 78-4774, EP 1035/98, LAET 75-3647; lt P3/4 EP 1554/98, EP 117/98, EP 1492/04, EP 1502/00, EP 2402/00,

EP 3692/00, EP 505/98, LAET 75-1194, LAET 75-1385, LAET 75-2150, LAET 75-985, LAET 78-5406, EP 591/00; rt M1/2 EP 038/01, EP 1080/98, EP 120B/98, EP 3664/00, LAET 78-4651, EP 1064/04, EP 1217/98, EP 1611/00, EP 2027/03, EP 2223/00, EP 2401/00, EP 366c/98, EP 3691/00, EP 595/04, LAET 75-1306, LAET 75-1378, LAET 75-1615, LAET 75-2040, EP 1080/98, EP 120B/98, LAET 75-2760, LAET 75-492; lt M1/2 EP 1080/98, EP 982/03, LAET 78-4949, EP 634/98, EP 090/00, EP 1037/98, EP 119/98, EP 1358/00d, EP 1551/03, EP 156/00, EP 264/99, EP 2738/00, EP 761/03, LAET 75-1378, LAET 75-1872, LAET 75-507, LAET 75-543, LAET 78-4964, EP 1080/98, EP 120A/98, LAET 75-3648; rt M3 EP 089/00, EP 1080/98, EP 275/99, LAET 75-1378, LAET 75-2149, LAET 75-2208, LAET 78-4938; lt M3 EP 1080/98, EP 120A/98, EP 1509/03, EP 413/98, EP 414/98, EP 672/00, EP 763/03, EP 865/98, LAET 74-51, LAET 75-3042, LAET 78-4640; rt p2 EP 1178/98, EP 923/01, LAET 78-4651; lt p2 EP 147/03, EP 2645/00, EP 762/04, EP 874/01, LAET 75-1378; rt p3/4 LAET 75-1378, EP 1962/00; lt p3/4 EP 1359d/00, EP 1635/98, EP 556/00, LAET 75-987, LAET 74-188, LAET 75-1378, LAET 78-4755; rt m1/2 EP 027/00, LAET 75-3530, LAET 78-4883, LAET 78-5328, EP 026/00, LAET 75-2760; lt m1/2 EP 3693/00, EP 3883/00, LAET 74-153, LAET 74-188, LAET 75-1378, EP 037/01, EP 1177/98, EP 1239/01, EP 1359c/00, EP 1501/98, LAET 75-1135, LAET 75-544, EP 1359e/00, EP 3883/00, LAET 74-188, LAET 76-3847; rt m3 EP 1039/98, EP 211/01, LAET 78-4742; lt m3 EP 1298/03, EP 3883/00, LAET 74-188, LAET 75-472, LAET 78-4964, LAET 78-5141, LAET 78-5191.

Probably Upper Laetolil Beds (KNM)

Rt DP3 LIT 59-119; lt DP3 LIT 59-116; lt DP4 LIT 59-195; lt P2 LIT 59-418, rt P3/4, LIT 59-118; lt P3/4 LIT 59-346, LIT 59-439; rt M3 LIT 59-194; P/M frgts LIT 59-117, LIT 59-193

Upper Ndolanya Beds (NMT)

Cranium EP 1041/00; lt p2 LAET 75-413; m/p frgt EP 3786/00

Laetoli Specimens (BMNH)

Almost 60 rhinocerotid specimens from Laetoli are housed in the collections of the Natural History Museum of London. About 35% of them represent dental elements, while the rest are postcranial elements. The specimens originate from the collections made by Louis Leakey during 1935 and bear their original field numbers. Three Laetoli sites are indicated: LIT.AS, LOL.S and 1710.S. The material forms a rather uniform sample, and there is no indication for the presence of *Diceros*: all dental specimens demonstrate the characteristic morphological features of *Ceratotherium efficax* detailed in the diagnosis, and the postcranial elements are consistent in size and proportions. In particular, complete metapodials are absolutely longer and relatively more slender with respect to extant *Ceratotherium simum*.

Remarks and Comparisons

Before proceeding with the description we feel obliged to comment on what differences one may reasonably expect to demonstrate between species of the tribe Dicerotini. As our discussion shows, it has been commonplace in the literature to identify individual specimens at the species level. For complete cranial material and well-preserved dentitions and teeth this is generally entirely reasonable. However, even in these cases it might be difficult to support an identification based solely on metric comparisons. Fig. 11.1 shows that the skulls of the extant *Diceros* and *Ceratotherium* are quite well separated based on a length-width bivariate plot, although, even in this case, some individuals from the two genera overlap. Fig. 11.2 shows that the molars of the same specimens overlap almost completely in terms of their basal length-width measurements. We have accordingly desisted from attempts to use simple linear metrics to assign Laetoli teeth taxonomically, and based our identifications only on clearly defined morphological criteria.

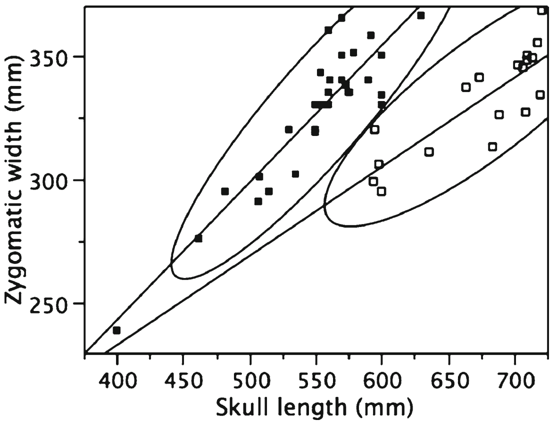

Fig. 11.1 Zygomatic width as a function of total skull length in Recent *Ceratotherium simum* (*white*) and *Diceros bicornis* (*black*), including subadult individuals, scale in cm. Some specimens have essentially identical dimensions but separation is good and the allometric relationship is different, *Diceros* having a more rapid increase in width with increasing length. Least squares regression lines and 95% density ellipses shown. Unpublished data; specimens from the collections of (Tervuren, Leiden, Copenhagen, Stockholm, Gothenburg, and Helsinki)

Crania

Guérin (1987a) assigned the crania LAET 74-323 (Loc. 7) and LAET 78-4979 (Loc. 3) from the Upper Laetolil Beds to *C. praecox*, reporting a close resemblance between the concave frontal profile of the latter specimen and the type cranium of "*C. praecox*" from Kanapoi (Hooijer and Patterson 1972). However, as noted by Geraads (2005), the frontal area of the LAET 78-4979 cranium is deformed rather than originally concave, and the cranial morphology is, in fact, very similar to the skulls from the Lower Awash Valley, which he referred to as *C. mauritanicum*. The dentition of the LAET 78-4979 cranium is very incomplete; the axis of the metaloph appears to pass distally to the medifossette, similar to the Lower Awash specimens. The dentition of the cranium LAET 74-323 is completely missing and the nuchal crest is seriously damaged; the available morphology of the occipital and frontal portion clearly distinguishes it from *Diceros*. The partial cranium EP 1041/00 from the Upper Ndolanya Beds is poorly preserved, but its dentition is in excellent condition and demonstrates all characteristic features of *C. efficax* described in the diagnosis (Fig. 11.3).

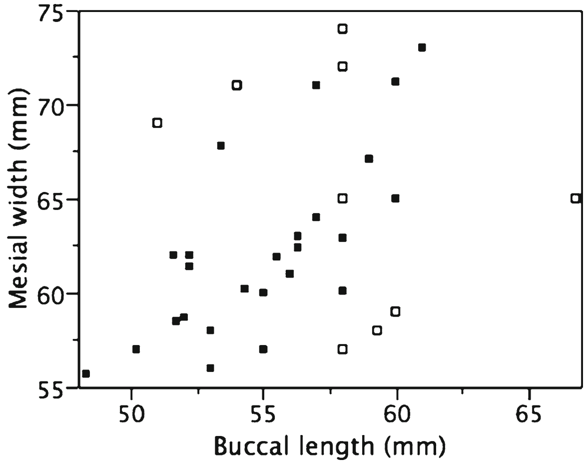

Fig. 11.2 Plot of mesial width as a function of buccal length in second upper molars of Recent *Ceratotherium simum* (*white*) and *Diceros bicornis* (*black*), from the skulls shown in Fig. 11.1. Note complete lack of separation of teeth by size or proportions

Permanent Upper Dentition

Although the Laetoli teeth assigned by us to *C. efficax* appear quite similar to those of modern *C. simum* in general characteristics, there are several distinct and constant differences. The dentition of *C. efficax* is absolutely and relatively less high crowned than *C. simum* and the occlusal surfaces of the teeth are less flattened. In *C. efficax*, the protoloph and particularly the metaloph bend less markedly distolingually than in *C. simum*. On the premolars of *C. efficax*, a moderately expressed and usually continuous cingulum is developed, the crista is weak and forms rarely after moderate stages of wear a closed medifossette with the strong crochet, the entrance of the medisinus remains usually open until late

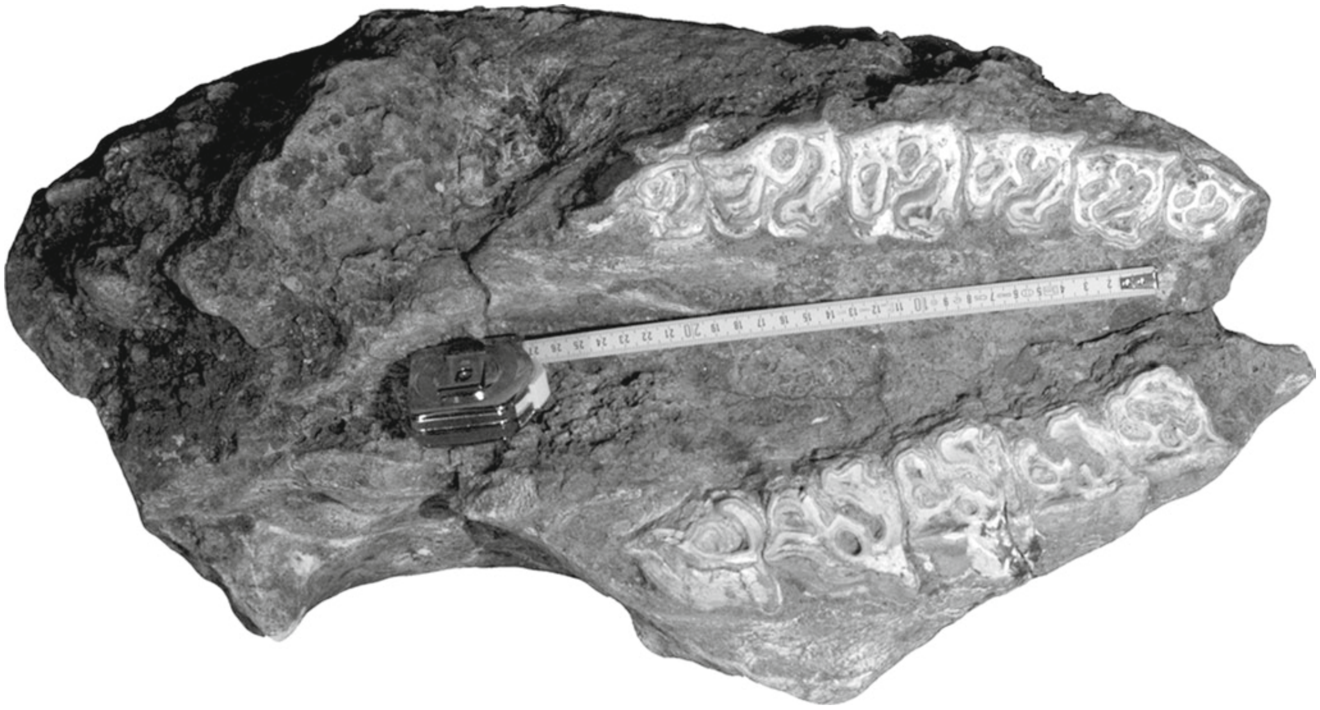

Fig. 11.3 *Ceratotherium efficax*, cranium NMT: EP 1041/00

stages of wear (except on P2), and a weak paracone fold is present on the buccal wall of the ectoloph. On the premolars of *C. simum*, the lingual cingulum is virtually absent, a closed medifossette is mostly formed during early stages of occlusal wear, the protoloph and metaloph fuse early closing the entrance of the medisinus, and the mesostyle bulge is the most prominent fold on the buccal wall of the ectoloph. On the molars of *C. efficax*, a conspicuous lingual protocone groove is nearly always present (sometimes also on premolars, but much weaker), a closed medifossette is variably formed, a faint protocone fold is usually evident, and the M3 features a continuous ectometaloph without postfossette. On the molars of *C. simum*, a marked lingual protocone groove is not developed (due to the more extreme bending of the protoloph), a closed medifossette is always formed at very early stages of wear, the paracone fold is completely suppressed by a deep parastyle groove, the mesostyle bulge is more acute, and on the M3 the ectoloph and metaloph are always markedly separated forming a postfossette.

Upper Deciduous Dentition

The upper deciduous teeth are generally quite similar to those of *C. simum*, with a slightly undulating ectoloph and a prominent parastyle, which is more markedly expressed than in *D. bicornis*. The mesial cingulum is weaker than in *D. bicornis* and the protoloph bends more markedly distolingually. The crista is strong and often expressed as multiple folds. The buccal enamel surface is rough, suggesting that a cement covering was originally present, but has not been preserved.

Mandible and Lower Dentition

Several mandibular fragments have been recovered from the Laetolil Beds, but unfortunately they are rather incompletely preserved. The mandibular symphysis and the ascending rami are usually broken off or severely crushed. The mandibular ramus, which is usually better preserved, is relatively high and features a concave dorsal profile. On its lingual side, the mylohyoid line is often expressed as a shallow longitudinal depression. The posterior margin of the symphysis extends variably below the level of p3. The enamel of the lower teeth is rough and cement traces can be often observed on the buccal wall and the internal valleys of the teeth. The dp1 does not persist in adulthood. On p2, the paralophid is single and there is no evident buccal groove or depression on the buccal wall of the trigonid. A rising mesiobuccal cingulum can be observed in some molars. The buccal wall of the metalophid is often slightly flattened, especially on the upper part of the crown, but not to the extent observed in extant *C. simum*, where it can be even slightly depressed, particularly on the molars. The ectoflexid is smoothly marked, but not particularly deep. It usually terminates before the base of the crown, especially on the premolars. The hypolophid is oblique and rounded, except sometimes on m3, where it may be less markedly rounded. In extant *C. simum*, the hypolophid on m3 and sometimes on m2 is less oblique and nearly straight. The lingual sinuses are situated high above the base; in molars, the profile of the anterior sinus is U-shaped and the distal sinus V-shaped. The lingual wall of the metaconid is rather flattened; in extant *C. simum*, the lingual wall of the metaconid is usually shallowly depressed. On the premolars, the metaconid bends frequently distolingually, but, contrary to the extant *C. simum*, the formation of closed fossetids is rare.

Tribe Dicerotini Ringström, 1924
Genus *Ceratotherium* (Gray, 1868)
Ceratotherium cf. *simum*

Material

Upper Ndolanya Beds (NMT)

Cranium LAET 81-74 (Fig. 11.4); lt p2 LAET 78-5017

Remarks and Comparisons

The LAET 81-74 cranium (Fig. 11.4) from Loc. 14 of the Upper Ndolanya Beds was assigned to *C. simum* by Guérin (1987a). The left P4-M3 are moderately well-preserved and show several derived features with respect to *C. efficax*. On

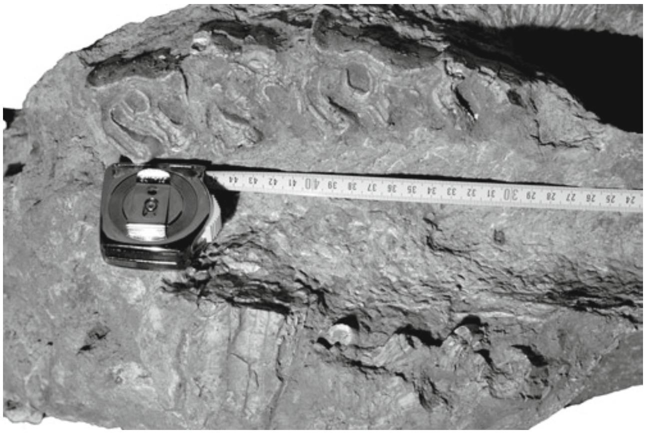

Fig. 11.4 *Ceratotherium* cf. *simum*, cranium NMT: LAET 81-74, left P4-M3

P4 a closed medifossette is formed, the metaloph is relatively longer than in *C. efficax*, and the mesostyle bulge more prominent. However, contrary to extant *C. simum*, the protoloph and metaloph of the P4 do not fuse lingually and the medisinus valley remains open even during this late stage of wear. The molars are fragmentary. The axis of the metaloph passes clearly through the medifossette. On the buccal wall of the ectoloph, the mesostyle bulge is the dominant fold, but it is not as prominent as in extant *C. simum*. The available comparative material presently prevents a more accurate assignment of this specimen to *C. germanoafricanum* or primitive *C. simum*, since the molars of both species share the features listed above.

Tribe Dicerotini Ringström, 1924
Genus *Ceratotherium* Gray, 1868
Ceratotherium sp.

Material

Upper Ndolanya Beds (NMT)

Lt mandible LAET 75-2469; P frgt EP 4022/00

Remarks and Comparisons

LAET 75-2469 is an incompletely preserved mandibular fragment, which may be referred to *Ceratotherium*.

Tribe Dicerotini Ringström, 1924
Genus *Diceros* Gray, 1821
Diceros sp.

Restricted Synonymy

1987a. *Diceros bicornis (L.)* - Guérin: p. 327, pl. 9.5, Figs. A, B; (Laetoli).
2005. *Diceros* cf. *praecox* (Hooijer and Patterson, 1972). - Geraads: p. 457, tab. 4; (Laetoli).

Material

Upper Laetolil Beds (NMT)

Cranium LAET 75-3065

Remarks and Comparisons

The genus *Diceros* has generally been regarded as morphologically constant from the Early Pliocene to the present day. According to Harris and Leakey (2003) even the teeth from 6.24–5.5 Ma (Leakey et al. 1996) Upper Nawata, Lothagam, are similar to the teeth of the recent *D. bicornis*, even though, as Hooijer (1978) and Geraads (2005) noted, such longevity is extremely rare for a recent mammal species. Although *Diceros* appears to have been a less common element in the Laetoli fauna than it may have been previously assumed (Guérin 1987a), it clearly was present as evidenced by the LAET 75-3065 cranium. During an exhaustive survey of the entire collections of the Laetoli rhinoceros material preserved in the National Museums of Tanzania and Kenya, as well as in London and Berlin, we found only a few dental specimens that potentially could be attributed to *Diceros*. It is possible that some of the postcranial elements may also represent *Diceros*, as Guérin (1987a) has suggested, but we were not able to document reliable quantitative or qualitative criteria for distinguishing two genera among the available material.

Cranium

The cranium LAET 75-3065 originates from Loc. 10W of the Upper Laetolil Beds and was described and figured by Guérin (1987a, pl. 9.5). The cranium is crushed and deformed, and bears multiple fractures. It belongs to a very old individual, as indicated by its heavily worn teeth. The right P3-M3, as well as the left M2 and part of the left M3, are fragmentary. All molars are lingually broken and their ectoloph is poorly preserved. The relatively complete P4 shows a well-developed and continuous lingual cingulum, and an ectoloph coronal profile similar to extant *D. bicornis*. There is no evidence of a paracone fold at this late stage of wear. Both the protoloph and metaloph are rather straight and only slightly oblique, similar to extant *D. bicornis*. These features are in sharp contrast to *Ceratotherium efficax* (and subsequent congeneric species), where the lingual cingulum is weaker, the ectoloph profile more flattened, and the protoloph is bending markedly distolingually.

Geraads (2005) proposed that the cranium LAET 75-3065 might be referred to *Diceros praecox* (Hooijer and Patterson 1972) from Kanapoi, together with the skull AL-126-21 from Hadar. According to Geraads (2005), both specimens combine a dental morphology similar to extant *Diceros* with a “primitive” [sic] *Ceratotherium* occipital morphology. However, we could not detect the combination of cranial and dental features described by Geraads (2005) for the Hadar and Laetoli crania. The teeth of the Laetoli specimen LAET 75-3065 are too worn to show any reliable differences, while the apparent shortness of the transverse lophs noted by Geraads (2005) for the Hadar specimen AL-126-21 does not, in our opinion, differ significantly from extant *D. bicornis* teeth at a similar early stage of wear. The large size of the teeth reported for the Hadar specimen actually fall within the range of variation of the large-sized genotypic subspecies *Diceros bicornis bicornis*. In addition, the teeth of the holotype cranium of the purported *Diceros praecox* from Kanapoi (KNM-KP 36) are too worn and incomplete to allow metric comparisons (Hooijer and Patterson 1972: Fig. 9a). The occipital region of both Laetoli and Hadar specimens is quite fragmentary. According to our comparisons, the available morphology seems to fall well within the range of variation that we have observed among the various subspecies of extant *D. bicornis*, for both the extension of the nuchal crest and the angle of the occipital level; a resemblance with the derived occipital morphology of *Ceratotherium* is not justified.

Tribe Dicerotini Ringström, 1924
Dicerotini gen. et sp. indet.

Material

Lower Laetolil Beds (NMT)

Postcrania (incomplete listing): Ulna EP 1184/04; magnum LAET 78-5023; unciform EP 005/99, EP 200/03.

Upper Laetolil Beds (NMT)

Permanent teeth: Rt P3 EP 1061/03; lt M1/2 LAET 75-757; rt p3 EP 628/98.

Postcrania (incomplete listing): Scapula EP 1761/00; humerus EP 462/04; radius EP 160/98, EP 413/04, EP 2163/00, scaphoid EP 154/98, EP 871/03, EP 602/98, EP 2674/00, EP 1963/00, LAET 75-581, EP 2783/00, EP 3826/00, EP 3908/00, EP 1043/98, EP 462/04; lunar EP 908/04, EP 1526/98, EP 1041/98; cuneiform EP 2484/00, EP 1322/04; trapezoid EP 424/98; magnum EP 809/98, EP 1322/04, EP 1504/00, EP 1183/98, unciform EP 496/98, LAET 75-2358, LAET 75-3284, EP 039/04, EP 124/98, EP 125/98, LAET 78-4743, EP 1133/04, EP 1363/98, LAET 78-4811, EP 2335/00, LAET 75-3048, EP 2648/00, EP 677/00, LAET 75-3653, EP 212/01, EP 1646/04, LAET 75-2890, EP 1322/04, EP 2134/03, EP 2518/00, EP 758/03, EP 462/04, mc II EP 3610/00, EP 1491/04, EP 383/03, EP 1361/00, LAET 75-1110, LAET 75-1118, EP 1505a/00, EP 1045/98; mc III EP 1844/00, EP 676/00A, EP 676/00B, LAET 75-1729, EP 515/00, EP 679/03, LAET 78-4924, EP 1361/00, EP 1423/04, LAET 75-1246, LAET 75-819, LAET 9b; mc IV LAET 75-3562, LAET 75-3564, EP 659/98, EP 810/98, EP 4300/00, LAET 78-4800, LAET 75-3656, LAET 76-3888, EP 1614/00, EP 1320/04, EP 1423/04, EP 1505b/00, EP 2517/00, EP 1236/01, tibia EP 2994/00, EP 3926/00; astragalus EP 039/01, EP 1009/98, EP 1146/00, EP 1319/04, EP 1429/01, EP 1434/98, EP 1572/03, EP 1845/00, EP 1964/00, EP 2199/03, EP 2219/00, EP 2363/00, EP 2456/00, EP 2457/00, EP 408/00, EP 4229/00, EP 751/00, EP 788/98, EP 789/98, EP 879/04, LAET 75-1231, LAET 78-5079; calcaneum EP 1141/00, EP 1142/00, EP 2051/00, EP 2133/03, EP 2293/00, EP 2483/00, EP 2647/00, EP 309/00, EP 3828/00, EP 879/04, LAET 75-1117; navicular EP 1697/00, EP 2135/03; ectocuneiform EP 1070/98, EP 462/04, EP 654/98; cuboid EP 1695/00, EP 2050/00, EP 3064/00; mt II EP 1107/98, EP 1262/00, EP 1364/98, EP 406/00, EP 462/04, LAET 75-3445, LAET 75-3529; mt III EP 337/99, EP 038/04, EP 1061/04, EP 1255/04, EP 1299/03, EP 1364/98, EP 462/04, EP 514/00, EP 793/98, LAET 74-18, LAET 75-1227, LAET 75-1339, LAET 75-2171, LAET 75-2825, LAET 75-3207, LAET 75-3654, LAET 75-583; mt IV EP 128/04, EP 1479/03, EP 267/03, EP 462/04, EP 978/01, LAET 74-9, LAET 75-3657, LAET 75-3658, LAET 75-814.

Probably Upper Laetolil Beds (KNM)

Permanent tooth: Lt P2 LIT 59-582.
Postcrania (incomplete listing): Mc II LIT 59-265; mc III LIT 59-580; mc IV LIT 59-263, LIT 59-263; tibia LIT 59-423; astragalus LIT 59-248, LIT 59-433; calcaneum LIT 59-22, LIT 59-23, LIT 59-345; mt II LIT 59-262, LIT 59-343; mt IV LIT 59-264.

Upper Ndolanya Beds (NMT)

Postcrania (incomplete listing): Magnum LAET 78-5023; unciform LAET 75-1653; femur, EP 1038/00; calcaneum EP 1214/03; navicular EP 705/03.

Ngaloba Beds (NMT)

Permanent tooth: Lt P3 EP 381/04

Remarks and Comparisons

Permanent Dentition

For some isolated dental fragments, a definite identification as *Ceratotherium* or *Diceros* is very difficult. The upper premolars LIT 59-582 and EP 1061/03, and the lower premolar EP 628/98 are incompletely preserved and do not offer reliable diagnostic features. The ectoloph profile of the upper molar LAET 75-757 appears to have some similarity with *Diceros* morphology, but it is difficult to ascertain, as almost half of the tooth is missing. The upper premolar EP 381/04 is clearly rounded by transportation and it may actually be subrecent.

Postcrania

Among the available postcranial material the most notable specimens are several complete metapodials. They are absolutely longer than the metapodials of both extant African species, and relatively slender. There is little doubt that these specimens represent *C. efficax*. The size and proportions of the Laetoli metapodials are closer to the size and proportions of the abundant Langebaanweg sample (Hooijer 1972; Guérin 1979, 1987a). This was one of the key arguments used by Guérin (1987a) for referring the Laetoli material to *C. praecox*, since this name was previously widely used for the Langebaanweg sample. Guérin (1987a) did not assign any metapodials or long bones to *Diceros*, but only a few carpal and tarsal bones with somewhat smaller dimensions. Based on the proportions and morphology, it seems difficult to unequivocally recognize different groups among the carpals and tarsal bones. Since the majority of cranial and dental specimens belong to *C. efficax*, one could reasonably assume that the majority of the postcranials, if not all, represent this species. Alternatively, some of the smallest postcranial elements may indeed belong to the genus *Diceros*, as Guérin (1987a) has suggested. We believe that more postcranial material and comparative studies are required to establish reliable quantitative and/or qualitative criteria for their discrimination and we have accordingly not attempted an identification of the Laetoli postcranial specimens in the present study.

Discussion

Taxonomic History of the Laetoli Rhinoceroses

The first detailed studies of fossil rhinoceroses from Laetoli were published by Dietrich (1942, 1945). His material, consisting of a large number of isolated teeth and bones, had been collected by the Kohl-Larsen Expedition from 1938–1939 in the volcanic tuffs of the Garusi River area (“Vogelflussgebiet”; Dietrich 1941; T. Harrison, personal communication) of the Southern Serengeti, known today as Laetoli (Leakey 1987). Dietrich identified specimens that in his opinion could not be referred to either of the living African species, the white rhino *Ceratotherium simum* or the black rhino *Diceros bicornis* (Dietrich 1942). He considered these specimens to represent a species intermediate between the living species, although closer to *C. simum*. He named this species *Serengeticeros efficax* and believed it to be the direct ancestor of *C. simum*. According to Dietrich the diagnostic character of *S. efficax* was found in the upper molar teeth, in which the protoloph curves towards distal but the metaloph is straight (Dietrich 1942). In a more detailed description of the stratigraphic context of the rhinoceros remains (Dietrich 1945), he noted that *S. efficax* was found in the grey volcanic tuff, corresponding to the Upper Laetolil Beds of current usage (T. Harrison, personal communication). According to Dietrich, fossils attributable to the living species were only found in younger strata, probably corresponding to the Ndolanya Beds or the Pleistocene Ngaloba Beds (Leakey 1987; T. Harrison, personal communication).

The specimens described and illustrated by Dietrich as *Serengeticeros efficax* (e.g., Dietrich 1942, Fig. 2; Dietrich 1945, Table XII:1, 6) correspond precisely to subsequently collected material of the most common rhinoceros species from Laetoli. Dietrich’s line drawings show the characteristics of this species well, including the lingual curvature of the protoloph towards the distal, the straight metaloph with an axis that does not bisect the medifossette, the lingual protocone groove, and the mesostyle bulge, distinct but less developed than in *C. simum*. The lack of any specimens of *Diceros bicornis* from the grey tuffs as noted by Dietrich matches our finding that *Diceros* is very rare in the Laetolil Beds.

Much earlier, Pomel (1885) had mentioned and later described (Pomel 1888, 1895) a Pleistocene rhinoceros from Ternifine (age ca. 0.8 Ma, see e.g., Guérin 1987b), Algeria, as *Rhinoceros mauritanicus*. Pomel did not assign a holotype, but Geraads (2005) selected an isolated M2 (MNHNP TER-2261) drawn by Pomel (1895, plate 1, Fig. 2) as the lectotype of this species, and transferred it to *Ceratotherium* as *C. mauritanicum*. In Pomel’s drawing the specimen appears rather similar to second upper molars from Laetoli: the medifossette is closed, the metaloph axis runs distal to the postfossette, the protoloph turns lingually towards distal, and the mesostyle bulge is significantly less pronounced than in *C. simum*. Among other specimens, Pomel also illustrates a right M3 (1895, Plate 1, Fig. 4), which also resembles specimens from Laetoli to a large degree.

Geraads (2005) attributed the Pliocene material from the Lower Awash to *C. mauritanicum*. The skull AL-129-25 figured by him (Geraads 2005, Fig. 1) matches the material from Laetoli perfectly in both cranial and dental features. We, however, feel that the name *Ceratotherium efficax* (Dietrich 1942) is more appropriate for this East African Pliocene species than the name *Ceratotherium mauritanicum* suggested by Geraads (2005).

North African Pleistocene *C. mauritanicum* retains similar craniodental and postcranial sizes and proportions as *C. efficax*, but demonstrates slightly more derived dental features. For example, M3s are more frequently quadrangular in shape with an expression of a shallow buccal depression slightly demarcating the continuity of the ectolometaloph. Also in upper premolars the lingual cingulum is often weaker and discontinuous, and the fusion of the protoloph and the metaloph happens earlier, and lower premolars more often form closed fossetids during moderate stages of wear. The morphology of *C. mauritanicum* is thus closer to the common ancestor of *C. germanoafricanum* and *C. simum*. *C. mauritanicum* managed to retain the *C. efficax* morphotype with few modifications in North Africa considerably longer than in East Africa, where *C. efficax* was replaced by the more derived species *C. germanoafricanum* and *C. simum* (Geraads 2005; Giaourtsakis et al. 2009). According to the interpretation presented here, the Pliocene *C. efficax* represents the common ancestor of *C. mauritanicum*, *C. germanoafricanum* and *C. simum*.

Hilzheimer (1925) described a subspecies of the white rhino from Olduvai Gorge as *Rhinoceros simus germanoafricanus*. Hilzheimer's description was based mostly on a broken skull, which according to Geraads (2005) has since been lost. Hilzheimer did not publish a stratigraphy of his material, but according to Dietrich, Hilzheimer's taxon was probably based on material of mixed provenance and age, an opinion supported by the notes of the original collector, Reck, who was uncertain whether the skull was derived from the basal Olduvai Beds proper or from a much younger horizon ("Steppensinter") (Dietrich 1945). Dietrich excluded Hilzheimer's material from *S. efficax* and suggested that *R. simus germano-africanus* might be synonymized with the white rhino, *Ceratotherium simum*, an opinion with which Geraads (2005) concurred.

Hilzheimer's drawing (Hilzheimer 1925, text Fig. 1) shows two teeth, M2 and M3, which appear somewhat less derived compared to those of modern *C. simum*, and are, in our opinion, best associated to the species *Ceratotherium germanoafricanum*. As already noted by Geraads (2005), the metaloph axis of M2 bisects the medifossette, resembling in this feature the modern *C. simum* and differing from the Pliocene *C. efficax* and Pleistocene *C. mauritanicum*. However, the protolophs of the M2 and M3 are straighter than in the modern *C. simum*, so that they do not turn distally except at their lingual tips. In addition, the protocone of the M3 is clearly marked by a lingual protocone groove, which is absent or only faintly expressed in molars of *C. simum*. The medifossette of the M3 is open, with a tiny crista and faint ectoloph bulge, and the overall shape of the tooth is rather triangular. Another of Hilzheimer's drawings (Hilzheimer 1925, text Fig. 2) shows an isolated M3 similar to modern *C. simum* with a closed medifossette and a quadrangular form.

In published Laetoli faunal lists, *C. simum germanoafricanum* remained the only rhinoceros taxon until Leakey et al. (1976) reported finding skulls belonging to both *Diceros* and *Ceratotherium* from Laetoli (Guérin 1987a). Soon after, Leakey and Hay (1979) reported numerous teeth and some postcranial remains from Laetoli attributed to *Diceros*, and expressed the opinion that both *Diceros* and *Ceratotherium* were represented by tracks in the footprint tuff, even though their separation by other criteria than size was not possible (Leakey and Hay 1979; Leakey 1987).

Guérin (1987a) found three species of fossil rhinoceros at Laetoli: *Ceratotherium praecox* and *Diceros bicornis* in the Laetolil Beds, and *Ceratotherium simum* in the overlying Upper Ndolanya Beds. He regarded *Serengeticeros efficax* Dietrich, 1942 as synonymous with *Ceratotherium praecox* Hooijer and Patterson, 1972, but preferred to use the junior nomen because of its wider usage, pending a decision by the ICZN that does not appear to have materialized. Guérin, (1987a) did, however, note that the dental material assigned by him to *C. praecox* differed from the teeth assigned to this species from Kanapoi, Ekora, Lothagam, and Langebaanweg, in it being more derived, similar to teeth from Hadar also assigned to *C. praecox*. Earlier Guérin (1980b) had also remarked that dental material from Sidi Hakoma of Hadar was morphologically intermediate between the species *C. praecox* and *C. simum*, and referred it to *Ceratotherium* cf. *praecox*. Given the wide concept of *C. praecox* adopted by other workers at the time (see below), Guérin's decision to call the Laetoli species *C. praecox* was understandable. However, as noted above, the name *C. efficax* now appears appropriate for this material.

Relationships of the Plio-Pleistocene Dicerotini

Scott (1907, plate XVII Fig. 3) erected the new species *Opsiceros simplicidens* based on an isolated left M2 from superficial coastal deposits in Zululand. From the same deposits, he illustrated also two isolated teeth of *Diceros bicornis* (Scott 1907, Plate XVII, Fig. 4, 5). Scott (1907) compared this mixed material with the extant *Diceros bicornis* only, and the unusual morphology of the isolated M2 led him to the creation of a new species. However, the tooth is morphologically indistinguishable from fossil and extant *Ceratotherium simum*. Hopwood (1926) inappropriately reported that the species name *Opsiceros simplicidens* was a previously occupied (junior homonym of *Rhinoceros simplicidens* Lydekker) and proposed the species name *Rhinoceros scotti* as a replacement. Thus, *Rhinoceros scotti* Hopwood, 1926 is an objective junior synonym of *Opsiceros simplicidens* Scott, 1907, which is a subjective junior synonym of *Ceratotherium simum* and therefore neither of these names affects the usage of *Ceratotherium efficax*. Hopwood (1926, Fig. 3) referred an upper molar (BMNH 12616) from the Kaiso Bone Beds in Uganda to his *Rhinoceros scotti*. Dietrich (1945) considered that this molar may be conspecific with *C. efficax* from Laetoli and our direct comparisons seem to support this assignment, although the stratigraphic context of the specimen is somewhat imprecise.

Arambourg (1947), in his study of fossil rhinoceros material from the Omo, synonymized *Serengeticeros efficax* with Hilzheimer's taxon, which he referred to as *Atelodus simus germano-africanus*. Furthermore, Arambourg synonymized Hopwood's *Rhinoceros scotti* (and Scott's *R. simplicidens*) with *A. simus germano-africanus*. Like Arambourg, Hooijer (1959, 1969) and Harris (1983) regarded *R. simus germano-africanus* Hilzheimer as synonymous with *Serengeticeros efficax* Dietrich. According to Hooijer (1972), this taxon, named *C. simum germanoafricanum*, occurs at Laetoli, Chemeron, and Olduvai. In Hooijer's view, its skull is indistinguishable from that of *C. simum*, but its upper molars differ from those of *C. simum* in having a transverse metaloph and a protoloph that begins to curve towards distal only at its lingual end (Hooijer 1969). Hooijer (1969, Plate 1, Figs. 1–2) illustrated a skull of *C. simum germanoafricanum* from Chemeron, J.M.91, which he considered similar to the material from Laetoli described by Dietrich as *S. efficax*, an opinion with which we concur; under the nomenclature employed here, this skull would thus be assigned to *Ceratotherium efficax.* In the same publication, Hooijer illustrated material from Olduvai, which he assigned either to *C. simum germanoafricanum* or to *C. simum* subsp. Unfortunately the quality of the figures does not permit a precise identification of the species in all cases.

The species *Ceratotherium praecox* was described by Hooijer and Patterson (1972), who interpreted it as an offshoot of *Diceros*, the first representative of *Ceratotherium* and a direct ancestor of the living *C. simum* by way of the intermediate form *C. simum germanoafricanum* (Hooijer and Patterson 1972; Hooijer 1973). They selected a rather poorly preserved skull from Kanapoi, KNM-KP 36 (Hooijer and Patterson 1972, Fig. 9A) for the holotype. Both sides of this skull as well as the occiput are damaged; the teeth are very worn as well as damaged, making comparisons with other material difficult. Hooijer and Patterson also referred to *C. praecox* a somewhat younger crushed skull from the Ekora Formation (KNM-KP 41; Hooijer and Patterson 1972, Fig 10 A-B) and a rather older isolated upper molar from the late Miocene of the Lower Nawata Formation of Lothagam (KNM-LT 89; Hooijer and Patterson 1972, Fig 8 C-D). Hooijer and Patterson regarded the holotype skull as not far removed from living *Diceros* in shape, but somewhat larger and postdentally more elongated. As for molar morphology, they noted that the metaloph is transverse and the protoloph bulges posteriorly in its lingual third, and that the molars of the type skull are similar to those of the isolated specimen from Lothagam KNM-LT 89. In the Ekora skull KNM-KP 41 Hooijer and Patterson also observed postdental elongation, but the skull is badly crushed and distorted. Its molars are damaged on the buccal sides, but the relatively well preserved premolars were observed by Hooijer and Patterson to be very similar to those of *Diceros bicornis*, differing only in the lack of a paracone style and in the ectoloph being flatter and undulating. The molars of the Ekora skull have a weak lingual cingulum, noted by Hooijer and Patterson as their only difference from the Lothagam molar KNM-LT 89.

According to Geraads (2005), *Ceratotherium praecox* should be transferred to *Diceros*. He regarded the Ekora skull KNM-KP 41 as belonging to *Diceros bicornis*, but retained the cranium KNM-KP 36 for *Diceros praecox*. We agree that both the Kanapoi skull KNM-KP 36 and the Ekora skull KNM-KP 41 belong to *Diceros*, but see no compelling reason to assign them to different species. Instead, we observe other signs of heterogeneity in the original *C. praecox* hypodigm. Thus, the teeth of the Kanapoi skull are in our opinion indistinguishable from those of modern *D. bicornis*, including the distal bulging of the protoloph noted by Hooijer and Patterson (1972), commonly seen in worn specimens. We would add that some Kanapoi specimens, such as KNM-KP 32, KNM-KP 30216 and KNM-KP 30472, are morphologically similar to *D. bicornis* in shape, but others, such as KNM-KP 38, KMN-KP 30217 and KNM-KP 30554 appear distinctly derived, and can be assigned to *C. efficax*. KNM-KP 38, a right P4, has a closed medifossette and, despite loss of the lingual enamel, a distinct vertical groove is observable on the lingual face of the protocone. KNM-KP 30217 is a left mandibular fragment with a lightly worn p3 in place. This tooth is quite hypsodont, with derived features such as a flattened buccal wall of the metalophid, flattened lingual walls, deep V-shaped lingual sinuses and rough enamel. KNM-KP 30554 is a worn left first or second molar with a flattened lingual wall, with the crown flaring out towards mesial and distal above the base, and rough enamel.

The dentition of the Ekora skull is similar to *D. bicornis*, as noted by Geraads (2005). Of the features noted by Hooijer and Patterson, the presence or absence of a paracone style in the molars cannot be determined on the buccally damaged molars, while in the premolars this feature, which depends very much on the stage of wear, is often weak or even missing in the living species; the ectoloph profile of these teeth also appears *D. bicornis*-like to us. In contrast, the isolated upper molar KNM-LT 89 again shows a more derived morphology: the ectoloph is slightly swollen in its middle part and the protocone has a vertical groove lingually.

Hooijer (1972) referred the rhinoceros from Langebaanweg to *C. praecox*, although the teeth show distinctly more derived features than in the Kanapoi and Ekora skulls. In particular the M1s show the presence of a lingual protocone groove (Hooijer 1972, Plates 21–24). We agree with

Hooijer that the Langebaanweg rhinoceros is a primitive form of the *Ceratotherium* lineage, as also noted by Geraads (2005) and Giaourtsakis et al. (2009). Since the Langebaanweg material, however, clearly represents a less derived form, with respect to both dental features and the features of the posterior part of the skull, than the Laetoli material attributed to *C. efficax* (see Giaourtsakis et al. 2009), we leave the actual taxon to be specified in later works.

Hooijer (1972) also transferred to *C. praecox* several specimens from the Mursi Formation of the Omo Basin and from the Chemeron Formation in Kenya, previously assigned by him to *C. simum germanoafricanum* (Hooijer 1969). These Mursi specimens are a palatal portion of a skull with the left M2-3 in place and a skull fragment with a broken left P4 (Hooijer 1969, Plate 5, Figs. 4–5). They are definitely more derived than those of the *C. praecox* type cranium from Kanapoi (which actually represents *Diceros*), and also more derived than the dental material of the Langebaanweg *Ceratotherium*, suggesting that an attribution to *C. efficax* would be reasonable. Both P4 and M2 have a lingual vertical groove on the protocone, the protolophs expand towards distal, and the metaloph of the M2 is straight. The medifossettes are open on these teeth but closed in the M3, as noted by Hooijer (1972) as exceptional for the Langebaanweg material; the ectolophs are damaged and their shape cannot be assessed. In *C. efficax* the medifossettes are usually, but not always, closed on the molars and often open on the premolars. The Chemeron specimen is a left maxilla with poorly preserved M1-3 (Hooijer 1969, Plate 2, Fig. 1). Only the M2 is sufficiently complete to allow comparisons; Hooijer (1972) regarded it as similar to the Mursi specimens, and it appears derived in comparison with the *Ceratotherium* material from Langebaanweg. Hooijer continued to add such morphologically derived specimens to *C. praecox*, from the Aterir Beds in the Baringo area, Kenya (Hooijer 1973, Plate 1, Figs. 1–3) and from the Omo (Hooijer 1975, Plate 2, Figs. 1–2). The latter material consists of milk teeth, which are considered indeterminate Dicerotini by Geraads (2005). They appear more derived than corresponding deciduous teeth from Langebaanweg and might therefore fit *C. efficax* better than other known forms.

The material referred to the species *C. praecox* by its original authors is thus quite heterogeneous, and the applied concept rather quickly drifted away from the original type material towards a more derived state. A considerable amount of fossil material has subsequently been assigned to what appears to be this secondary concept of *C. praecox*. Harris (1983) found this species in the Kubi Algi Formation of Koobi Fora, Guérin (1987a) found it at Laetoli, Harris et al. (2003) found more material at Kanapoi, and Harris and Leakey (2003) found it at Lothagam. Geraads (2005) noted that the type material of *C. praecox* belongs to the genus *Diceros* (as *Diceros praecox*), and he found that species at Hadar.

Early Evolution of Dicerotini

Several Miocene taxa have been described and phylogenetically associated with the extant African genera (Wagner 1848; Gaudry 1862–1867; Osborn 1900; Thenius 1955; Hooijer 1968, 1978; Guerin 1966, 2000, 2003; Arambourg 1959; Geraads 1986, 1988, 2005). Their status has been recently reviewed and updated by Giaourtsakis et al. (2009). Despite the number of described species, the early evolutionary history and radiation of the Dicerotini tribe remains presently unresolved, primarily due to the insufficient African Miocene record.

"*Diceros*" *neumayri* was the first recognized fossil relative of the extant African species (Wagner 1848; Gaudry 1862–1867) and until the 1960s their only Miocene representative. It is a very common element of the Hipparion faunas of the sub-Paratethyan mammalian province (*sensu* Bernor 1984) and has been documented in numerous localities from the Eastern Mediterranean, the Middle East and adjacent regions (Giaourtsakis 2009 and references therein). Because of its dental similarities with the extant *Diceros*, the taxon has been commonly assigned to this genus (Ringström 1924; Thenius 1955; Hooijer 1972, 1978; Heissig 1975, 1989; Guérin 1966, 1980a, 2003; Tsiskarishvili 1987). Geraads (1988) pointed out cranial similarities with *Ceratotherium*, which, however, represent early convergences (Giaourtsakis et al. 2009). Later, Geraads (2005) deemed "*Diceros*" *neumayri* (which he called *Ceratotherium neumayri*) as the common ancestor of both extant species, arguing that it is morphologically and ecologically intermediate between them. In his context, the known African Miocene taxa *Paradiceros mukirii* and *Diceros primaevus* were considered as being related forms with "*D*". *neumayri*, and *Diceros douariensis* as potentially conspecific. However, no arguments were provided by Geraads (2005) to support this grouping or the implied relationships among the Miocene taxa, whereas *Diceros australis* was excluded from the comparisons. Geraads (2005) further suggested that the two extant lineages split soon after the Miocene-Pliocene boundary, leading from an ancestral mixed feeder ("*Ceratotherium neumayri*") to a lineage of grazers (*Ceratotherium*) and a lineage of browsers (*Diceros*). However, based on our observations, the Late Miocene "*Diceros*" *neumayri* forms a monophyletic extra-African evolutionary lineage with no Pliocene descendants. The dispersal of these populations in the eastern Mediterranean and adjacent regions was followed by the gradual establishment of a unique combination of primitive and derived craniodental features, as well as several autapomorphies, notably in the postcranial skeleton (Giaourtsakis et al. 2009). The available Miocene fossil record indicates that the split between the extant lineages of *Diceros* and *Ceratotherium* must have taken place in Africa during the Miocene and that not only the common ancestor of the extant lineages should have been a browser, but also the ancestral stock of the *Ceratotherium* lineage probably favored a browsing diet for as long as available habitats could supply it.

A potential candidate of the ancestral Dicerotini morphology is the relatively complete rhinocerotid sample from the early late Miocene locality of Bou Hanifia (Oued el Hammam), Algeria, recovered above a volcanic tuff radiometrically dated at 12.18 ±1.03 Ma (Ameur et al. 1976). The material was originally described as *Dicerorhinus primaevus* by Arambourg (1959), partly due to misleading comparisons (Giaourtsakis et al. 2009), but was later properly allocated to the genus *Diceros* by Geraads (1986). *Diceros primaevus* shows a dental and postcranial morphology that essentially persists, with relatively few modifications, in the extant black rhinoceros. The conservative morphology of *D. primaevus* may support a placement close to the split between the extant black and white rhinoceros lineages. In addition, populations similar to *D. primaevus* might have migrated outside Africa, around the middle-late Miocene boundary, and independently evolved into the Eastern Mediterranean "*Diceros*" *neumayri*.

A species considerably older than *D. primaevus* has been recently described by Guérin (2000, 2003) as *Diceros australis* from the locality of Arrisdrift in the Orange River Valley of Namibia, dated close to the early-middle Miocene boundary (ca. 17.5-17.0 Ma after Pickford and Senut 2003). Besides a small occipital and a few mandibular fragments, the hypodigm of *D. australis* comprises several isolated dental and postcranial elements. Based on Guérin's (2000, 2003) descriptions and illustrations, the morphology of the upper permanent cheek teeth indeed seems to follow the unspecialized Dicerotini pattern, similar to the extant *Diceros*. The well preserved, slightly worn P4 (Guérin 2000, Plate 1, Fig. 3) has a strong paracone fold, the mesostyle and metacone folds are not developed, a weak crochet is present but no crista, the protocone is not constricted by a distal groove, and a strong continuous crenullated lingual cingulum is developed. The described molars also bear a strong paracone fold, a weakly developed crochet without a crista and a distally unconstricted protocone (Guérin 2000, 2003). The most prominent feature of *D. australis*, however, is the significant size of its postcranial elements, especially the metapodials that are considerably longer than the maximum values recorded for the two extant species, as well as the early late Miocene *D. primaevus* and the side branch of the extra-African "*D*". *neumayri*. Similar size and proportions can be found on isolated specimens from the significantly younger Mpesida Beds of Kenya (~6.2 to 6.9 Ma), and Saitune Dora (~5.6 Ma, Giaourtsakis et al. 2009), as well as in the abundant material from the early Pliocene of Langebaanweg (Hooijer 1972) and the Late Pliocene *C. efficax*. If correctly identified and dated, the puzzling discovery of the large-sized *D. australis* as the oldest known representative of the Tribe Dicerotini perplexes the early radiation of the Tribe and the split between the black and white rhinoceros (sensu lato), as it would clearly pose a second center of evolution next to the younger and apparently more conservative *D. primaevus*.

Another Middle Miocene taxon traditionally associated with the Dicerotini lineage has been inaccurately described from the locality of Fort Ternan in Kenya (ca. 13.7 ± 0.3 Ma, after Pickford et al. 2006). Hooijer (1968) originally portrayed *Paradiceros mukirii* as a primitive collateral species of the ancestral *Diceros* stock, differing from extant and fossil *Diceros* in a combination of primitive and progressive features. However, the holotype and the majority of the specimens from Fort Ternan, if not the complete hypodigm, belong to "*Dicerorhinus*" *leakeyi* Hooijer, 1969, an early member of the Dicerorhinini tribe (Giaourtsakis et al. 2009).

The first Miocene taxon to show some progressive dental features similar to *Ceratotherium*, appears to be *Diceros douariensis*, Guérin, 1966 (Heissig 1989; Giaourtsakis et al. 2009). The type material originates from the Mines of Douaria, 2.5 km SW of the village Sedjerane, in the plateau of Couchet el Douharia in North Tunisia. The biostratigraphical context of the locality warrants a Late Miocene age (Guérin 1966, 2003). The material comprises an adult holotype and a juvenile paratype skull, however the latter belongs clearly to a different, hornless rhinoceros species (Geraads 2005; Giaourtsakis et al. 2009). Guérin (1966) originally considered *D. douariensis* as a circum-Mediterranean species showing a mixture of progressive and primitive features with respect to the Eastern Mediterranean "*D*." *neumayri*, the only established Miocene Dicerotini species at that time. Besides the reported large size and the apparent high crowned teeth of the holotype adult skull (Guérin 1966; Giaourtsakis et al. 2009), some derived dental features characterize the Douaria rhinocerotid and distinguish it from Plio-Pleistocene and extant *D. bicornis*, as well as from the extra-African *D. neumayri*. These include the obliquity of the protoloph on the molars and the development of a lingual protocone groove (Guérin 1966, Fig. 8). A similar dental morphology is also observed on an isolated upper molar (KNM LT-89) from the Lower Nawata formation of Lothagam (~7.5–6.5 Ma; McDougall and Feibel 1999, reprinted in 2003), originally referred to as *C. praecox* by Hooijer and Patterson (1972), and an almost complete cranium from Kuseralee of the Middle Awash Valley of Ethiopia (Giaourtsakis et al. 2009). The dental complexity was further advanced during the Pliocene by populations similar to the Langebaanweg sample (Hooijer 1972) and the late Pliocene *Ceratotherium efficax* detailed herein as a response to the expansion of more open habitats and the adaptation to more abrasive diet.

Paleoecology of the Laetoli Rhinoceroses

The available cranial morphology of the LAET 75-3065 *Diceros* falls within the variation observed in the extant *D. bicornis*. The Laetoli *Ceratotherium* crania are markedly longer, more dolichocephalic, and demonstrate an increased posterodorsal inclination of the occiput similar to extant *C. simum*. These cranial features suggest a lowering of the resting position of the head, and by implication, a shift towards feeding on lower vegetation, as originally suggested by Zeuner (1934) and Loose (1975). These observations are consistent with the commonly held view that *Diceros* has remained a browser throughout its history, whereas *Ceratotherium* experienced a more or less gradual shift towards grazing (Osborn 1900; Zeuner 1934; Dietrich 1945; Thenius 1955; Hooijer 1969, 1978; Guérin 1980a, 1987a; Heissig 1989; Harris and Leakey 2003; Giaourtsakis et al. 2009). The available data do not favor a sudden shift in proportions as caused by a mutation acting on ontogenetic development (Stanley 1979), and it is difficult to reconcile with the scenario of Geraads (2005), which suggests that *Diceros* arose from *Ceratotherium* through a process of evolutionary reversal from mixed feeding, or grazing, to browsing.

The available dental morphology of the Laetoli *Diceros* shows no significant difference with respect to extant *D. bicornis*. The recovered teeth are too few (as only the teeth of the cranium LAET 75-3065 can be securely assigned to *Diceros*), and too worn to allow a meaningful study of dental wear patterns. However, nothing suggests that the teeth were worn much differently from what is seen in the extant species. On the contrary, the dental morphology of the Laetoli *Ceratotherium* is functionally informative, since a sufficient number of specimens exist to allow a paleodietary reconstruction using the mesowear analysis (Fortelius and Solounias 2000).

The functionally relevant morphological features of the *Ceratotherium* teeth from Laetoli all point to a state intermediate between extant *Diceros* and extant *Ceratotherium*. These include, among others, the moderate degree of hypsodonty, the presence of thickened cement covering the crown, the mild distolingual bending of the transverse lophs, the incipient closing-off of the medifossette and the medially bulging curvature of the ectoloph. The distribution of these character states is discussed in detail in the taxonomic part of this chapter; here we only note that the dental morphology of the Laetoli *C. efficax*, while indeed intermediate, is significantly closer to the *C. simum* end of the spectrum and well separated from the plesiomorphic rhinoceros morphology demonstrated by *Diceros*, including *D. praecox* as understood by Geraads (2005). However, rather than trying to quantify the relative development of these features of long-term evolutionary change, we focus our attention here on the analysis of wear patterns reflecting the immediate dietary regimes of the animals.

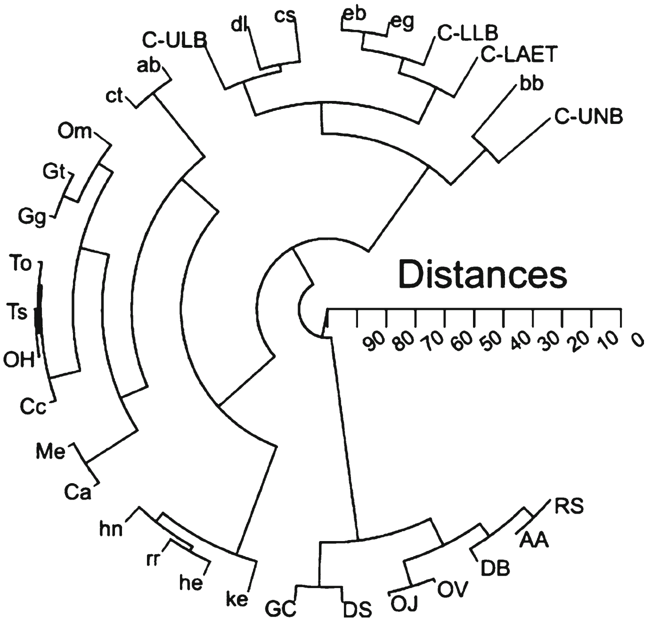

Fig. 11.5 Hierarchic cluster diagram of mesowear (Fortelius and Solounias 2000) in all *Ceratotherium* (C-LAET) from Laetoli and in stratigraphic subsamples from the Lower Laetolil Beds, Upper Laetolil Beds, and upper Ndolanya Beds (C-LLB, C-ULB, and C-UNB, respectively). Note that all samples cluster in the grazer part of the tree, indicated by species *acronyms in lower case*. *Acronyms in upper case* indicate browsers and *acronyms in mixed case* indicate mixed feeders. Species abbreviations: Browsers (conservative): AA = *Alces alces*, DB = *Diceros bicornis*, DS = *Dicerorhinus sumatrensis*, GC = *Giraffa camelopardalis*, OH = *Odocoileus hemionus*, OJ = *Okapia johnstoni*, OV = *Odocoileus virginianus*, RS = *Rhinoceros sondaicus*. Grazers (conservative): ab = *Alcelaphus buselaphus*, bb = *Bison bison*, cs = *Ceratotherium simum*, ct = *Connochaetes taurinus*, dl = *Damaliscus lunatus*, eb = *Equus burchelli*, eg = *Equus grevyi*, he = *Hippotragus equinus*, hn = *Hippotragus niger*, ke = *Kobus ellipsiprymnus*, rr = *Redunca redunca*. Mixed feeders (conservative): Ca = *Capricornis sumatrensis*, Cc = *Cervus canadensis*, Gt = *Gazella thompsoni*, Gg = *Gazella granti*, Me = *Aepyceros melampus*, Om = *Ovibos moschatus*, To = *Taurotragus oryx*, Ts = *Tragelaphus scriptus*

Hierarchic clustering of *C. efficax* from Laetoli, based on classical mesowear, places it within the grazer cluster, with stratigraphically defined subclusters ending up in distinct parts (Fig. 11.5). The result is insensitive with respect to which two of the three cusp sharpness states are included in the analysis, and to whether the relief is included as a parameter or not.

In order to evaluate the conventional mesowear study presented here, we used curvature analyses of scanned enamel profiles to illustrate and to compare the wear profiles in a small selection of upper and lower teeth from Laetoli with teeth of the extant species (Fig. 11.6). These profiles clearly show the exceptionally sharp edges (high curvature) seen in *Diceros*, indicated by a narrow band of white along the buccal edge of an otherwise smooth (black-colored) surface. In contrast, the teeth of derived *Ceratotherium* from the latest Pliocene and

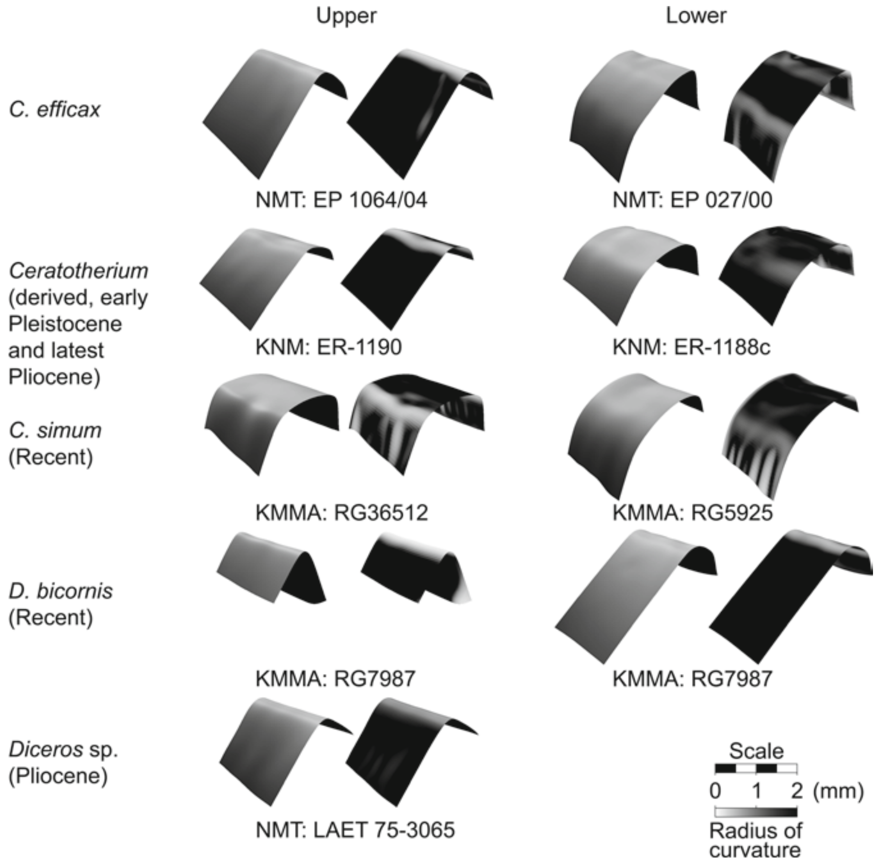

Fig. 11.6 Profiles and curvature maps of buccal upper and lower teeth enamel facets (all teeth are M2/m2, except KNM ER-1190 and LAET 75-3065, which are P4s) of *C. efficax* compared with the early Pleistocene (*left*) and the latest Pliocene (*right*) derived *Ceratotherium*, Recent *C. simum*, Pliocene *Diceros* and Recent *D. bicornis*. For each specimen, a topographic surface is shown on the left, and a curvature map overlaying the surface is shown on the right. Higher curvature (lower radius of curvature) is shown in *white*, with lower curvature in *black*. Topographic scale bar in mm, radius of curvature scale (*grayscale*) in mm

early Pleistocene, and particularly extant *Ceratotherium simum* show moderate curvature along the crest and a profusion of locally high curvature due to irregularities in the enamel surfaces. *C. efficax* from Laetoli occupies an intermediate state between these extremes, with relatively well-demarcated curvature maxima along the profile, but decidedly lower values at the edge between the main surfaces and with more irregularities within them than is seen in *Diceros*. This comparison also reveals that the profiles of the lower teeth, while geometrically different from those of the upper teeth, nevertheless show the same overall similarities and differences as the upper teeth, lending some independent support to our inclusion of lower teeth in the cusp sharpness analyses.

A box plot of cusp sharpness among selected taxa (Fig. 11.7) shows a clear separation between *Diceros* and *Ceratotherium*, with *C. efficax* occupying an intermediate position closer to *C. simum* than to *Diceros*. A marked but statistically insignificant difference is observed between the late Pliocene and early Pleistocene derived *Ceratotherium* and extant *C. simum*, suggesting that the extreme grazing diet of the extant species may

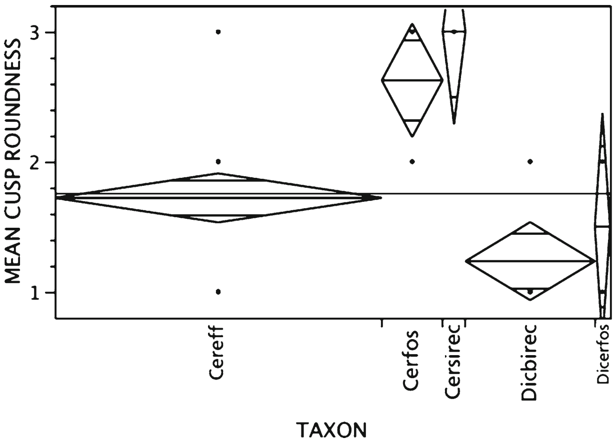

Fig. 11.7 Comparison of mean molar cusp roundedness in selected rhinoceros taxa: Cereff = *C. efficax*, Cerfos = derived *Ceratotherium* from the late Pliocene and the early Pleistocene, Cersirec = *C. simum* (recent), Dibicrec = *D. bicornis* (recent), Dicerfos = fossil *Diceros*. Note low rounding in *Diceros*, high in C. *simum*, and intermediate in *C. efficax*. Top and bottom of diamond, 95% CI; *horizontal lines* are "overlap marks", width of diamond signifies number of specimens

have developed during the beginning of the Pleistocene or even later. A similar plot for *Ceratotherium* across temporal groups within the Laetoli sequence shows the same relationships but with more resolution (Fig. 11.8). The minor fluctuations observed within the Laetolil Beds cannot be distinguished from random noise, but the small sample from the Upper Ndolanya Beds shows significantly higher rounding, indicating a more abrasive diet at this time. Thus, the dietary regime of *C. efficax* appears to fall within the grazing realm, but may still have included variable amounts of browse. In any case the food eaten was clearly less abrasive than the graze consumed by the late Pliocene and early Pleistocene *Ceratotherium* and especially extant *C. simum*. Figure 11.9 illustrates the mean molar cusp roundness of *Ceratotherium* in East Africa over time.

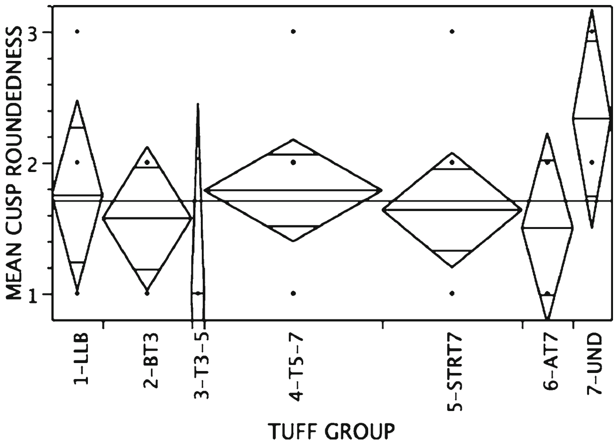

Fig. 11.8 Mean cusp roundedness in *Ceratotherium* in the Laetoli Sequence, separated into Tuff Groups. Note increase in unit 7-UND (Upper Ndolanya Beds). Other abbreviations: 1-LLB = Lower Laetolil Beds, 2-BT3 = below Tuff 3, 3-T3-5 = between Tuffs 3 and 5, 4-T5-7 = between Tuffs 5 and 7, 5-STRT7 = straddles Tuff 7, 6-AT7 = above Tuff 7. See Fig. 11.7 for diamond description

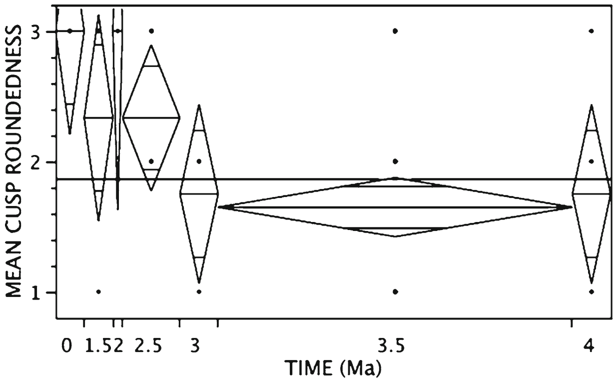

Fig. 11.9 Mean molar cusp roundedness in East African *Ceratotherium* over time. Note sustained increase in food abrasion through Late Pliocene and Pleistocene. See Fig. 11.7 for diamond description

Conclusions

The occurrence of true *Diceros* in the Laetolil Beds is indisputable, but, in contrast to Guérin (1987a), we find few specimens attributable with any confidence to this genus. We are also unwilling to assign the Laetoli *Diceros* material at the species level. We agree with Hooijer (1978) and Geraads (2005) that the existence of an extant species *D. bicornis* even in the Late Miocene locality Lothagam (Harris and Leakey 2003) would make its longevity rather unique among mammals. We were, however, unable to detect in the *Diceros* material from Laetoli features described by Geraads (2005) in *D. praecox* from Lower Awash. We agree with Guérin (1987a) on the identity of the larger and more abundant rhinoceros at Laetoli, which he assigned to *Ceratotherium praecox*, while mentioning the alternative nomenclatorial choice of *C. efficax*. We, however, chose to use the name *C. efficax* for this material, because of the mismatch with the holotype and the heterogeneity of the material referred to the species *C. praecox* by its original authors. The name *C. mauritanicum*, proposed by Geraads (2005), is restricted to the Pleistocene North African species, which is most likely a descendant of *C. efficax* and can be viewed as a "sister taxon" of *C. germanoafricanum* and *C. simum*. The more advanced cranium LAET 81-74 is so poorly preserved, that the precise identification to either *C. germanoafricanum* or *C. simum* is impossible. The vast majority of the Laetoli postcranials most likely belong to *C. efficax*.

As noted by several authors (Osborn 1900; Dietrich 1942; Fortelius 1985), the dental evolution of *Ceratotherium* shows a transition from a *Diceros*-like ectolophodont condition to the full-fledged plagiolophodonty seen in extant *Ceratotherium simum*. There cannot be any doubt that this morphological transition somehow reflects a dietary shift from browsing to grazing, but the rate and timing of these changes, as well as their precise relationship to the diet has largely remained a matter of speculation. Our results suggest, that the transition included a substantial period of stasis, spanning at least the interval represented by the Laetolil Beds, during which the dietary regime varied in the range from mixed feeding to grazing (Fig. 11.8). Our results clearly show that a shift in the dietary regime towards grazing had occurred by Upper Ndolanya times, and that the trend towards increased grazing continued from the Early Pleistocene to the Recent (Fig. 11.9).

Geraads (2005) proposed an alternative scenario according to which African *Ceratotherium* arose through an immigration of the Eurasian species "*Diceros*" *neumayri*, and in turn gave rise to *Diceros* through an evolutionary reversal to a browsing mode of life. However, we find this scenario difficult to reconcile with the available evidence, and believe that the Late Miocene "*Diceros*" *neumayri* actually forms a monophyletic extra-African evolutionary lineage with no Pliocene descendants (see Giaourtsakis et al. 2009).

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Chapter 12
Equidae

Miranda Armour-Chelu and Raymond L. Bernor

Abstract Equid teeth and postcrania from the Laetolil and Upper Ndolanya Beds are described and compared with other hipparion assemblages from East and South African Plio-Pleistocene localities. The hipparion from the Laetolil Beds is morphologically similar to *Eurygnathohippus hasumense* from Hadar, although of slightly smaller dimensions, and is referred to *Eurygnathohippus* aff. *hasumense.* The hipparion from the Upper Ndolanya Beds closely resembles the advanced hypsodont form found at Olduvai Gorge (Bed I-IV), and is referred to *Eurynathohippus* aff. *cornelianus*.

Keywords *Eurygnathohippus hasumense* • *Eurygnathohippus cornelianus* • Hipparion • Equid • Ectostylid • Metacarpal III • Metatarsal III • Phalanx • Pliocene • Laetoli • Olduvai Gorge

Introduction

Mary and Louis Leakey first collected fossils from Laetoli in 1935 (Leakey 1987), in the area that later became known as Localities 10, 10W and 10E, from sediments dated to between 3.6 and 3.8 Ma. The fauna included hipparion remains, which were curated in London and discussed by Boné and Singer (1965), Cooke and Coryndon (1970), Aguirre and Alberdi (1974), and Forsten (1996). Laetoli was further collected by Kohl-Larsen during his expedition to the Southern Serengeti in 1938–1939, and the material is housed in Berlin and described by Dietrich (1942).

Dietrich (1942) identified two taxa, *Hypsohipparion albertense* from the Vogel River and *Stylohipparion* sp. Dietrich (1941) erected the genus *Hypsohipparion* to describe a horse of relatively large size with rather hypsodont lower cheek teeth that lacked ectostylids. Arambourg (1947) questioned the validity of Dietrich's *Hypsohipparion* and suggested that the lower teeth attributed to this taxon (those lacking ectostylids) were derived from *Equus*. While Kohl-Larsen's collection are generally considered to contain material from unknown or mixed stratigraphic levels, Boné and Singer (1965) pointed out that most of the upper cheek teeth are hipparion and that the degree of contamination may be less than previously supposed.

The identification of *Stylohipparion* from Laetoli was based upon the presence of small-sized cheek teeth bearing ectostylids. Dietrich (1942) further observed that *Stylohipparion* was conspecific with *Eurygnathohippus*, the highly derived hipparion of Pleistocene age from Cornelia, South Africa (Van Hoepen 1930; Eisenmann 1983). Presumably this finding was based on a comparison between a mandibular symphysis from Laetoli and the symphysis from Cornelia, rather than the Olduvai specimens, as these were not discovered until the 1950s (OLD 55, BK II, 293, 067/5344). There is an equid symphysis with a low and flattened morphology from Gadjingero (Gadj. 10) that Forsten (1996) and Boné and Singer (1965) describe as lacking the third incisor and canine. All material from these early collections is of unknown stratigraphic provenance. However, this latter specimen may be derived from the Upper Ndolanya Beds, since Gadjingero is the equivalent of the present-day Locality 18, but it cannot be discounted that the specimen was derived from Pleistocene deposits that also occur in the Gadjingero River (see Harrison and Kweka 2011).

Eisenmann (1976, fig. 1) shows a bivariate plot of the proportions of the mandibular symphyses of a range of hipparion taxa including the Gadjingero specimen from Laetoli, which plots closely with a symphysis of *E. cornelianus* from Olduvai (067/5344). This suggests that the Gadjingero symphysis may be derived from *E. cornelianus*, except for the seemingly absent third incisors; perhaps these were originally present, but the alveoli are obscured by matrix. Cooke and Coryndon (1970) contended that only one taxon was represented at Laetoli and referred all material to *Hipparion albertense*, which is usually considered to be a *nomen vanum* on the basis of the inadequate type material (Hooijer 1975).

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Initially it was thought that the Laetoli deposits could be roughly correlated with Bed I and II at Olduvai until the discovery of hominin remains in 1974 (Leakey 1987). Detailed study of the local geology of the Laetoli area (Hay 1987; Leakey 1987) established a stratigraphic framework, which demonstrated that the "older fauna" was much earlier than previously supposed.

Further investigations in the Omo, Turkana, Olduvai and Laetoli regions during the 1970s led to a better understanding of hipparion systematics in East Africa (Hooijer 1975, 1976, 1987a, b; Hooijer and Churcher 1985; Hooijer and Maglio 1974; Eisenmann 1983).

After 1974, systematic collections of fossils at Laetoli with secure stratigraphic information stimulated further studies of the fauna. Hooijer (1979, 1987a, b) described almost one hundred hipparion teeth collected by Mary Leakey between 1974 and 1976. The 1979 paper was reprinted in the 1987 Laetoli monograph (Leakey and Harris 1987). After Hooijer's original report was completed he received further specimens from Mary Leakey, and these were published in the Laetoli volume. In this text we refer to Hooijer's original report as 1987a, and his additional analysis as 1987b.

Hooijer (1987a) identified two hipparion taxa from the Upper Laetolil and Upper Ndolanya Beds, although he refrained from giving a specific identity to the hipparion from the Upper Laetolil Beds, describing it as "*Hipparion* sp." Hooijer characterized this taxon as representative of the "Mpesida-Aterir" type hipparion, which he loosely correlated with the 7–4 Ma interval. This group included *Hipparion turkanense* from Lothagam, and a single specimen of this taxon from the Mursi Formation, Ethiopia, and material that Hooijer assigned to *H. primigenium* from Kanapoi and Ekora, which outcrop a few miles north and south of the Lothagam locality (Hooijer and Maglio 1974; Hooijer 1975).

The cheek teeth of the earlier group are generally larger, but not so hypsodont as later hipparions and have less well developed ectostylids on the permanent mandibular cheek teeth, when present. Hooijer found several features that characterized the upper cheek teeth such as bifid pli caballin, which is sometimes in contact with the protocone, but no single character to give this taxon a specific identity. These characters are generally primitive for Old World and, in particular, African hipparions.

Crown height of upper M1 is between 60 and 70 mm. Skulls from Kanapoi and Ekora have a preorbital fossa, whilst this is absent in the Lothagam skull of *Eurygnathohippus turkanense*, (KNM LT-136; figs. 9–7, Bernor and Harris 2003), and tends to be absent in later hipparions from East Africa. One small-bodied taxon was also reported from Lothagam, originally attributed to *H.* aff. *sitifense* by Hooijer and Maglio (1974) because its small size compared closely with the North African taxon from Saint Arnaud Cemetery, Algeria. Bernor and Harris (2003) cited Eisenmann's (V. Eisenmann, personal communication) observations that the St. Arnaud horse never had a type specimen designated and the assemblage has since been lost. Furthermore, the North African late Miocene has a number of small hipparions, and of these none compare in morphological details to the Lothagam small hipparion. As a result, Bernor and Harris (2003) assigned the Lothagam small hipparion material to *Eurygnathohippus feibeli.*

Ectostylids were not recorded from most of the permanent lower cheek teeth examined by Hooijer from the Laetolil Beds, but an associated tooth row (LAET 75-491) from Loc. 11 has ectostylids and is morphologically similar to dentitions of the same age (Hooijer 1987a). Ectostylids were found on an associated right lower dp3 and dp4 from Loc. 9S, Upper Laetolil (Hooijer 1987a), and deciduous premolars from the Upper Ndolanya Beds. Ectostylids are invariably present on hipparion deciduous teeth and accordingly have little phylogenetic significance in themselves (Hooijer 1975).

Hooijer (1987a) referred the material from the Upper Ndolanya Beds to *H.* cf. *ethiopicum*, after a taxon first described by Joleaud (1933) as *Libyhipparion ethiopicum* from unknown level(s) in the Omo. In Hooijer's (1975) revision of the "advanced hipparion" (*Stylohipparion*) group from eastern Africa he selected a single specimen from Joleaud's original type series as the lecotype for *H. ethiopicum*. This was a right m3 (Joleaud 1933, Plate 1, figs. 2 and 6, subsequently accessioned in the Museum National d' Histoire Naturelle, Paris [MNHN] as 1951-4-127), lacking specific stratigraphic provenance. The original material includes four additional topotypic lower cheek teeth. Three of these teeth seem likely to have been derived from the same individual as the lectotype. These cheek teeth may be characterized by their well developed ectostylids, angular, pointed metaconid-metastylids, as well as by their hypsodonty (Hooijer 1975). The metastylids of the associated cheek teeth are especially triangular in the Omo material and the ectostylids are more obliquely orientated than most material referred to this taxon. Protostylids and pli caballinid are also present. In many specific morphological characteristics, this material is similar to that from the Upper Ndolanya Beds, but otherwise they are similar to other mid-Pliocene and early Pleistocene African hipparion assemblages. The lack of complete metapodials, premaxillae with incisors and mandibular symphyses with incisors disallows any specific referral to other relevant hipparion assemblages. In effect, neither the temporal context nor the morphological features are sufficient to compare or verify the taxonomic identity of *Eurygnathohippus* "*ethiopicus*".

Hooijer considered the mandibular and maxillary symphyses recovered from site BK, Bed II, Olduvai, as the same taxon as the mandibular symphysis from Cornelia, South Africa described by van Hoepen (1930) as *E. cornelianus*. The further discovery of a skull from the BK locality in 1973 (2845/2846) convinced Hooijer that *Stylohipparion* and *Eurynathohippus* were congeneric. However, Hooijer retained the nomen *ethiopicum* (Hooijer 1975; Hooijer and Churcher 1985) because he acknowledged that differences between the northern, southern and eastern forms might exist, but that they could only be differentiated when further skulls were found. Hooijer concluded that if a different generic name was required it should be *Eurygnathohippus.* We agree.

Despite Hooijer's best efforts, the taxonomy of the African hipparions is still incompletely resolved. The earlier hipparion group dating from the 7–4 Ma have generally larger cheek teeth and lack ectostylids, or if these are present they are small. Later hipparions are characterized by having smaller sized lower teeth with well developed ectostylids. These characteristics are thought to indicate the "advanced stage of evolution" as seen in *Stylohipparion* (Hooijer 1975). The genus *Stylohipparion* was first erected by van Hoepen (1930) for material from Cornelia, South Africa but it has also been used to describe a grade of evolution that categorizes African Pleistocene hipparions.

The occurrence and size of ectostylids upon the lower cheek teeth of Plio-Pleistocene hipparions has been considered an important source of taxonomic and paleoecological information (Hooijer 1975). Small, inconstant ectostylids from lower cheek teeth have been reported from a series of Pliocene localities, including Kanapoi, Chemeron Formation, locality J.M. 493 (Hooijer 1975) and it has been shown how these become a constant feature and enlarge in size through the Plio-Pleistocene (Hooijer and Churcher 1985). Boné and Singer (1965) found that ectostylids are particularly constant in p4 and m1.

Presence or absence of ectostylids has been used to assign teeth at the specific level. However, this may be problematic. First, the frequency of ectostylids varies between populations. Early African hipparions have small (length and width) and short (height) ectostylids and unless the tooth is well worn, the ectostylid does not present on the occlusal surface. However, in early populations one can often discern an ectostylid "bulge" on the labial aspect of the crown. Ectostylids become longer and wider and ascend higher on the crown in the medial Pliocene, as exhibited in the 3.4–2.9 Ma assemblages at Hadar, Ethiopia. Beginning around Upper Ndolanya Beds time, 2.66 Ma, African hipparions have longer, wider and higher crowned ectostylids and it is at this time that they are persistent and usually visible features on the hipparion crown (Bernor and Armour-Chelu 1999; Bernor and White 2009).

Of further relevance is the taphonomy of equid cheek teeth. Equid cheek teeth are extremely resilient and become incorporated into fossil concentrations with many years of time represented. When teeth from time successive horizons become mingled frequency counts can only be seen as estimates subject to a wide margin of error. An example of this type of problem is shown at Laetoli where ectostylids were originally considered absent in the lower cheek teeth derived from the Laetolil Beds. Further collecting by Harrison has recovered a few specimens bearing ectostylids from the early part of the sequence, where they were formerly considered absent (Hooijer 1987a).

In the original description of the *Eurygnathohippus* type specimen van Hoepen (1930) mistook the third incisor for a canine tooth; this was subsequently corrected by Cooke (1950). Hooijer (1975) and others questioned whether the advanced representatives of *Eurygnathohippus* possessed canines, but they are now known to be present in two mandibles, likely male individuals, from Koobi Fora and Laetoli (Eisenmann 1976; Hooijer 1987a). The canines preserved in the Laetoli specimen (LAET 74-253, Loc. 18) show they were directly tucked behind the third lower incisor (Hooijer 1987a, Plate 9.1). Canine teeth are not yet recorded from maxillary dentitions, including the 2845/2846 skull from BK, Bed II Olduvai, and it is possible that canines are absent in later representatives of the species.

This present study includes material collected by Terry Harrison between 1998 and 2005 and some specimens collected by Mary Leakey and curated in the National Museum of Tanzania in Dar es Salaam. The oldest material, from the Lower Laetolil Beds, derives from localities at Esere, Noiti 3 and Kakesio, dating to around 3.85–4.4 Ma. Material from the Upper Laetolil Beds dates from 3.6 to 3.85 Ma and the younger material from the Upper Ndolanya Beds (at Locs. 7E, 14, 15, 18, 22S, 22E) is dated at 2.66 Ma (Deino 2011) and mixed deposits occur at Locs. 15 and 22E.

Abbreviations, Definitions and Methods

AMNH	American Museum of Natural History, New York
KNM	Kenya National Museum, Nairobi
MA	Middle Awash Project, Ethiopia
MNHN	Museum National d'Histoire Naturelle, Paris
SAM	South African Museum of Natural History, Cape Town
SMNK	Staatliches Museum für Naturkunde, Karlsrhue

The taxon hipparion has been applied in a variety of ways by different authors. We utilize the following definitions in this work: Hipparionine or hipparion: horses with an isolated protocone on maxillary premolar and molar teeth and, as far as known, tridactyl feet, including species of the following genera: *Cormohipparion*, *Neohipparion*, *Nannippus*, *Pseudhipparion*, *Hippotherium*, *Cremohipparion*, *Hipparion*, "Sivalhippus," *Eurygnathohippus* (= senior synonym of "*Stylohipparion*"), *Proboscidipparion*, "Plesiohipparion." Characterizations of these taxa can be found in MacFadden (1984), Bernor and Hussain (1985), Webb and Hulbert (1986), Hulbert (1988), Hulbert and MacFadden (1991), Qui et al. (1988), Bernor et al. (1988, 1989, 1996, 1997, 2003, 2005, 2008, 2010), Bernor and Armour-Chelu (1999), Bernor and Harris (2003), Scott et al. (2005a, b), Armour-Chelu et al. (2006), Bernor and Kaiser

(2006), Kaiser and Bernor (2006), Woodburne (1989, 2007), Woodburne (2007) and previous publications by him cited therein.

Hipparion s.s.: The name is restricted to a specific lineage of horses with the facial fossa positioned high on the face (MacFadden 1980, 1984; Woodburne and Bernor 1980; Woodburne et al. 1981; MacFadden and Woodburne 1982; Bernor and Hussain 1985; Bernor 1985; Bernor et al. 1987, 1989, Bernor et al. 2008, 2010; Woodburne 1989). The posterior pocket becomes reduced and eventually lost, and confluent with the adjacent facial surface (includes Group 3 of Woodburne and Bernor 1980). Bernor's definition departs from some investigators in not recognizing North American species of *Hipparion* s.s. Bernor (1985) and Bernor (in Bernor et al. 1989) have argued that any morphologic similarity between North American "Hipparion s.s." and *Hipparion* s.s. is due to homoplasy.

"Hipparion": several distinct and separate lineages of Old World hipparionine horses once considered to be referable to the genus *Hipparion* (Woodburne and Bernor 1980; MacFadden and Woodburne 1982; Bernor and Hussain 1985; Bernor 1985; Bernor et al. 1980, 1988, 1989).

"Cormohipparion" as explicitly used herein: not determinable as strictly a member of the *Cormohipparion* lineage as recently defined by Woodburne (2007). As such, we recognize the likely paraphyly of North and East African "Cormohipparion" *africanum* and the possibility that it will be assigned to a new genus as the result of a detailed phylogenetic analysis. However, "Cormohipparion" *africanum* is determined to exhibit a morphologic pattern closest to *Cormohipparion* and not the *Hipparion* s.s., *Hippotherium*, *Eurygnathohippus* clades, or any other Old World clade recognized by us or previous authors. Phylogenetic systematic studies are underway that will likely allow eventual assignment of African "Cormohipparion" to a known, or new genus rank (Wolf and Bernor, in progress).

Hipparion: purposely not capitalized and used as a non-formal taxonomic abbreviation for hipparionine.

Measurements are in mm. All postcranial measurements are as defined by Eisenmann et al. (1988) and Bernor et al. (1997) and rounded to 0.1 mm; all dental measurements are as defined by Bernor et al. (1997). The osteological nomenclature, the enumeration, and/or lettering of the figures have been adapted from Nickel et al. (1986). Getty (1982) was also consulted for morphological identification and comparison. Hipparion monographs by Gromova (1952) and Gabunia (1959) were consulted after the French translations. Log10 ratio diagrams were calculated and plotted in Excel 2008 for MAC (MacIntosh OSX).

Abbreviations in Text

Ma: mega-annum in the geochronologic time scale

Africa: ages in m.y. usually based on radio isotopic analyses or magnetostratigraphic analyses. North Africa: localities may be referred to the MN biochronologic time scale.

North America: Hemingfordian, Barstovian, Clarendonian, Hemphillian, Blancan; intervals of the North American land mammal age sequence (e.g., Woodburne 1987, 2004), based on characteristic associations of mammalian taxa. Western Eurasia: Vallesian, Turolian, and Ruscinian; intervals of the European land mammal age sequence, commonly termed units (*sensu* Fahlbusch 1991).

Measurement Table Abbreviations

Sex: M = male; F = female; ? = unknown. Sex can be defined by the size of a canine tooth, male being large, female being small.

Side: lt. = left; rt. = right

Element abbreviations: MCIII = metacarpal III; premax = premaxilla; MTIII = metatarsal III; MPIII = Metacarpal III or metatarsal III; 1PHIII = First phalanx III (central digit) of either the anterior or posterior limb, which are difficult to distinguish in hipparion.

tx = maxillary tooth; tm = mandibular tooth; mand = mandible. M1-M38 refers to measurements as described by Eisenmann et al. (1988) and Bernor et al. (1997).

Many figures present plots with abbreviations for different taxa and fossil samples. These abbreviations are as follows:

General Analyses

A = Awash (Middle), Ethiopia
B = Baringo Basin, Kenya
C = Langebaanweg, South Africa
D = Abu Dhabi
E = Eppelsheim, Germany
G = Omo, Ethiopia
H = Hoewenegg, Germany
I = Laetoli, Tanzania
K = Ekora, Kenya
L = Lothagam, Kenya
O = Olduvai, Tanzania
M = Manonga Valley, Tanzania
P = Potwar Plateau, Pakistan

R = Hadar, Ethiopia
S = Sahabi, Libya
T = Sinap, Turkey
U = Uganda
Z = Morocco

Abbreviations for Laetoli Horizons

N = Upper Ndolanya Beds
U = Upper Laetoli Beds
L = Lower Laetoli Beds
P = No provenance

Metric Procedures

Measurements are all given in millimeters and rounded to 0.1 mm. Measurement numbers (M1, M2, M3, etc.) refer to those published by Eisenmann et al. (1988) and Bernor et al. (1997) for the skulls and postcrania. Tooth measurement numbers refer to those published by Bernor et al. (1997) and Bernor and Harris (2003).

Bernor and Armour-Chelu (1999), Bernor and Harris (2003), Bernor and Scott (2003), Bernor et al. (2004, 2005, 2010) Gilbert and Bernor (2008), Bernor and Haile Selassie (2009) and Bernor and White (2009) have compared African hipparions to an extensive series of Late Miocene-Pleistocene Eurasian and African assemblages. In various studies, Eisenmann, (see Eisenmann 1995 for a comprehensive summary), has used log 10 ratio diagrams to evaluate differences in hipparion metapodial proportions as a basis for recognizing taxa and their evolutionary relationships. Bernor et al. (2003) and Bernor and Harris (2003) have used multiple statistical tests, including univariate, bivariate and multivariate statistics as well as log 10 ratio diagrams to evaluate and resolve the alpha systematics of hipparionine horses. Bernor et al. (2005) used log 10 ratio diagrams together with multivariate statistics to evaluate metapodial and first phalangeal evidence for postcranial evolution in Ethiopian hipparions. We incorporate these previously used methodologies in this work.

Our statistical analysis uses two recognized population standards. For postcrania we use the skeletal population from Höwenegg (Hegau, southern Germany, 10.3 Ma; Bernor et al. 1997) for calculating 95% confidence ellipses used in bivariate plots, and log10 mean standard values for all log10 ratio diagrams (MPIIIs and 1PHIIIs). We use the Eppelsheim standard for calculating 95% confidence ellipses for cheek tooth variables (Bernor and Franzen 1997; Kaiser et al. 2003; Bernor and Harris 2003).

Statistical Analysis

Tables 12.1–12.3 provide measurements of the Laetoli specimens used in this analysis. Comparative measurements were taken from Bernor's unpublished equid database. Analyses of Laetoli Equidae included bivariate plots of maxillary P2, calcanea, astragali, MC III, MT III and 1PHIII. All of these skeletal elements are clearly differentiated with the exception of 1PHIII. While anterior and posterior 1PHIII can be clearly differentiated in living *Equus*, the same cannot be said for all hipparions. The Höwenegg hipparion skeletons were found in articulation and thus the anterior versus a posterior 1PHIII are known. However, the statistical differences between these phalanges are minor at best, which has led us to analyze all 1PHIII together. Some advanced African hipparions may in fact differ significantly in anterior versus posterior 1PHIII dimensions, but this has not been adequately demonstrated. Bivariate plots will include two parallel sets of plots: one of our broad Eurasian – African samples to provide relevant ranges of variability in the sample under consideration, and the other that is specifically targeted to variability in the Laetoli sample by stratigraphic unit. The statistical analysis will be followed by the description of the material by stratigraphic horizon.

Metrical Results

Maxillary P2

Bernor et al. (2003) argued that P2 is the best tooth to statistically analyze for length and width measurements because it varies the least in these dimensions throughout ontogeny. Figure 12.1a is a bivariate plot of maxillary P2 occlusal width (measurement M3) versus occlusal length (measurement M1) for a large sample of African hipparions. Most of the sample falls within the Eppelsheim 95% confidence ellipse, with the largest specimens falling outside and above the ellipse originating from the Middle Awash, Potwar Plateau and Hadar. The smallest specimens, found just outside the lower border of the ellipse are from Lothagam and the Middle Awash. Figure 12.1b compares the known P2s from the Upper Ndolanya Beds and Upper Laetolil Beds; all specimens fall either within or just inside the Eppelsheim ellipse and are neither extraordinarily large, nor small. Cheek teeth are highly variable and change in size and shape becoming progressively smaller and square in outline with age. This is particularly the case with the advanced, high crowned hipparions that occur during the late Pliocene and Pleistocene of Africa (Bernor et al. 2010).

Table 12.1 Measurements (mm) of *Eurygnathohippus* aff. *hasumense* specimens from the Laetolil Beds, Laetoli (Tooth measurements after Bernor et al. 1997; Bernor and Harris 2003 – see text for further description of measurements). Loc = Laetoli collecting locality. KK = Kakesio; ES = Esere; N3 = Noiti 3

Specimen	Loc	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
Upper deciduous fourth premolar															
EP 1405/03	8	28.7	28.1	17.7		26.7									
EP 1013/98	9S	30.7	28.1	25.7	26.2	16.3	4.0	5.0	2.0	1.0	9.4	4.9			
LAET 75-2024	10	31.1		20.9		27.7									
EP 2321/03	13	33.8	31.7	21.6	24.0	27.4		2.0	1.0		8.3	3.5			
Upper second premolar															
EP 2989/00	1	28.2	26.1	29.6	28.5	38.6	1.0	6.0	1.0	1.0	16.6	10.0			
EP 1367/00	6	34.0	33.2	22.9	0.0	13.0	2.0	1.0	3.0	0.0	13.1	8.3	4.4		
EP 1967/00	6	24.1	21.8	25.5	26.4	15.9	0.0	5.0	2.0	0.0	10.8	5.4			
LAET 75-3534	8	38.7	37.8	25.9	26.6	24.7	2.0	2.0	0.0	0.0	9.1	5.6			
EP 512/98	10	35.5	32.7	25.9	21.3	54.2	3.0	3.0	0.0	0.0	9.7	4.1			
EP 404/00	12	37.6	36.8	0.0	23.8	35.6	2.0	2.0	2.0	1.0	11.6	0.0			
EP 071/98	KK	65.6	27.9	8.8	22.1										
Upper third/Fourth premolar															
LAET 78-5231	8	34.3	26.7	8.84	25.3										
EP 3531/00	12E	29.3	27.5	28.4	29.0	40.4	1.0	5.0	3.0	1.0	11.3	5.6			
EP 3532/00	12E	29.1	28.2	28.0	28.4	42.6	3.0	5.0	3.0	1.0	11.5	4.9			
Upper third premolar															
EP 2989/00	1	28.2	26.1	29.6	28.5	38.6	1.0	6.0	1.0	1.0	16.6	10.0			
EP 1706/04	2	31.5	25.9	30.0	27.2	52.8	3.0	7.0	4.0	1.0	8.5	3.4			
LAET 75-2114	2	27.8	26.0	25.6	23.6	26.5					9.4	4.5			
EP 1967/00	5	24.1	21.8	25.5	26.4	15.9	0.0	5.0	2.0	0.0	10.8	5.4			
EP 1969/00	5	26.3	23.1	24.7		41.2					10.2	4.7			
LAET 75-1193	6	28.4	26.7	23.3	51.7						9.8	3.8			
EP 1186/98	9	26.5	26.7	27.6	22.7	0.0	2.0	1.0	0.0		10.7	5.3			
EP 1187/98	9	24.7	24.6	24.9	26.3	28.9	1.0	5.0	0.0	0.0	10.0	4.4			
LAET 75-1430	9S	29.2	23.5	26.2	25.1	58.1	4.0	4.0	1.0	1.0	11.8	3.9			
LAET 75-3583	9S	29.9	26.5	27.0	24.8	49.8					8.4	3.1			
EP 1431/01	12	29.8	28.4	29.6	26.7	36.5	1.0	5.0	5.0	1.0	10.2	4.7			
EP 3531/00	12E	29.3	27.5	28.4	29.0	40.4	1.0	5.0	3.0	1.0	11.3	5.6			
EP 3532/00	12E	29.1	28.2	28.0	28.4	42.6	3.0	5.0	3.0	1.0	11.5	4.9			
EP 1443/01	21	29.2	29.0	23.1	21.2	38.4	3.0	4.0	1.0		9.6	4.3			
LAET 75-3437	21	27.3	24.9	24.1		39.4					9.4	4.7			
Upper fourth premolar															
EP 435/04	2	28.2	24.0	26.9	27.8	65.1	5.0	5.0	3.0	2.0	65.1	9.7			
EP 4222/00	2	29.7	25.4	23.8	25.8	66.9	2.0	5.0	1.0	0.0	8.9	3.4			
EP 1967/00	5	23.0	22.0	23.7	25.4	14.9	0.0	4.0	3.0	0.0	9.5	4.4			
EP 1420/04	6	27.3	25.9	31.5	22.7	0.0	6.0	0.0	0.0		9.8	5.6			
EP 1494/98	9	29.0	25.6	25.2	29.1	60.5	1.0	4.0	3.0	1.0	10.9	3.1			
EP 1012/98	9S	26.1	23.7	21.1	20.9	43.4	2.0	6.0	2.0	2.0	8.3	3.8			
EP 978/03	10	24.1	22.3	24.1	24.5	43.1		5.0	1.0	2.0	9.7	4.3			
LAET 75-2070	10	27.7	24.5	22.9	64.2	1.0	3.0	1.0	1.0		9.8	3.7			
EP 205/98	10E	24.7	23.3	26.1	25.8	49.7	3.0	6.0	3.0	1.0	8.5	4.3			
EP 1606/00	10W	27.1	24.3	29.2	28.3	32.5					9.9				
EP 1553/98	10E	26.3	24.6	28.1	28.0	25.9	1.0	10.0	2.0	1.0	9.4	5.1			
EP 420/01	13	25.4	24.4	24.0	25.5	28.0	3.0	5.0	2.0	1.0	9.2	4.2			
LAET 75-3358	21	28.1	22.6	25.2	25.4	65.8					8.0	3.9			
LAET 75-3667	22	23.7	23.3	24.3	24.1	20.3	1.0	4.0	1.0		9.9	5.0			

(continued)

Table 12.1 (continued)

Specimen	Loc	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
Upper first molar															
EP 435/04	2	26.2	22.8	24.5	25.9	62.6	4.0	5.0	4.0	1.0	62.4	9.2	3.9		
EP 685/00	2	27.9	23.9	23.1	23.2	68.1	1.0	3.0	3.0	0.0	10.2	3.0			
EP 959/05	2	28.1	25.1	23.7	24.0	68.0	1.0	5.0	1.0	1.0	9.4	4.4			
EP 1967/00	5	22.6	22.3	22.6	23.8	18.3	0.0	4.0	3.0	1.0	9.5	4.6			
EP 1942/03	7	24.0	22.1	23.4	25.1	24.5	1.0	4.0	2.0	0.0	9.6	4.9			
LAET 75-1320	8	25.8	23.4	25.1	25.0	52.6									
EP 766/03	9	26.8	24.4			68.5	4.0	6.0	1.0	3.0					
EP 2422/03	9S	23.6	23.9	21.7	23.9	32.7	1.0	4.0	1.0		10.0	4.6			
EP 172/99	10	23.5	22.9	23.8	24.7	30.9	0.0	3.0	2.0	1.0	9.0	5.0			
EP 1326/98	13	31.2	28.1	25.3	29.2	75.4	1.0	6.0	4.0	1.0	11.6	3.9			
LAET 75-3187	20	27.3	22.9	23.5	26.5	68.2		5.0	3.0	2.0	9.3	3.9			
EP 198/03	KK	27.8	22.8	23.5	23.9	63.1					9.4	3.6			
Upper second molar															
EP 4222/00	2	63.4	30.1	11.1	25.2										
EP 1967/00	5	20.5	23.5	10.5	25.1										
EP 1694/00	5	25.2	23.8	23.3	23.4	58.2	2.0	4.0	3.0	0.0	8.3	3.9			
LAET 75-1052	7E			21.1	20.8	63.4	2.0	4.0	1.0	3.0	10.3	3.1			
LAET 75-3532	8	25.4	22.2	23.3	24.1	60.9	3.0	5.0	3.0	2.0	10.4	3.6			
EP 764/03	9	25.5	25.3	22.7	22.8	45.5	5.0				9.1	4.0			
EP 765/03	9	26.3	24.9	21.3	24.0	72.7	2.0	2.0	2.0	1.0	10.0	3.6			
EP 1011/98	9S	24.9	22.2	22.0	24.1	35.2	1.0	4.0	1.0	0.0	8.8	4.1			
LAET 75-1450	9S	28.0		23.3		76.3									
LAET 75-1529	9S	25.7	22.7	24.0	25.1	59.8	3.0	5.0	3.0	1.0	9.8	4.0			
EP 171/99	10	24.5		23.8			2.0	10.0	3.0	1.0					
EP 513/98	10	23.0	22.1	21.4	23.4	22.9	0.0	5.0	0.0	0.0	9.2	4.2			
LAET 75-1781	10W	24.9	21.5	22.5	23.1	65.5	1.0	6.0	1.0	1.0	10.6	3.4			
EP 071/98	KK	26.8	23.5	22.2	25.3	59.4			2.0	1.0	8.2	4.4			
EP 086/98	KK	25.8	24.7	22.2	25.6	41.2	4.0	7.0	3.0	1.0	8.7	4.0			
Upper third molar															
EP 81/04	2	23.7	25.4	15.7	20.7	67.4	0.0	0.0	0.0	0.0	8.7	2.6			
EP 434/04	2	25.4	26.5	21.4	22.8	54.5	4.0	7.0	3.0	1.0	8.6	3.6			
EP 502/01	2	23.0	27.9	20.1	23.2	60.1	3.0	2.0	2.0	2.0	9.1	3.4			
EP 1842/00	2	26.0	25.5	21.5	22.5	35.8	2.0	5.0	3.0	1.0	11.2	4.2			
LAET 78-5068	2	23.4	25.3	17.6	20.8	63.3	2.0	4.0	1.0	0.0	11.1	2.3			
EP 1606/00	3	25.7	26.8	21.9	21.7	53.4					8.6	3.6			
EP 1967/00	5	26.4	26.7	20.8	20.8	23.3					10.9	4.1			
EP 1419/04	6	23.5	22.6	18.5	20.9	28.2	1.0	6.0	1.0	1.0	9.3	3.9			
EP 1185/98	9	27.2	24.6	21.2	23.0	19.2	1.0	5.0	3.0	1.0	12.4	3.9			
LAET 75-1991	10E	23.3	23.3	19.3	20.9	48.6	3.0	3.0	4.0	1.0	8.6	3.6			
EP 625/04	10W	25.6	27.1	20.3	24.0	44.0		5.0	3.0	1.0	9.7	3.8			
EP 698/05	10W	24.6	23.0	20.0	19.5	18.9	0.0	4.0	0.0	0.0	10.5	4.7			
EP 1295/03	11	24.0	25.2	20.4	21.3	41.7	3.0	5.0	3.0	1.0	9.4	2.3			
EP 533/05	12	22.9	25.7	20.1	19.5	53.2		2.0	1.0		7.4	3.2			
EP 403/00	12E	26.5	29.3	22.0	23.9	49.8	3.0	3.0	3.0	1.0	12.6	3.6			
EP 1512/03	12E	26.4	28.0	21.1	23.8	52.4									
EP 2043/00	13	25.6	25.8	21.8	22.7	41.2	1.0	6.0	2.0	1.0	8.5	3.4			
EP 2361/03	13E	28.9	29.3	22.3	24.8	38.3									
EP 161/04	15	24.1	26.1	20.9	21.8	36.7	4.0	5.0	1.0	1.0	8.1	3.8			

(continued)

Table 12.1 (continued)

Specimen	Loc	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
Lower second deciduous premolar															
EP 977/04	16	37.3	36.3	15.0	11.6	15.6	14.5	16.4	11.4	13.4	9.2	6.0	2.2	6.9	
Lower fourth deciduous premolar															
EP 977/04	9	30.9		13.4	9.1	11.0	16.3	16.9	12.5	12.0	11.8	9.0	3.4	7.6	
Lower second premolar															
EP 1190/98	9			13.1	9.7	10.2	14.4	15.1	12.4	13.0	31.6	5.9	2.0	37.3	
EP 1192/98	9	29.7	29.8	13.4	6.7	14.4	14.3	14.4	12.1	13.8	24.3				
LAET 75-1431	9S	32.1	31.3	15.6	10.3	16.5	15.8	13.5	12.3	14.4	31.8				
EP 1015/98	9S	29.4	28.3	14.2	8.4	16.3	15.3	15.0	12.6	13.5	42.2				
Lower fourth premolar															
LAET 81-48	9S	27.6	25.7	16.2	8.8	14.9	17.0	15.1	14.7	15.3	49.6				
EP 1016/98	9S	29.4	27.7	18.1	9.1	16.6	15.2	15.3	15.9	43.9					
EP 321/05	10W	26.8	26.8	24.8	16.1	9.1	11.5	16.8	17.5	15.1	14.2	29.3			
EP 617/98	10W	26.4		15.9	9.1	13.1	17.1	16.1	14.2	14.4					
EP 790/98	10W	24.5	24.0	15.4	8.3	9.6	15.7	15.8	13.5	12.8	18.5				
EP 3170/00	10W	25.1	24.3	14.5	8.4	11.0	14.1	12.6	12.7	12.0	26.3				
EP 594/00	22E	27.7	27.1	16.5	8.1	17.1	16.7	15.9		14.9	51.3				
Lower first molar															
LAET 76-3983	2	24.7	22.6	14.7	6.3	9.1	14.6	16.8	13.9	13.4	15.1				
LAET 78-5008	2	28.0	26.7	17.7	9.3	11.9	13.8	14.8		12.9	55.4				
LAET 76-4041	5	26.8		16.0	8.5	11.1	11.0		12.4	12.3					
EP 1496/98	9	24.7	24.5	14.8	8.8	10.7	13.0	13.9	12.0	11.6	47.1	3.8		45.4	
EP 1216/04	9S	25.4	23.4	16.5	7.8	11.4		15.2	15.3	13.6	35.9				
EP 2452/00	13E	27.2	23.4	15.2	8.1	10.8	13.1	14.5	12.6	11.9	35.9				
EP 3606/00	21	26.9	22.9	15.0	6.7	9.8	14.0	15.5	10.7	13.5	42.7				
EP 3732/00	22	27.7	24.4	12.9	7.5	10.3	11.6	12.0	10.0	8.6	65.1				
Lower second molar															
LAET 78-4974	2	25.4	25.3	15.1	7.4	12.2	15.3	15.6	16.1	15.0	26.8				
EP 2196/03	7	26.1	25.0	15.0	8.5	9.2	14.8	15.3	13.4	12.2	28.1				
EP 1017/98	9S	28.2	27.0	14.8	8.6		18.3	13.6	15.1	15.9	63.2				
EP 2480/00	13	26.1	25.1	15.7	8.1	9.1	12.8	13.5	12.7	12.6	42.1	3.0	1.7	37.5	
Lower third molar															
EP 2196/03	7	30.2	30.4	14.4	7.7	10.2	12.6	12.7	12.9	10.4	25.7				
EP 1241/01	9S	27.3		13.2	8.1	10.3	12.6	13.0	12.7	11.5	40.3				
EP 1242/01	9S	25.6	27.6	12.8	6.7	9.3	10.9	12.1	10.6	9.6	68.6				
LAET 75-3667	22	28.0	22.7	21.4	20.1	17.7	1.0	2.0	1.0	1.0	11.4	5.3			
Metacarpal III															
EP 1528/00	3										38.8	39.2	32.1	28.4	30.0
LAET 75-1128	6					47.3	34.4	41.4							
EP 1107/00	8					44.5	32.1	41.0	11.9	7.0					
EP 4123/00	8														
EP 1244/01	9S										45.0	43.8	29.9	25.3	27.0
LAET 75-2250	10E					47.5	31.5								
LAET 78-4752	11										46.2	43.6	35.0	28.5	29.6

(continued)

Table 12.1 (continued)

Specimen	Loc	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
Metacarpal III															
LAET 75-1589b	13			30.6	27.9	46.7	34	40.2	11.3	5.4					
LAET 75-3138	12					45.5	33.1	40.2	10.7	6.0					
LAET 75-1589	13					45.6	33.6	41.4	10.5	5.8					
LAET 75-3442	21					47.6	35.6	43.2	10.8						
EP 1222/98	22														
EP 1668/98	ES										42.4	38.7			
Tibia															
LAET 75-2891	4							72.9	51.6						
EP 300/00	8							73.0	52.2						
EP 146/98	10E							75.0	51.5						
Calcaneus															
LAET 75-2549	2			18.1			60.5	54.3							
LAET 75-1886	10			22.9			57.5	48.1							
EP 2572/00	11			23.2			49.3								
EP 2454/00	13E	115.9	76.1	22.3	28.4	50.9	58.4	44.8							
EP 1748/03	22			22.6			55.6	55.5							
Astragalus															
EP 678/00	2	62.1	62.5		62.9	49.5	38.9	52.0							
LAET 75-1897	2	66.8	63.7	31.4	66.8	55.6	38.8	56.4							
LAET 75-2530	2	65.2	66.8	30.8	64.1	54.0	37.4								
LAET 75-3756	6	62.9	63.7	34.6	62.2	51.2	36.2	46.9							
EP 3822/00	6	63.1	63.9	32.8	63.9	49.2	36.8	53.2							
EP 307/00	8	64.4	62.1	30.6	61.8	49.1	37.4	49.0							
LAET 75-1244	8	62.7	61.7	30.9	62.2	49.0	35.7	50.0							
LAET 75-1498	9	62.1	60.0	29.1	61.7	47.1	35.4								
EP 655/98	10W	61.3	57.1	30.1	48.8	48.5	34.3								
EP 3171/00	10W	59.9	59.8	28.3	56.2	46.2	35.2	46.2							
EP 364/98	10E	69.0	69.7	33.8	65.2	51.2	38.8	49.0							
LAET 75-3145	12	69.9	68.1	34.0	70.1	53	38.6	53.9							
EP 1130/04	13	61.3	62.1	31.9	61.4	47.9	35.2								
LAET 75-2944	16	66.1	67.3	31.5	58.5	55.8	38.3								
EP 1422/01	21	61.9	57.2	30.8	64.8	44.3	34.2	44.0							
LAET 75-3670	22	63.5	61.6	30.1	61.4	55.2	36.4								
Metatarsal III															
EP 2197/03	7										47.8	44.2	32.9	31.4	32.1
EP 3881/00	7														
EP 4122/00	8										43.2	41.0	34.5	26.9	31.5
EP 128/98	10E					45.02									
EP 558/00	22												33.6		29.8
EP 1669/98	ES										44.0	44.1	35.9	29.6	31
EP 463/04	N3					45.5	37.4	42.3	10.1	7.2					
First phalanx (1 ph3)															
EP 4221/00	2				46.5	32.9				26.4					
LAET 78-5160	9	68.6	61.2		48.0	33.6	40.0	39.6	24.0	22.7					
EP 893/00	10W	67.5	59.9	29.6			38.5	36.9	23.4	20.5	46.3	46.4	11.9	11.9	
EP 2481/00	13	70.7	63.0	33.0	47.6	37.6	40.1	40.5	24.5	15.2	41.4	47.3	17.4	16.5	

Table 12.2 Measurements (mm) of *Eurygnathohippus* aff. *cornelianus* specimens from the Upper Ndolanya Beds, Laetoli (Tooth measurements after Bernor et al. 1997; Bernor and Harris 2003 – see text for further description of measurements). Loc = Laetoli collecting locality. SA = Silal Artum

Specimen	Loc	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
Upper fourth deciduous premolar															
EP 445/05	18	31.5	28.9	13.9	9.9	10.6	13.8	14.5	8.9	8.6	23.6			19.3	
Upper first incisor															
LAET 75-2461	14	23		11.5		29.5									
EP 032/03	SA	17.3	11.1	14.7	14.6	29.6									
Upper second incisor															
LAET 78-5117	7E	12.3	13.8	13.5	13.7	24.5									
Upper third incisor															
LAET 75-3793	7E	31.2	17.9	10.9	11.6	33.8									
EP 1495/04	22E	18.3	11.3	13.1	12.3	34.6									
Upper second premolar															
LAET 75-2458	14			25.1		53.5					11.0				
EP 1033/00	15	35.4		22.5		60.0									
LAET 78-4872	18	32.1	29.9	23.8	21.3	30.4	2.0	1.0	2.0	1.0	7.7	4.8			
EP 781/01	18		32.4	22.7	22.9	29.4					6.8	3.9			
Upper third premolar															
EP 1213/03	7E	23.1	23.3	25.3	23.5	22.1	1.0	6.0	6.0	1.0	8.1	3.5			
EP 4010/00	7E	20.0	18.5	20.6	21.6	30.1	1.0	5.0	1.0	1.0	9.1				
EP 4011/00	7E	22.7	21.3	25.2	26.1	30.8	1.0	6.0	4.0	1.0	9.5	5.4			
EP 1183/04	14	26.5	23.0	24.9	27.3	43.0					7.2	2.9			
LAET 78-5049	14	28.9	25.5	28.3	25.3	69.7									
EP 1033/01	15	29.5				58.3									
EP 980/00	18	26.4	23.7	25.4	23.5	24.3	1.0	6.0	7.0	1.0	8.5	4.3			
EP 986/00	18	25.3	24.5	27.3		42.8					8.0	4.9			
LAET 78-4872	18	22.3	20.6	21.8	23.3	29.4	4.0	7.0	2.0	1.0	8.3	4.2			
EP 1495/05	22	24.8	21.5			19.1		4.0							
EP 1308/98	22S	24.1	23.0		23.6	40.9	3.0	3.0			7.3	3.7			
Upper fourth premolar															
LAET 75-906	7E	23.6	23.4	24.3	24.3	12.8	0.0	4.0	1.0	0.0	10.8	6.7			
EP 1213/03	7E	23.4	22.5	22.8	23.5	17.7	1.0	5.0	3.0	1.0	9.6	4.5			
LAET 75-1696	14	25.5	25.4	25.9	26.1	34.7	1.0	7.0	5.0	1.0	8.7	3.9			
EP 986/00	18	27.9	0.0	26.6	0.0	49.9	0.0				8.5	4.4			
Upper first molar															
EP 4018/00	7E	21.1	20.2	21.3	21.9	40.0		6.0	4.0	1.0	8.3	3.2			
EP 3470/00	15	29.0	22.6	22.9	23.7	80.0									
EP 986/00	18	25.6	24.1	25.2		51.2									
Upper second molar															
LAET 75-1685	14	25.4	19.7	23.1	73.4		4.0	2.0		10.9	3.6				
EP 1517/01	SA	23.6	22.1	22.0	23.4	50.2									
Upper third molar															
LAET 75-1639	14	25.5	27.4	20.1	22.6	50.3	1.0	2.0	1.0	1.0	9.1	3.5			
LAET 78-4872	18	21.8	22.3	18.9	18.8	33.5	3.0	4.0	4.0	1.0	7.9	3.3			
EP 1495/04	22E	23.6	23.2	19.7	19.9	28.3		4.0			10.0	4.0			

(continued)

Table 12.2 (continued)

Specimen	Loc	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
Lower first incisor															
LAET 78-4815	18	14.7	12.3												
Lower second premolar															
EP 4012/00	7E	31.2	31.7	13.7	6.3	13.9	16.2	17.8	11.7	13.8	24.4	5.5	3.6	19.6	
LAET 81-73	14	31.3	30.8	12.0	7.0	13.9	13.5	15.4	10.3	12.3	19.0	6.4	3.6	14.1	
LAET 75-3765	14			14.8		14.6	16.0	16.1		14.0	23.1	5.1	3.6	19.3	
LAET 78-4815	18	30.7	30.5	13.2	3.9	15.5	12.8	15.3	10.6	11.4	16.3	8.5	3.8	18.0	
Lower third premolar															
LAET 78-4815	18	25.2	23.0	15.6	8.6	13.0	15.4	15.2	14.3	12.1	13.8	8.0	3.0		
Lower fouth premolar															
LAET 78-4815	18	24.4		15.3	8.5	11.4	16.1		14.6	12.5		6.5	2.9		
Lower third/Fourth premolar															
LAET 75-778	7E	24.3	23.6	15.3	7.2	12.8	16.7	16.8	15.2	13.3	20.6	4.8	3.1	24.0	
LAET 75-804	7E	23.9		14.2	8.6	12.0	14.2		13.4	13.9					
LAET 75-905	7E	24.5	22.5	15.6	9.5	12.8	15.4	14.7	14.0	12.1	12.5	3.5	2.4	17.4	
EP 034/00	18	28.0	25.9	16.3	9.1	13.5	16.6	16.5	14.5	14.9	54.0	7.4	2.3	44.5	
LAET 75-2460	18	29.4		14.0	8.5	12.8	13.7		11.2	13.9					
Lower first molar															
LAET 75-1685	14	28.3	16.0	9.1	11.7	12.8	12.1	11.7	12.2	65.8			53.0		
LAET 78-4815	18	22.8		13.0	6.7	9.8	13.8		10.9	11.2	33.8	6.0	2.3		
Lower second molar															
EP 1210/03	7E	23.8	23.7	13.1	8.6	9.3	13.4	13.0	13.4	11.6	28.1	5.5	2.5	20.7	
EP 1211/03	7E	29.0		10.7	9.5	12.3		13.0	10.0	9.2	75.1			50.7	
LAET 76-3948	18	23.0	22.0	12.2	6.6	10.1	12.1	12.3	12.0	10.2	49.4	5.1	12.6	46.7	
LAET 78-4815	18	23.2	20.3	13.3	6.9	9.9	13.3		11.5	11.0	39.1	5.5	3.0	32.3	
Lower third molar															
LAET 78-5031	14	24.4	23.8	14.6	7.7	11.4	11.9	11.9		11.3	29.2	1.6	0.9	27.0	
LAET 78-4815	18	27.3	29.4	12.0	6.9	10.6	11.9	10.5	10.7	9.1	32.2	3.9	2.3	27.4	
Metacarpal III															
LAET 75-904	7E										36.2	32.4	31.5	25.1	28.2
EP 1208/03	7E										44.1	43.5	34.2	29.5	31.9
LAET 78-5095	7E										40.5	39.8	31.2	25.3	27.2
LAET 78-5027	14					45.0	30.9	39.1	13.0						
LAET 78-5036	14					45.4	29.0	37.2	13.3						
LAET 76-153	18										42.9	39.5	38.0	26.7	28.3
EP 926/00	18					44.1	29.4	38.6	10.8	6.5					
EP 927/00	18					42.1	29.0	36.0	11.8	5.1					
EP 976a/00	18										37.1	36.2	30.3	26.5	26.6
EP 976b/00	18										36.1	36.5	30.6	25.9	26.7
LAET 78-4857	18										39.0	35.3	30.7	27.7	28.7
EP 2352/00	18					44.5	31.3	37.5	12.8	7.6					
EP 1838/03	SA										51.6	51.7	39.5	31.1	33.4
Tibia															
LAET 75-927	7E							68.1	47.5						
LAET 75-930	7E			47.5	32.7			66.6	46.2						
LAET 75-1073	7E								44.5						

(continued)

Table 12.2 (continued)

Specimen	Loc	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
Calcaneus															
LAET 75-802	7E	112.2	73.7	20.5	33.5	51.3	54.5	54.3							
LAET 76-473	18	107.0	68.5	21.0	33.8	50.8	53.1	54.6							
Astragalus															
LAET 75-1640	14	66.7	64.2	31.7	66.3	52.5	38.6								
LAET 75-1659	14	56.9	59.0												
LAET 78-5056	14	57.2	55.1	29.8	54.8	45.6	32.2								
EP 083/03	18	56.4	57.4	26.7	54.5	47.4	38.2								
LAET 76-55	18	59.9	57.1	27.8	53.4	44.4	31.5	44.0							
Metatarsal															
LAET 75-903	7E										43.5	39.2	33.2	27.4	
LAET 75-904	7E											32.5	32.0	25.8	
LAET 75-928	7E					42.4	35.5	37.7	9.6						
LAET 75-2471	14	265.0	264.0	30.4	31.1	42.5	35.9	40.2			46.5	38.2	34.0	28.0	
EP 207/04	15										42.4	37.1	33.7	26.4	
EP 1687/03	15										41.5	40.0	32.3	25.9	
EP 157/76	18					43.8	35.2	42.1	8.8						
EP 284/76	18			28.22	26.48						43.74	41.53	37.14	28.1	
EP 286/76	18					47.5	37.5	42.7	13.3	4.8					
EP 357/76	18					39.3	31.8	37.9							
EP 1515/01	SA										42.9	39.4	34.6		
First phalanx (1 ph3)															
EP 163/76	7E				41.8	32.6									
LAET 75-800	7E	63.1	56.2	32.8	45.6	35.7	37.9	35.3	20.9	18.9	39.9	38.6	13.3	16.3	
LAET 75-1065	7E				45.8	37.5				18.8					
LAET 75-1077	7E				45.6	30.3									
EP 1493/00	7E	65.5	57.6	31.6	42.7	34.0	36.9	36.1	20.7	19.5	40.8	41.6	15.2	15.3	
LAET 75-2467	14	72.3	63.4	33.5	42.6	36.6	40.0	39.5	24.2	23.4	51.3	49.3	12.5	18.0	
EP 5030/75	14				39.9	32.2				10.6					
EP 208/76	18	64.2	60.0	28.5	39.8	31.4	34.5	34.0	22.0	19.0	44.9	45.3	12.5	11.8	
EP 084/03	18	63.6	56.7	30.5	42.4	33.7	36.8	35.5	20.1	9.9	49.8	50.0	11.4	12.3	
EP 3289/01	18	62.0	53.3	31.4	42.8	34.3	34.9	34.6	22.1	19.3	35.3	36.7	19.2	18.4	
EP 8418/03	18	63.8	58.0	30.1	42.4	32.9	36.5	35.5	21.2	18.4	40.1	39.7	16.7	17.3	
EP 1310/98	22S				43.5	34.8				23.5					

Table 12.3 Measurements (mm) of *Equus* sp. phalanges from Emboremony (EM, Ngaloba Beds) – (see text for explanation of measurements)

Specimen	Loc	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13
First phalanx (1 ph3)														
EP 367/99	EM	76.7	70.7	31.6	50.7	35.0	42.0	39.3	23.8	42.8	53.1	50.6	18.6	19.8
EP 2105/03	EM	78.4	69.1	33.3	53.8	37.4	43.9	39.0	20.3		52.3	54.9	17.3	14.4

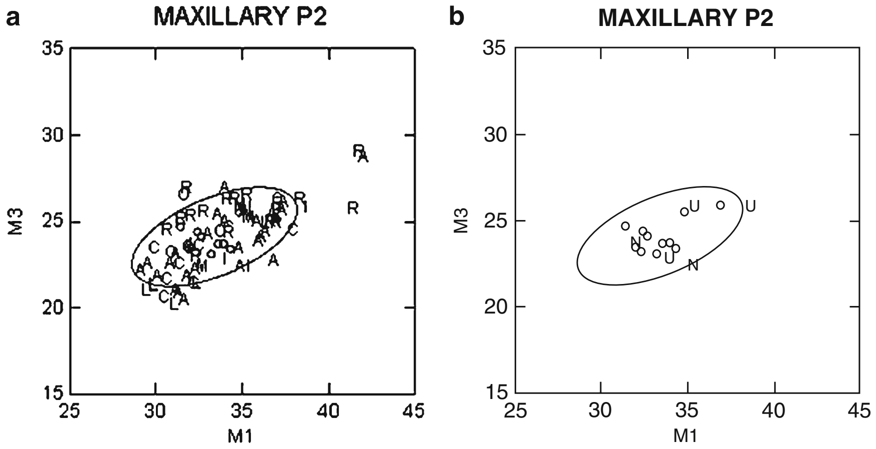

Fig. 12.1 (**a**) Bivariate plot of maxillary P2s occlusal width, (measurement M3) versus occlusal length (measurement M1) from the African hipparion sample plotted relative to the Eppelsheim ellipse (*A*=Middle Awash, *L*=Lothagam, *R*=Hadar). (**b**) Bivariate plot of maxillary P2s (occlusal width versus occlusal length) from the Upper Laetoli (*U*) and Upper Ndolanya Beds (*N*)

Calcanea

Figure 12.2a plots calcaneal maximum length (M1) versus maximum width (M6) for our sample compared to the Höwenegg 95% confidence ellipse. All but one of the Laetoli (I) specimens fall either within, or immediately outside the ellipse; Hadar specimens (R) plot at the upper border, or above the Höwenegg ellipse; Langebaanweg, C, plots at the bottom, or below the Höwenegg ellipse. One Laetoli specimen falls very far below the ellipse and is a smaller form. Figure 12.2b plots the Laetoli specimens by horizon, the two Upper Ndolanya Bed specimens fall within the ellipse, the Upper Laetolil Bed specimen at the upper limit of the ellipse and a single specimen falls well below the ellipse.

Astragali

Astragali are usually far more common than calcanea in collections, and this is reflected in our sample plotted in Fig. 12.3. In our larger sample (Fig. 12.3a) we find that astragali vary in size far beyond the range represented by Höwenegg 95% confidence ellipse of *Hippotherium primigenium*. This plot shows a number of larger astragali specimens from Hadar (R) and Laetoli (I), some from Awash (A) and Olduvai (O) and smaller specimens from Olduvai, Lothagam (L), Langebaanweg (C) and Omo (G). The large specimens from Hadar are referable to *Eurygnathohippus hasumense* (*sensu* Bernor et al. 2005), and those from Awash are perhaps *Eu.* aff. *turkanense*. Small taxa have been reported from Lothagam (*Eu. feibeli*, Bernor and Harris 2003), Olduvai and Omo (Armour-Chelu et al. 2006). The Olduvai specimen far to the right of the ellipse may be referable to *Equus oldowayensis*, having a wide distal facet (re Gilbert and Bernor 2008). Figure 12.3b plots the Laetoli specimens by horizon and here we find that the Upper Ndolanya specimens mostly fall within the ellipse, while most of the Upper Laetolil Beds specimens fall either above or to the left of the ellipse. This suggests that the dominant morph (and potentially species) in the Upper Ndolanya Beds is smaller (the size of the Höwenegg species), while the Upper Laetolil sample may include more than a single species, one large and the other small. The larger Laetoli form overlaps extensively in size with the Hadar hipparion and could be referable to *Eurygnathohippus* cf. *hasumense* as found in the Beredi Member of the Manonga Valley fauna in Tanzania, (Bernor and Armour-Chelu 1997). We further plotted, but do not figure here, distal articular facet depth (M6) versus width (M5) and this analysis exhibits very much the same result as illustrated in Figs. 12.3a and b.

Metacarpal III

There are no complete hipparion MCIIIs in the Laetoli sample available to us. In Fig. 12.4a we provide a broad sample of complete MCIIIs plotting maximum length (M1) versus distal articular width (M11) exhibiting the great variation in size of African hipparions compared to the Höwenegg population. Most remarkable are the extremely long MCIIIs from Hadar (R) and the extremely small specimen from Sahabi (Bernor and Scott 2003; Bernor et al. 2008); the large Olduvai specimens to the far right of the ellipse are likely *Equus* cf. oldowayensis (Gilbert and Bernor 2008). Fig. 12.4b is a similarly large sample of MCIII measurements

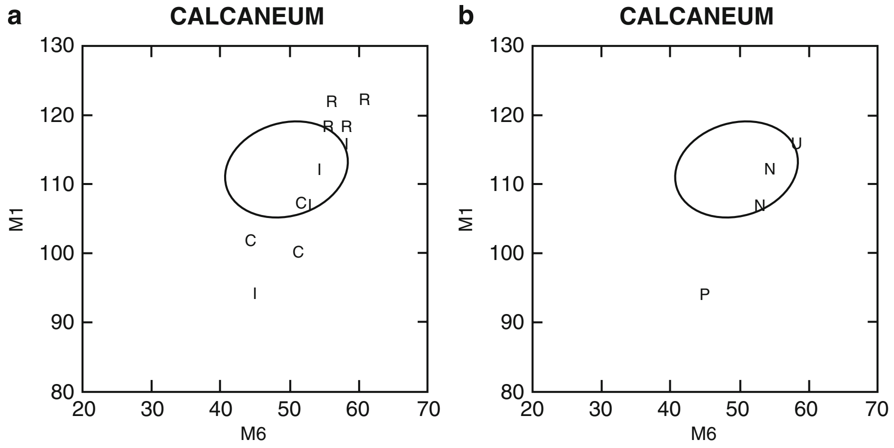

Fig. 12.2 (**a**) Bivariate plot of calcaneum from Laetoli (*I*), Hadar (*R*) and Langebaanweg (*C*) (maximum length vs maximum width) relative to the Höwenegg ellipse. (**b**) Bivariate plot of calcaneum (maximum length vs maximum width) from the Upper Laetolil (*U*) and Upper Ndolanya Beds (*N*) relative to the Höwenegg ellipse

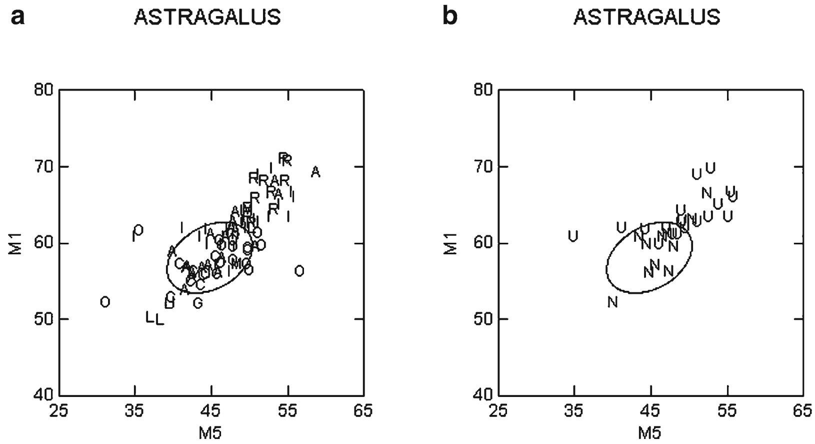

Fig. 12.3 (**a**) Bivariate plot of astragali maximal length (measurement M1) versus distal articular width (measurement M5) from the African hipparion sample plotted relative to the Höwenegg ellipse. (**b**) Bivariate plot of astragali maximal length (measurement M1) versus distal articular width, (measurement M5) from the Upper Laetolil (*U*) and Upper Ndolanya Beds (*N*) plotted relative to the Höwenegg ellipse

on proximal articular depth (M6) versus proximal articular width (M5): most Laetoli specimens plot at the upper limit, or somewhat above the Höwenegg ellipse, while Hadar and Olduvai specimens fall much further above the ellipse; specimens within the ellipse include those from Olduvai (O), Langebaanweg (C), Manonga Valley (M), Lothagam (L; likely *Eurygnathohippus feibeli*) and Middle Awash (A; also likely *Eurygnathohippus feibeli*). The Hadar specimens have greater proximal width dimensions than the Upper Laetolil specimens with the former being referable to *Eu. hasumense*. The same can be said for the large and very broad Olduvai specimens, which are most likely referable to *Equus oldowayensis*. The smaller Laetoli specimens are from the Upper Ndolanya Beds and overlap extensively with some of the Olduvai specimens. Referring back to Fig. 12.4b, it can be seen that Olduvai specimens show the greatest variation in size of all sites and this undoubtedly indicates multiple equid taxa, which certainly include species of *Equus* and *Eurygnathohippus.*

Figure 12.4c plots Laetoli proximal MCIIIs by horizon: the Upper Ndolanya specimens plot at the upper extreme and above the Höwenegg ellipse while the Upper Laetolil Beds specimens overlap slightly and are larger than the Upper Ndolanya specimens. Figure 12.4d plots a large sample of distal MCIII specimens distal sagittal keel (M12) versus distal articular width (M11); this graph exhibits that great range of variability among taxa under consideration and the extreme development of the distal sagittal keel, most prominent in the Hadar (R) *Eurygnathohippus hasumense* sample (Bernor et al. 2005). Figure 12.4e plots the Laetoli specimens by stratigraphic unit and includes substantial diversity in the Upper Ndolanya sample, which may well represent more than one taxon and specimens from the Upper Laetolil Beds and unknown provenance to the right and above the Höwenegg ellipse.

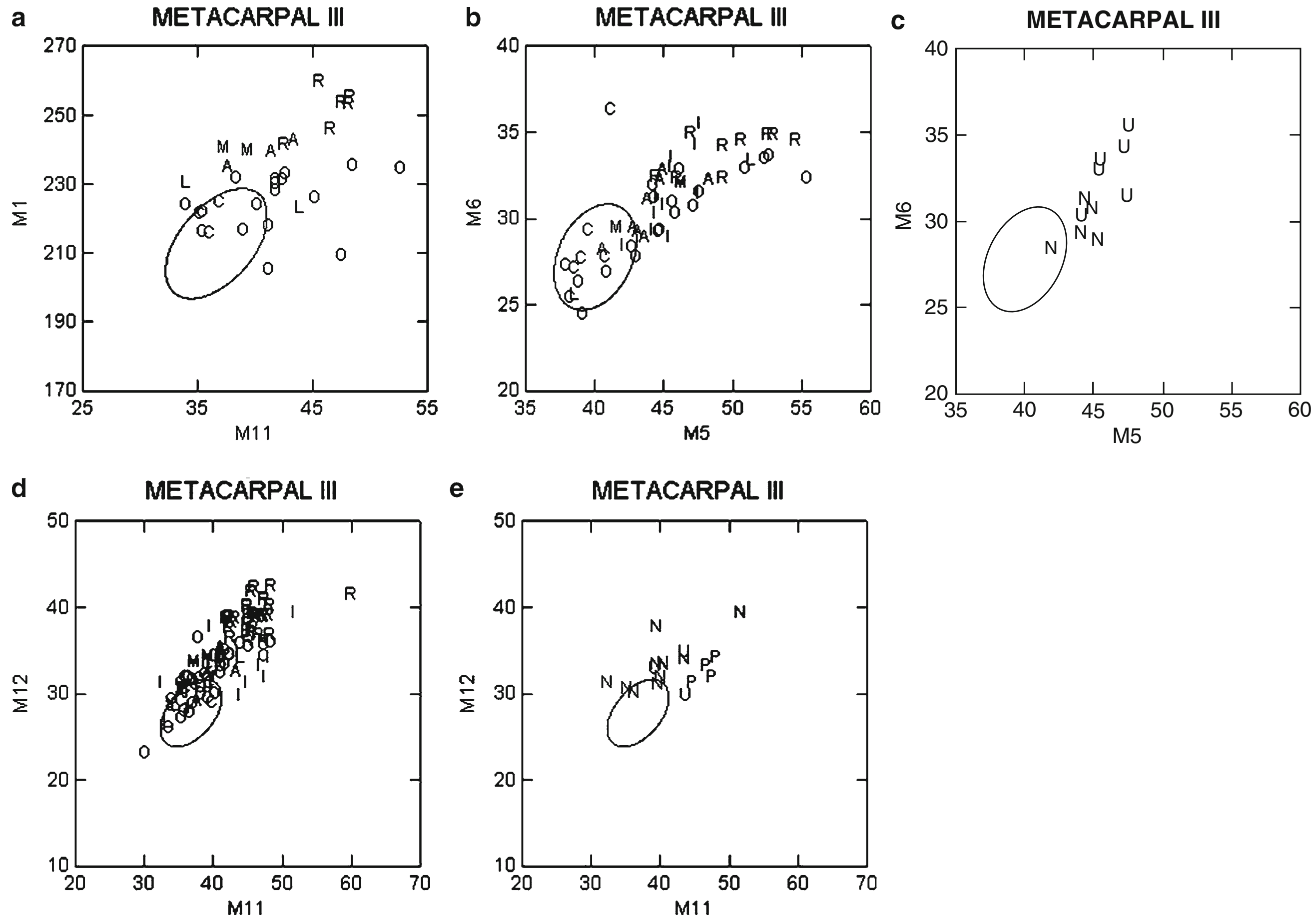

Fig. 12.4 (**a**) Bivariate plot of complete MCIII from the African sample, plotting maximum length (M1) versus distal articular length (M11) compared to the Höwenegg ellipse. (**b**) Bivariate plot of proximal articular width (M5) versus proximal articular depth (M6), showing Laetoli specimens relative to Höwenegg ellipse and the African sample. (**c**) Bivariate plot of proximal articular width (M5) versus proximal articular depth (M6) plotted by horizon and compared to the Höwenegg ellipse. (**d**) Bivariate plot of distal articular width (M11) versus sagittal keel (M12) of African sample of distal MCIIIs. (**e**) Bivariate plot of distal articular width (M11) versus sagittal keel (M12) of Laetoli specimens plotted by stratigraphic unit

Metatarsal III

Figure 12.5a is a bivariate plot of MT III length (M1) versus width (M11) comparing a large sample of African specimens to the Höwenegg sample. The majority of specimens are derived from Olduvai, most of which plot within the Höwenegg ellipse, but with some smaller and larger specimens. Langebaanweg *Eurygnathohippus hooijeri* (Bernor and Kaiser 2006) overlaps with the Höwenegg population, being at the top or above its range. Middle Awash specimens plot just to the right or above the ellipse being somewhat larger than the Höwenegg population. The largest MT III is derived from Hadar *Eurygnathohippus hasumense* (Bernor et al. 2005). The single Laetoli specimen (I), plotting slightly above the ellipse, is from the Upper Ndolanya Beds (Fig. 12.5b), and overlapping with the intermediate range of the Olduvai specimens. Figure 12.5c represents a large sample of African proximal MT IIIs for which we plot proximal articular depth (M6) versus width (M5). Significant features here include: most of the Olduvai specimens plot within the ellipse, but there is a significant dispersion of specimens above and to the left of the ellipse as well as just above the ellipse, likely indicative of at least two hipparionine taxa; Hadar *Eurygnathohippus hasumense* (R) again plots well above the ellipse overlapping with the massively built Lothagam *Eurygnathohippus turkanense* (L). Figure 12.5d plots the Laetoli sample by horizon and all specimens from the Upper Ndolanya Beds (five from N), Lower Laetolil Beds (one from L) and uncertain provenance (one from P) plot within the Höwenegg ellipse. Figure 12.5e is important documentation of the significant increase in MT III distal sagittal keel dimensions in African hipparions, with Hadar (R) being the most prominent. Figure 12.5f plots the Laetoli sample by horizon: most Upper Ndolanya specimens plot within or just outside the ellipse (mostly above indicating increased M12 dimension), with a few specimens plotting above the ellipse from the Upper Ndolanya, Upper Laetolil, Lower Laetolil and unknown provenance.

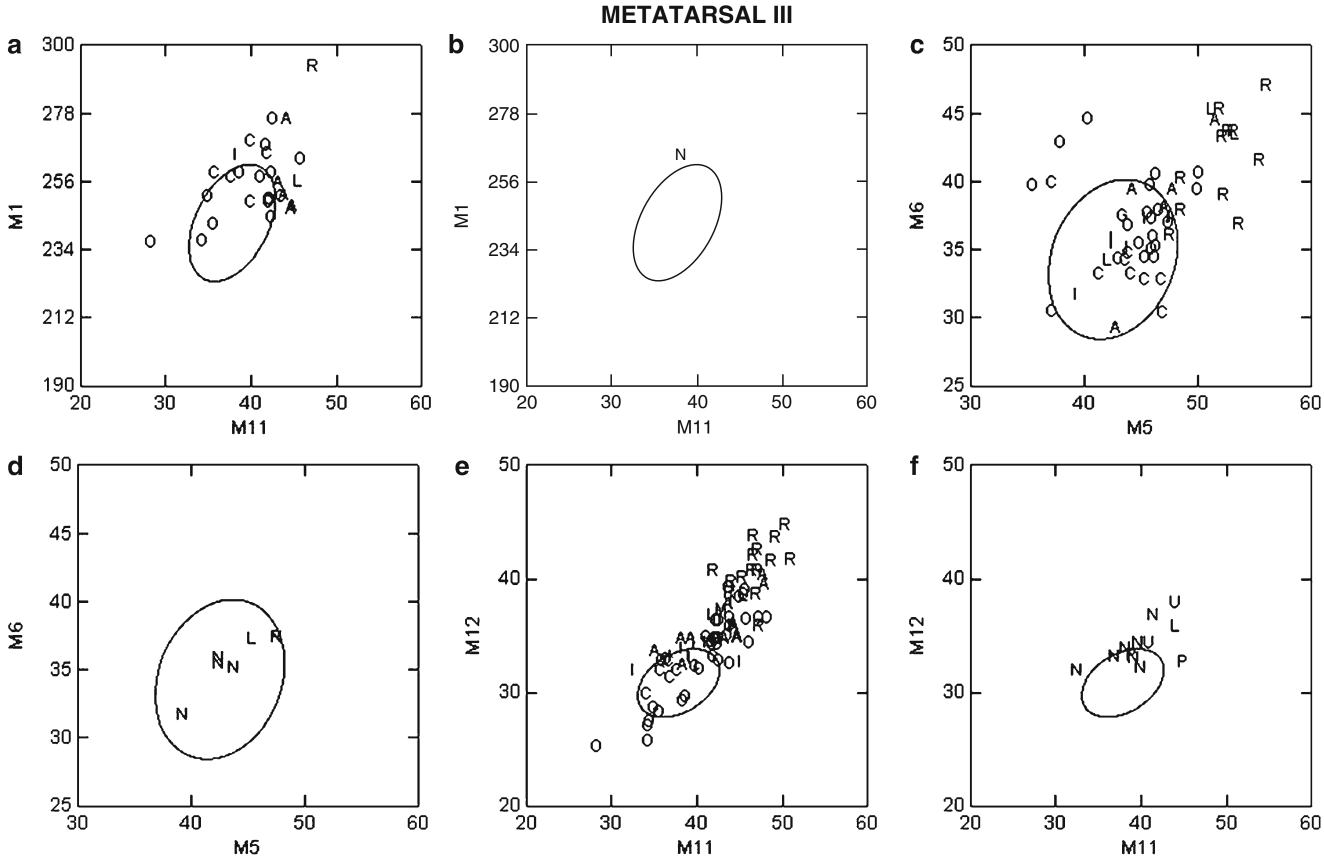

Fig. 12.5 (**a**) Bivariate plot of MTIII maximum length (M1) versus distal width (MII) of African sample compared with the Höwenegg ellipse. (**b**) Bivariate plot of MTIII maximum length (M1) versus distal width (M11) of complete MTIII from Upper Ndolanya Beds. (**c**) Bivariate plot of MTIII proximal articular width (M5) versus proximal articular depth (M6) from the African sample compared to the Höwenegg ellipse. (**d**) Bivariate plot of MTIII proximal articular width (M5) versus proximal articular depth (M6) from the Laetoli sample by horizon compared with the Höwenegg ellipse. (**e**) Bivariate plot of MTIII distal sagittal keel dimension, (M11 – distal maximal articular width) versus M12 (distal maximal depth of the keel) in the African sample. (**f**) Bivariate plot of MTIII distal sagittal keel dimensions from Laetoli plotted by horizon (distal maximal articular width M11 versus distal maximal depth of the keel M12)

We calculated a number of MT III log10 ratio plots all using the mean Höwenegg log10 standard. Figure 12.6a compares the Höwenegg standard to the mean Sinap *Cormohipparion sinapensis* sample (Turkey; AS_Mean2; Bernor et al. 2003), the Langebaanweg sample (South Africa; SAM_Mean2; Bernor and Kaiser 2006), Daka (Ethiopia; BOU-VP-26/13) *Eu.* aff. *cornelianus* (Gilbert and Bernor 2008), Olduvai *Eu. cornelianus* (Armour-Chelu et al. 2006) and the Upper Ndolanya specimen EP 75-2471R. The Sinap mean is believed to represent the primitive condition for Old World hipparions (Bernor et al. 2003; Bernor and White 2009) with particular regard to: its length (M1) is only slightly less than the Höwenegg mean, its mid-shaft width (M3) is very narrow and its depth slightly less than Höwenegg; other dimensions are less, reflecting slighter build than the Höwenegg hipparion. The Langebaanweg specimen is longer (M1) than in the Höwenegg sample, but a mid-shaft width (M3) versus mid-shaft depth (M4) proportion is virtually identical to Daka *Eu.* aff. *cornelianus*. The remainder of Langebaanweg's dimensions is similar to *H. primigenium*. The Laetoli MT III most closely compares with Olduvai *Eu. cornelianus* and the Daka hipparion, except for M11 (distal articular width), which is lower and overlaps with Langebaanweg. The close comparison of the Upper Ndolanya MT III dimensions to Olduvai and Daka hipparions supports Armour-Chelu et al.'s (2006) observation that the *Eu. cornelianus* lineage extends back to Upper Ndolanya horizons at 2.66 Ma.

Figure 12.6b compares the Laetoli MT III (EP75-2471) with samples from Hadar (AL 155-6AZ), Olduvai (OLDEoldMEAN), Ahl al Oughlam, Morocco (AaOMTIII Mean) and Sinap (AS_Mean2). This plot clearly shows the dramatically different dimensions and larger size of Olduvai *Equus oldowayensis* (OLDEoldMEAN) compared to all hipparions considered (Gilbert and Bernor 2008); M1 is relatively short, midshaft width (M3), midshaft depth (M4), proximal articular width and depth (M5 and M6) and distal dimensions (M11, M12 and M13) are greatly elevated compared to all other hipparions, except *Eu. hasumense* for M11, M12 and M13. The Hadar *Eurygnathohippus hasumense* metatarsal has the greatest overall length (M1) and midshaft width (M3)

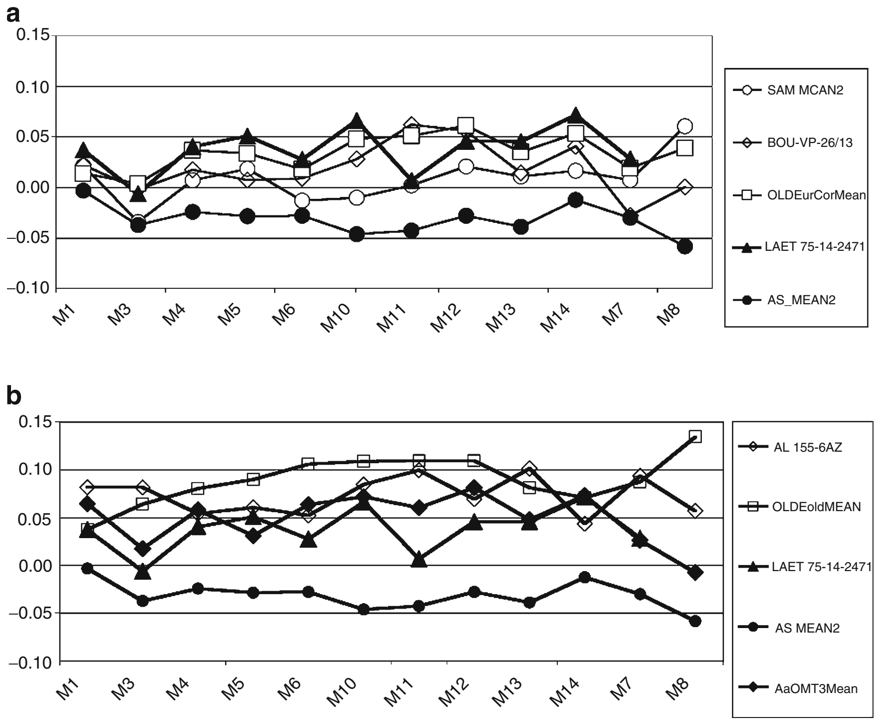

Fig. 12.6 (**a**) Metatarsal III log10 ratio diagram (Höwenegg Standard) showing more slender limbed equids from Langebaanweg, Daka, Olduvai, Laetoli and Sinap. (**b**) Metatarsal III log10 ratio, Hp. Std., larger equids from Olduvai, Hadar and Ahl al Oughlam (AaO) compared to primitive *Cormohipparion sinapensis* and Laetoli Upper Ndolanya Beds

followed by the Moroccan MTIII (*Eurynathohippus pomeli*). While the Moroccan *Eurygnathohippus pomeli* metatarsals (Eisenmann and Geraads 2007; Bernor et al. 2010) are clearly longer than the Laetoli specimen, the proportions for most dimensions (except M11) track the Laetoli specimen quite closely and, on face value, suggest a possible evolutionary relationship. The possibility that *Eu. pomeli* and *Eu. cornelianus* are sister taxa is an observation contrary to Eisenmann and Geraad's (2007) recent interpretations.

First Phalanges III

We undertook a number of bivariate calculations and have found the maximum length (M1) versus proximal articular width (M4) is the most useful (Fig. 12.7). Figure 12.7a exhibits the major increase in length of first phalanges in several African hipparions, and in particular the Hadar hipparions (R). Lothagam (L), Langebaanweg (C), Middle Awash (A), Laetoli (I) all have several specimens plotting within the Höwenegg ellipse and as such are conservative in their morphology. Figure 12.7b plots the Laetoli specimens by stratigraphic horizon: most of the Upper Ndolanya specimens fall within the Höwenegg ellipse (six within, only one above), whereas the Upper Laetolil Beds specimens plot just outside the ellipse. Figure 12.8a is a log10 ratio plot of 1PH III Laetoli *Eurygnathohippus* aff. *cornelianus* (mean) compared to Daka *Eurygnathohippus* aff. *cornelianus* (BOU-VP-12/89; Gilbert and Bernor 2008), Hadar *Eurygnathohippus hasumense* (AL155-6X; Bernor et al. 2005), Lothagam *Eurygnathohippus turkanense* (mean; LTEurturkMean; Bernor and Harris 2003) and Langebaanweg *Eurygnathohippus hooijeri* (mean; SAM_MEAN2; Bernor and Kaiser 2006). The log10 ratio profile of the Laetoli mean is virtually identical to that of the Daka 1PH III (BOU-VP-12/89), supporting our conclusion that they are both members of the *Eurygnathohippus cornelianus* lineage.

Eurygnathohippus hooijeri (SAM_Mean2) is virtually identical to the Daka specimen, except for the slightly elevated maximum length measurement, which is more like the Laetoli EuMean. Hadar *Eurygnathohippus hasumense* is a larger form being the longest of all the sampled 1PH III. Lothagam *Eurygnathohippus turkanense* 1PH III is no longer than the comparative sample, but has a midshaft width (M3), proximal width (M4), depth (M5) and distal articular width measurement virtually identical to *Eu. hasumense*: it is a relatively short, massively built 1PH III. Overall, this plot shows the similarities in the proportions of the Laetoli, Daka and Langebaanweg samples.

Figure 12.8b compares individual specimens of Laetoli *Eurygnathohippus* aff. *cornelianus* first phalanges with the mean of Laetoli *Eu.* aff. *cornelianus*, Daka *Eu.* aff. *cornelianus*, Langebaanweg *Eu. hooijeri* and Laetoli *Equus*. These plots exhibit the striking intrapopulation similarity of all Laetoli

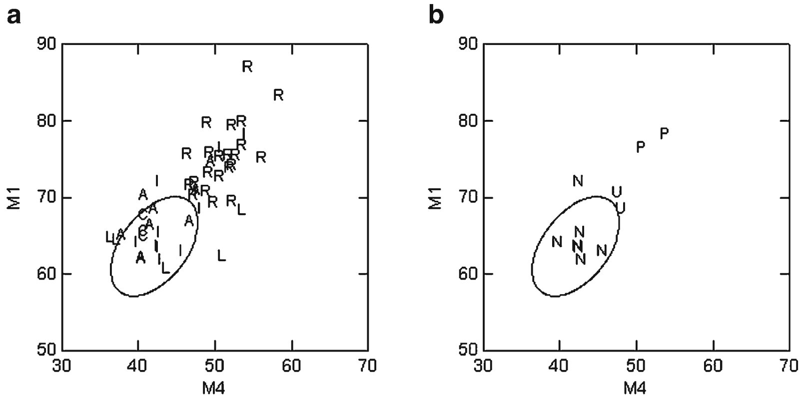

Fig. 12.7 (**a**) Bivariate plot of maximum length (M1) of 1PHIII versus proximal articular width (M4) in African hipparion sample plotted with the Höwenegg ellipse. (**b**) Bivariate plot of maximum length (M1) of 1PHIII versus proximal articular width (M4) in Laetoli sample plotted with the Höwenegg ellipse

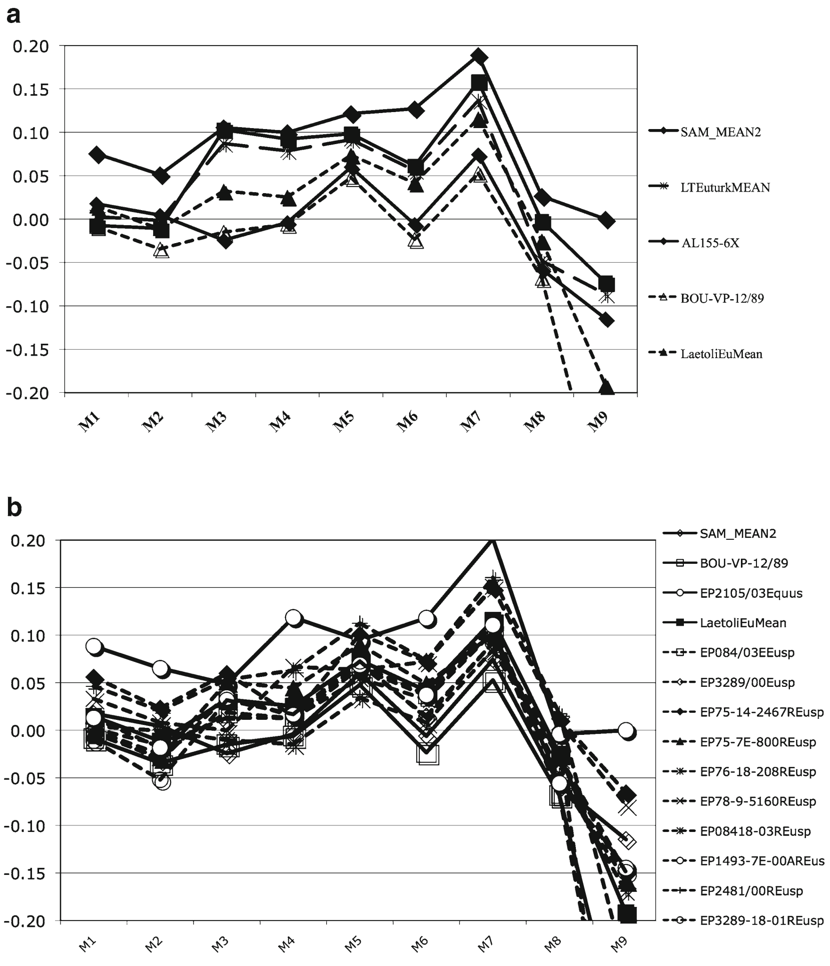

Fig. 12.8 (**a**) Comparison of Laetoli, Langebaanweg, Hadar and Daka *Eurynathohippus* 1 PHIII's (Höwenegg Std.). (**b**) Comparison of Langebaanweg, Daka, Laetoli *Eurynathohippus* aff. *cornelianus* with Laetoli 1PHIII, (Höwenegg Std.)

Eu. aff. *cornelianus,* the close resemblance of Daka *Eu*. aff. *cornelianus* to this sample (albeit at the smaller size of the range), the similar line profile of *Eu. hooijeri* to *Eu*. aff. *cornelianus,* the distinct morphology of Laetoli *Equus* 1PH III, particularly the higher values of maximum length (M1), proximal articular width and distal width measurements (M6 and M7).

Summary of Metrical Results

This analysis supports the conclusion that there are likely three equids from Laetoli: an Upper Laetolil Beds hipparion, which is larger than the Upper Ndolanya Beds form, and *Equus* is identified from Emboremony 2 (Ngaloba Beds). The results from P2 (Fig. 12.1) generally show a great size distribution but, in itself, is not conclusive. The calcanea plots (Fig. 12.2) revealed how much larger the Hadar *Eu. hasumense* was compared to the rest of the hipparion sample. The astragali bivariate plots (Fig. 12.3) revealed larger individuals from the Upper Laetoli Beds and smaller ones, plotting mostly within the Höwenegg ellipse, from the Upper Ndolanya beds. There were no complete MC IIIs from Laetoli, but analyses on proximal articular depth (M6) versus width (M5) dimensions revealed that the Upper Ndolanya beds specimen overlapped the Höwenegg ellipse and intermediate sized Olduvai specimens. Our analysis of MT III bivariate (Fig. 12.5) revealed much the same thing. Our log10 ratio analysis on MT IIIs (Fig. 12.6) revealed that the Laetoli sample was distinct from Olduvai *Equus oldowayensis*, Hadar *Eurygnathohippus hasumense* and is closest in its proportions to Moroccan *Eurygnathohippus pomeli*. The 1PH IIIs again revealed that the Hadar hipparion is distinct in its large size, the Upper Ndolanya Beds hipparion are similar in size to Höwenegg *Hippotherium primigenium*, while the Upper Laetolil Beds specimens are somewhat larger. The 1PH III log 10 ratio diagrams we present here (Figs. 12.8a, and b) overall reveal the close identity of Upper Ndolanya Beds, Daka and Langebaanweg samples. We suggest here that *Eu. pomeli* is possibly the sister taxon of the *Eu. cornelianus* lineage and, these may be related to Langebaanweg *Eurygnathohippus hooijeri* (Bernor and Kaiser 2006).

Description of the Material

Maxillary Teeth

Upper Laetolil Beds

There are a number of maxillary teeth that we have measured and photographed from the Upper Laetolil Beds and we discuss representative samples serially.

LAET 75-1430 is a right P3 with a mesostyle height of 58.1 mm (Fig. 12.9a, b). The labial view (Fig. 12.9a) has the characteristic mesialward slant of a P3, has strongly developed parastyle and mesostyle and both the mesial and distal ectoloph enamel bands are worn blunt, indicative of a diet that was predominantly graze. Occlusally (Fig. 12.9b), there are the following salient features: parastyle is pointed labialward while mesostyle is squared labialward; fossette plications are complex on the mesial and distal borders of the prefossette and the mesial wall of the postfossette, only; pli caballins are double, protocone is elongate, flattened lingually and rounded labially; hypoglyph is deeply incised.

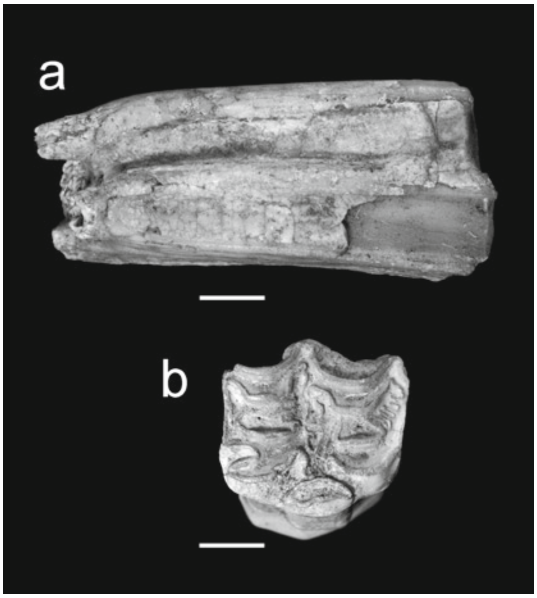

Fig. 12.9 (**a**) LAET 75-1430 rt P3 (*labial* view). (**b**) LAET 75-1430 rt P3 (*occlusal* view). Scale = 1 cm

EP 1494/98 (Fig. 12.10a, b) is a right P4 that is in wear and has a 60.5 mm crown height. Figure 12.10a is a labial view that shows the prominent parastyle and mesostyle. The enamel band ectoloph is absolutely flat mesially, low and rounded distally, suggesting that the individual had a diet that was predominantly composed of graze. Figure 12.10b has an occlusal surface that is worn, but not yet in middle wear, yet the following salient features can be identified: parastyle and mesostyle have pointed aspects labialward; the distal border of the prefossette and mesial border of the postfossette are complex, while their opposing borders are simple; pli caballin is clearly double, protocone is flattened, elongate and is rounded labially and flattened lingually; the hypoglyph is very deeply incised.

LAET 75-2070 is a left M1, in relatively early wear with a mesostyle crown height of 64.4 mm. Figure 12.11a is a labial view that reveals the slight backward slant of an M1 and a mesial ectoloph that is flat and a distal ectoloph that is low and rounded; the wear pattern is typical of a grazer. The occlusal view (Fig. 12.11b) reveals an eroded crown surface with the following salient features: labially squared parastyle and mesostyle; pre- and postfossettes in too early wear to adequately express their plication frequency; pli caballin not preserved; protocone elongate with labially rounded and lingually flattened surfaces; hypoglyph only moderately incised.

LAET 75-3532 is a right M2 that has a mesostyle crown height of 60.2 mm. The labial view (Fig. 12.12a) exhibits the

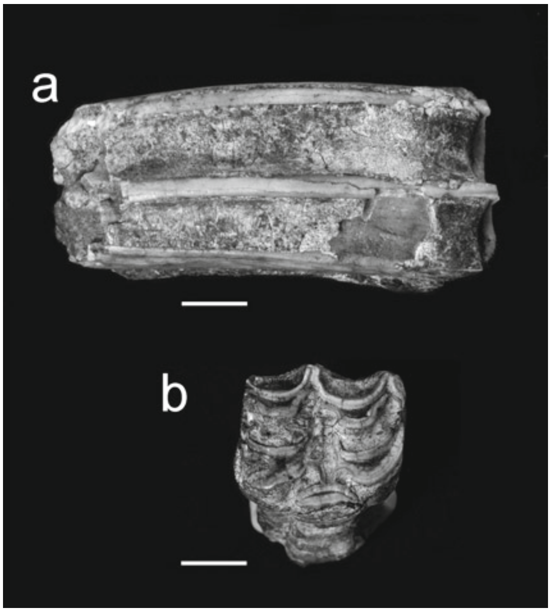

Fig. 12.10 (**a**) EP 1494-98, rt P4 (*labial* view). (**b**) EP 1494-98, rt P4 (*occlusal* view). Scale = 1 cm

Fig. 12.11 (**a**) LAET 75-2070, lt M1 (*labial* view). (**b**) LAET 75-2070, lt M1 (*occlusal* view). Scale = 1 cm

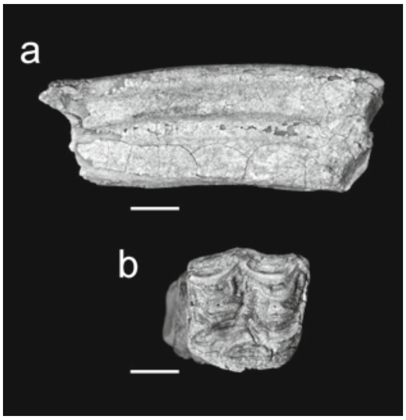

Fig. 12.12 (**a**) LAET 75-3532, rt M2 (*labial* view). (**b**) LAET 75-3532, rt M2 (*occlusal* view). Scale = 1 cm

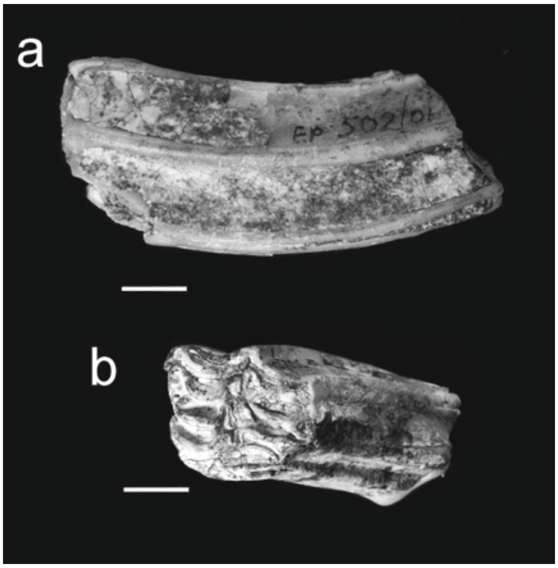

Fig. 12.13 (**a**) EP 502/01, lt M3 (*labial* view). (**b**) EP 502/01 lt M3 (*occlusal* view). Scale = 1 cm

sharp distalward slant typical of the M2 and the ectoloph is worn low and flat mesially and is low and rounded distally. The occlusal surface (Fig. 12.12b) is well worn and exhibits the following salient features: parastyle is pointed labialward while mesostyle is squared labialward; both the mesial and distal borders of the prefossette are complex while on the mesial border of the postfossette is complex; pli caballin is large, but single; hypoglyph is moderately deeply incised; protocone is as in the other maxillary dentition described thus far being elongate with a rounded labial and flattened mesial surface.

EP 502/01 is a left M3 with a mesostyle height of 60.1 mm. Figure 12.13a exhibits the characteristically sharp distalward curvature typical of an M3, the ectoloph mesial enamel band is low and rounded while the distal one is virtually flat as is found in grazers. The occlusal surface (Fig. 12.13b) exhibits essentially the same morphology as is found in other specimens from the Upper Laetolil Beds: parastyle pointed and mesostyle squared labially; the prefossette mesial and distal borders are complex as is the mesial border of the postfossette; pli caballin is weakly double; protocone is elongate being rounded labially and flattened distally; hypoglyph is deeply incised.

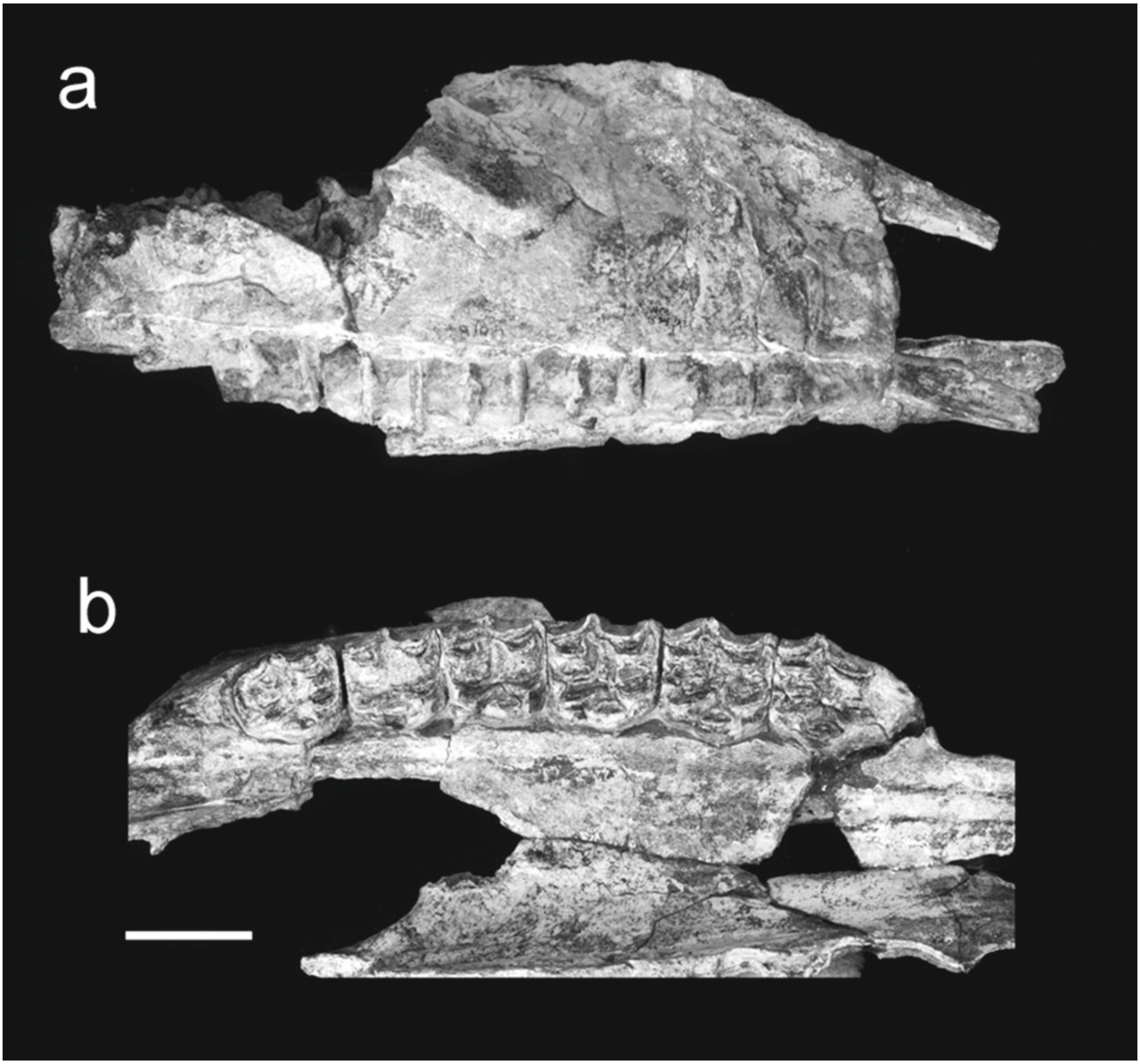

Fig. 12.14 (**a**) WM 1528/92, Beredi 3, Manonga Valley. Lateral view of skull. (**b**) WM 1528/92, Beredi 3, Manonga Valley. *Occlusal* view of P2-M3. Scale = 3 cm

For comparison with the Upper Laetolil Beds, we illustrate here the Beredi 3 skull. Figure 12.14a is a lateral view of WM 1528/92. As with the Upper Laetolil Beds cheek teeth the ectoloph cusps are either flat, low and rounded, or as in the mesial portion of M3 ectoloph actually concave. This morphology is indicative of grazing. Figure 12.14b provides a close-up view of the P2-M3 occlusal surfaces. The poor contrast of this specimen does not allow occlusal details to be exhibited, but the morphology of parastyle, mesostyle, fossettes, pli caballin, protocone and hypocone is essentially identical to the Upper Laetolil Beds hipparion and is undoubtedly closely related or conspecific with that taxon.

Upper Ndolanya Beds

LAET 75-3793 is a left maxillary I3 that is well worn. Both the labial (Fig. 12.15a) and lingual views (Fig. 12.15b) reveal a mesiodistally long (31.2 mm) dimension, with strong lingual grooving and a distinct distal taper. The tooth is derived for a *Eurygnathohippus*, but does not seem as derived as Olduvai Bed II *Eu. cornelianus.*

LAET 75-2458 is an unworn left P2 that preserves too little morphology to warrant description or figuring. There is a worn associated P2 and P3, LAET 78-4872 from Loc. 18, Upper Ndolanya Beds. There are two P4s, EP 986/00 from Loc. 18

Fig. 12.15 (**a**) LAET 75-3793, lt I3 (*labial* view). (**b**) LAET 75-3793, lt I3 (*lingual* view). Scale = 1 cm

Fig. 12.16 LAET 75-1685 lt M1 (*occlusal* view). Scale = 1 cm

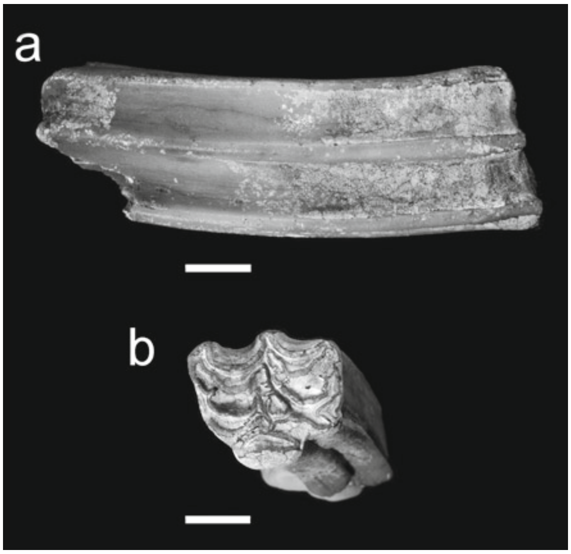

Fig. 12.17 (**a**) LAET 75-1685, lt M2 (*labial* view). (**b**) LAET 75-1685, lt M2 (*occlusal* view). Scale = 1 cm

and EP 1213/03 from Loc. 7E which are too worn for description. A rolled and damaged M1, EP 4008/00 is known from the Upper Ndolanya Beds. The specimen is too damaged to obtain an accurate crown height, but enough is present to state that it is an adult tooth, well in wear with fossette morphology and protocone shape as in other Upper Ndolanya Bed specimens.

There is an associated tooth row LAET 75-1685 from Loc. 14, Upper Ndolanya Beds, comprising left M1, M2, and right M1, M2. These teeth were described by Hooijer (1987b). The teeth are in early to middle wear, they are associated with a lower cheek tooth, (left m1), which by its state of preservation and stage of wear would likely be from the same individual. The left M1 with a mesostyle crown height of 75.0 mm, is the best preserved. As shown in Fig. 12.16, the tooth is well worn despite its relatively high crown height preserving the following salient features: parastyle is pointed labialward while mesostyle is narrow but squared labialward; both the mesial and distal surfaces of the prefossette are complex, while in the postfossette only the mesial side is complex. The pli caballin is single, hypoglyph is deeply incised and protocone is elongate, labially rounded and lingually flattened. The protocone of the left M^1 measures 10 mm anteroposteriorly and 4 mm transversely. The M2 (left) LAET 75-1685 has a mesostyle crown height of 75.3 mm. The labial view (Fig. 12.17a) reveals the strong distal curvature of the tooth, typical for an M2, and the low rounded (mesially) and flat (=blunt, distally) ectoloph enamel band. The occlusal surface is in early wear but reveals some occlusal ornamentation (Fig. 12.17b): the fossettes are not well developed, but the opposing borders of the pre- and postfossette have rich plications coming into wear; the pli caballin is single; hypoglyph is moderately deeply to deeply incised, protocone is elongate, rounded labially and flattened lingually.

The Upper Ndolanya Beds hipparion upper cheek teeth exhibit a number of similarities with the Upper Laetolil Beds although they differ in crown height: the Upper Ndolanya Beds have a higher maximum crown height, which we estimate as being 80 mm (compared to 70 mm in the Upper Laetolil Beds). In this regard, the Upper Ndolanya Beds hipparion resembles the Olduvai species *Eurygnathohippus cornelianus*.

Mandibular Cheek Teeth

Lower Laetolil Beds

There are two mandibular cheek teeth from the Lower Laetolil Beds: EP 035/98 (Fig. 12.18), a left dp4 and EP 032/98 a left p4. Both only preserve the occlusal surfaces well. The dp4 (Fig. 12.18a) is elongate, has a rounded metaconid and distally pointed metastylid, the pre- and postflexids have simple margins, the linguaflexid is broad and the deep protoconid has a flattened enamel band labially and there is a very small, pointed ectostylid. The p4 occlusal surface is well preserved and has a rounded metaconid, distally pointed metastylid; linguaflexid is a deep V-shape, preflexid has relatively simple margins while the postflexid has more complicated margins, pli caballinid is distinct, ectostylid is a distinctly rounded feature on the labial margin of the tooth (Fig. 12.18b).

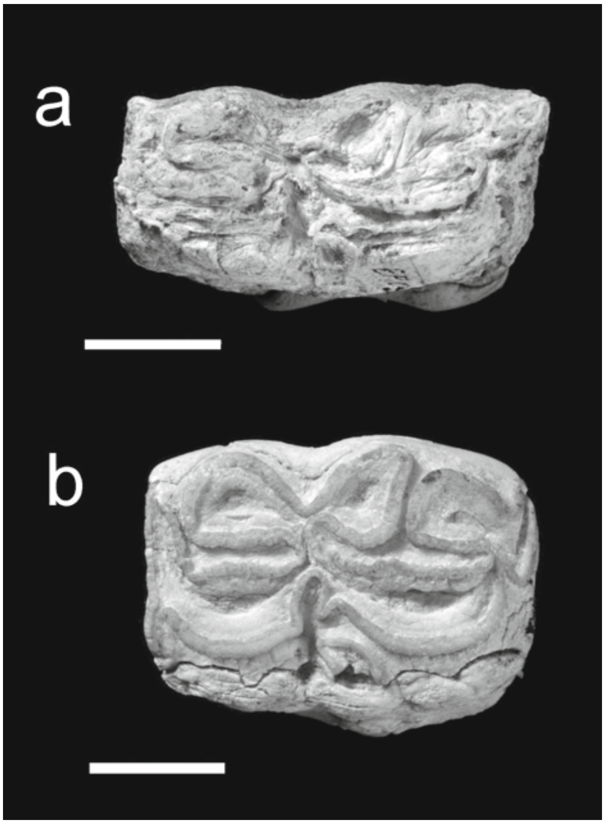

Fig. 12.18 (**a**) EP 035/98, lt dp4 (*occlusal* view). (**b**) EP 032/98, lt p4 (*occlusal* view). Scale = 1 cm

Upper Laetolil Beds

EP 363/98 is a right i2 and i3 from the same individual, extremely worn and in poor condition. The crown height of i2 is 18 mm to the cementum-enamel junction and 12 mm transversely at the occlusal surface. Labiolingual diameter is 13 mm at the occlusal surface. The tooth tapers towards the root, its basal diameters at the enamel junction are 8 mm transversely by 13 mm. This agrees with the incisors of the "Mpesida to Aterir" hipparion as shown by Hooijer (1987a). Mandibular i3 is unreduced unlike *Eurynathohippus*, its mesiodistal diameter is 13 mm and maximum labiolingual diameter is 10 mm at the occlusal surface.

EP 1341/01 is a left i1 (Fig. 12.19a, b). The tooth is long mesiodistally and both margins exhibit distinct, albeit light grooving.

LAET 75-1431 is a left p2 in middle wear. Figure 12.20a is a labial view showing a distinct, albeit slender ectostylid ascending the labial margin of the tooth. The ectostylid is not expressed on the occlusal surface (Fig. 12.20b) due to its relatively early stage of wear (crown height = 31.8 mm). The occlusal surface also exhibits a round metaconid, irregular kidney-shaped metastylid (not uncommon in early wear lower teeth), the linguaflexid is irregularly shaped, preflexid and postflexid have simple margins and the ectoflexid is deeply incised.

There is no p3 from the Upper Laetolil Beds. Figure 12.21 (a and b) are of a right p4, LAET 81-48 with a crown height of 49.6 mm. The labial view (Fig. 12.21a) reveals the straight mesial and distal walls typical of a p4 and a distinct ectostylid that is mesiodistally long at the base and tapers to a shorter length as the feature ascends the labial side of the crown. Figure 12.21b is of the occlusal surface, which includes a kidney-shaped metaconid, distolingually pointed

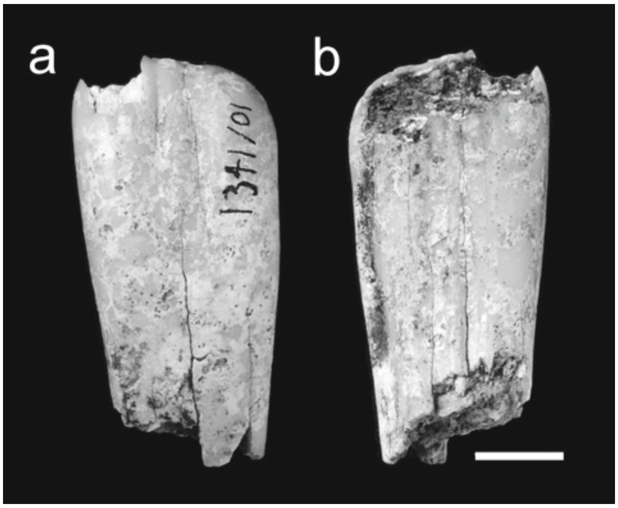

Fig. 12.19 (**a**) EP 1341/01, lt i1 (*labial* view). (**b**) EP 1341/01, lt i1 (*lingual* view). Scale = 1 cm

Fig. 12.20 (**a**) LAET 75-1431, lt p2 (*labial* view). (**b**) LAET 75-1431, lt p2 (*occlusal* view). Scale = 1 cm

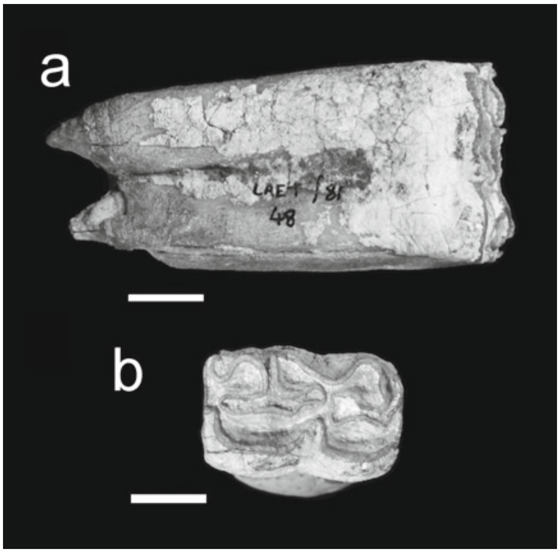

Fig. 12.21 (**a**) LAET 81-48, rt p4 (*labial* view). (**b**) LAET 81-48, rt p4 (*occlusal* view). Scale = 1 cm

metastylid, shallow linguaflexid, preflexid and postflexid with simple margins, ectoflexid deep with a distinct pli caballinid and the ectostylid is not expressed at the occlusal surface.

EP 1242/01 (Fig. 12.22) is a left m3 with a crown height of 68.6 mm. The labial view (Fig. 12.22a) shows the strong curvature of the mesial and distal margins typical of an m3. There is no evidence of an ectostylid in this view. The occlusal surface is worn enough to reveal a kidney-shaped metaconid and square shaped metastylid; linguaflexid is a deep and broad U-shape; preflexid has simple margins and postflexid has slightly complex margins; pli caballinid is distinct; ectoflexid is deep; hypoconulid has a double loop (Fig. 12.22b).

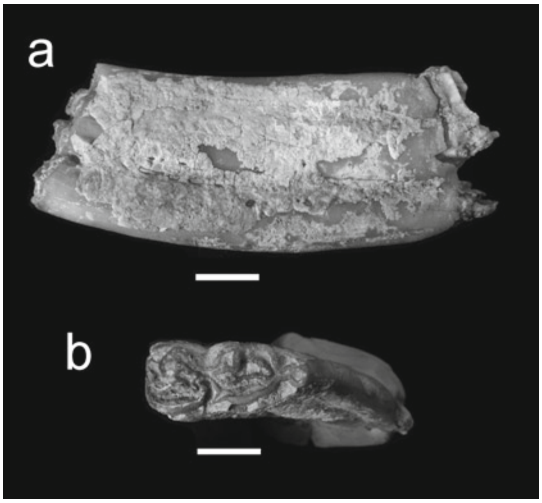

Fig. 12.22 (**a**) EP 1242/01, lt m3 (*labial* view), (**b**) EP 1242/01, lt m3 (*occlusal* view). Scale = 1 cm

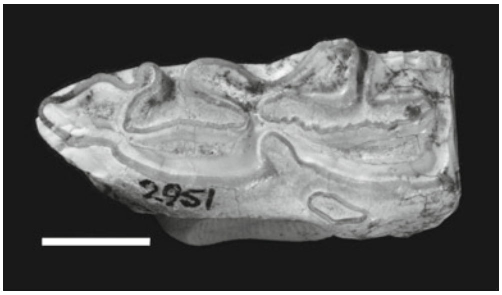

Fig. 12.23 LAET 75-2951, lt dp2 (*occlusal* view). Scale = 1 cm

Upper Ndolanya Beds

LAET 75-2951 is a left dp2 (Fig. 12.23). The crown is short (9.2 mm high) and elongate and preserves the following salient features: metaconid is elongate and metastylid is square-shaped, linguaflexid is a deep, narrow U-shape, preflexid has simple margins whereas postflexid has a finely serrated margin, ectoflexid is shallow and a large oval structure.

LAET 74-253 from Loc. 18 is a mandibular symphysis that bears a canine described by Hooijer (1987a).

LAET 78-4815 is a left mandibular fragment with i1 and p3-m3, the dentition is much worn. Height of incisor crown from occlusal surface to enamel root border is 20.9 mm, width at enamel root junction is 10 mm and labiolingual

Fig. 12.24 (**a**) LAET 78-4815, lt mandible (*labial* view). (**b**) LAET 78-4815, lt mandible (*occlusal* view). Scale = 1 cm

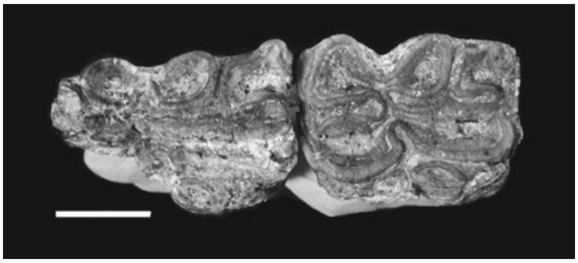

Fig. 12.25 LAET 75-3765, lt p2, p3 (*occlusal* view). Scale = 1 cm

diameter is 14.6 at this point. The labial view (Fig. 12.24a) includes only a little bone that covers p3-m3. Crown height is low on the m1 (33.8), m2 (39.1) and m3 (32.2) due to the advanced age of the specimen. The crown morphologies exhibit deep V-shaped linguaflexids on p3 and p4, deep and broader U-shapes on m1-m3; pre- and postflexids are labio-lingually compressed on p3 and p4, not so compressed on the molars; ectostylids present at the occlusal surface of p2-m3 and are very large on all cheek teeth, pli caballinids are not developed on any teeth and ectoflexid is deep only on the m3 and the m3 has a double hypoconulid. The metaconid and metastylid are somewhat angular, especially the metastylid. Length of tooth row is 158 mm.

LAET 75-3765 is a much worn p2 and p3 (Fig. 12.25). The p2s mesial and mesolabial margins is markedly eroded, however what is significant here is the compressed pre- and post-flexids, shallow U-shaped linguaflexid and very prominent, large, oval ectostylid. The p3 is better preserved and has a very deep U-shaped linguaflexid; pre- and postflexids lacking any complexity, no pli caballinid and a very large ectostylid.

LAET 75-1685 is a left m1 with an ectostylid, which extends up to the occlusal surface. The height of the ectostylid as preserved is 60 mm. There is a protostylid. This is an important specimen because it is one of the few examples of a lower tooth associated with an upper dentition in this taxon.

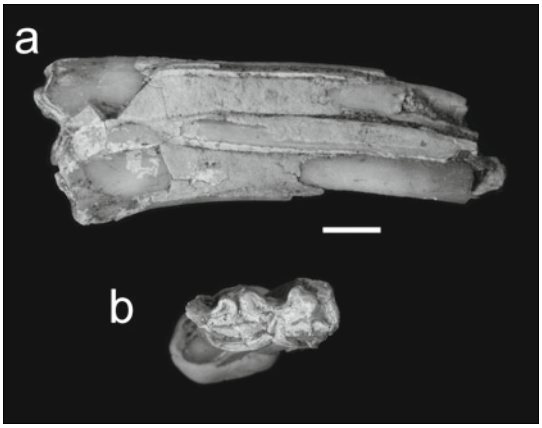

Fig. 12.26 (**a**) EP 1211/03, m2 (*labial* view). (**b**) EP 1211/03, m2 (*occlusal* view). Scale = 1 cm

EP 1211/03 is an early wear m2 with a crown height of 75.1 mm. Figure 12.26a exhibits the very large ectostylid on the labial wall of the tooth. The occlusal view (Fig. 12.26b) reveals that the tooth was in wear and must have been about 80 mm high preserving the following salient features: metaconid irregular shaped and metastylid pointed distally; pre and postflexid is compressed; linguaflexid is a broad U-shape; ectoflexid is deep; pli caballinid is lacking and ectostylid is not expressed on the occlusal surface.

We compare here the Upper Ndolanya Beds mandibular cheek teeth with the following Ethiopian mandibles (Fig. 12.27): Hadar AL 425-1 *Eurygnathohippus hasumense* mandible (Fig. 12.27a, Denen Dora 2, 3.2 Ma); Hadar AL 177-21, paratype of *Eurygnathohippus "afarense"* (Eisenmann 1977; Bernor and Armour-Chelu 1997; Bernor et al., 2010), mandibular symphysis (Fig. 12.27b, Denen Dora 2, 3.2 Ma); the Middle Awash BOU-VP-8-45 mandible (Fig. 12.27c) from the 2.5 Ma horizon (T.D. White, personal communication).

The AL 425-1 right mandible exhibits a number of characteristics common for *Eurygnathohippus hasumense*, and the Upper Laetolil Beds hipparions, metaconid is mostly rounded while metastylid is pointed posteriorly, premolar and m1 linguaflexids are a deep V-shape, while m2 is a deep U-shape. The AL 425-1 mandible is of an early adult stage-of-wear and the ectostylids are not well developed, nor is the i3 (only remaining incisor) fully erupted and in wear. The lack of ectostylid development in this specimen is due to its age, only, in that the ectostylid does not ascend to occlusal level in young adults. The cheek teeth do have the characteristic strongly developed pli caballinid typical of *Eu. hasumense.* AL 177-21 was referred to *Eurygnathohippus afarense* by Eisenmann (1977) based on its large incisors, but this was questioned by Bernor and Armour-Chelu (1997) and Bernor et al. (2010). Recently, Eisenmann and Geraads (2007) suggested that this specimen be reassigned to *Eurygnathohippus hasumense*.

Fig. 12.27 (**a**) AL 425-1 *Eu. hasumense* mandible from Denen Dora. (**b**) AL 177-2 *Eu. afarense* mandible paratype (Eisenmann 1977). (**c**) BOU-VP-8-45 mandible, Middle Awash. Scale = 5 cm

It may, in fact be referable to that taxon. What is important here is the large size of the erupted left i1-i2 and right i2. Mandibular i3 is in eruption, but would not have been very large when at full height. The symphysis is not mesiodistally strongly expanded as seen in *Eurygnathohippus cornelianus*. Hadar *Eurygnathohippus hasumense* mandibular tooth morphology compares well with the Upper Laetolil Beds cheek teeth and has a comparable maximum crown height of around 70 mm (Bernor et al., 2010). It also compares well with Upper Ndolanya Beds worn adult mandible LAET 78-4815 (see Fig. 12.24b).

The Middle Awash BOU-VP-8-45 mandible (Fig. 12.27c, 2.5 Ma) is slightly younger than the Upper Ndolanya Beds hipparion and is advanced in its morphology. It would appear to be of a young adult individual. The mandible is very deep, indicating advanced high crown height. The p3-m2 have elongate and narrow occlusal outlines, very broad and deep U-shaped linguaflexids, metaconids and metastylids that are sharply pointed lingualward and large (albeit broken) ectostylids. Upper Ndolanya Beds mandible fragment LAET 75-3765 (see Fig. 12.25), has large ectostylids on the p2 and p3, and a very deep linguaflexid on the p3. The Upper Ndolanya Beds EP 1211/03 right m2 exhibits the advanced characters seen in the BOU-VP-8-45 mandible, including: broad U-shaped linguaflexid, lingual pointing of the metaconid and metastylid and a large ectostylid.

Eisenmann and Geraads (2007) recently described a large, well-preserved sample of hipparion, *Eurygnathohippus pomeli* (*sensu* Bernor et al. 2010) from the 2.5 Ma Ahl al Oughlam fissure fills, Morocco. The mandibular material (Eisenmann and Geraads 2007, fig. 8) exhibits critical morphological features shared by the Upper Ndolanya and 2.5 Ma Middle Awash BOU specimens, most prominent being the large ectostylids, deep linguaflexids and propensity to have pointed metaconids and metastylids, particularly on the molar dentition. These features are likewise shared by the

Daka *Eurygnathohippus* cf. *cornelianus* from Ethiopia (Gilbert and Bernor 2008, figs. 6–19). We follow Bernor et al. (2010) in recognizing the increasing likelihood that these late Pliocene-Pleistocene taxa are closely related to one another.

Postcrania

We have described the size and proportions for astragali, calcanea, MC III, MT III and 1PH III in the statistical analysis. There is nothing further to add here for the astragali and calcanea because there are no discrete morphological characteristics by which they differ between stratigraphic levels at Laetoli and other Pliocene African hipparions that we have studied or have been reported by others. We do develop, albeit briefly below, some aspects of MP III and 1PH III morphology.

As noted earlier in the statistical summary we have no complete MC IIIs from Laetoli. The plots of proximal MC III width (M5) versus depth (M6) revealed an overlap in the Upper Laetolil and Upper Ndolanya Bed sample, but with most Upper Ndolanya specimens being smaller than the Upper Laetolil sample. Moreover, the Upper Ndolanya specimens are similar in size to the Höwenegg, Langebaanweg, and Manonga Valley specimen and some Olduvai specimens. The Upper Laetolil specimens overlap with the smaller specimens from Hadar. Figure 12.28 includes two specimens from the Upper Laetolil Beds (Fig. 12.28a, LAET 75-3138; Fig. 12.28b, LAET 75-2250) and the Upper Ndolanya Beds (Fig. 12.28c, EP 026/00; Fig. 12.28d, EP 927/00). All four specimens are similar in the extensive development of the magnum–hamate facet indicating well developed functional tridactyly. The two specimens from the Upper Ndolanya Beds do have a broader caudal articular surface than the two from the Upper Laetolil Beds. Whether this is a consistent and species-level difference has yet to be determined.

There is a single complete MT III from Laetoli, LAET 75-2471 from the Upper Ndolanya beds (Fig. 12.29a, b), and we compare it here to a Hadar MT III from the AL 155 skeleton collected from Denen Dora 2 (3.2 Ma; AL 155-6AZ, Fig. 12.29c, d). The bivariate plot comparisons (see Fig. 12.5a) and log 10 ratio comparisons (see Fig. 12.6b) clearly reveal that the Hadar specimen is much longer and the mid-shaft dimension is greater in the Hadar specimen than the Upper Ndolanya Bed specimen, but their basic proportions are otherwise very similar. Both the Laetoli and Hadar MT IIIs have prominently developed distal sagittal keels and distal epicondylar eminences, suggesting an adaption for open country running (Bernor et al. 2005). Interestingly, the MT III mean measurement of the Moroccan 2.5 Ma *Eurygnathohippus pomeli* (AaO) has an overall shape and proportion closer to the Upper Ndolanya Beds MT III than the Hadar hipparion (see Fig. 12.6b), and in turn, the Upper Ndolanya MT III compares closely with both the Daka (BOU-VP-13) and Olduvai *Eurygnathohippus cornelianus* mean measurements. These results suggest that the Upper Ndolanya Beds hipparion, the Moroccan mid-Pliocene hipparion and *Eurygnathohippus cornelianus* are potentially related and distinct from the *Eurygnathohippus hasumense* lineage.

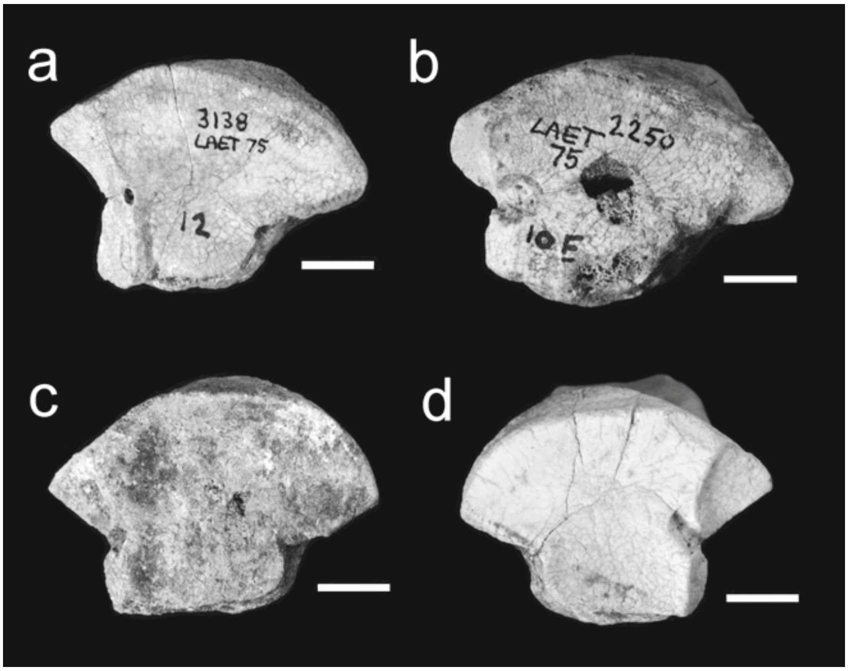

Fig. 12.28 (**a**) LAET 75-3138, proximal MCIII showing magnum-hamate facet from Upper Laetolil Beds. (**b**) LAET 75-2250, proximal MCIII showing magnum-hamate facet from Upper Laetolil Beds. (**c**) EP 026/00, proximal MCIII showing magnum-hamate facet from Upper Ndolanya Beds. (**d**) EP 927/00, proximal MCIII showing magnum-hamate facet from Upper Ndolanya Beds. Scale = 1 cm

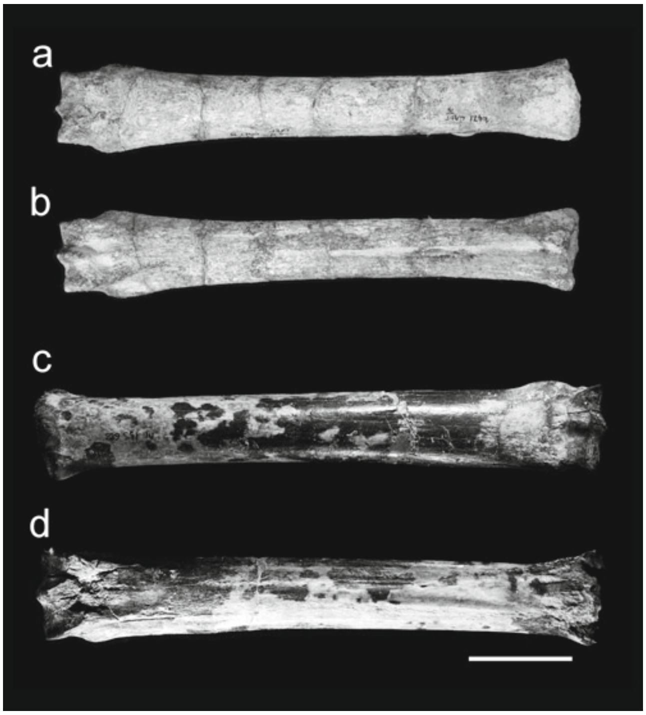

Fig. 12.29 (**a**) LAET 75-2471 MTIII (*anterior* view). (**b**) LAET 75-2471 MTIII (*posterior* view). (**c**) AL 155 MTIII (*anterior* view) Denen Dora. (**d**) AL 155 MTIII (*posterior* view) Denen Dora. Sacle = 5 cm

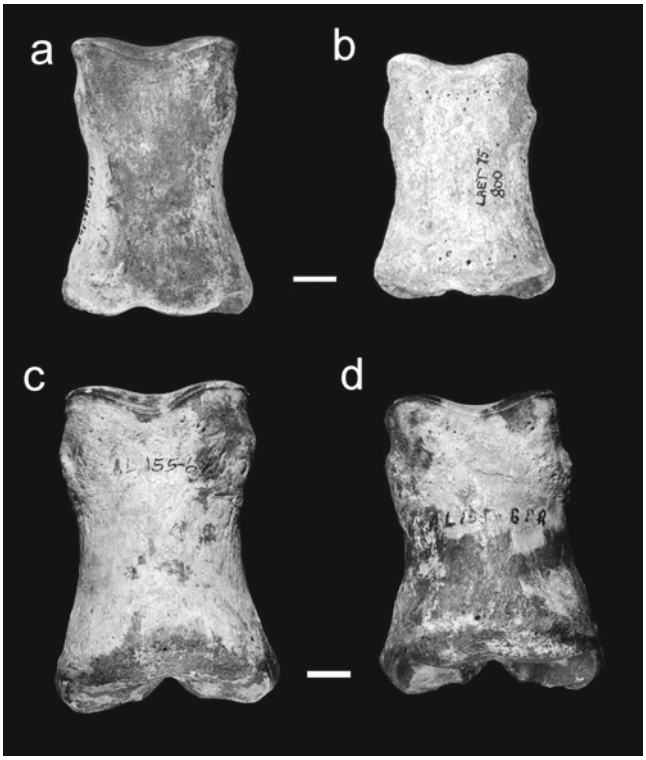

Fig. 12.30 (**a**) EP 3281/01, 1PHIII, Upper Laetolil Beds. (**b**) LAET 75-800 1PHIII, Upper Ndolanya Beds. (**c**) AL 155-6 X 1PHIII fore, Hadar. (**d**) AL 155-6 AA 1PHIII hind, Hadar. Scale = 1 cm

1PH III – Cranial and Caudal Comparisons

1PH IIIs reveal a similar pattern to the metapodials. Figure 12.30 includes four 1PH IIIs: EP 3281/01 (Fig. 12.30a, Upper Laetolil Beds), LAET 75-800 from 7E (Fig. 12.30b, Upper Ndolanya Beds) and AL 155-6 (6-AA is Fig. 12.30c and 6X is Fig. 12.30d). All four of these have the same basic morphology although they are of variable length. Figures 12.7a, b reveal that both the Upper Laetolil and Upper Ndolanya specimens are consistently smaller than those from Hadar. The log10 ratios diagrams show that the Hadar hipparion is longer than the Laetoli *Eurygnathohippus* mean, Langebaanweg and the Daka specimen (BOU-VP -12/89). An interesting point is that the AL 155 fore and hind phalanges show variation in length with AL 155-6AA being distinctly shorter (hind) than AL 155-6X (fore). The same proportional differences are found between the Upper Laetolil specimen (Fig. 12.30a) and Upper Ndolanya specimen (Fig. 12.30b). Finally, the bivariate plot of Laetoli 1PH III maximum length (M1) versus proximal articular width (M4, Fig. 12.7b) reveals that five Upper Ndolanya specimens lie in the middle of the Höwenegg ellipse, while one is distinctly above the ellipse, being somewhat longer. It is possible that these advanced Pliocene African hipparions are exhibiting differences in anterior versus posterior length as in extant *Equus*. Too little data exists to support this contention at this time.

Later Material

Equus from Emboremony 1 and 2 (Ngaloba Beds)

A few postcranial bones from Emboremony 1 and Emboremony 2 (Ngaloba Beds), dating to about 200 ka, can be referred to *Equus* sp. First phalanges EP 367/99, EP 2105/03, EP 351/99 are at the lower end of the range for *E. oldowayensis* and also overlap in size with *E. burchellii* (M1 greatest length 76–78 mm).

Systematics

EQUIDAE Gray, 1821
Eurygnathohippus van Hoepen, 1930

Generic Diagnosis: All African hipparions of the genus *Eurygnathohippus* are united by the synapomorphy of ectostylids on the permanent cheek teeth. Eurasian and North

American hipparions do not have this character, except rarely in extremely worn hipparion teeth from the Dinotheriensandes. Within *Eurygnathohippus* species crown height increases and ectostylid length, width and maximum height increase from older to younger stratigraphic horizons.

Eurygnathohippus cornelianus van Hoepen, 1930
The type specimen of *Eurygnathohippus cornelianus,* (COR 556), consists of a mandibular symphysis and associated lower incisors from Cornelia, South Africa, (van Hoepen 1930), and dated to around 900 ka. The type represents one of the latest specimens known of this taxon and may show some morphological advances over the earlier representatives from East Africa. The holotype of *Eu. cornelianus* is essentially defined by a set of lower incisors without any associated lower cheek teeth or upper dentition. Further material from the type locality described as *Eu. steytleri* may derive from the same taxon (Hooijer 1975).

Eurygnathohippus hasumense Eisenmann, 1983
Hipparion hasumense was first described from a lower tooth row (KNM-ER 2776) from Area 204 below the Hasuma Tuff in zones B and C of the Kubi Algi Formation (Eisenmann 1983). The Hasuma Tuff has a K–Ar date of 2.82 Ma, and is thus correlated with the early part of Member C of the Shungura Formation. It is also identified from zone A of the Kubi Algi Formation and the *Notochoerus scotti* zone, which lies below the KBS Tuff at Koobi Fora. Cranial remains from Hadar originally assigned to *Hipparion* sp. (AL 340-8, AL 116-115) are now also referred to this taxon (Eisenmann and Geraads 2007). AL 177-21 from the Denen Dora member, Hadar is the type specimen for *H. afarense*, and now referred to *Eu. hasumense* (Bernor and Armour-Chelu 1999; Eisenmann and Geraads 2007).

Eurygnathohippus hasumense is a large bodied taxon, especially individuals from the Hadar Formation, where its maximum size is documented. Individuals from the Turkana area, Laetoli and Manonga Valley are 10% smaller in postcranial dimensions, but larger than average upper cheek teeth from Laetoli are known from Locs. 1, 2, 9 and 12E (between Tuffs 5 and 8).

The muzzle is long and narrow (Eisenmann and Geraads 2007). Eisenmann (1983) found that the third and fourth lower premolars are notably larger than the first and second molars in this taxon. In Eisenmann's type specimen the cheek teeth are rather narrower than found in the Omo B11 (L1-40) mandible or Laetoli specimens, but are otherwise similar. In the material from Koobi Fora the lower cheek teeth usually possess ectostylids, which taper apically and are more visible in worn teeth. Forsten (1996) observed that the teeth from the lower Koobi Fora Formation resemble the large teeth from Vogel River, which lack or have small ectostylids and teeth from Members B and C of Shungura Formation identified as *Hipparion* sp.

VO MB 9/10 38 is a mandibular symphysis with the first incisors from Vogel River (synonymous with the Garusi River) attributed by Dietrich (1942) to *Hypsohipparion albertense*. The third incisors are missing, but were originally present and it is not *Eurynathophippus cornelianus* (Dietrich 1942, Plate 16).

Eurygnathohippus aff. *hasumense*
Upper Laetolil Beds. Differs from Hadar in relatively smaller size, less robust MP IIIs and 1PH IIIs than Hadar, smaller, less well-developed incisors, not as hypertrophied and lacking as strong labial and lingual grooving. The upper incisor arcade is more rounded and incisors of more equal mesiodistal length compared to *Eu. cornelianus*. Similar to Hadar hipparion in skull and cheek tooth morphology. Lower premolars larger than molars, as reported by Eisenmann (1983) for the type material of *Eu. hasumense*, and like Hadar in not having as well developed ectostylids, which are variably present in the Laetoli population. Pli caballinid (called the ptychostylid by Hooijer) is present in lower cheek teeth (Hooijer 1987a). Metaconid and metastylid somewhat angular. This species is similar to Moroccan *Eu. pomeli* in its MTIII proportions.

Eurygnathohippus aff. *cornelianus*
The Laetoli sample of *Eu.* aff. *cornelianus* is similar in cheek tooth crown height and MC III, MT III and 1PH III dimensions to *Eu.* aff. *cornelianus* from Daka and in postcranial proportions to *Eu. cornelianus* from Olduvai. Crown height in Olduvai Bed IV hipparions approaches 90 mm, whereas in Bed II, as well as in the Upper Ndolanya Beds they are approximately 80 mm. The length of the lower cheek tooth row is 158 mm in LAET 78-4815, (Loc. 18), and similar or slightly shorter than found in *Eu. hasumense* (161 mm) in AL 177-21 (Eisenmann 1976) and 169 mm in LAET 74-491 from Loc. 11, Laetoli. The length of the premolar row is around 75 mm and approximately of subequal length with the molar row. Eisenmann (1983) notes that the premolars are relatively small. Metaconids and metastylids often have a rounded morphology and the longitudinal enamel crests of the preflexid and postflexid are often rather straight, described as the "caballoid" condition (Forsten 1996).

Discussion

One of the points of difference between *Eu. hasumense, Eu. turkanense, Eu.* aff. *hasumense* and *Eu. cornelianus* is the degree of hypsodonty of the incisor teeth (Hooijer 1975), although mesiodistal dimensions of the occlusal surface of lower first and second incisors are similar. We do not have measurements for unworn upper incisor teeth of *Eu.* aff. *hasumense.* However, LAET 75-3473, I1 has a mesiodistal length of 18 mm and a height of 25 mm (Hooijer 1987a).

Hooijer (1987a) notes the similarity between this incisor and those found in the type skull of *Eu. turkanense* and the same dimensions in the I2 of the WM 1528/92 skull are 18 mm at a height of 39 mm.

Hooijer (1975) reports a maximum height of 80 mm in a relatively unworn first upper incisor BK II, 264 of *Eu. cornelianus* (measured along the curvature of the tooth). The mesiodistal length is unknown in this specimen, but in the associated I2 it is 22 mm.

The Olduvai series described by Hooijer (1975) gives the range of dimensions of the occlusal surfaces of the incisor teeth from early to late wear stages. Mesiodistal dimensions of upper first and second incisors ranges between 17 and 22 mm (Hooijer 1975), whilst the maximum mesiodistal length of *Eu. hasumense* I2s is 18 mm.

The morphology of incisors attributed to *Eu. hasumense* also differs from the condition found in *Eu. cornelianus*. In *Eu. hasumense* the crown of the incisors tapers to the tooth root, whereas in *Eu. cornelianus* they are relatively broader at the cementum–enamel border. *Eurygnathohippus cornelianus* typically has broad ridge along the labial surface of the upper first incisor, but this feature is also found in some *Eu. hasumense* material.

The height of the i2 in *Eu. hasumense* (AL 155-6), a young adult, is 49 mm (Eisenmann 1976). The mesiodistal dimensions of the first and second lower incisors of *Eu. hasumense* (AL 177-21), which is also a young adult are 18 mm for i1 and 23.5 for i2 (Eisenmann 1976), similar to the mesiodistal length of 21 mm in the i2 from Manonga Valley (WM 1470/92), compared with 21 mm in an unworn i1 of *Eu. cornelianus* from Olduvai, (SHK II, 749).

Dimensions of the Upper Ndolanya lower incisors appear slightly smaller than the material described by Hooijer (1975) from Bed II, Olduvai, but the Laetoli sample are largely derived from old animals where the crown height does not exceed 25 mm.

The sequence of hipparion remains from Laetoli is important in that it documents the replacement of *Eu.* aff. *hasumense* with fairly hypsodont cheek teeth and variably present ectostylids, (usually more evident in the later tooth wear stages), by an early member of the *Eu.* aff. *cornelianus* lineage. The cheek teeth of *Eu.* aff. *cornelianus* are more hypsodont although slightly smaller than *Eu.* aff. *hasumense* and have well developed ectostylids which are consistently present throughout the population.

The earliest occurrence of *Eu.* aff. *cornelianus* appears to be the Upper Ndolanya Beds at Laetoli, which is interesting in the regard that this immediately postdates an intense climatic drying phase at around 2.8 Ma. During the 2–1 million year interval the taxon is widely represented throughout East Africa, (Daka and the Omo Valley, Ethiopia; Olorgesaillie, Kenya; and Olduvai Gorge, Tanzania). Its last reasonably well calibrated occurrence is in eastern Africa at 900 ka and at Olduvai, Bed IV. There may be later occurrences in South Africa (for type site Uitsoek, Cornelia dated between 1.0 and 0.6 Ma), but these are not well calibrated (Bernor et al. 2010).

Despite some similarities between *Eu. cornelianus* and *Eu. hasumense* such as grooving on incisor teeth, some reduction in the size of the lower third incisor, relatively hypsodont cheek teeth, *Eu. cornelianus* is not likely descended from *Eu. hasumense*. In *Eu. hasumense* the proportions of the postcrania are dissimilar to *Eu. cornelianus* and are more derived. The proportions of limbs may suggest a closer affinity to *Eu. hooijeri* from Laangebaanweg (Bernor and Kaiser 2006), which also shows advances in the degree of hypsodonty and ectostylid development.

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Chapter 13
Suidae

Laura C. Bishop

Abstract This contribution discusses over 200 suid specimens recovered from Laetoli by the Eyasi Plateau Paleontological Expedition (EPPE) between 1998 and 2005. Earlier collections from the site included just three taxa, *Notochoerus euilus* and *Potamochoerus porcus* from the Laetolil Beds, and *Kolpochoerus limnetes* (= *heseloni*) from the Upper Ndolanya Beds. In addition, the more recent collections establish the presence of *Nyanzachoerus kanamensis* and *Notochoerus jaegeri* in the Laetolil Beds and extend the range of *Kolpochoerus heseloni* into this earlier geological unit. *Potamochoerus* material from the Upper Laetolil Beds has been assigned to *P. afarensis*. *Metridiochoerus andrewsi* is present in the Upper Ndolanya Beds. The suid fauna can now be shown to be taxonomically similar to that from other comtemporaneous sites. The autecology of the suid taxa from Laetoli has implications for the paleoenvironmental reconstruction of the site, and suggests that a range of environments were present in the region.

Keywords Suids • Laetoli • Pliocene • *Notochoerus euilus* • *Potamochoerus porcus* • *Kolpochoerus limnetes* • *Nyanzachoerus kanamensis* • *Notochoerus jaegeri* • *Metridiochoerus andrewsi*

Introduction

Suid fossil remains collected by the Eyasi Plateau Paleontological Expedition (EPPE) between 1998 and 2005 are discussed here with special attention paid to those from the Laetolil Beds. Continued research by that project greatly increased both the number of specimens and of species of pig that are now known from Laetoli. As was the case for the previous major study of suids from this locality (Harris 1987) most of the fossil remains are fragmentary. Thus the discussion of them here does not present new taxonomic observations, but rather describes the new specimens and how they change the perception of variability in the suid fauna from the site. Suid representation at different localities and over the time range of the Laetolil Beds (~4.4–3.6 Ma) and Upper Ndolanya Beds (~2.66 Ma) can help to examine paleoecology and paleoenvironments at Laetoli.

Harris (1987) observed the apparent absence of *Nyanzachoerus kanamensis*, a taxon commonly recovered from African Pliocene sites of similar age to the Laetolil Beds, such as Kanam, the Chemeron Formation of the Tugen Hills, and Kanapoi. This suid can now be demonstrated to be present, as the increased sample now includes several specimens that can be attributed to this taxon. The present study also identifies both *Notochoerus jaegeri* and *Kolpochoerus heseloni* from the Laetolil Beds, the former from the lower unit and the latter from the upper unit. The identification of these taxa presents a slight dilemma in that it somewhat reduces the perceived uniqueness of the Laetoli fauna, which previously had seemed taxonomically impoverished relative to sites of similar age. The large faunal sample collected since 1998 has increased our understanding of Laetoli and of the time period during deposition. Since the taxa vary in their distribution in time and space at Laetoli, the suid fauna presents an opportunity to examine the paleoecology of the site, and re-examine the extent to which this fauna is unique amongst contemporary sites.

Materials and Methods

Over 200 suid specimens have been collected by the Eyasi Plateau project in successive field seasons. These complement the samples previously collected and described by Harris (1987). The current sample is housed in the National Museum of Tanzania in Dar es Salaam. It consists largely of fragmented specimens and isolated teeth. There are a few gnathic fragments that contain fragmentary partial dentitions. Only 31 specimens were sufficiently well preserved to allow their identification to species following the taxonomic

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framework of Harris and Liu (2007). Twenty-one specimens were complete enough to measure using the scheme of Harris and White (1979). Luckily our knowledge of the suid fauna from other African paleontological sites of this time period is quite good, so it is easier to ascribe even fragmentary specimens to taxa with some level of confidence when there are diagnostic features preserved.

Systematic Paleontology

Family Suidae Gray, 1821
Subfamily Tetraconodontinae Lydekker, 1876

The Suidae from Laetoli represent two subfamilies, the Suinae and the Tetraconodontinae, the latter of which is extinct, but by far dominates the Laetoli assemblage. Tetraconodontinae are an archaic subfamily of pigs, with a distribution in the later Miocene of Africa, Asia and Europe. They can be identified by their relatively large third and fourth premolars, amongst other features. The later forms of African tetraconodonts, belonging to the genus *Notochoerus*, have secondarily reduced the size of the third and fourth premolars, but otherwise greatly expanded the breadth of their muzzles and the length of their cheektooth rows. This last has been accomplished by elaboration of the length and complexity of the third molars, and in later *Notochoerus* (although not usually *No. jaegeri*) by expansion of the second molar, particularly in inflation of the anterior and posterior cingula. *Nyanzachoerus* cheekteeth have relatively thick enamel, and when the cusps of the molars are worn, they expose dentine lakes that have a characteristic star-shaped appearance. *Nyanzachoerus* teeth are relatively bunodont and brachydont; their third molars have little pillar differentiation throughout the length of the tooth. In *Notochoerus*, worn lower molars have dentine lakes that appear to be H-shaped. Their third molars are hypsodont and can be greatly elongated by the addition of numerous talon/id pillar pairs, especially in the most derived species of this genus.

Three species of tetraconodont pig can be recognized from the Laetolil Beds – *Nyanzachoerus kanamensis*, *Notochoerus jaegeri*, and *Notochoerus euilus*. Previous collections contained just one species, *No. euilus*. The genus *Nyanzachoerus*, which was not known from the earlier collections from Laetoli, can now be demonstrated to be present. Two species of its descendant taxon, *Notochoerus*, are present in the Eyasi Plateau project assemblage: *Notochoerus jaegeri*, not known from earlier collections, and its daughter species *No. euilus*, which remains the most numerous suid from the Laetolil Beds (Harris 1987).

Genus *Nyanzachoerus* Leakey, 1958
Species *Nyanzachoerus kanamensis* Leakey, 1958

Holotype: M15882, a partial left mandibular corpus from Kanam, Kenya housed at the Natural History Museum, London.
Laetoli localities: Locs. 3, 7, 9, 13, 15
Laetoli time range: Upper Laetolil Beds, between Tuffs 7 and 8, with possible occurrences above Tuff 5, but not earlier.

Nyanzachoerus kanamensis is a derived species of *Nyanzachoerus*. Its dentition is large and massive, but there is relatively little expansion of the postcanine tooth row. The third and fourth premolars are very large, if less massive than in *Ny. syrticus*. The third molar is expanded and relatively hypsodont for this genus, with separated cusps that have a more pillar-like form. The exterior of these pillars have a simple star shape when viewed from the occlusal surface, and when the tooth is worn the exposed dentine lakes have this appearance.

Nyanzachoerus kanamensis is present in several of the later horizons of the Laetolil Beds, but there are only a few specimens and they are fragmentary. It is represented by two partial right M3s, EP 649/04, from Loc. 3, and EP 2282/00 from Loc. 7, both from the Upper Laetolil Beds between Tuffs 7 and 8. Both specimens have thick enamel and are relatively low-crowned, with a well-developed talon, the pillars of which are at the same crown height as those of the trigon. Molar fragments EP 1101/98 from Loc. 9, EP 2118/00 from Loc. 13 and EP 1436/98, from Loc.15 show *Ny. kanamensis* patterns of crown height, molar morphology and pillar shape, but are relatively fragmentary and can only give the possibility that this taxon is present at these localities, which are lower in the stratigraphic sequence than the more definite specimens listed above.

Nyanzachoerus kanamensis is thought to have preferred woodland or intermediate habitats on the basis of its postcranial ecomorphology (Bishop 1994; Bishop et al. 1999). At least in the later part of their temporal distribution, they were browsers to mixed feeders (Harris and Cerling 2002). It is a common suid elsewhere in Africa during its documented temporal range, so its apparent absence from earlier Laetoli collections had presented a conundrum. Since the then prevailing view of Laetoli habitats was that they were relatively dry and sparsely vegetated (see Andrews and Bamford 2008) the absence of *Ny. kanamensis*, in combination with what we know of their paleoecology, could be used to bolster this interpretation of Laetoli paleoenvironments as being similar to their present-day condition. Thus, the demonstrable, if somewhat rare, presence of *Ny. kanamensis* can contribute to a building consensus that Laetolil Beds environments may have been both more variable, and more densely vegetated, than previously thought.

Genus *Notochoerus* Broom, 1925

The type species of *Notochoerus* is one of the most derived examples of the genus, *Notochoerus capensis* Broom, 1925.

The taxon was originally described based on South African material, but once recognized has been identified in deposits from all over the continent. *Notochoerus* is large-bodied, with an evolutionary reduction in the primarily enlarged third and fourth premolars otherwise typical in tetraconodonts. They had long and massive heads and relatively broad snouts, with long, horizontally projecting sabre-shaped canines in the lower jaw. The genus is characterized by increased length, complexity and hypsodonty of the third molar crown through time. The lateral pillar pairs of the third molar can be relatively isolated. They have invaginations in the enamel on the mesial and distal aspects of each pillar, with the appearance of H-shaped dentine lakes resulting from wear.

The examples of *Notochoerus* from Laetoli are from the earlier, less derived species of the genus: *No. jaegeri* and *No. euilus*. As was the case for *Nyanzachoerus kanamensis*, most of the *Notochoerus* remains are highly fragmentary and consist largely of isolated teeth and tooth fragments.

Species *Notochoerus jaegeri* (Coppens, 1971)

Holotype: Partial mandibular corpus with p2-m3 from Hamada Damous, Tunisia, housed at the Muséum National d'Histoire Naturelle, Paris.

Laetoli localities: Locs. 9S, 10W and Kakesio 4

Laetoli time range: Lower Laetolil Beds and Upper Laetolil Beds below Tuff 2.

The hypodigm of *No. jaegeri* was originally assigned to the genus *Nyanzachoerus*, from which all *Notochoerus* doubtless descend. Later studies of the more complete specimens from Lothagam and Kanapoi identified features that suggested the placement of the species *jaegeri* in the more derived genus *Notochoerus* (Harris and Leakey 2003; Harris et al. 2003). These features include the broader and deeper mandibular symphysis and a reduction in the size of the posterior premolars. *Notochoerus jaegeri* third molars are more derived than in earlier *Nyanzachoerus*. They are hypsodont and lengthened through the addition of talon/id pillars, most of which are the full trigon/id occlusal height of the tooth. The third molars have pronounced invagination of the enamel on the lateral tooth pillars; this gives the cusps and dentine lakes a more complex star-shaped appearance, particularly on the M3.

The remains of *No jaegeri* from Laetoli are fragmentary and rare. They only occur early in the sequence – in the Lower Laetolil Beds and below Tuff 2 in the Upper Laetolil Beds. Measurements of some of the more complete specimens attributable to this species are given in Table 13.1. One example of the taxon is EP 043/98, a right M3 fragment from the Lower Laetolil Beds at Kakesio 4, with moderate crown height development, some major and minor pillars and, although unworn, star-shaped cusp appearance (Fig. 13.1). EP 608/98, a right M3 fragment from below Tuff 2 of the Upper Laetolil Beds at Loc. 10W shows similar characteristics (Fig. 13.2). This specimen is in light wear and shows the complex, star-shaped enamel lakes that are typical of this species. It is relatively hypsodont and has several accessory pillars on the buccal side of the tooth. EP 1020/98, a third molar from Loc. 9S, below Tuff 2 of the Upper Laetolil Beds, is a relatively long, narrow tooth, which shows the cusp morphology and relatively lower crown height that suggest it represents this species rather than the more derived *No. euilus*.

Table 13.1 Measurements (in mm) of identified *Notochoerus jaegeri* upper teeth from the Laetolil Beds. Measurements marked E are approximations. Measurements marked + are minimum estimates

	M3	
	M-D length	Trigon length
Notochoerus jaegeri	B-L breadth	Crown height
EP 043/98	–	–
Kakesio 4, Lower Laetolil Beds	26.1	32.2
EP 1020/98	–	–
Loc. 9S, Upper Laetolil Beds, below Tuff 2	33.3	31+
EP 608/98	75E	–
Loc. 10W, Upper Laetolil Beds, below Tuff 2	32+	–

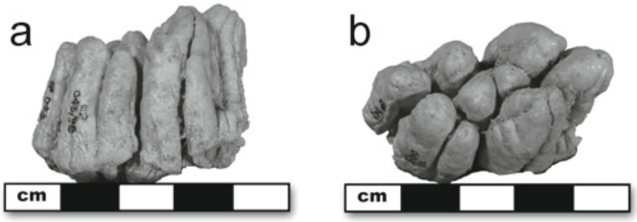


Fig. 13.1 EP 043/98, RM3 fragment of *Notochoerus jaegeri* from Kakesio 4, Lower Laetolil Beds. (**a**) buccal view; (**b**) occlusal view

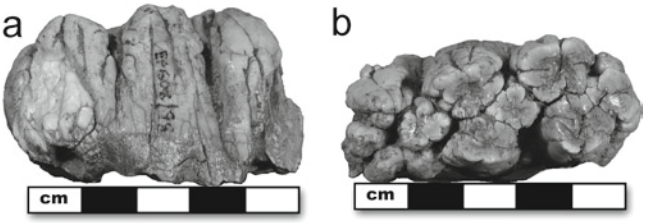


Fig. 13.2 EP 608/98, RM3 fragment of *Notochoerus jaegeri* from Loc. 10W, Upper Laetolil Beds, below Tuff 2. (**a**) buccal view; (**b**) occlusal view

Notochoerus jaegeri was determined to be a mixed feeder through carbon stable isotope studies, with both browse and tropical grasses consumed by specimens from the Tugen Hills (Bishop et al. 1999) and more grassy diets for examples from Kanapoi (Harris and Cerling 2002). An exception to this is *No.* cf. *jaegeri* from Langebaanweg, which did not show a C_4 grass component to its diet due to the lack of C_4 grasses in the region, which today is a Mediterranean biome within the Cape Floristic Region (Franz-Odendaal et al. 2002).

Variation in *No. jaegeri* diet may also have a temporal component, perhaps linked with the lengthened and higher-crowned third molars in later examples.

Species *Notochoerus euilus* (Hopwood, 1926)

Holotype: M12613A, a talonid of a right m3, from the Kaiso Formation of Uganda housed at the Natural History Museum, London.
Laetoli localities: Locs. 2, 6, 7, 8, 9, 9S, 10, 10E, 10S, 11, 13, 15, 16, 21, 22, and 22E
Laetoli time range: Lower Laetolil Beds and throughout the Upper Laetolil Beds.

Notochoerus euilus is a large-bodied tetraconodont with a broad muzzle. They have an expanded cheek tooth row, lengthened by elaborated third molars and a long second molar that compensates the tooth row length for their secondarily reduced third and fourth premolars. Their morphology follows a trend set by their presumed ancestor, *No. jaegeri*, from which they are distinguishable on the basis of larger, more developed third molars and relatively smaller posterior premolars in *No. euilus*. *Notochoerus euilus* also possesses the molar cusp morphology of later *Notochoerus*, which is H-shaped in wear due to pronounced vertical grooves in the mesial and distal aspects of each pillar.

Notochoerus euilus is the most common suid at Laetoli, identified at 16 localities and throughout the Laetolil Beds. As is the case for most other suid taxa from the Eyasi Plateau project collections, the remains are highly fragmentary and few yield comparative metric data (see Tables 13.2 and 13.3). Despite their incomplete and damaged nature it is possible to attribute a large number of specimens to the taxon, due to their possession of distinctive *No euilus* characteristics and the previously well-documented presence of the taxon throughout the sequence (Harris 1987). EP 1029/98 from Loc. 9S in the Upper Laetolil Beds below Tuff 2 is a fragmentary right m3, which possesses the characteristic H-shaped dentine lakes in wear and the aligned pillar organization of *Notochoerus*. EP 367/01, from Loc. 2 between Tuffs 5 and 7 in the Upper Laetolil Beds, shows the size, pillar morphology and potential crown height of the talon that typifies M3s of this taxon (Fig. 13.3). EP 1138/00, from Loc. 8 from the same stratigraphic horizons, consists of associated isolated and mainly unerupted teeth representing a lower mixed deciduous and permanent dentition. The dp4 is fragmentary and, of the permanent teeth, only the m1 shows light wear with the m2 still having incompletely formed roots. This tooth, although expanded through the infilling of cracked surfaces during diagenesis, has the inflated mesial and distal cingula typical of *No. euilus.* The p3 and p4

Table 13.2 Measurements (in mm) of identified *Notochoerus euilus* upper teeth from the Laetolil Beds. Measurements marked + are minimum estimates

	M3	
	M-D length	Trigon length
Notochoerus euilus	B-L breadth	Crown height
EP 147/00	–	–
Loc. 16 Upper Laetolil Beds, between Tuffs 7+8	–	30+
EP 367/01	72.9	38.7
Loc. 2 (W) Upper Laetolil Beds, between Tuffs 5+7	32.2	–

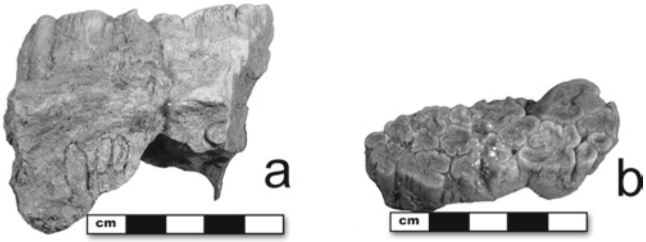


Fig. 13.3 EP367/01, *Notochoerus euilus* RM3 from Loc.2 (West), Upper Laetolil Beds, between Tuff 5 and Tuff 7. (**a**) buccal view; (**b**) occlusal view

Table 13.3 Measurements (in mm) of identified *Notochoerus euilus* lower teeth from the Upper Laetolil Beds. Measurements marked + are minimum estimates

	m1	m2	m3	
	M-D length	M-D length	M-D length	Trigonid length
Notochoerus euilus	B-L breadth	B-L breadth	B-L breadth	Crown height
EP 1138/00	22.1	35.7		
Loc. 8, Upper Laetolil Beds, between Tuffs 5+7	16.1	21.9		
EP 4118/00		32.7		
Loc. 8, Upper Laetolil Beds, between Tuffs 5+7		20.0		
EP 419/01		32.4		
Loc. 13, Upper Laetolil Beds, between Tuffs 6+8		24.3		
EP 1437/98			–	–
Loc. 15, Upper Laetolil Beds, below Tuffs 7+8			25.0	35+
EP 148/00			–	–
Loc. 16, Upper Laetolil Beds, between Tuffs 7+8			25.0	–

are also greatly reduced, typical of later tetraconodonts. EP 1354/00, from the same context is a similar m2, with flaring cingula and H-shaped cusp morphology in wear. EP 1353/00, from between Tuffs 5 and 7 of the Upper Laetolil Beds at Loc. 6 represents fragments of a high-crowned and narrow m3 with H-shaped pillars. It lacks accessory lateral cuspules, which distinguishes this taxon from earlier tetraconodonts. EP 1437/98 is a left m3 from between Tuffs 7 and 8 at Loc. 15, which has the cusp morphology, tooth breadth and crown height to identify it as *No. euilus*.

From a paleoecological standpoint, the presence of *No. euilus* throughout the Laetolil Beds may suggest the continuous availability of closed habitats, since postcranial ecomorphology suggests that this taxon preferred them (Bishop 1994, 1999; Bishop et al. 1999). Carbon stable isotopic studies on specimens from Kanapoi and Koobi Fora suggest that the diets of these tetraconodonts consisted mainly of tropical grasses, although some other vegetation was also consumed (Harris and Cerling 2002). The carbon isotope signature from the dental enamel of numerous *No. euilus* specimens from the Laetolil Beds have also been analyzed and found to be from mixed feeders, trending towards the grass-dominated side of the dietary spectrum (Kingston and Harrison 2007; Kingston 2011).

Subfamily Suinae Gray, 1821
Genus *Potamochoerus* Gray, 1854
Species *Potamochoerus afarensis* (Cooke, 1978)

Holotype: AL 147-10, a partial cranium with P3-M3 housed in the Ethiopian National Museum, Addis Ababa.
Laetoli localities: Locs. 2, 8, 10, 10W, 17, 22E
Laetoli time range: Throughout the Upper Laetolil Beds.

Specimens from the Pliocene of Africa originally described as *Kolpochoerus afarensis* by Cooke (1978) have subsequently been sunk into *Potamochoerus*, the genus of the extant bush pig and red river hog (Cooke 1997). Since the extinction of the tetraconodonts, suines have been the sole pigs in Africa. *Potamochoerus afarensis* is the most primitive suine pig found in African deposits and it or its ancestors presumably arrived from Eurasia some time before 4.5 Ma. It was recognized at Laetoli by Harris (1987).

Potamochoerus afarensis is distinguishable from the modern *P. porcus* and from the extinct *Kolpochoerus heseloni* on the basis of its craniodental morphology. Cranially, it is more similar to *Kolpochoerus*, having the characteristic inferiorly oriented zygomatic morphology and inflated mandibular rami of this genus. Dentally, *P. afarensis* has generally larger third molars than does *P. porcus*, with less reduction of the premolars than is seen in the extant species, and more strongly columnar molar cusp morphology. The cheektooth row can have a slightly lophodont appearance due to the more well-defined cusps which can be strongly aligned buccolingually.

Several specimens from the Eyasi Plateau project assemblage can be attributed to this taxon. There are no complete dentitions, only isolated teeth for which the third molar morphology is the most diagnostic (for measurements of the more complete specimens see Tables 13.4 and 13.5). EP 3162/00 from below Tuff 3 in the Upper Laetolil Beds at Loc. 10W, a right m3 fragment can be identified to this species on the basis of its cusp morphology, enamel thickness and the morphology and relative size of the trigonid and talonid cusps. EP 368/01, a left M3 from Loc. 2 between Tuffs 5 and 7, is a small, worn specimen with relatively large and well-defined pillars in the trigon and no development of cusps in the talon (Fig. 13.4). EP 590/00, a right m3 from between Tuffs 5 and 7 at Loc. 22E has similar morphology in the lower tooth, with strong cusp morphology in the trigonid and no talonid development.

Potamochoerus afarensis is relatively rare in the African fossil record; it is unclear whether this is because its temporal range is relatively poorly sampled or whether it preferred habitats that are less well represented in the fossil record. Originally described from Hadar on the basis of some complete material (Cooke 1978), it has been more fragmentary when recovered elsewhere, including the material found at Laetoli from the current collection and earlier ones (Harris 1987). It has been reported from the Shungura, Nachukui, Koobi Fora and Chemeron Formations, as well as from the Middle Awash.

Table 13.4 Measurements (in mm) of identified *Potamochoerus afarensis* upper teeth from the Upper Laetolil Beds

	M1	M3	
	M-D length	M-D length	Trigon length
Potamochoerus afarensis	B-L breadth	B-L breadth	Crown height
EP 1058/04	16.4		
Loc. 11, Upper Laetolil Beds, between Tuff 7 + just above 8	12.6		
EP 1875/00	17.0		
Loc. 2W, Upper Laetolil Beds, between Tuffs 5 + 7	14.3		
EP 1363/05		37.5	26.7
Loc. 22E, Upper Laetolil Beds, between Tuffs 5 + 7		23.0	
EP 368/01		35.0	23.5
Loc. 2W, Upper Laetolil Beds, between Tuffs 5 + 7		21.1	

Table 13.5 Measurements (in mm) of identified *Potamochoerus afarensis* lower teeth from the Upper Laetolil Beds. Measurements marked E are approximations

	p3	p4	m3	
Potamochoerus afarensis	M-D length B-L breadth	M-D length B-L breadth	M-D length B-L breadth	Crown height Trigonid length
EP 1056/03	12.4			
Loc. 10W, Upper Laetolil Beds, below Tuff 2	8.9			
EP 1031/98		15E		
Loc. 9S, Upper Laetolil Beds, below Tuff 2		12.5		
EP 3162/00			–	22.5
Loc. 10W, Upper Laetolil Beds, below Tuff 3			22.6	–
EP 323/04			45E	30.1
Loc. 8, Upper Laetolil Beds, between Tuffs 5+7			22.0	
EP 590/00			39.3	26.8
Loc. 22E, Upper Laetolil Beds, between Tuffs 5+7			20.2	19.7

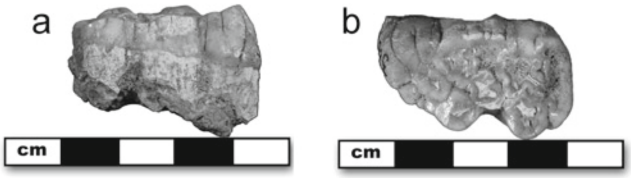


Fig. 13.4 EP368/01, *Potamochoerus afarensis* LM3 from Loc.2 (West), Upper Laetolil Beds, between Tuff 5 and Tuff 7. (**a**) lingual view; (**b**) occlusal view

Little is known about the paleoecology of *Potamochoerus afarensis*. It is tempting to infer their habitat and dietary preferences on the basis of their living relatives, *P. porcus*¸ which have diets relatively rich in C_3 vegetation but are considered browsers to mixed feeders. Results of carbon stable isotope analysis of tooth enamel from several *P. afarensis* from the Laetolil Beds reveal a range of values, across the spectrum of mixed feeding diets (Kingston 2011). Modern examples of this genus prefer bushland habitats, and are common in riverine or gallery forests as well (Grubb 1993). The presence of *P. afarensis* at Laetoli argues for the availability of this type of vegetation in the region during the times and near the localities from which it has been recovered.

Genus *Kolpochoerus* Van Hoepen and Van Hoepen, 1932
Species *Kolpochoerus heseloni* (Leakey, 1943)

Holotype: (Syntypes) M17118a, left mandibular fragment with p4-m3 and M17118b, right mandibular fragment with p4-M3 from the Shungura Formation, Omo, Ethiopia housed at the Natural History Museum, London.
Laetoli localities: Locs. 3, 5, and 18
Laetoli time range: Upper Laetolil Beds between Tuffs 3 and 5 (Loc. 5) and between Tuffs 7 and 8 (Loc. 3). Upper Ndolanya Beds (Loc. 18).

Table 13.6 Measurements (in mm) of identified *Kolpochoerus heseloni* lower teeth from the Upper Laetolil Beds

	m3	
Kolpochoerus heseloni	M-D length B-L breadth	Trigon length Crown height
EP 375/03	59.4	36.7
Loc. 5, Upper Laetolil Beds between Tuffs 3+5	23.6	–

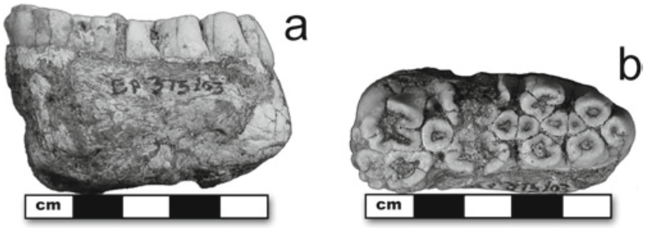


Fig. 13.5 EP 375/03, *Kolpochoerus heseloni* Lm3 from Loc. 5, Upper Laetolil Beds, between Tuff 3 and Tuff 5. (**a**) buccal view; (**b**) occlusal view

Kolpochoerus heseloni (= *K. limnetes*) is a common suid during the later Pliocene and early to middle Pleistocene of Africa, where it has been reported from most, if not all, sites attributable to this time range. It has not been reported previously from the Laetolil Beds. There are relatively few specimens attributable to *K. heseloni* from the Upper Laetoli Beds, and these are relatively fragmentary (for measurements see Table 13.6). Nonetheless, they possess the characteristic morphology that enables relatively confident attribution to this species.

EP 375/03 from Loc. 5 between Tuffs 3 and 5 is a left m3, which is relatively complete and well worn (Fig. 13.5). It has a developed talonid, with two major pairs of pillars, which are separated by double median pillars. EP 1603/00 from between Tuffs 7 and 8 at Loc. 3 is a left m3 fragment, which preserves both a partial distal pillar pair from the trigonid and the talonid (Fig. 13.6). These two regions of the tooth are separated by a double median pillar, which is diagnostic, as it is always present in the genus *Kolpochoerus*. The presence

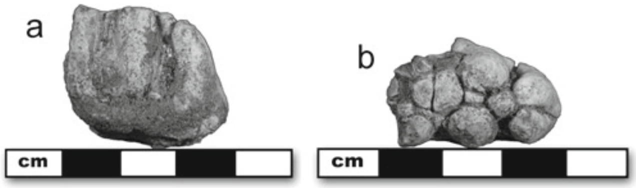


Fig. 13.6 EP 1603/00, *Kolpochoerus heseloni* Rm3 from Loc. 3, Upper Laetolil Beds, between Tuff 7 and Tuff 8. (**a**) buccal view; (**b**) occlusal view

of a highly developed pillar pair on the talonid and its crown height, exclude it from *Potamochoerus*, which does not have these features.

Kolpochoerus heseloni has previously been reported from the Upper Ndolanya Beds (Harris 1987) and the Eyasi Plateau project has recovered at least one more specimen attributable to this taxon. EP 122/03 from Loc. 18 is a fragmentary left m3, which is relatively high-crowned compared to the specimens from the earlier Laetolil Beds.

Due to its relative ubiquity in the fossil record, the paleoecology of *K. heseloni* is relatively well understood. It does evince change in its diet and habitat preference throughout its relatively long time range and temporal distribution (Bishop et al. 2006). Carbon stable isotope analysis of specimens from the Upper Ndolanya Beds suggest a mixed C_3/C_4 diet, tending towards the grassy end of that dietary range (Kingston and Harrison 2007; Kingston 2011). Later specimens from the Koobi Fora Formation seemingly have diets more dominated by grasses (Harris and Cerling 2002). Over its geographic and temporal range, the diets of *K. heseloni* are quite variable, with C_4 grasses comprising between half and all the diet of specimens examined, so it may be unwise to generalize (see Bishop et al. 2006 for a summary). Similarly, the studies of postcranial ecomorphology for this taxon show variability through time. Earlier specimens seemed to have preferred closed habitats and later examples show a preference for more mixed habitats (Bishop 1994; Bishop et al. 2006). It is tempting to relate this apparent temporal trend with the concurrent one of increasing crown height and elaborated third molars for this taxon. However, it is equally possible that the taxon exhibits a high level of ecological variability as would befit its wide temporal and geographic range.

Genus *Metridiochoerus* Hopwood, 1926
Species *Metridiochoerus andrewsi* Hopwood, 1926

Holotype: M14007, a right M3 from near Homa Mountain, Kenya, housed at The Natural History Museum, London.
Laetoli localities: Loc. 1 and Silal Artum.
Laetoli time range: Upper Ndolanya Beds

Metridiochoerus andrewsi is an early member of the suine radiation that dominates many of the African fossil assemblages of the later Pliocene to middle Pleistocene (Harris and White 1979). *Metridiochoerus* is extremely rare in the Eyasi Plateau Project's collections, despite the fact that the Upper Ndolanya Beds are within its known temporal range. It was not recognized in the previous collections from the Upper Ndolanya Beds (Harris 1987). Later representatives of this genus achieved relatively large size and a high degree of dental specialization, particularly in loss of the anterior cheek tooth row through wear during life, and huge cusp elaboration and tooth crown height of the third molars. This radiation gave rise to the modern warthog, *Phacochoerus*.

Table 13.7 Measurements (in mm) of identified *Metridiochoerus andrewsi* upper teeth from the Upper Ndolanya Beds

	P4
	M-D length
Metridiochoerus andrewsi	B-L breadth
EP 1519/01	9.5
Silal Artum, Upper Ndolanya Beds	11.2

The dentition of *Metridiochoerus andrewsi* is relatively primitive and unspecialized compared to its descendants. It is recognizable in the Laetoli assemblage on the basis of several fragmentary teeth from the Upper Ndolanya Beds. *Metridiochoerus andrewsi* is represented by EP 1519/01 from Silal Artum in the Upper Ndolanya Beds, a crushed and broken maxilla fragment with associated tooth fragments (see Table 13.7 for measurements). It is attributable to *Metridiochoerus andrewsi* on the basis of its premolar and molar pillar morphology, and the nature of the M3 pillars, which, although well defined, would appear to merge together in wear. Another specimen from Loc. 1, in the Upper Ndolanya Beds, EP 1118/05 is a third molar fragment which appears to have the talon pillar morphology of *Metridiochoerus*, with numerous cylindrical terminal accessory cusps, however it is too fragmentary to be definite about the species attribution.

The paleoecology of *Metridiochoerus andrewsi* is not particularly well known considering how common it is in the Plio-Pleistocene fossil record of Africa. Studies of carbon stable isotopes in its dental enamel suggest that its diet may have changed through its temporal range, with earlier examples showing more mixed diets than later ones, which have a relatively pure C_4 grass dominated isotopic signal (Bishop et al. 1999; Harris and Cerling 2002). Its habitat preferences have not been determined at this stage.

Discussion

The fossils collected by the Eyasi Plateau project have improved our knowledge of the suid fauna of the Upper Laetolil Beds and the Upper Ndolanya Beds. Two species have been added to the taxonomic lists for the latter sequence, *Nyanzachoerus kanamensis* and *Notochoerus jaegeri*. *Metridiochoerus andrewsi* has now been recovered from the Upper Ndolanya Beds. The time period sampled by the Upper Laetolil Beds is relatively brief. However, there are changes in the representation of pig species through time, and these seem to correspond with their temporal ranges as recognized at other East African sites (Fig. 13.7; White 1995; Bishop 2010). Thus, some of the apparent differences in the presence of suid taxa compared to other contemporaneous sites in Africa have largely disappeared with the collection of a larger faunal sample by the Eyasi Plateau Project.

The vast majority of the Laetoli localities now have a good diversity of suid taxa, with most having more than one species represented; there are 27 documented locality/species occurrences (Table 13.8, Fig. 13.8). In addition to their fossilized bones, trace fossils attributed to the more common suids, *N. euilus* and *P. afarensis*, have been reported from the footprint tuffs at Laetoli (Leakey and Hay 1979). This would demonstrate that these pigs lived in the Laetoli area at least during some time intervals; the recovery of their fossils at the site is not anomalous.

The autecology of the suid taxa themselves can help provide information about the environments during the deposition of the Upper Laetolil Beds and the Upper Ndolanya Beds. With a broad range of dietary requirements, and habitat preferences which tend towards the more closed end of

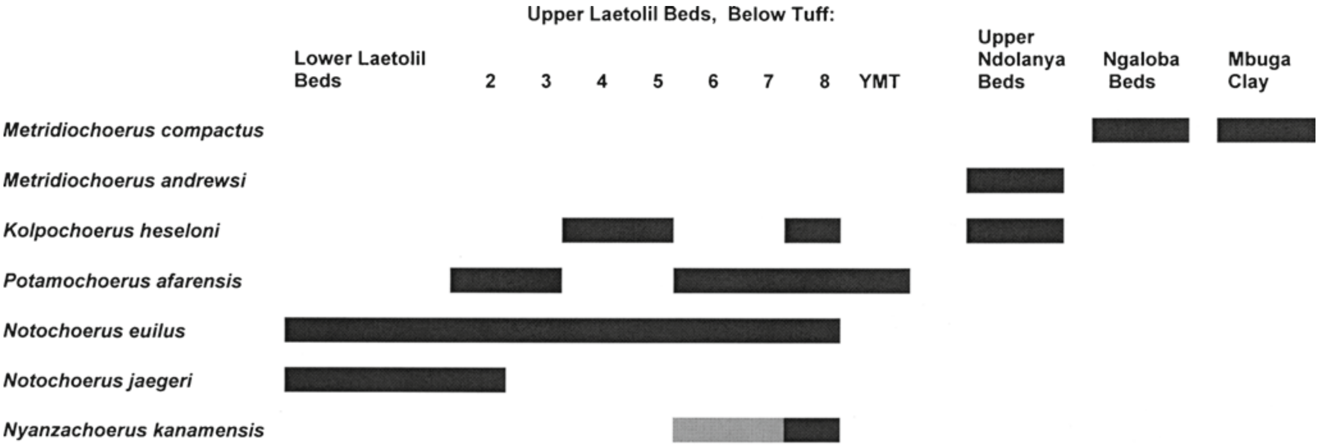


Fig. 13.7 Stratigraphic distribution of extinct pig taxa from Laetoli. Grey shading indicates inconclusive presence of the taxon. See text for details

Table 13.8 Representation of pig taxa at the different localities from the Eyasi Plateau Project collections by stratigraphic unit

Locality	Stratigraphic Unit	Taxa
Emboremony 1		
	Ngaloba Beds	*Phacochoerus*
	Ngaloba Beds	cf *Potamochoerus*//*Kolpochoerus*
	Lower Laetolil Beds	cf *Potamochoerus*//*Kolpochoerus*
Esere 1		
	Mbuga Clay	*Phacochoerus*
	Mbuga Clay	cf *Metridiochoerus compactus*
Esere 2		
	Lower Laetolil Beds	Suidae indet.
Garusi River		
	Lower Laetolil Beds	Suidae indet.
Kakesio 3		
	Lower Laetolil Beds	Suidae indet.
Kakesio 4		
	Lower Laetolil Beds	*Notochoerus jaegeri*
Kakesio 6		
	Lower Laetolil Beds	Tetraconodontinae indet.
Kakesio 8		
	Lower Laetolil Beds	Suidae indet.

(continued)

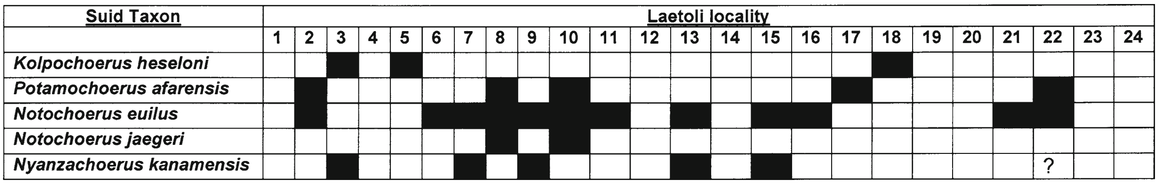
Table 13.8 (continued)

Locality	Stratigraphic Unit	Taxa
Silal Artum		
	Upper Ndolanya Beds	*Kolpochoerus heseloni*
	Upper Ndolanya Beds	*Metridiochoerus andrewsi*
Laetoli Localities		
1	Upper Ndolanya Beds	*Metridiochoerus* indet.
	Upper Laetolil Beds, between Tuff 7 – Yellow Marker Tuff	Suidae indet.
2	Upper Laetolil Beds, between Tuffs 5–7	*Potamochoerus afarensis*
	Upper Laetolil Beds, between Tuffs 5–7	*Notochoerus euilus*
	Upper Laetolil Beds, between Tuffs 5–7	Tetraconodontinae indet.
3	Upper Laetolil Beds, between Tuffs 7–8	*Kolpochoerus* cf. *heseloni*
	Upper Laetolil Beds, between Tuffs 7–8	*Nyanzachoerus kanamensis*
4	Ngaloba Beds	Suidae indet.
	Upper Laetolil Beds, between Tuffs 6–7	Suidae indet.
5	Mbuga Clay	Suidae indet
	Upper Laetolil Beds, between Tuffs 3–5	*Notochoerus* indet.
	Upper Laetolil Beds, between Tuffs 3–5	*Kolpochoerus heseloni*
6	Upper Laetolil Beds, between Tuffs 5–6	*Notochoerus euilus*
7	Upper Ndolanya Beds	*Kolpochoerus* indet.
	Upper Laetolil Beds, between Tuffs 7–8	Suidae indet.
	Upper Laetolil Beds, between Tuffs 7–8	*Nyanzachoerus* cf. *kanamensis*
	Upper Laetolil Beds, between Tuffs 7–8	*Notochoerus euilus*
	Upper Laetolil Beds, between Tuffs 5–7	*Notochoerus* indet.
	Upper Laetolil Beds, between Tuffs 5–7	*Kolpochoerus* indet.
	Ngaloba Beds	*Phacochoerus*
7E	Upper Ndolanya Beds	*Kolpochoerus* indet.
8	Upper Laetolil Beds, between Tuffs 5–7	*Notochoerus euilus*
	Upper Laetolil Beds, between Tuffs 5–7	*Potamochoerus afarensis*
	Upper Laetolil Beds, below Tuff 6	Suidae indet
9	Mbuga Clay	*Phacochoerus*
	Upper Laetolil Beds, between Tuffs 6–7	*Notochoerus euilus*
	Upper Laetolil Beds, between Tuffs 6–7	*Nyanzachoerus* cf. *kanamensis*
	Upper Laetolil Beds, between Tuffs 6–7	*Notochoerus euilus*
	Upper Laetolil Beds, between Tuffs 5–7	*Notochoerus euilus*
	Upper Laetolil Beds, between Tuffs 5–7	*Nyanzachoerus* indet.
9S	Upper Laetolil Beds, below Tuff 2	*Notchoerus jaegeri*
	Upper Laetolil Beds, below Tuff 2	*Notochoerus euilus*
10	Upper Laetolil Beds, below Tuff 3	*Notochoerus euilus*
	Upper Laetolil Beds, below Tuff 2	*Kolpochoerus afarensis*
	Upper Laetolil Beds, below Tuff 2	Tetraconodontinae indet.
10E	Upper Laetolil Beds, between Tuffs 6–7	Tetraconodontinae indet.
	Upper Laetolil Beds, between Tuffs 5–7	Suidae indet.
	Upper Laetolil Beds, between Tuffs 5–7	*Notochoerus euilus*
	Upper Laetolil Beds, between Tuffs 6–7	*Notochoerus euilus*
	Upper Laetolil Beds, between Tuffs 5–7	*Kolpochoerus* indet.
10W	Upper Laetolil Beds, below Tuff 3	Tetraconodontinae indet.
	Upper Laetolil Beds, below Tuff 3	*Potamochoerus afarensis*
	Upper Laetolil Beds, below Tuff 2	*Notochoerus jaegeri*
11	Upper Laetolil Beds	Tetraconodontinae indet.
	Upper Laetolil Beds, between Tuffs 7–8	*Kolpochoerus* indet.
	Upper Laetolil Beds, between Tuffs 7–8	*Notochoerus euilus*
	Upper Laetolil Beds, between Tuffs 7–8	Tetraconodontinae indet.
13	Upper Laetolil Beds, between Tuffs 6–8	*Notochoerus euilus*
	Upper Laetolil Beds, between Tuffs 6–7	cf. *Notochoerus*
	Upper Laetolil Beds, between Tuffs 6–7	*Nyanzachoerus* cf *kanamensis*

(continued)

Table 13.8 (continued)

Locality	Stratigraphic Unit	Taxa
15	Mbuga Clay	*Phacochoerus*
	Upper Laetolil Beds, between Tuffs 6–7	*Notochoerus euilus*
	Upper Laetolil Beds, between Tuffs 6–7	*Nyanzachoerus* cf. *kanamensis*
	Upper Laetolil Beds, between Tuffs 6–7	*Kolpochoerus*
16	Upper Ndolanya Beds	Suidae indet.
	Upper Laetolil Beds, between Tuffs 7–8	*Notochoerus euilus*
17	Upper Laetolil Beds, between Tuffs 7 and Yellow Marker Tuff	*Potamochoerus afarensis*
18	Upper Ndolanya Beds	*Kolpochoerus heseloni*
	Mbuga Clay	*Metridiochoerus* cf. *compactus*
20	Upper Laetolil Beds, between Tuffs 6–8	Suidae indet.
21	Upper Laetolil Beds, between Tuffs 5–7	*Nyanzachoerus kanamensis*
	Upper Laetolil Beds, between Tuffs 5–7	*Notochoerus euilus*
22	Ngaloba Beds	*Metridiochoerus compactus*
	Upper Laetolil Beds, between Tuffs 5–7	Tetraconodontinae indet.
	Upper Laetolil Beds, between Tuffs 5–7	*Nyanzachoerus* indet.
	Upper Laetolil Beds, between Tuffs 5–7	*Notochoerus euilus*
22E	Upper Ndolanya Beds	Suidae indet.
	Upper Laetolil Beds, between Tuffs 5–7	*Kolpochoerus*
	Upper Laetolil Beds, between Tuffs 5–7	*Kolpochoerus afarensis*
	Upper Laetolil Beds, between Tuffs 5–7	*Notochoerus euilus*
	Upper Laetolil Beds, between Tuffs 3–5	Tetraconodontinae indet.
22S	Upper Ndolanya Beds	Suidae indet.
23	Lower Ngaloba Beds	Suidae indet.
	Ngaloba Beds	*Phacochoerus*



Suid Taxon	Laetoli locality																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Kolpochoerus heseloni			■		■													■						
Potamochoerus afarensis		■						■		■							■					■		
Notochoerus euilus		■				■	■	■	■	■	■		■		■	■					■	■		
Notochoerus jaegeri								■		■														
Nyanzachoerus kanamensis			■				■		■				■		■							?		

Fig. 13.8 Occurrences of suid taxa at the different Laetoli localities. Black squares indicate the presence of the taxon at the locality

the vegetational spectrum, the paleoecology of the identified pig fauna would support more recent reconstructions of Laetolil paleoenvironments with a range of habitat types, including the woodland and forest (Andrews 1989; Andrews and Bamford 2008). *Nyanzachoerus kanamensis*, which may have preferred relatively wetter habitats, was initially conspicuous by its absence at Laetoli, since the site falls within the taxon's long temporal range (Harris 1987; Bishop 1997). However, its recognition now presents another question: what does its occurrence here, however rare, suggest about the environments? The pattern of its spatial distribution throughout the Laetoli localities does not help answer this, but the recognition that water periodically flowed through the Laetoli area may suggest that occasionally, wetter environments were available for faunal exploitation (Ditchfield and Harrison 2011).

The diets of all taxa occurring at Laetoli contain an identifiable proportion of C_4 grasses as shown by carbon stable isotope analysis, so C_4 grasses must have been locally available (Harris and Cerling 2002; Kingston and Harrison 2007; Kingston 2011). The possible exception to this, *Notochoerus* cf. *jaegeri* at Langebaanweg, showed a C_3 browsing diet; this relates to the demonstrated absence of C_4 vegetation at this early Pliocene site (Franz-Odendaal et al. 2002). The diversity of suid species would indicate that Laetoli paleoenvironments were significantly different from those that are prevalent in eastern Africa today. Some aspect of these past environments, perhaps with more inherent diversity, or larger and different ecotonal areas, may have supported this high species diversity amongst related taxa.

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Chapter 14
Giraffidae

Chris A. Robinson

Abstract 792 specimens attributed to the Giraffidae were recovered by the Eyasi Plateau Paleontological Expedition (EPPE) from the three Pliocene stratigraphic units at Laetoli, with *Giraffa stillei* the most common taxon in all three levels. Giraffids are notably well represented in the Upper Laetolil Beds, with further evidence gathered by EPPE for the three previously recognized species from this unit. In the Lower Laetolil Beds *Giraffa stillei* is provisionally identified, as is *Sivatherium*. A third, large giraffid species may also be present. Based on a specimen recovered by Kohl-Larsen's team during the first extensive exploration of Laetoli, we now provisionally recognize *Giraffa pygmaea* from the Upper Ndolanya Beds, along with *Giraffa stillei* and *Sivatherium maurusium*. Evidence for *Giraffa jumae* in the Upper Ndolanya Beds is not as convincing, as it is based on a small number of postcranial bones. In the time between the formation of the Upper Laetolil Beds and the Upper Ndolanya Beds, it appears that *Giraffa stillei* increased in size, which has been documented at other contemporary East African localities. This may relate to competition from the smaller *Giraffa pygmaea*.

Keywords Giraffidae • *Giraffa* • *Sivatherium* • Artiodactyla • Pliocene • Africa • Tanzania

Introduction

The diversity of giraffids in the Pliocene of Africa was considerably greater than it is today, and Laetoli is similar to most other African Pliocene sites in having multiple giraffid taxa represented in all of the stratigraphic units. In the Upper Ndolanya Beds, for example, four giraffid species are now identified with the recognition of *Giraffa pygmaea*, Harris 1991 based on a mandibular specimen described below. These same four taxa have been identified at the Pliocene sites of Hadar, Koobi Fora and the Omo Valley (Boaz et al. 1982; Harris 1991; Reed 2008). While the diversity of species is similar to other sites, previous studies of fossil giraffids have noted the unusually high number of giraffe specimens at Laetoli compared to other East African Plio-Pleistocene sites (Harris 1976a, 1987, 1991), which could be related to favorable ecological conditions and/or a reduced number of competitors compared to other early Pliocene sites. The Laetolil Beds are unusual with respect to the number of giraffids recovered, but this abundance diminishes in the Upper Ndolanya Beds, possibly due to competition from the increased number of bovids.

Three species of *Giraffa* have been at least provisionally identified from the various stratigraphic units at Laetoli, *Giraffa jumae*, Leakey 1965, *Giraffa pygmaea* and *Giraffa stillei*, Dietrich 1942. The earliest appearance of *Giraffa* in East Africa is currently in the late Miocene at Aramis and Lothagam (WoldeGabriel et al. 1994; Harris 2003). At that time it appears that the genus had already split into at least two species, probably *G. jumae* and *G. stillei*. The *G. stillei* specimens from the Lower Laetolil Beds described below represent some of the earliest fossils in East Africa that can be provisionally attributed to *Giraffa stillei*. Based on the current evidence, *G. pygmaea* does not appear until the late Pliocene, where competition with *G. stillei* seems to have resulted in increased size in the latter taxon (see below).

Also present at Laetoli, as it is in many East African faunal assemblages, is *Sivatherium maurusium*, Pomel 1892. The *S. maurusium* specimens from the Upper Laetolil Beds represent the earliest known representatives of that species, although there are a number of earlier sivathere specimens that cannot be attributed to species. A single sivathere premolar was recovered from the Lower Laetoli Beds, which are similar in age to sites in North, East and South Africa from which *Sivatherium hendeyi*, Harris 1976 has been identified (Harris 1976a, 1999; Likius 2002; Vignaud et al. 2002). The tooth could represent this taxon or its possible descendant, *S. maurusium*.

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Cranial Specimens and Taxonomic Attribution of Giraffids

Species of Giraffidae are generally differentiated from one another on the basis of size and cranial morphology, especially on the shape of their ossicones (Harris 1976a, b, 1987, 1991; Churcher 1978; Hamilton 1978; Geraads 1986, 1994; Likius 2002; Solounias 2007). No giraffid cranial specimens were recovered by EPPE. Harris (1987) described two *Giraffa stillei* ossicones from the Upper Laetolil Beds, and another (MB Ma 42325 in Berlin) was published by Dietrich (1942) that is likely to be derived from the Upper Laetolil Beds (T. Harrison, personal communication), confirming the presence of the smaller *Giraffa* in this unit. In addition, following publication of Harris (1987), right and left frontal ossicones (LAET 76-4193) from this unit were described and assigned to *Sivatherium maurusium* (Harris, 1991). This makes it possible to confidently recognize the presence of *Sivatherium maurusium* in the Upper Laetolil Beds. It should be noted that, while most authors identify the cranial appendages of sivatheres as ossicones (Harris 1987, 1991; Harris 2003; Harris et al. 1988; Solounias 1988, 2007; Churcher 1990), Geraads (1986, 1991) argues that this term should be reserved for the cranial appendages of *Giraffa*, *Okapia* and, possibly, *Palaeotragus*. Geraads (1991) describes the ossicone as "a bone originally independent from those of the cranial roof, ossifying from a cartilaginous matrix". He also notes that the "true" ossicones of extant giraffids are "hyper-ossified" and shifted posteromedially, further from the supraorbital region. The ramified cranial appendages of *Sivatherium*, which show evidence of having had blood vessels on them, appear to grow in a manner more similar to cervids or bovids than *Giraffa* and do not exhibit the extremely dense bone of that genus (Geraads 1986).

Other than in its cranial morphology, especially the form of its ossicones, *Giraffa jumae* closely resembles *Giraffa camelopardalis*, Linnaeus 1758 (Harris 1987, 1991; Geraads et al. 2004). There are no *G. jumae* cranial specimens known from Laetoli. Consequently, it is not possible to confirm the specific attribution of giraffid fossils that are similar in size to extant giraffes. However, the Upper Laetolil Beds, where a number of specimens similar in size and morphology to *G. jumae* from other sites are well documented, are dated to between approximately 3.5 and 3.8 Ma (Drake and Curtis 1987; Deino 2011), making it likely that these specimens represent *G. jumae* rather than *G. camelopardalis* (Harris, 1987). There are no specimens of *G. camelopardalis* from the Pliocene, whereas *G. jumae* is known from a number of Pliocene sites in East and South Africa (Harris 1976a–c, 1991; Churcher 1978; Harris et al. 2003; Kullmer et al. 2008). The earliest diagnostic evidence for *G. camelopardalis* is from the Nariokotome Member at West Turkana, dated to between 1.2 and 1.3 Ma (Harris et al. 1988; Harris 1991; McDougall and Brown 2006).

Because Dietrich (1942) did not designate a holotype for *Okapia stillei*, later referred to the genus *Giraffa* (Harris, 1976b), Harris (1987) selected two specimens from Laetoli to be lectotypes of *Giraffa stillei*. One of the lectotypes, based on Dietrich (1942) Figure 170, was identified as a partial mandible with P_3-P_4 and M_2-M_3, although the teeth in the figure are actually P_4-M_3 (Dietrich 1942; T. Harrison, personal communication). Moreover, as Dietrich often did, the lectotype is comprised of a composite of specimens from different individuals and localities (Geraads et al. 2004; T. Harrison, personal communication). It is proposed here that the mandibular fragment with M_2 and M_3 (MB Ma 39078) be retained as a lectotype, as it clearly belongs to the smaller *Giraffa* species from the Upper Laetolil Beds, and conforms to the concept of *Okapia stillei* as proposed by Dietrich (1942). The other unassociated specimens should be recognized as paralectotypes.

Lower Laetolil Beds

Eleven giraffid specimens were recovered from the Lower Laetolil Beds during the 1998–2005 field seasons (Table 14.1). All were identified to taxon on a provisional basis because of the lack of diagnostic specimens. Nine of these specimens are attributed to *Giraffa* aff. *stillei*.

In the following descriptions the terminology used for the postcranial elements follows that of Harris (1987, 1991) and colleagues (Harris et al. 2003) other than for the external cuneiform. The term external cuneiform is used rather than lateral cuneiform to avoid confusion, since this bone is formed by the fusion of the middle and lateral cuneiforms in fossil giraffids from Laetoli.

Giraffa aff. *stillei* is best represented by a left mandibular fragment from Kakesio retaining M_1-M_3 (EP 854/04) (Fig. 14.1). The preserved morphology and dimensions of its well worn molars are similar to those of smaller *G. stillei* specimens from the Upper Laetolil Beds (see Fig. 14.4). Small ectostylids are present on M_1 and M_2, and an entostylid on M_3, as they are on a number of *G. stillei* lower molars from the Upper Laetolil Beds. Three isolated dental elements and five postcranial specimens from Emboremony and Kakesio are also provisionally attributed to this species. The P^4 (EP 2097/03) is similar in size to smaller specimens from the Upper Laetolil Beds and indistinguishable morphologically. EP 291/99, a relatively small P_4 from Emboremony 1, shares an unusual feature with another smaller P_4 from the Upper Laetolil Beds, EP 3528/00, in that on both specimens the anterior arm of the hypoconid extends lingually into the talonid basin. The postcranial specimens resemble *G. stillei* fossils from the Upper Laetolil Beds in both size and morphology, with only the calcaneum (EP 202/03) and astragalus (EP 375/99) reasonably well preserved. Although

Table 14.1 Lower Laetolil Beds specimens. Measurements in mm

Specimen ID	Element	Locality	Taxonomic attribution	Measurements
EP 290/99	Distal radius fragment	Emboremony 1	*Giraffa* aff. *stillei*	
EP 291/99	Lower P4	Emboremony 1		BL – 16.2; MD – 21.3
EP 375/99	Astragalus	Emboremony 1		Lat. Length – 93.7; Med. Length – 86.1[a]
EP 2097/03	Upper P4	Emboremony 2		BL – 21.9; MD – 17.5
EP 027/99	Partial lower M3	Kakesio		
EP 202/03	Calcaneum	Kakesio 8		Length – 160.2; Artic. AP – 72.2
EP 854/04	Mandible with M1-M3	Kakesio 8		M1: BL – 17.6; MD – 23.1: M2: BL – 18.3; MD – 23.7: M3: BL – 17.9; MD – 34.0
EP 520/03	Astragalus fragment	Kakesio 10		Med. Length – 77.2[a]
EP 860/04	Astragalus fragment	Kakesio 10		Lat. Length – 86.3[a]; Med. Length – 76.7
EP 108/98	Magnum	Kakesio South	Giraffidae indet.	Length – 77.9; Ant. DV – 36.2
EP 1680/98	Upper P4	Esere	*Sivatherium* sp.	BL – 49.2

Note: The maximum distance was measured for all tooth dimensions

BL buccolingual breadth, *MD* mesiodistal length, *AP* anteroposterior, *DV* dorsoventral, Artic. *AP* anteroposterior breadth at the proximal end of the calcaneum

[a] Estimated measurement

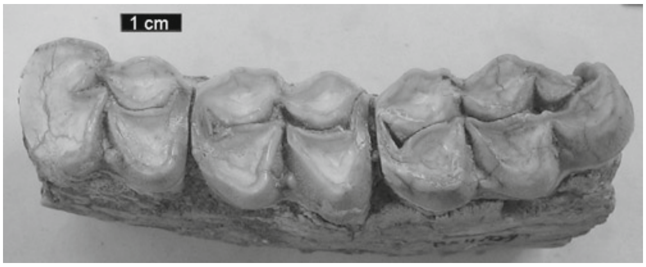

Fig. 14.1 Occlusal view of EP 854/04, *Giraffa* aff. *stillei* left mandibular fragment with M_1-M_3 from Kakesio, Lower Laetolil Beds

adhering matrix adds slightly to this dimension, the calcaneum is similar in its length to larger *G. stillei* specimens from the Upper Laetolil Beds. However, the Lower Lateolil Beds specimen more closely resembles smaller Upper Laetolil Bed calcanei in its more gracile tuber calcis. The astragalus is more robust and slightly larger than the largest of the *G. stillei* specimens from the Upper Laetolil Beds, being similar in size to smaller female *G. camelopardalis* specimens. It is possible that this specimen should be included in a separate taxon with the large magnum from the Lower Laetolil Beds described below but, pending further evidence that would help to identify that species, it is retained in *G.* aff. *stillei*.

Sivatherium is represented only by a single poorly preserved P^4 from Esere (EP 1680/98), which is the only giraffid fossil recovered from that site. The general morphology, highly rugose enamel and massive buccolingual breadth closely resemble those of *Sivatherium maurusium* P^4s recovered from the Upper Laetolil Beds. However, *S. maurusium* cannot be distinguished in its dental morphology from *Sivatherium hendeyi* and both species have been identified at contemporary or older African sites (Singer and Boné 1960; Harris 1976a; Churcher 1978; Likius 2002; Vignaud et al. 2002; Harris et al. 2003). Consequently, this specimen is provisionally assigned to *Sivatherium* sp.

A magnum (EP 108/98) does not fit comfortably in either of the two other giraffid taxa identified in the Lower Laetolil Beds. It is similar in size to EP 4298/00, a *Giraffa* aff. *jumae* specimen from the Upper Laetolil Beds, but its scaphoid facet is unusually expanded mediolaterally compared to other specimens from Laetoli. It also differs from EP 4298/00, but is similar to magnums from the Mary Leakey collection (Harris 1987), in that its anterolateral corner is not projecting as far laterally as on extant giraffe specimens. This specimen could be a representative of a third giraffid taxon in the Lower Laetolil Beds, possibly *Giraffa jumae*. However, without diagnostic fossils, it seems most appropriate to attribute the magnum to Giraffidae indet.

Upper Laetolil Beds

Over 700 giraffid specimens were recovered from the Upper Laetolil Beds (Table 14.2). Representatives of all three taxa previously recognized from this unit (Harris 1987) have been identified among these fossils.

Upper Laetolil Dento-Gnathic Specimens

All dento-gnathic specimens recovered by EPPE from the Upper Laetolil Beds were attributed, at least provisionally, to one of the three previously described giraffid species from these strata (Harris 1987). Many of the isolated dental specimens cannot be identified to a specific tooth because of morphological similarities between serial teeth (Harris 1991). Included in the EPPE collection are the first recorded giraffid incisors and canines from Laetoli.

Table 14.2 Upper Laetolil Beds giraffid specimen numbers at each locality

	Giraffa aff. *jumae*			*Giraffa stillei*			*Sivatherium maurusium*		
Locality	Dental	Postcranial	Total	Dental	Postcranial	Total	Dental	Postcranial	Total
1	2	2	4	5	8	13	4	4	8
1NW	0	0	0	1	3	4	1	0	1
2	3	6	9	16	16	32	6	2	8
3	0	1	1	11	5	16	2	1	3
4	3	2	5	0	3	3	0	3	3
5	1	5	6	14	7	21	3	4	7
6	2	3	5	17	8	25	1	3	4
7	3	2	5	4	13	17	8	5	13
8	4	4	8	14	7	21	4	5	9
9	7	8	15	14	8	22	2	1	3
9S	6	3	9	9	9	18	3	0	3
10	3	1	4	18	15	33	3	3	6
10E	10	5	15	25	19	44	4	5	9
10W	5	3	8	14	24	38	1	2	3
11	4	3	7	9	14	23	1	1	2
12	0	2	2	2	0	2	0	0	0
12/12E[a]	0	0	0	2	1	3	1	1	2
12E	3	1	4	6	4	10	1	1	2
13	2	7	9	6	8	14	5	0	5
15	0	5	5	10	1	11	0	0	0
16	0	10	10	5	3	8	1	5	6
19	0	0	0	1	2	3	1	0	1
20	1	0	1	0	2	2	0	0	0
21	5	3	8	6	11	17	5	5	10
22	1	5	6	9	10	19	3	0	3
22E	2	3	5	4	11	15	3	1	4
24	0	0	0	0	1	1	0	1	1
Totals	67	84	151	222	213	435	63	53	116

[a] When these five giraffid fossils were recovered, specimens from Locs. 12 or 12E were combined

Giraffa aff. *jumae*

Sixty-six isolated dental specimens attributable to *Giraffa* aff. *jumae* were recovered by EPPE from the Upper Laetolil Beds. In general, the teeth resemble those of *Giraffa camelopardalis* in both size and morphology, and they are substantially larger than specimens assigned to *Giraffa stillei*. Given the relatively low sexual dimorphism in the dentition of extant giraffes, it seems unlikely that specimens attributed to these two *Giraffa* species are males and females of a single species (Harris 1987).

Two incisors and two canines are provisionally assigned to *Giraffa* aff. *jumae*. One of the incisors, EP 4297/00, is unusually low crowned, due in part to its having been extensively worn, being more similar in crown height to *Giraffa stillei* specimens (Fig. 14.2). However, it has a long and broad crown and a thick root, which distinguishes it from specimens of the smaller *Giraffa* species. The two canines, EP 432/98 and EP 3172/00, have a bilobed crown typical of giraffids (Churcher 1978; Hamilton 1978; Geraads 1986; Harris 1991; Solounias 2007). However, the mesial and distal lobules are evenly rounded and more similar to one another morphologically than the asymmetrical lobules of extant giraffes (Fig. 14.3). They are also lower crowned than the canines of *Giraffa camelopardalis*, but which are otherwise similar in size. An isolated canine from Makapansgat, M 1801, attributed to *Giraffa* (Singer and Boné 1960), does not share this morphology with the Laetoli specimens, although it is approximately the same size. Its shape most closely resembles that of the *Sivatherium maurusium* canine (EP 498/00) from Laetoli (Fig. 14.3).

Five mandibular postcanine teeth are attributed to *Giraffa* aff. *jumae*, all with length and breadth measurements in the upper end of the extant giraffe size range, but otherwise indistinguishable (Table 14.3).

Many more maxillary than mandibular postcanine teeth of giraffids were recovered from the Upper Laetolil Beds. This makes it possible to compare the degree and pattern of variation between fossil and extant giraffe species for these teeth. Data for *Giraffa camelopardalis* are derived from 13 wild shot specimens housed at the American Museum of Natural History (AMNH) in New York. The coefficients of variation for the length and breadth of all of the *Giraffa* aff. *jumae* maxillary postcanine teeth are similar to, and more often less than, those of *Giraffa camelopardalis* (Table 14.3).

Fig. 14.2 Giraffid incisors from the Upper Laetolil Beds. *Top* row from *left* to *right* – EP 2425/03, 438/98, 4296/00, 618/01 and 619/01 (*Giraffa stillei*); *Bottom* row from *left* to *right* – EP 4297/00 and 2270/03 (*Giraffa* aff. *jumae*); EP 1625/98, 2126/03, 1124/00 and 165/99 (*Sivatherium maurusium*)

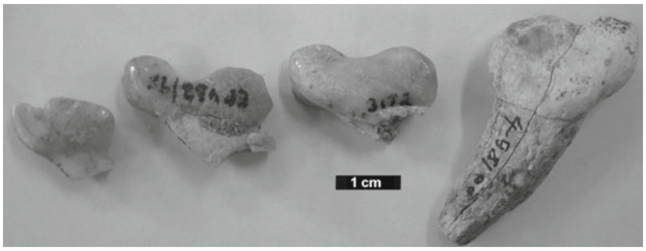

Fig. 14.3 Giraffid canines from the Upper Laetolil Beds. From *left* to *right* – EP 553/03 (*Giraffa stillei*); EP 432/98 and 3172/00 (*Giraffa* aff. *jumae*); EP 498/00 (*Sivatherium maurusium*)

Modeling the extent of variation to be expected in a fossil giraffid species from one site is difficult given that there is only a single living species and museums typically have individuals that have been collected from multiple populations. Consequently, the extent of variation among extant specimens may be greater due to the geographic variation of the sample. However, the Laetoli specimens sample a number of populations spread over a substantial amount of time, albeit seemingly under similar ecological conditions, possibly leading to increased variation in the fossil sample as well. Given the potential for temporal variation in a fossil sample even from one site, some have suggested that collecting data from multiple extant populations or subspecies is the most appropriate means of modeling the extent of variation to be expected in a fossil species (Richmond and Jungers 1995; Lockwood et al. 1996; Uchida 1996).

Giraffa aff. *jumae* upper molars are slightly larger than those of extant giraffes, but otherwise closely resemble them in morphology. In a bivariate plot of the buccolingual breadths and mesiodistal lengths of giraffid upper molars, most of the *G.* aff. *jumae* upper molars are positioned above those of extant giraffes on the Y-axis, indicating proportionately broader teeth (Fig. 14.4).

Giraffa stillei

Two hundred and thirteen isolated teeth and eight specimens with multiple associated teeth (EP 504/98 – M^2-M^3; EP 1594/00 – P_3, P_4 and M_2; EP 1122/00 – RdP^2-M^2 and LdP^2; EP 1600/00 – mandible with M_1-M_2; EP 292/01 – P_4-M_1; EP 483/01 – P^3-M^2; EP 1700/04 – M_2-M_3; EP 174/05 – P^3-M^1; EP 1294/05 – P^2-P^4) attributed to *G. stillei* were recovered from the Upper Laetolil Beds. Unless discussed below, these teeth are indistinguishable from those of *Giraffa camelopardalis* and *Giraffa jumae* other than by size (Harris 1976b, c, 1987, 1991).

Mandibular dentition: A tiny deciduous canine (EP 1098/00) that is most likely attributable to *Giraffa stillei* was recovered from Loc. 8. This specimen resembles permanent canines, although its mesial lobule is mesiodistally longer and more spatulate in shape. In addition, the specimen is over 20% smaller in its mesiodistal dimension than the smallest giraffid permanent canine from Laetoli. This is consistent with the difference in size between the deciduous and permanent canines of extant giraffes.

Table 14.3 Measurements (in mm) of giraffid dental elements from the Upper Laetolil Beds and those of extant giraffes

Element	Taxon	Sample size	Mean (range)		Standard Dev.		Coeff. of Variation	
Incisor			ML	BL	ML	BL		
	G. aff. *jumae*	2	14.7 (13.1–16.3)	12.3	2.26	N/A		
	G. stillei	11	11.4 (10.2–12.7)	8.3 (7.0–9.3)	0.60	0.70		
	S. maurusium	4	16.4 (13.3–18.9)	14.9 (13.6–15.8)	1.34	0.97		
	G. camelopardalis	14	14.4 (8.6–18.6)	9.8 (7.2–12.5)	2.86	1.77		
Lower dC			BL	MD	BL	MD		
	G. aff. *jumae*	0						
	G. stillei	1	5.1	12.6				
	S. maurusium	0						
	G. camelopardalis	2	6.0 (5.4–6.6)	20.1 (19.6–20.6)	0.88	0.68		
Canine			BL	MD	BL	MD		
	G. aff. *jumae*	2	7.5 (7.3–7.7)	22.6 (22.2–22.9)	0.28	0.50		
	G. stillei	2	6.2 (6.1–6.3)	16.8 (15.9–17.7)	0.14	1.27		
	S. maurusium	1	12.5	20.2				
	G. camelopardalis	5	8.4 (6.5–10.1)	23.4 (16.1–31.7)	1.63	6.28		
Lower dP3			BL	MD	BL	MD		
	G. aff. *jumae*	0						
	G. stillei	0						
	S. maurusium	2	17.0 (16.8–17.3)	30.7	0.35	N/A		
	G. camelopardalis	5	12.9 (12.5–13.9)	20.5 (18.4–23.2)	0.59	1.87		
Lower dP4			BL	MD	BL	MD		
	G. aff. *jumae*	0						
	G. stillei	2	13.6 (12.7–14.6)	24.7	1.34	N/A		
	S. maurusium	0						
	G. camelopardalis	5	15.6 (14.9–16.7)	32.1 (30.8–33.8)	0.68	1.08		
Lower P2			BL	MD	BL	MD		
	G. aff. *jumae*	0						
	G. stillei	2	10.6 (9.9–11.2)	18.1	0.92	N/A		
	S. maurusium	1	19.9					
	G. camelopardalis	11	15.7 (12.6–19.4)	19.6 (15.6–22.8)	2.12	1.98		
Lower P3			BL	MD	BL	MD	BL	MD
	G. aff. *jumae*	1	17.2	21.8			N/A	N/A
	G. stillei	8	15.3 (15.1–16.9)	21.0 (20.4–21.9)	0.97	0.71	0.063	0.034
	S. maurusium	4	22.9 (20.7–23.8)	34.0 (3.0–35.0)	1.48	1.41	0.065	0.041
	G. camelopardalis	12	20.4 (16.7–23.9)	23.1 (19.0–25.5)	1.73	1.47	0.085	0.064
Lower P4			BL	MD	BL	MD	BL	MD
	G. aff. *jumae*	1	24.2	29.1			N/A	N/A
	G. stillei	16	16.6 (14.2–18.4)	21.4 (18.4–23.9)	1.31	1.43	0.079	0.067
	S. maurusium	3	24.9 (21.0–28.0)	39.0 (37.8–40.2)	3.58	1.70	0.144	0.044
	G. camelopardalis	12	21.8 (15.8–23.4)	24.9 (21.3–26.6)	1.04	1.29	0.048	0.052
Lower M1/M2 [a]			BL	MD	BL	MD	BL	MD
	G. aff. *jumae*	2	23.8 (22.7–24.9)	32.9	1.56	N/A	0.066	N/A
	G. stillei	44	18.2 (15.1–22.0)	24.8 (21.0–27.5)	1.45	1.75	0.080	0.071
	S. maurusium	6	31.8 (29.5–33.9)	42.7 (41.5–43.6)	1.65	1.07	0.052	0.025
	G. camelopardalis	24	22.1	30.2 (26.5–34.5)	1.42	1.78	0.064	0.059
Lower M3			BL	MD	BL	MD	BL	MD
	G. aff. *jumae*	5	23.8 (21.8–25.5)	45.2 (43.9–46.5)	1.69	1.84	0.071	0.041
	G. stillei	18	18.4 (15.9–21.7)	34.6 (31.6–37.7)	1.69	1.83	0.092	0.053
	S. maurusium	1		65.5				
	G. camelopardalis	12	22.6 (18.8–25.1)	42.0 (37.5–44.7)	1.76	2.45	0.078	0.058
Upper dP2			BL	MD	BL	MD		
	G. aff. *jumae*	0						
	G. stillei	1	12.8	16.0				
	S. maurusium	0						
	G. camelopardalis	5	17.3 (16.9–17.7)	20.4 (18.9–22.4)	0.29	1.39		

(continued)

Table 14.3 (continued)

Element	Taxon	Sample size	Mean (range)		Standard Dev.		Coeff. of Variation	
Upper dP3			BL	MD	BL	MD		
	G. aff. *jumae*	0						
	G. stillei	2	16.9 (15.8–17.9)	19.6 (18.6–20.5)	1.48	1.34		
	S. maurusium	2	26.8 (24.3–29.4)	34.6 (33.6–35.7)	3.61	1.48		
	G. camelopardalis	5	19.9 (18.7–20.3)	24.4 (23.1–25.9)	0.70	1.34		
Upper dP4			BL	MD	BL	MD		
	G. aff. *jumae*	0						
	G. stillei	1	18.0	20.3				
	S. maurusium	0						
	G. camelopardalis	5	22.8 (21.2–25.7)	26.4 (24.4–28.0)	1.86	1.37		
Upper P2			BL	MD	BL	MD	BL	MD
	G. aff. *jumae*	7	26.2 (23.9–27.8)	23.5 (21.9–25.0)	1.67	1.03	0.064	0.044
	G. stillei	23	18.8 (16.5–21.2)	18.4 (15.9–21.1)	1.28	1.23	0.068	0.067
	S. maurusium	1	41.2	32.6				
	G. camelopardalis	10	25.2 (21.9–28.5)	21.3 (18.9–24.9)	1.78	1.78	0.071	0.084
Upper P3			BL	MD	BL	MD	BL	MD
	G. aff. *jumae*	6	27.3 (25.8–29.3)	23.7 (22.4–26.0)	1.19	1.62	0.044	0.068
	G. stillei	25	21.2 (18.9–22.8)	18.5 (16.7–28.5)	1.27	1.12	0.060	0.061
	S. maurusium	3	41.7 (39.7–44.2)	28.5	2.30	N/A	0.055	N/A
	G. camelopardalis	10	29.0 (24.9–32.7)	22.6 (20.3–24.3)	1.93	1.06	0.067	0.047
Upper P4			BL	MD	BL	MD	BL	MD
	G. aff. *jumae*	6	30.2 (29.2–32.0)	22.2 (21.4–23.3)	1.26	0.71	0.042	0.032
	G. stillei	16	23.8 (21.8–26.6)	19.2 (17.3–22.4)	1.29	1.51	0.054	0.079
	S. maurusium	2	49.8 (49.4–50.3)	36.9	0.64	N/A	0.013	N/A
	G. camelopardalis	11	29.8 (27.7–32.5)	22.9 (20.2–24.5)	1.78	0.87	0.060	0.038
Upper M [a]			BL	MD	BL	MD	BL	MD
	G. aff. *jumae*	15	35.6 (26.4–40.0)	32.1 (28.8–34.9)	1.99	2.14	0.056	0.067
	G. stillei	61	25.9 (20.5–29.5)	24.1 (19.2–28.5)	1.90	2.08	0.073	0.086
	S. maurusium	15	46.0 (41.0–52.0)	45.8 (36.4–49.1)	4.04	4.13	0.088	0.090
	G. camelopardalis	37	30.9 (26.9–34.1)	31.4 (24.8–36.6)	2.40	1.67	0.078	0.053

ML mediolateral breadth, *BL* buccolingual breadth, *MD* mesiodistal length

[a] It is not possible to consistently differentiate giraffid M_1s and M_2s or the three upper molars and, consequently, the data for these teeth are pooled

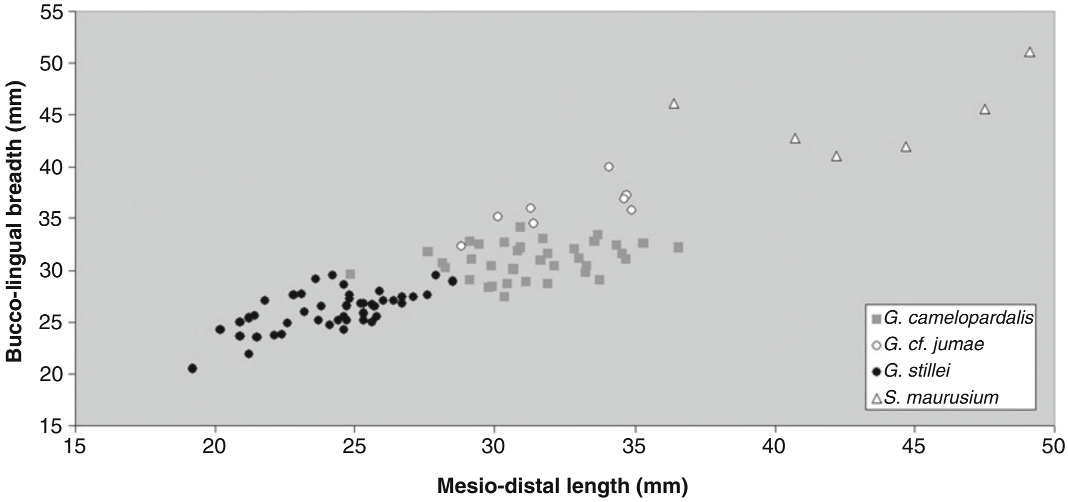

Fig. 14.4 Bivariate plot of the mesiodistal length and buccolingual breadth measurements taken on upper molars of giraffids from the Upper Laetolil Beds and extant *Giraffa camelopardalis* specimens

No consistent differences could be identified in *Giraffa camelopardalis* specimens to distinguish between the three lower incisors. Consequently, the isolated incisors from Laetoli are not attributed to serial position. The incisors from Laetoli ascribed to *Giraffa stillei* are substantially smaller than those of *G. camelopardalis* and it is possible that some of the smaller specimens could represent *Okapia* or *Giraffa pygmaea*. To explore this possibility further, the products of the length and breadth measurements for the incisors and lower molars (excluding M_3) were calculated and averaged for the three fossil giraffid species from Laetoli and extant giraffes. The results show that, on average, the incisors attributed to *G. stillei* are 26% of the size of *G. stillei* molars, while *G. camelopardalis* incisors are 21% of the size of their molars. This suggests that the incisors attributed to *G. stillei* are not unusually small. *G. stillei* incisors have considerably thinner roots than those of *G. camelopardalis*. On worn incisors (e.g., EP 618/01 and 619/01) a notch can form midway along the occlusal margin that causes these specimens to superficially resemble the bilobed canines of giraffids (Fig. 14.2). Some extant giraffes exhibit a similar wear pattern, although the notch is not as deep on any *G. camelopardalis* incisor in the AMNH collections.

Giraffa stillei canines from the Upper Laetolil Beds have a more asymmetrical crown than those attributed to *G.* aff. *jumae*, with a distal lobule that is lower and substantially longer mesiodistally than the mesial lobule (Fig. 14.3). This shape more closely recalls the typical morphology of extant giraffes.

The *Giraffa stillei* dP_4s from Laetoli are trilobed like those of extant giraffes, but lack the prominent lingual stylids observed in *G. camelopdardalis*.

Giraffa stillei P_2s are proportionately thinner buccolingually than those of extant giraffes, but resemble them in having a deep talonid basin and an elongated, buccolingually thin trigonid. P_3s from Laetoli exhibit little morphological or size variation, with the coefficients of variation for both the length and breadth of these teeth lower than in *G. camelopardalis* (Table 14.3). *Giraffa stillei* P_4s from the Upper Laetolil Beds are more variable than those of extant giraffes, with higher coefficients of variation for both the buccolingual and mesiodistal dimensions. EP 3528/00, the specimen that resembles the Lower Laetolil Beds P_4, is also unusual in having multiple stylids on its cingula, including a pronounced metastylid on the buccal cingulum.

There do not appear to be any consistent differences to separate the lower M1s and M2s of *Giraffa* species (Harris 1991). Therefore, unless a lower molar is part of an associated dental series, it is identified only as a lower molar or lower M3.

Accessory cusps are not common on the lower molars of *Giraffa stillei* other than a variably present ectostylid. Among the 22 lower M1 and M2s, there are two especially small specimens, EP 1427/98 and EP 2119/00, which are 10–15% smaller than the next smallest *G. stillei* lower molar. These specimens are nearly identical in size to a lower M2 (LAET 75-2215) in the Mary Leakey collection (Harris 1987). Earlier studies of the giraffid fossils from the 1959 Laetoli collections provisionally attributed some of the smaller specimens to *Giraffa pygmaea* (Harris 1976b), although Harris (1987) later revised this opinion. The three lower molars from Laetoli mentioned above are similar in their buccolingual breadth to the holotype of *G. pygmaea* (KNM-ER 778) but they are approximately 20% longer mesiodistally, and are probably best retained within *G. stillei*. Moreover, the smallest of the three lower molars, EP 2119/00, lacks an ectostylid, which is typically found on *G. pygmaea* lower molars (Churcher 1978; Harris 1991).

EP 1700/04 preserves M_2 and M_3 in association, with the M_3 not fully erupted. The dimensions of the M_3 clearly identify it as *Giraffa stillei*. However, the M_2 is mesiodistally longer than any other *G. stillei* specimen from Laetoli and overlaps slightly with the lower end of the *G. camelopardalis* range. It is also larger than five isolated molar specimens that were identified as *G.* aff. *jumae* (LAET 75-1491, 75-1578, 75-2207, 75-3047 and 75-3461) (Harris 1987). These molars are considerably smaller than the other specimens attributed to *G.* aff. *jumae* from Laetoli (EP 021/00, EP 1057/03 and LAET 76-3986) (Fig. 14.5). Given these data, the evidence that *G.* aff. *jumae* teeth are generally larger than those of extant giraffes, and the relative prevalence of these two taxa in the Upper Laetolil Beds, it is suggested that these five smaller molars be reassigned to *Giraffa stillei*.

To explore whether the inclusion of these smaller and larger specimens in the *G. stillei* sample from the Upper Laetolil Beds increases its intraspecific variation beyond what would be expected for a single giraffe species, the coefficients of variation (CVs) of the buccolingual and mesiodistal dimensions were calculated for all permanent postcanine teeth, other than P_2, of the three fossil giraffid species and *Giraffa camelopardalis* (Table 14.3). The CVs for the buccolingual breadth and mesiodistal length of *Giraffa stillei* lower molars are similar to, albeit slightly greater than, those of extant giraffes. Given the evidence discussed above from the type specimen of *Giraffa pygmaea* and from EP 1700/04 there does not appear to be sufficient cause to refute the single species hypothesis for the lower molars currently attributed to *Giraffa stillei*.

Most of the eight *Giraffa stillei* lower M3s recovered by EPPE from the Upper Laetolil Beds lack accessory cusps, although EP 862/03 has a prominent ectostylid and hypostylid on its buccal cingulum. EP 1078/01 is about 7% smaller than the other isolated M_3s, but it is similar in size to the M_3 in the LAET 75-563 mandible. Like the other smaller lower molars discussed above, these two specimens are mesiodistally elongated

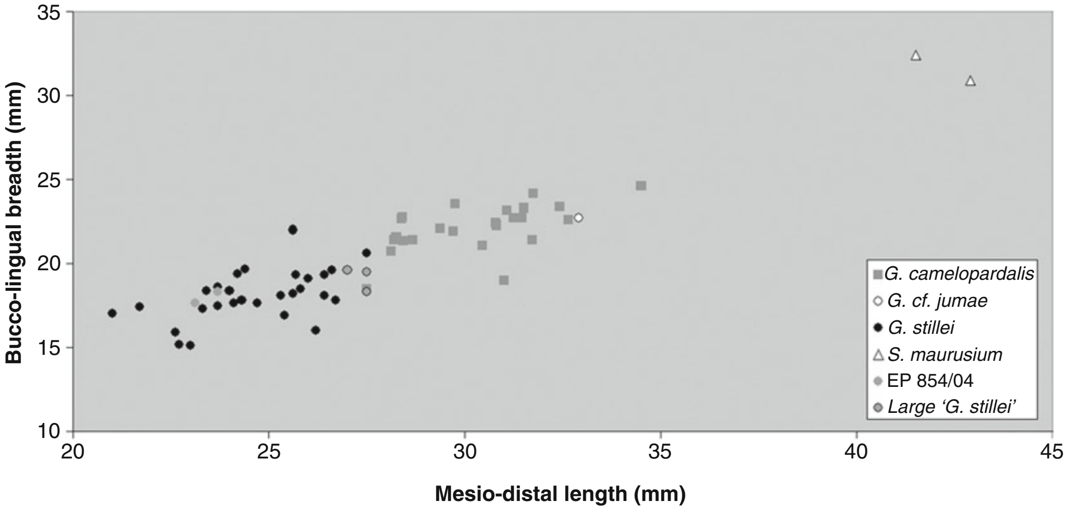

Fig. 14.5 Bivariate plot of the mesiodistal length and buccolingual breadth measurements taken on lower molars (M_1 and M_2) of giraffids from the Laetolil Beds and extant *Giraffa camelopardalis* specimens. EP 854/04 is a mandibular specimen from the Lower Laetolil Beds retaining M_1-M_3. The 'large' *Giraffa stillei* specimens are three of the lower molars identified as *Giraffa* aff. *jumae* specimens by Harris (1987) that may instead be large *G. stillei* specimens

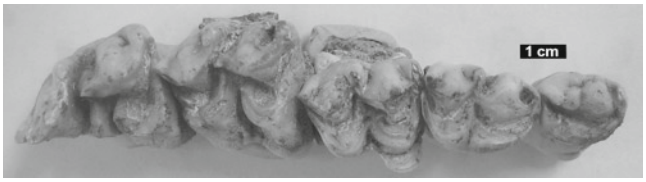

Fig. 14.6 Occlusal view of EP 1122/00, an associated series of upper teeth attributed to *Giraffa stillei* (RdP^2-M^2). Also associated with these teeth, but not pictured, is a left dP^2

compared to the M_3 of the *Giraffa pygmaea* holotype. Moreover, including these smaller molars within *G. stillei* does not result in its coefficient of variation being substantially greater than that of extant giraffes (Table 14.3).

Maxillary dentition: EP 1122/00 is an associated series of maxillary teeth of a juvenile (RdP^2-dP^4 and LdP^2), along with M^1 and M^2, attributed to *Giraffa stillei* (Fig. 14.6). These specimens were recovered from Loc. 8 and are the first deciduous maxillary teeth described from Laetoli. All the teeth are minimally worn and M^2 appears to have still been developing within its crypt. Deciduous P^{2}s of *Giraffa* resemble mesiodistally elongated permanent upper premolars and frequently have small accessory cuspules on their pronounced buccal cingula. Upper dP3s are also mesiodistally elongated, due primarily to a lengthening of the mesial cusps, but are otherwise similar morphologically to permanent upper molars. The EP 1122/00 dP^3 is notably longer mesiodistally than the other dP^3 from the Upper Laetolil Beds (EP 3599/00). Maxillary dP4s are morphologically indistinguishable from *G. stillei* upper molars, but are substantially smaller.

It is possible to divide the *G. stillei* permanent upper premolars from the Upper Laetolil Beds into two size groups. However, the coefficients of variation for the buccolingual and mesiodistal dimensions of these pooled teeth are similar to, and usually less than, those of modern giraffes (Table 14.3). This suggests that these two groups are more likely to be males and females of a single species rather than two different taxa.

Two P^{2}s, EP 398/00 and 1532/03, are distinct from the other *Giraffa stillei* specimens in having well defined mesostyles on their buccal cingula. EP 345/98, EP 347/98 and, to a lesser extent, EP 3163/00, three of the largest P^{3}s, resemble one another in having their lingual margins folded, such that they come to a point at approximately the midline of the crown. The other *G. stillei* upper P3s have a more evenly rounded lingual margin. The upper P4s exhibit less morphological variation, with the occlusal outline typically being more triangular in shape than that of P^3, due to the P^{4}s narrowing more sharply towards the lingual margin of the tooth.

There does not appear to be any consistent morphological criteria to identify the serial position of giraffid isolated upper molars (Leakey 1970; Harris 1987, 1991). Consequently, all isolated *G. stillei* specimens are simply identified, following Harris (1987), as upper molars. A small entostyle is present on two of the specimens (EP 2869/00 and EP 1667/04). The largest *G. stillei* specimens overlap in size with the smallest *G. camelopardalis* molars, but not with any *G.* aff. *jumae* specimens from Laetoli (Fig. 14.4). The coefficients of variation for the length and breadth dimensions of *G. stillei* upper molars are similar to those of *G. camelopardalis* (Table 14.3).

Sivatherium maurusium

Fifty four isolated teeth from the Upper Laetolil Beds are attributed to *Sivatherium maurusium* based on their size and greater hypsodonty compared with *Giraffa* specimens. In addition, four specimens with associated dental elements were assigned to this taxon (EP 588/00 – P_4-M_1; EP 1342/01 – M^1-M^3; EP 2324/03 – M^1-M^3; EP 1701/04 – P_4-M_1).

Sivatherium maurusium incisors are buccolingually thickened compared to those of *Giraffa*, so that when worn they have a more extensive occlusal surface area. The roots of *S. maurusium* incisors are more robust relative to the size of the crown than those of *Giraffa*. EP 1625/98 and EP 202/00 are more extensively worn on the buccal half of their crowns. In EP 1625/98 the crescent-shaped wear pattern formed is so pronounced that the apex of the crown comes to a point and the tooth is nearly worn down to the root on its buccal side (Fig. 14.2). This irregular wear pattern was not observed on any other fossil or extant giraffid incisor and could be due to a pathological condition, although the cause is difficult to determine given the lack of extant examples.

The *Sivatherium maurusium* canine, EP 498/00, resembles the incisors of this taxon in being relatively broader buccolingually than those of *Giraffa* (Fig. 14.3). In addition, the robusticity of its root matches that of the incisors. It is bilobed, with an elongated and lower distal lobule, comparable to specimens of *Giraffa stillei*, but substantially more robust. It is smaller, but otherwise resembles the canine associated with the *S. maurusium* skeleton from West Turkana (KNM-WT 16584). This is consistent with evidence suggesting that there may be an increase in the size of *S. maurusium* teeth through time (see discussion).

Sivatherium maurusium lower dP3s are longer mesiodistally both absolutely and relative to buccolingual breadth than those of *Giraffa*. Their talonids resemble those of *Giraffa* dP_3s, albeit with a mesiodistally expanded hypoconid more similar to the hypoconid of a permanent molar. Their trigonid is elongated, with a large separation on the buccal margin of the tooth between the relatively small metaconid and paraconid. Similar to the *S. maurusium* dP_3s from Ahl al Oughlam (Geraads 1996), the anterior lobe is almost closed on both specimens.

Sivatherium maurusium P_2s are elongated mesiodistally compared to those of *Giraffa camelopardalis*. They also narrow more sharply mesially, with the well developed protoconid in the midline of the tooth rather than being shifted buccally as in extant giraffes. The crest extending from the protoconid and curving lingually (Harris 1991) is weaker than in *G. camelopardalis*. The distal end of the crown is flattened compared to the more rounded and projecting distal margin of *Giraffa* P_2s (Harris 1991).

Sivatherium maurusium lower P3s typically differ from those of *Giraffa* in having a reduced trigonid, particularly the metaconid, and an expanded entoconid, although on the *S. maurusium* specimen from Laetoli (EP 206/01) the entoconid is not as pronounced, with the hypoconid dominating the talonid, leading to a buccolingually narrower tooth overall. This tooth has been described as in a more “primitive stage of molarization” than those of *Giraffa* in terms of its overall form (Geraads et al. 2004), although the lack of molarization in spite of the large size of this tooth has also been argued to be a derived feature of sivatheres (Geraads 1986).

The only identifiable *Sivatherium maurusium* P_4 recovered by EPPE was EP 588/00, a fragmentary specimen found in association with a partial M_1. The EP 588/00 teeth are relatively small, but they fall well above the range of *Giraffa camelopardalis*. Only one other *Sivatherium maurusium* lower molar was identified from the Upper Laetolil Beds (EP 695/05). This specimen is about 10% larger than the EP 588/00 M_1, but closely resembles it morphologically. While the CVs for both the buccolingual breadth and mesiodistal length of most *S. maurusium* postcanine teeth are smaller than those of extant giraffes, the coefficient of variation for the buccolingual breadth of P_4 is high (Table 14.3). This is seemingly due to the inclusion of the P_4 in the LAET 75-520 mandible, which is unusually narrow.

Sivatherium maurusium upper P3s from Laetoli exhibit similar morphological variation to that observed among *Giraffa stillei* specimens, with EP 401/04 resembling the small *Giraffa* specimens EP 345/98 and 347/98 in having a lingual margin that folds to create a point, while the other *Sivatherium* specimens have a flatter lingual margin that results in a more typically rectangular shape to their occlusal outlines. Two *Sivatherium* upper P^4s are identified, with the better preserved, but well worn, EP 1101/05 appearing to be more rectangular in shape than typical giraffid P4s, partly due to extensive wear, but also because of a glue-filled crack that distorts the lingual margin.

Two *Sivatherium maurusium* specimens, EP 1342/01 and EP 2324/03, retain all three associated upper molars, although none are well preserved. No entostyles were observed on any of the *S. maurusium* upper molars. EP 139/98 is a relatively small *S. maurusium* upper molar, but it is too broad buccolingually to be classified as *Giraffa*.

Upper Laetolil Beds Postcranial Specimens

Given the small sample sizes and range of intraspecific variation (Harris 1987; Harris 1991), it is frequently difficult to confidently attribute fragmentary and/or isolated giraffid postcranial specimens to particular species (Likius 2002). However, following comparison of the material from the Upper Laetolil Beds with extant and other fossil giraffe samples, most well preserved postcranial specimens from Laetoli were provisionally identified to species (Table 14.4). This was based primarily on size, although there are some notable differences between the postcrania of *Giraffa* and *Sivatherium* (Harris 1991; Likius 2002).

Giraffa aff. *jumae*

Two proximal radii and one distal radius are the only forelimb bones that can be provisionally attributed to *Giraffa* aff. *jumae* from Laetoli. They are similar in size and morphologically indistinguishable from those of extant giraffes.

The carpals of *Giraffa* aff. *jumae*, especially the cuneiforms, semilunars and unciforms, resemble those of *Giraffa camelopardalis*, apart from some relatively minor differences (Harris 1987). The anterolateral corner is more extensively projecting on the EP 4298/00 magnum than on specimens in the Mary Leakey collection (Harris 1987), which more closely recalls the morphology of extant giraffes. While *G.* aff. *jumae* scaphoids from Laetoli are similar in their mediolateral breadth and proximodistal width to those of extant giraffes, they are, on average, about 15% longer anteroposteriorly, partly due to a posterior extension of the bone. This gives the specimens the appearance of being mediolaterally compressed (Harris 1987).

Table 14.4 Measurements (in mm) of giraffid postcranials from the Upper Laetolil Beds

Taxon	Element	Sample size	Mean dimensions (range in parentheses)
G. aff. *jumae*	Proximal radius	2	AP – 65.9 (61.0–71.7); ML – 116.6 (111.8–121.4)
	Distal radius	1	
	Cuneiform	4	Length – 56.8 (56.1–58.3); Ant. DV – 52.9 (48.5–55.6); Post. DV – 65.5 (62.3–68.2)
	Semilunar	3	Length – 75.4 (69.0–79.5); Ant. ML – 47.7 (41.5–52.1); Ant. DV – 52.0 (50.4–53.8)
	Magnum	4	Length – 78.8 (75.3–82.2); Ant. DV – 34.4 (32.1–36.7); Post. ML – 54.2 (52.0–56.1)
	Scaphoid	10	AP Length – 75.4 (69.6–84.4); Ant. DV – 38.7 (33.7–45.5); Ant. ML – 50.1 (46.6–52.2)
	Unciform	2	Length – 70.8 (67.2–74.4); Breadth – 43.7 (42.3–45.1)
	Pelvis fragment	2	
	Fibula	1	
	Astragalus	15	Lat. Length – 104.7 (102.6–112.1); Med. Length – 91.0 (88.0–99.1)
	Calcaneum	6	Artic. ML – 89.4; t.c. AP – 60.3
	External cuneiform	1	DV – 21.8
	Naviculo-cuboid	3	ML Breadth – 97.6 (92.4–101.7); AP Length – 87.8 (84.4–91.3)
	Proximal metacarpal	1	AP – 70.4; ML – 104.2
	Proximal metatarsal	2	AP – 90.7; ML – 94.8
	Distal metapodial	10	AP – 64.3 (57.1–76.3); ML – 99.1 (91.9–106.3)
	Proximal phalanx	12	Length – 106.6 (106.1–107.1); Prox. AP – 49.5 (46.1–52.4); Prox. ML – 47.6 (43.9–52.4); Dist. AP – 33.1 (32.5–33.8); Dist. ML – 42.8 (40.8–44.9)
	Middle phalanx	4	Length – 60.0 (52.2–64.4); Prox. AP – 43.6 (43.1–47.1); Prox. ML – 42.8 (41.3–44.3); Dist. AP – 45.8 (43.7–49.5); Dist. ML – 38.4 (36.0–42.2)
G. stillei	Distal humerus	3	ML – 105.1
	Proximal radius	4	AP – 56.9 (52.7–60.8); ML – 105.3 (103.2–107.3)
	Distal radius	3	AP – 61.4 (59.1–63.7); ML – 87.9 (84.3–91.5)
	Proximal ulna	3	Artic. ML – 56.5 (55.4–58.3)
	Cuneiform	3	Length – 47.5 (46.2–48.7); Ant. DV – 40.1 (38.9–41.8); Post. DV – 54.6 (52.2–57.0)
	Semilunar	10	Length – 60.0 (57.8–62.2); Ant. ML – 37.3 (31.4–44.0); Ant. DV – 42.4 (37.0–47.7)
	Magnum	5	Length – 69.3; Ant. DV – 33.0 (31.3–33.9); Post. ML – 50.6 (50.0–51.2)
	Scaphoid	6	AP Length – 57.0 (56.1–58.6); Ant. DV – 27.9 (27.7–28.1); Ant. ML – 41.6 (40.5–43.2)
	Unciform	2	Length – 51.6 (51.3–52.0); Breadth – 40.2
	Pelvis fragment	1	Acetabulum diameter – 70.2
	Distal tibia	2	AP – 65.6; ML – 85.2 (84.6–85.8)
	Fibula	17	Length – 48.2 (44.6–52.9)
	Astragalus	57	Lat. Length – 87.3 (83.4–96.0); Med. Length – 76.5 (72.0–81.5)
	Calcaneum	37	Length – 156.8 (147.3–166.2); Artic. ML – 71.7 (64.0–80.1); t.c. AP – 48.3 (37.6–59.1); t.c. ML – 51.1 (40.0–59.1)
	External cuneiform	11	Length – 71.3; DV – 17.1 (14.6–20.0)
	Naviculo-cuboid	12	ML Breadth – 75.2 (66.7–85.2); AP Length – 71.9 (66.5–83.6)
	Proximal metacarpal	1	AP – 53.0; ML – 79.7
	Proximal metatarsal	2	AP – 69.6 (66.8–72.5); ML – 66.2 (62.3–70.2)
	Distal metapodial	27	AP – 49.5 (47.7–52.9); ML – 75.4 (73.8–80.7)

(continued)

Table 14.4 (continued)

Taxon	Element	Sample size	Mean dimensions (range in parentheses)
	Proximal phalanx	6	Length – 99.3 (94.1–102.8); Prox. AP – 46.1 (44.9–46.8); Prox. ML – 39.3 (36.5–43.2); Dist. AP – 28.2 (25.9–30.2); Dist. ML – 36.2 (30.6–43.3)
	Middle phalanx	3	Length – 48.4 (48.0–48.8); Prox. AP – 37.2 (37.2–37.3); Prox. ML – 39.0; Dist. AP – 38.0 (35.3–40.6)
S. maurusium	Cuneiform	3	Ant. DV – 58.8 (56.4–61.6); Post. DV – 74.9 (73.4–76.3)
	Semilunar	7	Length – 78.8 (74.9–81.1); Ant. ML – 53.3 (51.5–55.7); Ant. DV – 59.4 (57.3–62.9)
	Magnum	4	Length – 87.9 (87.1–88.7); Ant. DV – 37.4 (36.0–38.8); Post. ML – 56.2
	Scaphoid	6	AP Length – 93.9 (91.9–98.6); Ant. DV – 48.7 (42.7–54.1); Ant. ML – 56.2 (54.1–58.3)
	Unciform	3	Length – 69.7 (65.9–72.2); Breadth – 57.9 (57.1–58.7)
	Distal tibia	1	AP – 87.8
	Fibula	2	Length – 66.4[a]
	Astragalus	10	Lat. Length – 118.8 (114.2–120.6); Med. Length – 101.9 (98.6–104.3)
	Calcaneum	1	Artic. ML – 93.2
	External cuneiform	1	DV – 23.4
	Naviculo-cuboid	2	ML Breadth – 117.4
	Proximal metacarpal	1	AP – 81.9; ML – 114.8
	Distal metapodial	4	
	Proximal phalanx	8	Length – 135.2 (124.2–146.2); Prox. AP – 60.0 (58.4–64.1); Prox. ML – 53.1 (50.5–56.5); Dist. AP – 37.9 (35.9–39.0); Dist. ML – 49.3 (47.7–50.1)
	Middle phalanx	4	Length – 66.2 (62.7–69.6); Prox. AP – 55.9 (53.3–58.5); Prox. ML – 56.0 (52.8–59.2); Dist. AP – 54.2; Dist. ML – 49.0 (47.3–50.8)

AP anteroposterior, *DV* dorsoventral, *ML* mediolateral, *Artic. AP* anteroposterior breadth of the proximal end of the calcaneum, *t.c.* tuber calcis

[a] Estimated measurement

Table 14.5 Measurements (in mm) of all giraffid astragali recovered from the Upper Laetolil Beds and those of extant giraffes

		Mean		Standard Deviation		Coefficient of Variation	
Taxon	Sample size	Lateral	Medial	Lateral	Medial	Lateral	Medial
G. aff. *jumae*	16	107.1	93.6	6.98	5.84	0.065	0.062
G. stillei	48	86.7	76.2	3.61	2.87	0.042	0.038
S. maurusium	6	120.7	103.3	5.84	5.00	0.048	0.048
G. camelopardalis	6	100.3	88.8	6.16	4.49	0.061	0.051

No hindlimb long bone specimens of *Giraffa* aff. *jumae* were recovered by EPPE and the only fibula found was incomplete, although it does retain the relatively narrow tibial facet characterizing fossil *Giraffa* fibulae from Laetoli (Harris 1987).

Most of the giraffid postcranial specimens recovered from the Upper Laetolil Beds are carpals and tarsals (Harris 1987), with astragali making up approximately 25% of the taxonomically identifiable postcranials. Because of the large sample of astragali, measurements taken on this element can be used to compare the extent of variation in postcranial specimens of the three Laetoli giraffid taxa and *Giraffa camelopardalis*. *Giraffa* aff. *jumae* was found to have higher coefficients of variation for both lateral and medial dorsoventral lengths, while the other two fossil giraffid species had lower CVs than in *G. camelopardalis* (Table 14.5).

To explore the extent and pattern of intraspecific variation among giraffid astragali further, the medial and lateral dimensions of these specimens were graphed on a bivariate plot (Fig. 14.7) and the least-squares regression line was calculated ($y = 0.77x + 8.88$). The results show that giraffes scale consistently for these measurements ($r^2 = 0.95$), with larger giraffids, such as *Sivatherium*, having proportionately shorter lateral condyles.

The three fossil giraffid taxa from the Upper Laetolil Beds are reasonably well separated from one another, with some overlap in the ranges of *Giraffa* aff. *jumae* and *Sivatherium maurusium*. This overlap, due to four especially large *Giraffa* astragali in the Mary Leakey collection that could potentially be *Sivatherium maurusium* specimens, contributes to the higher CVs for *G.* aff. *jumae* noted above. The range of *G.* aff. *jumae* also overlaps with that of *G. camelopardalis*, but the fossil taxon has larger astragali on average.

Most of the giraffid calcanei from the Upper Laetolil Beds are distal or proximal fragments, with few preserving sufficient morphology for accurate measurements to be taken. The three fossil taxa are generally differentiated by the

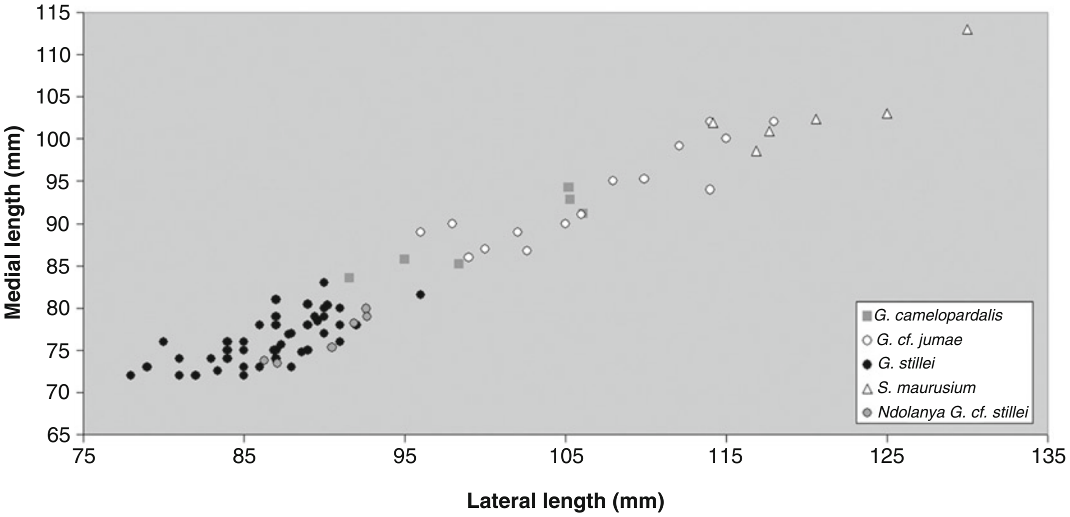

Fig. 14.7 Bivariate plot of the medial and lateral dorsoventral lengths for giraffid astragali recovered from the Upper Laetolil and Upper Ndolanya Beds and for extant *Giraffa camelopardalis* specimens

robusticity of the calcaneum, with the heel process being considerably thicker in the larger taxa. The calcanei, naviculo-cuboids and external cuneiforms of *Giraffa* aff. *jumae* from Laetoli are indistinguishable from those of extant giraffes.

Most of the distal metapodial specimens recovered from the Upper Laetolil Beds preserve only one of the condyles, which makes it difficult to attribute them to the hind- or forelimb. The identification of isolated condyles to species is equally problematic (e.g., they could either be large *G. stillei* metacarpals or small *G.* aff. *jumae* metatarsals). However, the two fossil *Giraffa* species can generally be distinguished from one another by their anteroposterior dimension and, consequently, most specimens can be tentatively identified to species. Only five giraffid metapodial specimens preserved enough of the distal end to allow for a measurement of their mediolateral breadths. The two attributed to *G.* aff. *jumae* are broad mediolaterally relative to their anteroposterior dimension and are likely to be metacarpals. These specimens are proportionately narrower anteroposteriorly than metacarpals of *G. camelopardalis*, like most of the *G.* cf. *jumae* specimens from Toros-Menalla and Kossom-Bougoudi (Likius 2002).

The three *G.* aff. *jumae* proximal metapodials, one metacarpal and two metatarsals, are larger, on average, than those of *G. camelopardalis*, but can clearly be attributed to *Giraffa*. The proximal metatarsals are differentiated from those of *Sivatherium* in having four articular facets rather than three, with *Sivatherium* lacking the posterior cuboid facet (Harris 1991).

Attributing isolated proximal phalanges, particularly the more fragmentary specimens from Laetoli, to taxon is difficult given the high levels of intraspecific variation among the various digits of the fore- and hindlimb of extant giraffes. The more complete specimens attributed to *G.* aff. *jumae* from the Upper Laetolil Beds have proportionately large proximal and distal ends relative to length compared to those of *G. camelopardalis*.

Giraffa stillei

Giraffid forelimb long bones are rare at Laetoli, and none preserve more than the proximal or distal ends. The only well preserved *Giraffa stillei* distal humerus recovered by EPPE from the Upper Laetolil Beds (EP 593/05) closely resembles in both size and morphology the two *G. stillei* distal humeri identified previously (Harris 1987). All three specimens are similar in size to female *G. camelopardalis* specimens, but with a relatively small medial condyle (Harris 1987). Two proximal radii and three distal radii are considerably smaller than those of *Giraffa camelopardalis*, but indistinguishable morphologically, and are assigned to *G. stillei*. The three similarly-sized *Giraffa stillei* ulnae recovered by EPPE are about 15% smaller in the mediolateral dimension of their humeral articular facet than LAET 75-1629, a proximal ulna in the Mary Leakey collection, which is approximately the size of an extant giraffe. These specimens likely represent female and male specimens of *G. stillei* as they share a reduced lateral facet for the radius compared to *G. camelopardalis* ulnae (Harris 1987).

Carpals of *Giraffa stillei* are relatively rare compared to other skeletal elements attributed to this taxon. Cuneiforms, unciforms and magnums of the two *Giraffa* species are similar morphologically to those of extant giraffes, differing from one another primarily in size and in the *G. stillei* specimens being somewhat less robust. Small *Giraffa* semilunars that articulate well with scaphoids attributed to *G. stillei* and have 'waisted' dorsal and ventral articular facets (Harris 1987) are placed in the smaller *Giraffa* taxon. The anteroposterior lengths of *G. stillei* scaphoids approach those of small female *G. camelopardalis* specimens, while mediolateral breadth measurements are on average about 20% smaller than those of extant giraffes, which matches previous descriptions of *G. stillei* scaphoids as being proportionately narrow (Harris 1987).

Giraffa camelopardalis tibiae exhibit considerable intraspecific variation in the anteroposterior width of the distal epiphysis compared to its mediolateral breadth. *Giraffa stillei* distal tibiae are considerably mediolaterally narrower than those of extant giraffes, but they overlap with smaller *G. camelopardalis* specimens in their anteroposterior width. The narrowness of *G. stillei* tibiae may be related to their relatively small and modestly projecting lateral condyles (Harris 1987) or to their smaller size as smaller ruminants are thought to typically have proportionately smaller mediolateral dimensions (D. Geraads, personal communication).

Of the giraffid fibula specimens recovered from the Upper Laetolil Beds, 85% are attributed, based on size, to *Giraffa stillei*.

Tarsals of *Giraffa stillei* are much more common at Laetoli compared to those of the other two fossil giraffid taxa. For example, over twice as many *G. stillei* astragali were recovered than those of the other two taxa combined. One *G. stillei* astragalus has an unusually long lateral condyle, but otherwise the specimens are quite similar to one another morphologically and they cluster tightly together when comparing their medial and lateral lengths (Fig. 14.7). Over five times as many calcanei were identified as *Giraffa stillei* than those attributed to the other two giraffids combined. Although they exhibit a large variation in size, like extant giraffes, all *G. stillei* calcanei are considerably smaller than those of *G. camelopardalis*. EP 662/00 is notably smaller than the other well preserved *Giraffa stillei* calcanei, particularly in the robusticity of its heel process, but is similar in size to LAET 76-3678 from the Mary Leakey collection (Harris 1987). The size and morphology of the tuber calcaneum is quite variable in *G. stillei*, with the morphology of some larger specimens resembling that of extant giraffes. As in the other tarsal elements, there is a substantially larger sample of *Giraffa stillei* external cuneiforms from the Upper Laetolil Beds than those of the other two taxa. However, only one *G. stillei* specimen (EP 144/98) is complete enough for a measurement of anteroposterior length and, while this dimension overlaps with the lower end of the extant giraffe size range, it is about 10% smaller than the mean for *G. camelopardalis*, and it articulates well with *G. stillei* naviculo-cuboids. Moreover, like *G. stillei* specimens in the Mary Leakey collection (Harris 1987), the metatarsal facets on the external cuneiform are almost continuous. There are slight differences among the three fossil taxa in the dorso-ventral breadth of their external cuneiforms, but the range of *G. stillei* for this measurement was extensive, and substantially overlapped the range of extant giraffes. The naviculo-cuboids follow the same pattern of relative abundance as the other tarsals, with considerably more *Giraffa stillei* specimens recovered than those of the other giraffids. The *G. stillei* specimens are mediolaterally narrower relative to their anteroposterior length than *G.* aff. *jumae* and *Giraffa camelopardalis* naviculo-cuboids, which is likely related to a mediolaterally reduced calcaneal facet. As Harris (1987) noted, the facet for articulation with the medial edge of the calcaneum does not extend posterior to the facet for the lateral trochlea of the astragalus in most of the *G. stillei* specimens from Laetoli.

Three *Giraffa stillei* distal metapodials are complete enough to identify one as a metatarsal and the other two as metacarpals. The metatarsal, EP 495/01, has both the proximal and distal ends preserved, but is missing about one-third of the shaft of the bone. It is also associated with a naviculo-cuboid specimen that is fused to the external cuneiform. The metatarsal shaft is typical of giraffine metapodials in being long and slender with a shallow posterior trough (Solounias 2007).

Giraffa stillei proximal phalanges are proximodistally shorter than those of extant giraffes but, as in *G.* aff. *jumae* specimens, they have proportionately large proximal and distal ends. Three middle phalanges are considerably smaller than those of *Giraffa* aff. *jumae* and, although they overlap with the lower end of *G. camelopardalis* size range for both length and the size of their proximal and distal ends, they are tentatively placed in *G. stillei*.

Sivatherium maurusium

Unlike at Koobi Fora (Harris 1991), massive postcranial specimens have been recovered from the Upper Laetoli Beds that seem likely to represent *S. maurusium* rather than extremely large *Giraffa* aff. *jumae* specimens.

The carpals attributed to *Sivatherium maurusium* from Laetoli are generally larger and more robust than those of *Giraffa*. None of the *S. maurusium* cuneiforms recovered by EPPE are complete, but they are substantially more robust than any *Giraffa* specimen and they articulate well with unciforms attributed to this taxon. The anteroposterior lengths of the *Sivatherium maurusium* semilunars overlap with those of large *Giraffa* specimens, while the breadth of these elements clearly separate specimens of the two genera from one another. Dorsoventral breadth measurements on magnums were not effective in differentiating giraffid taxa, and

S. maurusium and *G.* aff. *jumae* were also similar in their mediolateral dimension. Since *S. maurusium* had a substantially longer magnum than *G.* aff. *jumae*, this indicates that either *Giraffa* has a relatively broad magnum (Harris 1991) or *S. maurusium* has a proportionately longer magnum. No evidence of a longitudinal groove in the scaphoid facet (Harris 1987) was noted on the *S. maurusium* magnum recovered by EPPE (EP 3918/00). *Sivatherium maurusium* scaphoids are extremely robust compared to those of *Giraffa* and considerably larger in all dimensions. The proximal (radial) facet on the scaphoid is more excavated on *Sivatherium* specimens than on those of *Giraffa*, although a relatively deep facet has also been observed on some *G.* aff. *jumae* specimens (Harris 1987) and one *G. stillei* specimen (EP 1128/04). *S. maurusium* unciforms are similar to those of *G.* aff. *jumae* in their anteroposterior length, but considerably broader mediolaterally seemingly due to a mediolaterally expanded semilunar facet.

One *Sivatherium maurusium* partial distal tibia was recovered by EPPE (EP 402/00). It does not appear to be especially anteroposteriorly compressed compared to *Giraffa* tibiae like specimens from Koobi Fora (Harris 1991), although its mediolateral dimension could not be accurately measured due to incomplete preservation. The one sivathere fibula recovered by EPPE (EP 668/98) resembles those from the Mary Leakey collection in having a relatively broad tibial facet, but its spine projects upwards like *Giraffa* fibulae and not outwards like the other *S. maurusium* specimens from Laetoli (Harris 1987).

Well preserved tarsals of *Sivatherium maurusium* are relatively rare. Astragali of *S. maurusium* are notably more robust and larger than those of the two *Giraffa* species. Differences between this taxon and *Giraffa* in the morphology of the two trochleae that were noted on Koobi Fora specimens (Harris 1991) were not observed on these substantially larger *Sivatherium* astragali from Laetoli. Likius (2002) has argued that these characters are extremely variable in both genera and differentiating isolated astragali to genus based exclusively on them would be difficult. There was also a difference in the relative lengths of the medial and lateral condyles of *Sivatherium* and *Giraffa* astragali from Koobi Fora (Harris 1991). At Laetoli the disparity is less pronounced. *Sivatherium maurusium* has a lateral condyle that is about 17% longer on average than the medial condyle, while it averages about 14–15% longer on *Giraffa* astragali. The *S. maurusium* naviculo-cuboid from the Upper Laetolil Beds (EP 1885/03) can be differentiated from those of *Giraffa* by its massive size and reduced posterior ridge (Harris 1991), which leads to an anteroposteriorly narrower bone overall. Adhering matrix makes it difficult to assess the morphology of the articular facets. The *S. maurusium* calcaneum (EP 2543/00) recovered by EPPE only preserves the proximal end and has a large and saddled-shaped astragalar facet, with its medial margin extending further distally than on *Giraffa* specimens from Laetoli.

All *Sivatherium maurusium* distal metapodials recovered by EPPE from the Upper Laetolil Beds are fragments, but they appear to correspond to previous descriptions of these elements in being anteroposteriorly compressed with proportionately wide epiphyses (Harris 1976a, 1991). The epiphysis of the *Sivatherium maurusium* proximal metacarpal recovered by EPPE (EP 3604/00) was anteroposteriorly wider relative to its mediolateral breadth than *Giraffa* specimens, leading to a squarer outline to its articular surface. This is likely related to the medial and lateral facets remaining distinct on the articular surface of the *S. maurusium* specimen (Harris 1976a, 1991).

Sivatherium maurusium proximal and middle phalanges from the Upper Laetolil Beds are notable for having substantially enlarged proximal and distal ends compared to *Giraffa camelopardalis* specimens of similar length. This is consistent with descriptions of *Sivatherium* phalanges as being relatively short compared to those of *Giraffa* (Likius 2002).

Upper Ndolanya Beds

Sixty-two giraffid specimens were recovered from the Upper Ndolanya Beds by EPPE (Table 14.6). Since no diagnostic specimens have been found from this unit, species designations should be considered provisional. However, all three of

Table 14.6 Upper Ndolanya Beds giraffid specimen numbers at each locality

	Giraffa aff. *jumae*			*Giraffa* aff. *stillei*			*Sivatherium* aff. *maurusium*		
Locality	Dental	Postcranial	Total	Dental	Postcranial	Total	Dental	Postcranial	Total
7E	0	1	1	3	6	9	0	0	0
15	0	4	4	0	13	13	1	0	1
18	0	3	3	0	15	15	3	0	3
22S	0	2	2	1	2	3	0	0	0
Silal Artum	0	0	0	0	6	6	0	0	0
Totals	0	10	10	4	42	46	4	0	4

the giraffid taxa from the Upper Laetolil Beds, along with *Giraffa pygmaea*, appear to be represented in the Upper Ndolanya Beds.

Upper Ndolanya Beds Dento-Dnathic Specimens

Seven isolated giraffid teeth were recovered from the Upper Ndolanya Beds, with none of the specimens well preserved. Four fragmentary teeth, including one dP$_4$, were attributed to *Giraffa* aff. *stillei* (Table 14.7). All three of the permanent teeth are morphologically indistinguishable from, but larger than, the average *G. stillei* specimen from the Upper Laetolil Beds, although none overlapped with the size ranges of *G.* aff. *jumae* teeth.

One giraffid partial M$_3$ and two upper molar fragments were attributed to *Sivatherium* aff. *maurusium* because of their massive size and degree of hypsodonty. In addition, a rolled and fragmented partial mandible of *S.* aff. *maurusium* that retains the broken crowns of P$_4$-M$_2$ (EP 1040/00) was recovered from Loc. 18 (Fig. 14.8). The teeth in this specimen only preserve enough morphology to estimate their size. Based on these estimates, the mesiodistal length and buccolingual breadth of M$_1$ and M$_2$ are greater than those of the largest *S. maurusium* specimen known from the Upper Laetolil Beds. The mandible is more robust and approximately 40% deeper than the LAET 75-520 specimen from

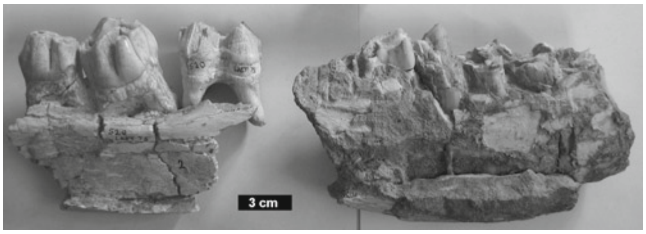

Fig. 14.8 Buccal view of the *Sivatherium maurusium* mandibular specimens LAET 75–520 from the Upper Laetolil Beds and EP 1040/00 from the Upper Ndolanya Beds

Table 14.7 Measurements (in mm) of giraffid specimens from the Upper Ndolanya Beds

Taxon	Element	Sample size	Mean dimensions (ranges in parentheses)
G. aff. *jumae*	Glenoid of scapula	1	Length – 94.3; Breadth – 79.6
	Proximal radius	1	AP – 71.9; ML – 113.6
	Distal radius	2	AP – 76.5; ML – 115.6
	Magnum	1	
	Distal tibia	1	AP – 67.7; ML – 92.7
	Calcaneum	1	Artic. ML – 75^{a}
	Naviculo-cuboid	1	ML Breadth – 91.3; AP Length – 84.5
	Distal metapodial	2	
G. aff. *stillei*	Lower dP4	1	
	Lower molar	1	MD – 26.0
	Upper P2	1	BL – 19.9
	Upper molar	1	MD – 25.3
	Glenoid of scapula	2	Length – 69.1; Breadth – 67.5
	Distal humerus	1	
	Cuneiform	1	Length – 46.8; Post. DV – 55.2
	Magnum	1	Length – 69.9; Post. ML – 47.8
	Scaphoid	1	AP Length – 67.8; Ant. ML – 41.4
	Distal tibia	3	AP – 64.6 (60.2–68.0); ML – 81.7
	Astragalus	10	Lat. Length – 90.2 (86.3–92.7); Med. Length – 77.4 (73.5–80.6)
	Calcaneum	4	t.c. AP – 43.0
	External cuneiform	1	DV – 18.5
	Naviculo-cuboid	2	ML Breadth – 76.6 (72.8–80.5); AP Length – 75.0 (66.5–83.6)
	Distal metapodial	5	AP – 47.7; ML – 80.7
	Proximal phalanx	10	Length – 95.4 (92.4–98.0); Prox. AP – 45.0 (43.2–46.3); Prox. ML – 43.3 (41.2–47.1); Dist. AP – 29.3 (28.5–30.3); Dist. ML – 41.8 (40.2–43.6)
	Middle phalanx	1	Length – 47.5; Prox. AP – 44.9; Prox. ML – 41.5; Dist. AP – 40.9; Dist. ML – 42.1
S. aff. *maurusium*	Mandible with P4-M2	1	Depth at P4/M1 – 73.7; Depth at M1/M2 – 82.8; M1: BL – 36.3^{a}; MD – 48.5^{a}; M2: BL – 35.0^{a}; MD - 50.1^{a}
	Lower M3	1	
	Upper Molar	2	

BL buccolingual breadth, *MD* mesiodistal length, *AP* anteroposterior, *DV* dorsoventral, *ML* mediolateral, *Artic. AP* anteroposterior breadth of the proximal end of the calcaneum, *t.c.* tuber calcis

[a] Estimated measurement

the Mary Leakey collection. While this could be attributed to sexual dimorphism, the difference is quite striking, particularly given that the depth of the LAET 75-520 mandible is artificially increased by crushing and, in spite of its poor preservation, this does not appear to be true of the EP 1040/00 mandible.

No cranio-dental specimens of *Giraffa* aff. *jumae* were identified among the giraffids from the Upper Ndolanya Beds. Harris (1987) assigned one dental specimen from Loc.14 to that taxon, but did not provide further details or metric data, which would suggest that it is an incomplete specimen.

Upper Ndolanya Beds Postcranial Specimens

Giraffa aff. *jumae*

Ten postcranial specimens are provisionally assigned to *Giraffa* aff. *jumae* pending recovery of cranio-dental elements that can be attributed to that taxon or another giraffid of similar size (Table 14.7). EP 3440/00 is a glenoid of a scapula that is similar in size to those of large male extant giraffes, although its articular surface is relatively narrow and, consequently, more ovoid. A proximal radius, EP 3434/00, is approximately the same size as those of extant giraffes and *G.* aff. *jumae* specimens from the Upper Laetolil Beds, but it is unusually wide anteroposteriorly compared to its mediolateral breadth. Two distal radii are similar in both size and morphology to large male *G. camelopardalis* specimens. A distal tibia (EP 1224/00) approximates the average size and typical morphology of female *G. camelopardalis* specimens, and is considerably broader mediolaterally than *G. stillei* specimens from Laetoli. A matrix encrusted and fragmentary proximal calcaneum (EP 1203/03) is similar in its robusticity to *G.* aff. *jumae* specimens from the Upper Laetolil Beds. A naviculo-cuboid (EP 1685/03) from the Upper Ndolanya Beds is approximately the same size as the smallest *G.* aff. *jumae* specimen from the Upper Laetolil Beds. It is considerably larger than any *G. stillei* specimen and does not share a reduced calcaneal facet with those specimens.

Giraffa aff. *stillei*

Forty two postcranial specimens recovered from the Upper Ndolanya Beds were assigned to *Giraffa* aff. *stillei*. These fossils comprise approximately 75% of the giraffid specimens collected by EPPE from this unit. Much of this material, including a distal humerus, is relatively fragmentary and is tentatively assigned to this taxon based on similarities to specimens from the Upper Laetolil Beds. Two scapular glenoids are smaller than, but indistinguishable morphologically from, those of extant giraffes.

Three carpals are attributed to *Giraffa* aff. *stillei*, with the cuneiform and magnum similar in size and morphology to those from the Upper Laetolil Beds. A scaphoid (EP 4003/00) is provisionally assigned to this taxon due to its being relatively narrow mediolaterally compared to *Giraffa camelopardalis* and *Giraffa* aff. *jumae* specimens, like the Upper Laetolil Beds *G. stillei* scaphoids, although it is over 15% longer anteroposteriorly than any *G. stillei* specimen from that unit.

Three distal tibiae were recovered that are morphologically similar to *Giraffa stillei* specimens from the Upper Laetolil Beds in being proportionately narrower mediolaterally than those of extant giraffes with a less protuberant lateral condyle.

Just as in the Upper Laetolil Beds, a large proportion, over 40%, of the postcranial specimens attributed to *Giraffa* aff. *stillei* from the Upper Ndolanya Beds are tarsals. Most of these specimens are astragali, and in general they fall within the upper end of the Upper Laetolil Beds *G. stillei* size range (Fig. 14.7). A number of *G.* aff. *stillei* astragali from the Upper Ndolanya Beds have a noticeably thicker medial condyle than specimens from the Laetolil Beds. All of the *G.* aff. *stillei* external cuneiforms and calcanei are fragmentary, although one calcaneum, EP 3286/00, retained parts of its proximal and distal ends and was associated with the smallest astragalus from this unit. One of the naviculo-cuboids, EP 1327/05, preserves a relatively broad articular facet for the medial condyle of the astragalus, which corresponds with the thicker medial condyles of the astragali mentioned above. Like many of the *G. stillei* specimens from the Upper Laetolil Beds it lacks a medial extension of the calcaneal facet.

Only one of the distal metapodial specimens attributed to *Giraffa* aff. *stillei* preserved enough morphology for the mediolateral breadth of the epiphysis to be measured and it is likely to be a metatarsal.

The relatively large number of *Giraffa* aff. *stillei* proximal phalanges from the Upper Ndolanya Beds generally have larger proximal and distal articular surfaces, but are dorsoventrally shorter, than *G. stillei* specimens from the Upper Laetolil Beds. A dorsoventrally short middle phalanx recovered from the Upper Ndolanya Beds also has relatively enlarged proximal and distal ends compared to *G. stillei* specimens from the Laetolil Beds. Based on the dimensions of the proximal phalanges from these strata, it is tentatively assigned to *G.* aff. *stillei*, although it may represent a dorsoventrally shortened *G.* aff. *jumae* specimen.

No postcranial specimens were recovered by EPPE from the Upper Ndolanya Beds that could be attributed to *Sivatherium* aff. *maurusium*, although four specimens of this taxon were listed as having been recovered from Loc. 7E by Harris (1987).

Additional Specimen from the Upper Ndolanya Beds

During an examination of the giraffid material recovered by Kohl-Larsen's team that is currently housed at the Museum für Naturkunde in Berlin, Terry Harrison noted an unusually small mandibular specimen retaining P_3-M_3 (MB Ma. 39792) that is likely to be derived from the Upper Ndolanya Beds (annotations on the specimen indicate that it was recovered from the Gadjingero, which is equivalent to Mary Leakey's collecting Loc. 18) and was identified as "*Okapia* 2 sp." (Fig. 14.9). The dimensions of all teeth are smaller than those of the holotype of *Giraffa pygmaea* (KNM-ER 778) with the M_2 nearly identical in size to two M_1s attributed to that species from Olduvai (Harris 1976b). As is typical for specimens of that taxon (Churcher 1978; Harris 1991), ectostylids are present on all three molars and there is a hypostylid on M_3. MB Ma. 39792 lacks an entostylid, present on the *G. pygmaea* M_3s from Koobi Fora. However, as discussed below, this appears to be a variable character found on some *G. stillei* specimens as well. The mandible is shallow, as in the type specimen of *G. pygmaea*, although the Laetoli specimen deepens posteriorly. Since only a tiny fragment of the mesiobuccal corner of the P_3 crown remains and P_4 is missing much of the mesial portion of the tooth, it is not possible to determine whether the specimen possesses the diagnostic premolar morphology of *Giraffa* (Harris 1976b, 1987). However, there are no known Pliocene *Okapia* fossils (Churcher 1978), while *Giraffa pygmaea* is present at a number of East African Pliocene sites (Harris 1991; Kullmer et al. 2008; Reed 2008). Thus, it seems likely that this specimen represents *Giraffa*. Since *Giraffa stillei* is diagnosed as a species with teeth that are "always" larger than those of *Giraffa pygmaea* (Harris 1991, 2003), this specimen cannot be attributed to the former taxon. Based on the size and morphology of its dental elements, MB Ma. 39792 is provisionally assigned to *Giraffa* aff. *pygmaea*.

Fig. 14.9 Occlusal and buccal views of the *Giraffa* aff. *pygmaea* mandibular specimen (MB Ma. 39792) from "Gadjingero", which is thought to correspond to Loc. 18 in the Upper Ndolanya Beds

Discussion

Lower Laetolil Beds

Giraffa aff. *stillei*

The Lower Laetolil Beds are dated to between 3.8 and older than 4.3 Ma and they could date to as old as 4.6 Ma (Drake and Curtis 1987; Su and Harrison 2007). If *Giraffa stillei* can be confirmed from these strata, it would represent one of the earliest known occurrences of this taxon in East Africa. This species has also been identified from the Apak Member at Lothagam, Kanapoi, and, provisionally, Aramis; three East African sites that are of similar age to the Lower Laetolil Beds (WoldeGabriel et al. 1994; Harris 2003; Harris et al. 2003). The specimens thus far recovered from the Lower Laetolil Beds appear to be typical of the species and closely resemble those found in the Upper Laetolil Beds.

Sivatherium

Two *Sivatherium* species have been identified from sites dated to the late Miocene and early Pliocene, *Sivatherium maurusium* and *Sivatherium hendeyi*. The latter is known from earlier sites and considered to be more primitive in its ossicone morphology (Harris 1976a; Likius 2002), although some researchers have argued that the differences between the two species represent intraspecific variation (Churcher 1978).

Most of the earliest fossils attributed to *Sivatherium* from sub-Saharan Africa cannot be identified to species because of the lack of diagnostic cranial specimens or complete metapodials. The earliest well documented *Sivatherium* specimens in East Africa come from the Middle Awash in Ethiopia, dated to between 5.2 and 5.8 Ma (Haile-Selassie et al. 2004). A fragmentary lower molar from the late Miocene/early Pliocene Nkondo Formation in the Albertine Rift Valley of Uganda also appears to represent *Sivatherium* (Geraads 1994). *Sivatherium* may also be present in the late Miocene Lower Nawata Formation at Lothagam, although this is based on only one large distal metapodial (Harris et al. 1988). Finally, Gentry (1997) has tentatively identified *Sivatherium* from the early Pliocene site of Kiloleli 2 in the Manonga Valley. *Sivatherium hendeyi* is best known from the early Pliocene site of Langebaanweg, in South Africa, where it is the most common artiodactyl in the faunal assemblage (Harris 1976a; Franz-Odendaal et al. 2003), but it has also been provisionally identified on the basis of what was described as an "ossicone fragment" at Kanapoi (Harris et al. 2003). The *Sivatherium* mandibles and postcranial material from the late Miocene and early Pliocene sites of Toros-Menalla and Kollé in Chad are provisionally assigned to that species as well, based primarily on the metapodial specimens being elongated compared to those of *S. maurusium* (Likius 2002; Vignaud et al. 2002), which is one of the diagnostic characters of *S. hendeyi*. Thus, it appears that both *Sivatherium* species are present in Africa by the early Pliocene, although the first diagnostic evidence of *S. maurusium* in sub-Sarahan Africa is from the Upper Laetolil Beds. Since the only evidence for *Sivatherium* so far recorded from the Lower Laetolil Beds is an isolated P^4, and these species are not distinguishable by their dental morphology (Harris 1976a; Harris 2003; Likius 2002), the specimen is provisionally identified as *Sivatherium* sp.

Giraffidae indet.

The magnum recovered from the Lower Laetolil Beds is substantially larger than those attributed to *Giraffa stillei* from Laetoli, and is not proportionately elongated like the *Sivatherium maurusium* specimens from the Upper Unit. It is approximately the size of *Giraffa* aff. *jumae* specimens from the Upper Laetolil Beds and could potentially be attributed to that taxon, although the shape of its scaphoid facet is unusual. *Giraffa jumae* has been identified from the late Miocene and early Pliocene sites of Kanapoi, Langebaanweg, and, provisionally, Aramis and the various Mio-Pliocene sites in the Djourab Desert of Chad (Harris 1976a; WoldeGabriel et al. 1994; Likius 2002; Harris et al. 2003). However, *Palaeotragus* is also known from late Miocene and early Pliocene sites, including the Upper Nawata Formation at Lothagam, the Middle Awash and, provisionally, the Pelletal Phosphorite Member at Langebaanweg (Churcher 1978, 1979; Hendey 1981; Harris 1991, 2003; Franz-Odendaal et al. 2003; Haile-Selassie et al. 2004). There is also a giraffid maxilla recovered from Asbole (below the "top conglomerate" fossils), that Geraads and colleagues (2004) speculate could possibly be a Pliocene palaeotragine based on differences in the premolar morphology between this specimen and those of *Giraffa* species. Finally, Geraads (1985) argued that an anterior ossicone from the Pelletal Phosphorite Member at Langebaanweg, attributed by Harris (1976a) to *S. hendeyi*, is probably instead a palaeotragine. *Palaeotragus germaini* Arambourg, 1959 the largest known species within this genus (Harris et al. 2003), is not substantially smaller than extant giraffes (Churcher 1978, 1979; Harris 2003) and has "characteristically giraffid" limb bones (Churcher 1978). While Harris and colleagues (2003) argue that sivatheres and giraffines replaced palaeotragines at the end of the Miocene, it is conceivable that some late surviving members were present in the Lower Laetolil Beds and at Asbole and Langebaanweg. Consequently, it seems prudent to not assign this specimen to a genus at this time.

Upper Laetolil Beds

In the Mary Leakey collections from the Upper Laetolil Beds *Giraffa stillei* specimens are approximately twice as common as *G.* aff. *jumae* specimens, while there are about 60% more specimens of the large *Giraffa* taxon than those attributed to *Sivatherium maurusium* (Harris 1987). During the 1998–2005 field seasons EPPE recovered three times as many *G. stillei* specimens as *G.* aff. *jumae* specimens (Table 14.2). While more specimens were attributed to *G.* aff. *jumae* by EPPE than to *Sivatherium maurusium*, the difference in their numbers was not as substantial as in the Mary Leakey collection.

Previously either *Giraffa* aff. *jumae* or *Sivatherium* was the most common giraffid at 8 of the 25 Upper Laetolil localities (Harris 1987). When the specimens recovered by EPPE from the 28 currently recognized localities where giraffids have been found in the Upper Laetolil Beds are added to these totals, *G.* aff. *jumae* is the most common species only at Localities 4 and 12 (Table 14.2). However, three *Giraffa stillei* fossils were recovered when collections from Locs. 12 or 12E were combined, and if these are added to the totals from Locality 12 then *G.* aff. *jumae* would no longer be the most common species at that locality. There are no localities at which *Sivatherium* is the most common taxon, although the only giraffids recovered from Loc. 24 were one *S. maurusium* and one *G.* aff. *jumae* specimen. Thus, there are only three out of 28 localities in the Upper Laetolil Beds at which *G. stillei* is not the most prevalent taxon. These three sites are among the least productive sites for giraffids (and mammals in general) in the Upper Laetolil Beds, suggesting that the relative numbers of giraffids at these localities may not be representative due to inadequate sampling.

Some unusual preservational patterns were observed among the giraffid fossils recovered from the Upper Laetolil Beds. First, postcranial remains were more common than dental specimens only for *Giraffa* aff. *jumae*, although the difference between the three giraffid taxa with respect to this ratio was not as extreme as previously recorded (Harris 1987). It is not readily apparent why there is a persistent difference between *G.* aff. *jumae* and the other two giraffid taxa in the proportion of postcranial specimens. Second, a comparison of the relative numbers of podials from the Upper

Laetolil Beds shows that almost three times as many *Giraffa stillei* tarsals were recovered than those of the other two giraffid taxa combined, while for the carpals there have been fewer *G. stillei* specimens found than those of the other two taxa. This does not appear to be due to search image bias as two different teams working a number of years apart produced similar results (Harris 1987). It seems unlikely, given the similarities in the overall density of these bones that this is due to a greater fragility of *G. stillei* carpals compared to tarsals. Another possibility is that carnivores were preferentially consuming the forelimbs of the smaller *G. stillei* individuals. However, 11 of the 16 forelimb long bones recovered from the Upper Laetolil Beds were attributed to *G. stillei*, which suggests that carnivore predation is unlikely to be the causal factor.

Giraffa aff. *jumae*

Giraffa jumae and *Giraffa camelopardalis* are distinguished from one another primarily based on cranial morphology (Harris 1987, 1991; Geraads et al. 2004). However, a few additional differences between these two taxa were provisionally identified above. These include *G. jumae* having: (1) bilobed lower canines that are lower crowned, with mesial and distal lobules that are more evenly rounded and more similar in shape to one another; (2) relatively buccolingually broad upper molars (see discussion below) and; (3) metacarpals that are relatively narrow anteroposteriorly.

The teeth of *Giraffa jumae* have been described as similar in size to the largest extant giraffe males (Leakey 1965, 1970; Harris 1976b; Churcher 1978), and Harris (1987) previously stated that the lower molars of *Giraffa* aff. *jumae* from the Upper Laetolil Beds are buccolingually broader than those of extant giraffes. However, it seems likely that he was referring to the upper molars, rather than the lowers, since, as mentioned above, five of the six M_1s and M_2s in the Mary Leakey collection are smaller than those of *G. camelopardalis*, while the upper molars from the Upper Laetolil Beds are relatively broad compared to those of extant giraffes. Measurements taken on *G. jumae* upper molars from Koobi Fora and Bed II at Olduvai housed at the National Museum of Kenya are similar to those from Laetoli. Published data indicate that *G. jumae* specimens from Langebaanweg, Kanjera and the type specimen from Rawe also have proportionately broader upper molars than extant giraffes (Harris 1976a, b). When all available data on *Giraffa jumae* specimens are pooled, their upper molars are found to be significantly broader (Student's two-tailed *t*-test; $p<0.0001$), approximately 15% broader on average, than those of *G. camelopardalis*, while there is no significant difference ($p=0.08$) between the mesiodistal lengths of these teeth. Data from Laetoli and Langebaanweg astragali suggest that *G. jumae* is also larger than *G. camelopardalis* postcranially, with the medial and lateral condyles significantly longer in the fossil taxon ($p<0.01$).

Unlike *G. stillei* (see below), there is no apparent trend for *Giraffa jumae* to increase in dental size through time. It is more difficult to assess whether a change occurred in the size of the postcranial elements, given the problems with being confident about the taxonomic attribution of isolated giraffid postcranial bones at many sites. Harris (1991) suggests that this possible stasis in size may be because potential food sources, such as *Acacia* trees, place an upper size limit on giraffes, which *Giraffa jumae* may have reached.

Giraffa stillei

While most of the *Giraffa stillei* from the Upper Laetolil Beds are quite similar to specimens attributed to that taxon from other East African sites, a few smaller lower molars could potentially be derived from a fourth, smaller giraffid species, possibly *Giraffa pygmaea*. It is not uncommon for the two smaller *Giraffa* species to co-occur. *Giraffa stillei* is known from many East African Pliocene sites including Hadar, Kanapoi, Koobi Fora, Lothagam, Omo and South Turkwel (Harris 1976b, c, 1991, 2003; Ward et al. 1999; Harris et al. 2003; Reed 2008), while *Giraffa pygmaea* has been identified at Hadar, Koobi Fora, Omo and, provisionally, Galili (Harris 1991; Kullmer et al. 2008; Reed 2008). As discussed above, the smaller dental specimens from the Upper Laetolil Beds are substantially longer mesiodistally than those of the holotype of *G. pygmaea*, and the smallest of them lacks an ectostylid, which has been observed on other lower molars attributed to that species (Churcher 1978; Harris 1991). Since these two *Giraffa* species are distinguished dentally primarily by size, the data suggest that the lower molars from the Upper Laetolil Beds should all be retained within *G. stillei*.

There is an M_3 from Koobi Fora attributed to *Giraffa pygmaea* (KNM-ER 3912) that is substantially larger than the type specimen and is similar in its mesiodistal and buccolingual dimensions to typical *Giraffa stillei* M_3s from Laetoli (Harris 1991). It seems that this specimen was placed in *G. pygmaea* because the *G. stillei* teeth from Koobi Fora are considerably larger than those from Laetoli, and that this specimen is much smaller than any *G. stillei* M_3 from Koobi Fora. KNM-ER 3912 has an extra cusp joining the posterior arm of the entoconid with the hypoconulid that has been suggested to be potentially a characteristic of *G. pygmaea* (Harris 1991). This appears to be an entostylid and is present on one of the smaller M_3s from Laetoli (LAET 75-563), but not the other (EP 1078/01). This cuspid is also observed on the largest isolated *G. stillei* M_3 from Laetoli, EP 862/03, the M_3 on the mandible from the Lower Laetolil

Beds, and the lectotype of *G. stillei* (MB Ma. 39078), which suggests that it is a variable feature on smaller *Giraffa* M_3s.

Upper Ndolanya Beds

Giraffa aff. *stillei* is the most common taxon at all of the Upper Ndolanya Beds localities other than Loc. 22S, from which only five giraffid specimens were recovered. The taxon makes up an even greater proportion of the total number of giraffids recovered from these strata than in the Upper Laetolil Beds, as noted previously (Harris 1987), with there being over three times as many *G.* aff. *stillei* specimens recovered than the other two giraffids combined.

Giraffa aff. *jumae*

Given the additional large-bodied *Giraffa* postcranial fossils recovered by EPPE, it seems probable that *Giraffa jumae* was present in the Upper Ndolanya Beds, although without cranial specimens to confirm its taxonomic identity, it is possible that the material represents *Giraffa camelopardalis*. It is also possible that some of the larger postcranial specimens could be attributed to *Sivatherium*, particularly with the documented reduction in the size of the *Sivatherium maurusium* postcrania in the late Pliocene (Harris 1976b, 1991; Harris et al. 1988; Geraads 1996) and the lack of more than a few fragmentary sivathere postcrania identified from the Upper Ndolanya Beds. However, until further, more complete specimens are recovered, it will be difficult to resolve this issue. Therefore, because of their size and overall morphological similarities to *Giraffa*, the specimens are provisionally retained in *Giraffa* aff. *jumae*.

Giraffa aff. *stillei* and *Giraffa* aff. *pygmaea*

If the same species is present in the Upper Laetolil Beds and the Upper Ndolanya Beds, it appears that *Giraffa stillei* increased in size through time at Laetoli. The dimensions of all teeth that could be measured from the Upper Ndolanya Beds are larger than the means of those from the Laetolil Beds. In addition, the average sizes of the two postcranial elements with relatively large samples from the Upper Ndolanya Beds, astragali and proximal phalanges, are greater than those of specimens from the Upper Laetolil Beds. This seems to have been a general trend for *G. stillei* in East Africa, with dental specimens from Koobi Fora and Omo being larger than those from the Laetolil Beds, Kanapoi and Lothagam (Harris 1976b, 1987, 1991, 2003; Harris et al. 2003). The difference was notable enough for the more recent specimens from Koobi Fora and Omo to have been initially placed into a different species, *Giraffa gracilis* (Harris 1976b; Churcher 1978).

It is possible that the reason for this size increase is the appearance of *Giraffa pygmaea* in the faunal assemblages of East Africa during this time period, with interspecific competition driving *Giraffa stillei* to increase in size. The first documented appearance of *G. pygmaea* is at Hadar, but it also co-occurs with *G. stillei* at Koobi Fora and in the Omo Valley. The teeth of *G. stillei* from Koobi Fora, where the same four giraffids from the Upper Ndolanya Beds co-occurred throughout much of the sequence, are notably larger than those of *G. stillei* from the Upper Laetolil Beds, where *G. pygmaea* appears to be absent. Data on *G. stillei* specimens from the Denen Dora and Kada Hadar Members at Hadar and Member B in the Omo Valley, where the two small *Giraffa* species also co-occurred (Boaz et al. 1982; Reed 2008), would provide a test of this hypothesis.

Sivatherium aff. *maurusium*

Although *Sivatherium hendeyi* is indistinguishable from *S. maurusium* in its dental morphology, the most recent diagnostic specimens of the former taxon are from the early Pliocene at Langebaanweg (Harris 1976a). Thus, it seems reasonable to provisionally attribute the *Sivatherium* dentognathic specimens from the Upper Ndolanya Beds to *Sivatherium* aff. *maurusium*.

A comparison of *Sivatherium maurusium* M_1s and M_2s from Laetoli and specimens from Olduvai and East and West Turkana found that those from the Upper Laetolil Beds were smaller than those from the late Pliocene and early Pleistocene sites (Fig. 14.10), which suggests that *Sivatherium* aff. *maurusium* may also have undergone a size increase through time. One might expect a change in dental morphology as sivatheres shift from browsing to more grazing near the end of the Pliocene (Harris 2003; Harris et. al. 2003), although at Laetoli there is no indication from stable isotope analyses of any significant dietary shift in *S. maurusium* between the two stratigraphic levels (Kingston and Harrison 2007).

This hypothesis is supported by data from three lower molars collected by Kohl-Larsen from "Gadjingero", thought to be equivalent to Loc. 18 in the Upper Ndolanya Beds, which show them to be considerably larger than the Upper Laetolil Beds specimens (T. Harrison, personal communication) and also by the partial mandible from the Upper Ndolanya Beds, EP 1040/00, that is substantially deeper than the LAET 75-520 specimen from the Upper Laetolil Beds, and more similar to specimens from Koobi Fora (Harris 1991; Likius 2002). Moreover, *Sivatherium maurusium*

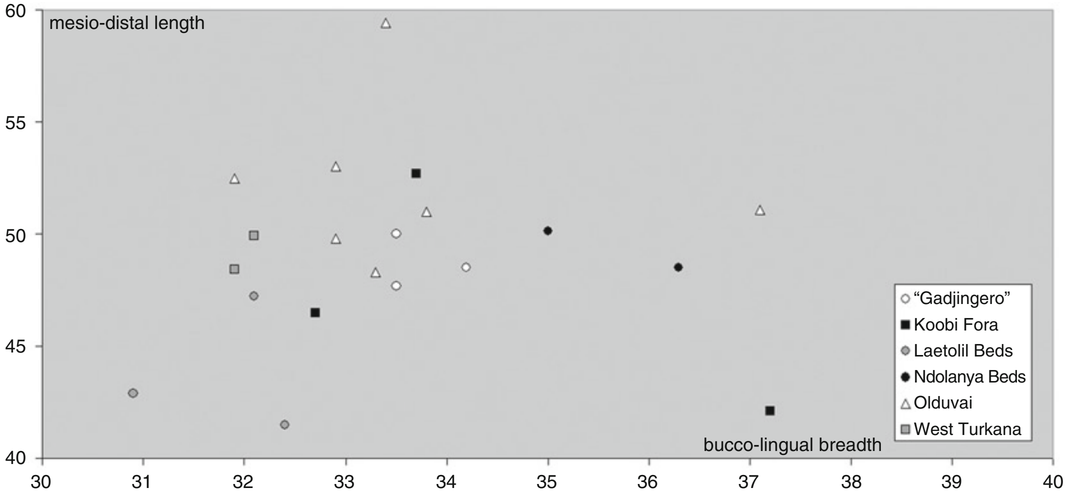

Fig. 14.10 Bivariate plot of the mesiodistal length and buccolingual breadth measurements (mm) of *Sivatherium maurusium* lower molars (M_1 and M_2) from Koobi Fora, Laetoli, Olduvai and West Turkana. This includes three specimens from "Gadjingero", regarded as equivalent to Loc. 18 in the Upper Ndolanya Beds

teeth from Hadar are said to be of similar size to, or slightly smaller than, those from the Upper Laetolil Beds (Harris 1987). However, since M_1s and M_2s are combined in the above analyses and only three of these teeth were recovered from the Upper Laetolil Beds, it is possible that these three teeth are all relatively small M_1s. Moreover, a comparison of two M_3s from "Gadjingero" and two from the Upper Laetolil Beds collected by Kohl-Larsen finds that the Laetolil Beds specimens are considerably larger (T. Harrison, personal communication). Finally, two isolated teeth from the Upper Ndolanya Beds collected by Mary Leakey's team are noted to be approximately the same size as those from the Upper Laetolil Beds (Harris 1987). These conflicting results are consistent with Harris (1991) statement that there is no obvious trend in *Sivatherium* cheek tooth size in East Africa and Likius (2002) contention that the extent of variation and small sample sizes make it impossible to be confident of any trend.

With no complete metapodials or limb bones attributed to *S. maurusium* from the Upper Ndolanya Beds, it is not possible to determine whether the reduction in the length of these elements at more recent sites, documented in specimens from Ahl al Oughlam, Olduvai, West Turkana and the Upper Burgi Member at Koobi Fora (Harris 1976b, 1991; Harris et al. 1988; Geraads 1996), also occurs at Laetoli. Limb length reduction in *S. maurusium* is thought to be related to a shift from browsing to grazing (Harris 2003; Harris et al. 2003), as it would have brought sivatheres closer to ground level foods (Harris 1991). Stable isotope analyses indicate that *Sivatherium maurusium* retained its browsing lifestyle between the Upper Laetolil and Upper Ndolanya Beds (Kingston and Harrison 2007), which suggests that, if there is a link between dietary behavior and limb bone length, its limb elements may have been relatively elongated compared to individuals from contemporary sites.

Diversity of Giraffids at Laetoli

The Upper Laetolil Beds are remarkable among Pliocene sub-Saharan African localities in having such a high proportion of giraffids among its mammalian faunal assemblage, with only Langebaanweg having a greater percentage, due to an exceptional number of *Sivatherium hendeyi* specimens (Harris 1976a, 1987, 1991). In the Upper Laetolil Beds, giraffids make up approximately 15% of the ruminant artiodactyls recovered by EPPE. They are also relatively common in the Lower Laetolil Beds, making up 12% of the ruminants. In the Upper Ndolanya Beds the percentage of giraffids is substantially reduced, to only 4% of ruminants. This change partly reflects the extraordinary increase in the proportion of bovids in the Upper Ndolanya Beds from 35% of the faunal assemblage to 81% (Kingston and Harrison 2007).

Giraffids are relatively rare at late Miocene sites, such as the Middle Awash and Upper and Lower Nawata Members at Lothagam (Harris 2003; Haile-Selassie et al. 2004), making up 6–8% of the ruminants in the Nawata Members (Harris et al. 2003). By the early Pliocene at Kanapoi and the Apak and Kaiyumung Members at Lothagam, they have become more common, being over 10% of the ruminants at all of these sites (Harris et al. 2003), although they are still rare at other early Pliocene sites, such as Galili (Kullmer et al. 2008). It has been suggested, though, that the fauna from the Apak and Kaiyumung Members may not be representative due to the limited numbers of mammalian fossils derived from these strata (Leakey and Harris 2003). After the early Pliocene, giraffid numbers, but not taxonomic diversity, become reduced at Hadar, Koobi Fora, West Turkana, and the Upper Ndolanya Beds (Harris 1976b, 1991; Harris et al. 1988). In the Omo, giraffids represent less than 10% of the ruminant artiodactyls in all relatively fossiliferous members, other than Upper Member B and Member C, dated to between about 2.5 and 3.1 Ma (Bobe et al. 2002), in the later part of the interval between the Upper Laetolil Beds and Upper Ndolanya Beds.

It may be that the environmental conditions at Laetoli are particularly well suited to a diverse and abundant giraffid guild. Stable isotope analyses have found that the large herbivore fauna from Laetoli is unusual in having a large percentage of taxa adapted to a more generalized diet (Kingston and Harrison 2007). This potentially could have enabled giraffids to fill the specialized browser niche with little competition, and could explain their diversity and relative abundance.

Although the most recent stable isotope analyses do not provide evidence for a significant change in paleoenvironmental conditions between the Upper Laetolil Beds and the Upper Ndolanya Beds (Kingston and Harrison 2007), previous analyses of the fossil mammal community structure (Kovarovic et al. 2002) and the paleosol carbonates (Cerling 1992), suggest that there was a shift to a more savanna-like environment. If so, it could be that the reduced number of giraffids in the Upper Ndolanya Beds is associated with this environmental change.

The giraffids from Laetoli are generally considered to be obligate browsers (Harris and Cerling 1998; Harris et al. 2003; Leakey and Harris 2003; Kingston and Harrison 2007; Solounias 2007). With three to four species surviving on broadly similar foods at Laetoli, they must have occupied slightly different niches. It may be that their diversity in size allowed them to feed at different optimum heights (Harris 1976b, 1987; Kingston and Harrison 2007). For example, it has been suggested that the prevalence of *G. stillei* is related to there being a predominance of shorter trees at Laetoli (Harris 1991). Alternatively, giraffids may have browsed on different food items or in different microhabitats (Harris 1976b, 1991; Kingston and Harrison 2007). For example, Harris (1991) suggests that *Giraffa stillei* may have fed in the upper slopes or in riverine woodland, while *G. jumae* ranged primarily in taller mid-slope woodland and *G. pygmaea* in the valley-bottom korongo thickets. Evidence from carbon isotopes from Laetoli indicate that *Sivatherium maurusium* was feeding in more forested areas than *Giraffa* species (Kingston and Harrison 2007). This is supported by the robust tooth roots and massive crowns of *Sivatherium* which may indicate that it was subsisting on more obdurate foods.

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Chapter 15
Bovidae

Alan W. Gentry

Abstract Substantial revisions are made to the account of the Bovidae of the Laetolil Beds and the Upper Ndolanya Beds given in Gentry (1987). Both beds have 17 or 18 species with a wide range of tribal affiliations. The bovids of the Laetolil Beds are unlike those in the "Plio-Pleistocene" faunas of Olduvai Gorge and the Shungura and Koobi Fora Formations. Some species are primitive, others are divergently specialized. Reduncini may well be totally absent, and a few teeth of a larger *Cephalophus* represent a rarely fossilized tribe. A little-advanced *Hippotragus* is more abundant than in later faunas. One or two links can be discerned between the bovids in the Upper Ndolanya Beds and those in the Laetolil Beds, but the differences are more striking. There are signs of a "Plio-Pleistocene" fauna being in place, and some of its species reach a large size. A new species of *Aepyceros* is described from the Laetolil Beds and of an alcelaphine from the Upper Ndolanya Beds.

Keywords Mammals • Pliocene • Africa • Laetoli • Descriptions • Taxonomy • Revision

Introduction

> At that meeting he was struck for the first time by the endless variety of men's minds, which prevents a truth from ever presenting itself identically to two persons.
>
> Count Tolstoy, *War and Peace*

Knowledge of fossil mammals at Laetoli, Tanzania, dates back to a 10-day visit made to the Ngarusi (= Garusi) area by Louis and Mary Leakey and others starting on 5 June 1935. Hopwood (in Kent 1941) thought that the fauna was of early Pleistocene age and a little older than Bed I at the nearby Olduvai Gorge. Hence, it became convenient to view the Laetoli mammals in terms of their likenesses to or differences from Olduvai species. Dietrich (1942, 1950) reported more comprehensively on Laetoli ruminants collected in 1939 by Kohl-Larsen and drew attention to the material being of different geological ages. Gentry and Gentry (1978) surveyed the Laetoli bovids in comparison with Olduvai ones. It seemed to us that many bovids from Laetoli were more puzzling and difficult to identify than were the Olduvai bovids.

Mary Leakey took a new and prolonged interest in Laetoli from 1974 onwards. She invited me to study the Bovidae from her new collections, and my wife and I visited her camp at Olduvai Gorge in 1977 to do so. This visit was truncated by the closure of the Tanzania/Kenya border at that time. Mary continued collecting until 1981, and I saw material from several of her later seasons. During her period of work, it was shown more precisely how the fossils came from a number of beds, of which the two most important were the upper unit of the Laetolil Beds, dating from 3.76 to 3.46 Ma, and the Upper Ndolanya Beds, at probably a little over 2.5 Ma. All this resulted in an improved account of the bovids of the Laetolil and Upper Ndolanya Beds (Gentry 1987). With the renewed investigations of 1998–2005, another revision of the previous accounts has become desirable. Most of this chapter is taken up with the Bovidae of the upper unit of the Laetolil Beds (i.e., Upper Laetolil Beds) and of the Upper Ndolanya Beds. Notes on the bovids of the more sparsely fossiliferous lower unit of the Laetolil Beds (i.e., Lower Laetolil Beds) will also be given. Except where the lower unit is specified, the phrase "Laetolil Beds" will be used in the text for the upper unit of those beds. For locality names within the Laetoli area used by Dietrich and others, see the notes in the chapter by Harrison and Kweka (2011). A list of cranio-dental bovid specimens collected from 1998–2005 is given as an Appendix.

Table 15.1 shows a classification of Bovidae. Following the early and long-extinct Hypsodontinae, these are Bovini and allied tribes, a cluster centered around Antilopini, and the caprine plus alcelaphine group. Molecular classifications often show only two clades, the Bovini and allies and then all the rest. Morphological descriptions and summaries of the extant species in the tribes of African Bovidae are given in Gentry and Gentry (1978). The species lists for the Upper

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Table 15.1 Classification of Bovidae into subfamilies and tribes. (A) The early and perhaps diphyletic Hypsodontinae, (B) Bovini and allied tribes, (C) a cluster centred around Antilopini, (D) the caprine-alcelaphine group. Based on Gentry (1992), Gatesy et al. (1997), Hassanin and Douzery (1999), Vrba and Schaller (2000), Matthee and Davis (2001), Hernández Fernández and Vrba (2005), Price et al. (2005)

(A) Subfamily †HYPSODONTINAE	
†HYPSODONTINI	- Middle Miocene, perhaps diphyletic to other bovids
(B) Subfamily BOVINAE:	
BOSELAPHINI	- Nilgai and four-horned antelope
TRAGELAPHINI	- Kudu, bushbuck group
BOVINI	- Cattle, buffalo
(C) Subfamily ANTILOPINAE:	
CEPHALOPHINI	- Duikers
NEOTRAGINI	- Dik dik, steinbok and other small antelopes. Also Vaal rhebok, *Pelea capreolus*
ANTILOPINI	- Blackbuck, impala, gazelles, saiga antelope
†*CRIOTHERIUM*	- Turolian, plus †*Palaeoreas*, coming from Antilopini
Subfamily REDUNCINAE:	
REDUNCINI	- Waterbuck and reedbuck group, springing from within Antilopinae (?near *Pelea*)
Subfamily †OIOCERINAE	
†OIOCERINI	- Turolian of Eurasia, includes †*Urmiatherium*
(D) Subfamily HIPPOTRAGINAE:	
HIPPOTRAGINI	- Roan, sable antelope, oryx, addax
ALCELAPHINI	- Hartebeest and wildebeest group. This and the preceding tribe arose near the complicated base of the Caprinae
?Subfamily of its own:	
†*TETHYTRAGUS*	- Middle Miocene. Relationship with Oiocerini, Hippotragini, *Pantholops* or Caprinae still to be decided
?Subfamily of its own:	
PANTHOLOPS	- Chiru, one genus near the origin of Caprinae
Subfamily CAPRINAE:	
RUPICAPRINI or NAEMORHEDINI	- Chamois, serow, goral
BUDORCAS	- Takin, not in the Ovibovini
OVIBOVINI	- Muskox
CAPRINI	- Goats, but tribe for sheep still to be decided

Laetolil Beds and the Upper Ndolanya Beds are shown in Tables 15.2 and 15.3.

African localities and formations other than Laetoli mentioned in the text are as follows:

Table 15.2 Bovid species in the Laetolil Beds, upper unit. Listed according to the new sequence of tribes since Gentry (1987)

Laetolil Beds, upper unit	
CURRENT VIEW	CHANGES FROM GENTRY, 1987
TRAGELAPHINI	
Tragelaphus sp.	Only slight overlap of specimens with *Tragelaphus* sp. of 1987
BOVINI	
Bovini sp.	An addition to the fauna, separate from the next one
Simatherium kohllarseni	
aff. CEPHALOPHINI or BOVINI	
[a]*Brabovus nanincisus*	
CEPHALOPHINI	
Cephalophini sp. or spp.	
NEOTRAGINI	
?Raphicerus sp.	
[a]*Madoqua avifluminis*	
ANTILOPINI	
[a]*Aepyceros dietrichi* sp.nov.	Horn cores of 1987 "?Hippotragini sp.nov." + teeth of "aff.*Pelea*"
[a]"*Gazella*" *kohllarseni*	Teeth intermediate in size and morphology between *Aepyceros dietrichi* and *Gazella janenschi*
[a]*Gazella janenschi*	
Gazella granti	Problematical
REDUNCINI	
?Reduncini indet.	New since 1987 but very rare
HIPPOTRAGINI	
[a]*Hippotragus* sp.	Very common but formerly muddled with next species
Oryx deturi	Now conceived as rare. Genus name *Praedamalis* abandoned
ALCELAPHINI	
[a]*Parmularius pandatus*	
Alcelaphini, larger sp.indet.	
Alcelaphini, small sp.?	Such a species may not be present

[a] = Common species

- Adu-Asa Fm., Middle Awash, Ethiopia, Late Miocene (Haile-Selassie et al. 2004). (Haile-Selassie et al. reported on a composite latest Miocene fauna that also passed upward into the lower Sagantole Fm.).
- Ahl al Oughlam, Morocco, Late Pliocene (Geraads and Amani 1998).
- Aïn Boucherit, Algeria, Late Pliocene (Arambourg 1979).
- Aïn Maarouf, Morocco, Middle Pleistocene (Geraads and Amani 1997).
- Aramis, Sagantole Fm., Middle Awash, Ethiopia, Early Pliocene (Vrba 1997).
- Asbole, Ethiopia, Middle Pleistocene (Geraads et al. 2004)
- Bouri 1–2, Ethiopia, Early Pleistocene (Vrba 1997).
- Djebel Krechem, Tunisia, Late Miocene (Geraads 1989).
- Elandsfontein, South Africa, Middle Pleistocene (Klein et al. 2007).
- Fort Ternan, Kenya, Middle Miocene (Gentry 1970).

Table 15.3 Bovid species in the Upper Ndolanya Beds

Upper Ndolanya beds	
CURRENT VIEW	CHANGES FROM GENTRY, 1987
TRAGELAPHINI	
Tragelaphus sp. cf. *T. buxtoni*	
BOVINI	
Bovini sp. or spp.indet.	One species is very large, perhaps a *Simatherium*
CEPHALOPHINI	
?Cephalophini sp.	Two new possible records
NEOTRAGINI	
?Raphicerus sp.	One specimen cited in 1987. No new ones
[a]*Madoqua ?avifluminis*	
ANTILOPINI	
Aepyceros sp.	Could be a lingering *Aepyceros dietrichi*
Gazella sp.	= Antilopini sp.1 of 1987 pl.10.12
Gazella janenschi	
Gazella granti	Still problematical, even in the Ndolanya Beds
[a]*Antidorcas recki*	
REDUNCINI	
Reduncini sp.indet.	
HIPPOTRAGINI	
Hippotragus sp. aff. *cookei?*	= Hippotragini gen. et sp. indet.
Oryx sp.	= "*Praedamalis deturi*" of Gentry, 1987 :pl.10.7
ALCELAPHINI	
Megalotragus kattwinkeli or *isaaci*	May include *Parestigorgon gadjingeri* Dietrich, 1950
?Connochaetes sp.	New since 1987
[a]*Parmularius ?altidens*	
Parmularius parvicornis sp. nov.	= Alcelaphini, small sp. and *?Pelea* sp. of Gentry, 1987

[a] = Common species

- Gamedah, Ethiopia, Late Pliocene (Vrba 1997).
- Hadar Fm., Ethiopia, mid-Pliocene (Vrba 1997; Alemseged et al. 2005).
- Kaiso Village, Uganda, Late Pliocene (Geraads and Thomas 1994).
- Kanam, Kenya, Late Pliocene-Early Pleistocene (Ditchfield et al. 1999).
- Kanapoi, Kenya, Early Pliocene (Harris et al. 2003).
- Kanjera, Kenya, Late Pliocene-Middle Pleistocene (Ditchfield et al. 1999).
- Karmosit Beds, north of the Tugen Hills, Kenya, Pliocene (?ca. 3.5 Ma, Bishop et al. 1971).
- Katwe Ashes, Semliki, easternmost DR Congo, Late Pleistocene (Boaz 1990).
- Koobi Fora Fm., Kenya, Pliocene-Middle Pleistocene (Harris 1991).
- Koro Toro, Chad, mid-Pliocene (Geraads et al. 2001).
- Kromdraai A (= Kromdraai Faunal Site), South Africa, Early (-Middle?) Pleistocene (Vrba 1996).
- Langebaanweg, South Africa, Early Pliocene (Gentry 1980).
- Lothagam, Nawata and Nachukui Fms., Kenya, Late Miocene-Early Pliocene (Leakey and Harris 2003).
- Lukeino, Kenya, Late Miocene (Thomas 1980; Deino et al. 2002).
- Lukenya Hill, Kenya, Late Pleistocene (Marean 1992).
- Maka, Middle Awash, Ethiopia, Early Pliocene (Vrba 1997).
- Makapansgat Limeworks, South Africa, Late Pliocene-Early Pleistocene (Vrba 1987a).
- Manonga (= Wembere), Tanzania, Late Miocene-Early Pliocene (Harrison and Baker 1997).
- Matabaietu, Ethiopia, Late Pliocene (Vrba 1997).
- Middle Awash, Ethiopia, Late Miocene-Early Pliocene (Haile-Selassie et al. 2004).
- Mpesida, Kenya, Late Miocene (Thomas 1980; Kingston et al. 2002).
- Mursi Fm., Omo, Ethiopia, mid-Pliocene (Brown 1994).
- Nkondo and Warwire Fms., Uganda, Early Pliocene and mid-Pliocene (Geraads and Thomas 1994).
- Olduvai Gorge, Tanzania, Late Pliocene-Middle Pleistocene (Gentry and Gentry 1978).
- Sahabi, Libya, Late Miocene (Boaz 2008).
- Shungura Fm., Omo, Ethiopia, mid-Pliocene-Early Pleistocene (Gentry 1985).
- Sterkfontein, South Africa, Late Pliocene (Clarke 2006).
- Swartkrans, South Africa, Early Pleistocene (De Ruiter 2003).
- Tighenif (formerly Palikao, later Ternifine), Algeria, Early Pleistocene (Geraads 1981).
- Toros-Menalla, Chad, Late Miocene (Geraads et al. 2008).
- Usno Fm. (= White Sands and Brown Sands), Omo, Ethiopia, mid-Pliocene (Gentry 1985).
- Wee-ee, Middle Awash, Ethiopia, mid-Pliocene (Vrba 1997).

Horn core measurements are given as anteroposterior diameter × transverse diameter at the bases. Degree of compression is given as a percentage: (transverse diameter × 100) ÷ anteroposterior diameter. Tooth measurements are given as occlusal length × width × height, but the height is often unavailable. Lt, rt = left, right. DAP × TS for postcranial bones = anteroposterior dimension × transverse width.

Systematics: Bovidae of the Upper Unit of the Laetolil Beds

SUBFAMILY BOVINAE Gray, 1821
TRIBE TRAGELAPHINI Blyth, 1863

TYPE GENUS *Tragelaphus* Blainville, 1816

Tragelaphini includes *Tragelaphus*, with seven living species, and *Taurotragus*, with one or two. They have twisted or spiralled horn cores with keels. The torsion is anticlockwise on the right side or heteronymous. Females in *Tragelaphus* are horned only in *T. eurycerus*. Frontals without internal sinuses and little elevated between the horn insertions. Cranial roofs are little inclined, as in Boselaphini. Molar teeth are less high crowned than in most other bovids and have a simple occlusal pattern. Basal pillars absent on upper molars and small or absent on lower molars, upper molars without ribs between the styles, lower molars without goat folds, premolar rows quite long, with large P^2s and P_2s, P_4s have paraconid-metaconid fusion to form a closed lingual wall.

Tragelaphus Blainville, 1816

TYPE SPECIES *Tragelaphus scriptus* (Pallas, 1766)

Tragelaphus sp.

Tragelaphus sp. Gentry, 1987: 379.

Material

- LAET 75-722, Loc. 1. Lt upper molar frag.
- LAET 75-1301, Loc. 8. Lt upper molar, middle wear, 17.2×14.7×10.1.
- LAET 75-3105, Loc. 12. Poorly preserved horn core in three pieces, possibly tragelaphine. Combined length ca. 140 mm.
- EP 903/98, Loc. 9 S. Below Tuff 2. Rt M_3 in mandible frag., middle wear, occlusal length ca. 32.5.
- EP 010/00, Loc. 4. Between Tuffs 6 and 8. Lt upper molar, early middle wear, 20.6×14.8×10.8.
- EP 1283/00, Loc. 6. Between Tuffs 5 and 6. Rt upper molar, middle wear, ca. 23.7×ca. 17.5×ca. 14.0.
- EP 2977/00, Loc. 1. Between Tuffs 6 and 8. Distal metapodial.
- EP 088/01, Loc. 6. Between Tuffs 5 and 6. Rt upper molar, early middle wear, 20.0×14.3×13.1.
- EP 1372/03, Loc. 8. Between Tuffs 5 and 6. Rt upper molar, early middle wear, 19.0×12.4×14.8.
- EP 494/03, Loc. 3. Between Tuffs 6 and 8. Rt P^2, 13.0×9.0.

Description

The diameters of the horn core LAET 75-3105 change rather little along its course and are approximately 20 mm for both dimensions, but it is not known how much length above the original base has been lost. The cross-section approaches a triangular shape. Unfortunately, there is no clear indication of torsion that would have increased the probability of it being tragelaphine.

Of the teeth in the Leakey collection listed by Gentry (1987: 379) under *Tragelaphus*, LAET 75-1300 and LAET 75-2652 are now thought likely to be alcelaphine. Many of the others, including the mandible LAET 76-4131 (Gentry 1987: pl. 10.2), are probably better identified as *Brabovus*. The most convincing tragelaphine teeth – for example, LAET 75-722 and EP 1283/00 – are larger. The upper molars listed here are from a species about the size of extant *Tragelaphus spekei* or *T. imberbis*, with EP 1283/00 as a larger specimen. LAET 75-1301 could also join this tragelaphine species, provided it were an M^1. The upper molar EP 010/00 is shown in Fig. 15.1. The distal metapodial EP 2977/00 looks tragelaphine, in that it is quite thick anteroposteriorly and has narrow, high condyles with deep hollowings immediately above them posteriorly. It is slightly too small to be a comfortable match for a species the size of *T. imberbis*. The M_3 EP 903/98 is close to the size of modern *Tragelaphus strepsiceros* or of *T. nakuae* from the Shungura Fm. It looks tragelaphine, but the lingual walls of the two preserved main lobes are well outbowed, and the central fossettes are anteroposteriorly shorter. It could be a primitive bovine instead.

Discussion

Tragelaphini are not common at Laetoli. Dietrich (1942: 118, fig. 154) described a tragelaphine frontlet, supposedly from the Laetolil Beds, under the name '*Tragelaphus* sp. cf. *buxtoni* Lydekker, 1910'. *Tragelaphus buxtoni* is the mountain nyala, a living large species with horns so strongly lyrate as to approach the spiralling of those of a greater kudu, *T. strepsiceros*. It is endemic to Ethiopia, east of the Rift Valley at 3,000–3,500 m. Gentry and Gentry (1978: 305) thought that Dietrich's frontlet was more like a sitatunga or nyala, *T. spekei* or *T. angasi*, but failed to comment on its large size. It will be further discussed below. The teeth listed above as Tragelaphini are rather small to go with the frontlet, with the possible exception of EP 1283/00. They would be of a size to be expected for the unknown teeth of *T. kyaloae* Harris, 1991, a species from the Lower Lokochot Mb. (~3.5 Ma) of the Koobi Fora Fm. and also present in other early members of that formation and at Kanapoi and Lothagam. It is conceivable that two different-sized tragelaphine species coexisted in the Laetolil Beds, but this remains unknown for the present.

TRIBE BOVINI Gray, 1821
TYPE GENUS *Bos* Linnaeus, 1758

Gentry (1980) postulated two lineages of African Bovini: the smaller short-horned *Ugandax* to *Syncerus* and the larger long-horned *Simatherium* to *Pelorovis*. The *Ugandax* to *Syncerus* lineage or group is still a plausible concept,

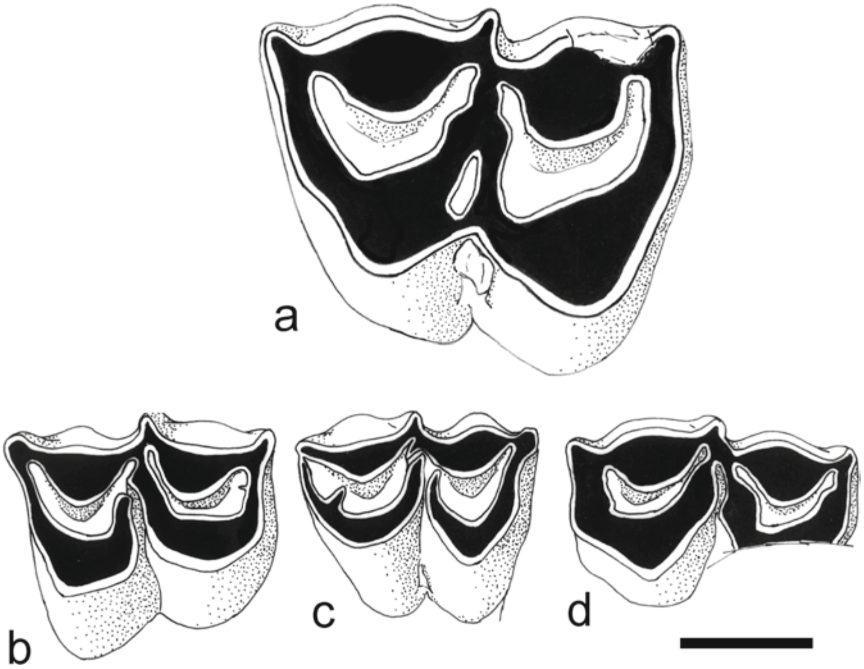

Fig. 15.1 Upper molars from the Laetolil Beds in occlusal view. Labial sides to the top. (**a**) right upper molar of *Simatherium kohllarseni*, EP 393/04. (**b**) left upper molar of *Tragelaphus* sp. EP 010/00. (**c**) right upper molar of *Brabovus nanincisus* EP 385/04. D, right upper molar of ?Reduncini sp. EP 815/03. Scale = 10 mm

but Gentry (2006) came to think that *Simatherium* was difficult to characterize and unlikely to be ancestral to *Pelorovis*. *Simatherium* was founded on a Laetoli species, but only the holotype of the type species can be taken with reasonable safety as unlikely to be congeneric with *Ugandax*.

Simatherium Dietrich, 1941

1941 *Simatherium* Dietrich: 221.
1942 *Simatherium* Dietrich: 119.
TYPE SPECIES *Simatherium kohllarseni* Dietrich, 1941

Other Species and Occurrences

Simatherium shungurense Geraads, 1995: 89, pl.1, Mb. G, Shungura Fm.. The former *Simatherium demissum* Gentry, 1980 from Langebaanweg is now seen as more likely to belong to *Ugandax* (Gentry 2006). Hence, the diagnosis of *Simatherium* has changed from that in Gentry (1987).

Occurrence and Range

Mid-Pliocene to Late Pliocene.

Generic Diagnosis

Moderate- to large-sized bovines. Horn cores moderately long to long; of irregular or rounded rather than a neater, more or less triangular cross-section; and little compressed. They are divergent, but the degree of divergence diminishes as they ascend, inclined backwards, inserted widely apart and postorbitally, and with an incipient temporal fossa below their bases. Sinuses within frontals and horn pedicels, slightly raised frontals between the horn bases, a short and wide cranium, slightly sloping cranial roof with a smooth area in front enclosed by temporal ridges and a rugose raised area at the back. Strong nuchal crests, low and wide, flat-topped occipital surface, moderate to large mastoids. Basioccipital wide posteriorly, with a longitudinal ridge just behind the small anterior tuberosities.

Remarks

Simatherium differs from *Ugandax* Cooke and Coryndon, 1970 (type species *U. gautieri* Cooke and Coryndon 1970) in having longer horn cores with less indication of keels, variably greater divergence, perhaps wider insertions of its horn cores, higher frontals between the horn insertions, and a wider and shorter cranium. *Simatherium* may not always have been characterized by large size, if a small cranium of *Simatherium* cf. *S. kohllarseni* of unknown date in the Koobi Fora Fm. (Harris 1991: fig. 5.15) is correctly identified at generic level. The poor preservational state of the holotype of the type species of *Simatherium*, added to the variable cross-sections of bovine horn cores even among the subspecies of living *Syncerus*, continues to confuse generic and specific delineations in African bovines.

***Simatherium kohllarseni* Dietrich, 1941**

Simatherium kohllarseni Dietrich, 1941: 221.
Simatherium kohllarseni Dietrich, 1942: 119, pl. 20, figs. 161, 163, 165.
Simatherium kohllarseni Gentry and Gentry, 1978: 311, 62.
Simatherium kohllarseni Gentry, 1987: 380, pl. 10.3.

Holotype

A poorly preserved cranium, Vo 670, in the Museum für Naturkunde der Humboldt-Universität, Berlin. Dietrich, 1942: pl. 20, figs. 161, 163, 165. No other material was assigned to the species at the time.

Type Locality

Garusi in the Laetoli area, Tanzania.

Horizon and Range

Dietrich (1942, 1950: 49) assigned the holotype to the oldest of the Laetoli faunas, as would be expected for Garusi. Some matrix anteroventrally on the holotype appeared to be a grey tuff resembling those of the Laetolil Beds.

Material

- EP 420/98, Loc. 10. Below Tuff 3. Rt lower molar, early middle wear.
- EP 1202/98, Loc. 22. Between Tuffs 5 and 7. Lt M_3, middle wear. 38.0 long.
- EP 042/99, Loc. 10E. Between Tuffs 5 and 7. Rt dP_3 germ, 26.8 long.
- EP 743/00, Loc. 2. Between Tuffs 5 and 7. Lt upper molar, early middle wear. ca. 35.0 long and ca. 28.4 broad.
- EP 3553/00, Loc. 12. Between Tuffs 5 and 7. Rt M_2, late middle wear. 30.8 × 17.8 × 10.3.
- EP 3683/00, Loc. 21. Between Tuffs 5 and 8. Lt P_3 or P_4, late wear. 20.5 × 14.6 × 7.7.
- EP 259/03, Loc. 16. Between Tuffs 7 and 8. Lt M_3, middle wear. ca. 38.4 long.
- EP 393/04, Loc. 16. Between Tuffs 7 and 8. Rt upper molar, middle wear. 32.1 × 23.5 × 20.0.

Among the postcranial bones are:

- EP 2308/00, Loc. 17. Between Tuff 7 and Yellow Marker Tuff. Lt astragalus with lateral height 72.7, width 51.6, anteroposterior dimension 40.4.
- EP 2638/00, Loc. 2. Between Tuffs 5 and 7. Rt calcaneum.
- EP 2460/00, Loc. 13. Between Tuffs 5 and 8. Rt astragalus.
- EP 1135/01, Loc. 1. Between Tuffs 6 and 8. Middle phalanx with a length of 48.5 mm and proximal height and width of 30.2 × 29.5.
- EP 1254/04, Loc. 10E. Between Tuffs 5 and 7. Rt naviculocuboid, width 63.0.
- EP 1516/04, Loc. 22E. Between Tuffs 3 and 8. Distal metatarsal.

Diagnosis

A large *Simatherium* with very divergent horn cores.

Description

The original much-damaged cranium of *Simatherium kohllarseni* was from a very large animal, a striking find for the middle Pliocene, and its horn cores were both large and transversely widened at the base (index 76.5 × 126). This strong compression, although present only in the vicinity of the base, is unlike other specimens with any claim to be *Simatherium*. The horn cores show no sign of keels, but both compression and absence of keels may have arisen from or been affected by postmortem damage. The left horn core suggests that the degree of divergence is beginning to lessen distally. The horn cores overhang the sides of the braincase as is well shown in Dietrich (1942: pl. 20, fig. 165). The species account given in Gentry (1987) centered around a second bovine cranium with right horn core, LAET 75-3064 from Loc. 4, now on loan to the National Museum in Nairobi, and the difficulties of making it conspecific with the holotype. It differs in its smaller size, shorter and more stocky horn cores with little compression (Gentry 1987: pl. 10.3), horn cores less inclined in side view, and more steeply sloped cranial roof. It is similar in having horn cores without clear signs of keels, with strong divergence basally but less divergence distally, and with wide insertions.

Bovine teeth and postcranials continue to be uncommon in the 1998–2005 collections, as was also the case in the Leakey collection. They are less advanced than in the modern *Syncerus caffer* of East and southern Africa. The upper molar EP 393/04 is shown in Fig. 15.1. Another upper molar EP 743/00 shows limited hypsodonty, has a primitive, unlocalized outbowing of the metacone labial wall, a posterolingual cingulum, and a small- to moderate-sized basal pillar. The middle phalanx EP 1135/01 is less robust than examples of the somewhat larger Middle Pleistocene *Bos primigenius* from Ilford, England.

Discussion

The *Simatherium kohllarseni* holotype differs from the Middle Pliocene *Ugandax coryndonae* of Gentry (2006) in greater size, longer horn cores with less indication of keels, greater divergence of horn cores, wider insertions of horn cores, higher frontals between the horn insertions, and a wider and shorter cranium. The cranium LAET 75-3064 differs from *U. coryndonae* in larger size, more massive and divergent horn cores, and a shorter cranium, characters making it more advanced than *Ugandax*. If it were seen as separate from *S. kohllarseni*, it would not fit with the horn core pieces referred below to "Bovini sp.," and we would draw near to having to postulate three bovine species in the Laetolil Beds. The underlying problem is to work out the course of African bovine phylogeny. Have numbers of long-horned and sometimes large bovines evolved at different times and places through the later Tertiary? If so, *Simatherium shungurense* (~2.2 Ma) may not be connected after all with *S. kohllarseni*. A Hadar Fm. horn core piece, AL 114-1c in DD-2 (~3.2 Ma), is an example of yet another bovine in search of a place in an evolutionary story (Gentry 1981). This horn core was large, curved, compressed, without keels, and too early to be a *Pelorovis*. For the present, I leave LAET 75-3064 in *S. kohllarseni* and *S. shungurense* in *Simatherium*.

Bovini sp.

Material

A few pieces of short, stumpy horn cores:

- LAET 74-23, Loc. 2.
- LAET 75-2643, Loc. 5.
- LAET 75-816, Loc. 7.
- LAET 75-1592, Loc. 13.
- EP 1119/98, Loc. 9, between Tuffs 6 and 8.
- EP 4202/00, Loc. 2, between Tuffs 5 and 7.

Description

Of these horn cores, LAET 75-816, probably of the left side, is the best preserved (Fig. 15.2). It must have been short when complete. Its preserved part has a length of ca. 130 mm, and the greatest diameter at the thickest end is ca. 49 mm. There is no compression. One (?dorsal) surface is slightly flattened, suggestive more of a triangular than a rounded cross-section. LAET 74-23 is certainly conspecific with LAET 75-816. LAET 75-2643 is much curved, and its proximal end is compressed. EP 1119/98 is smaller than the others. EP 4202/00 could be the tip of a short curved horn core.

Discussion

These horn cores can be tentatively assigned to Bovini but would not be conspecific with *Simatherium kohllarseni*, nor do they have any characteristics of *Ugandax*. They are of similar build to the larger horn cores assigned to *Syncerus* in Shungura C – for example, L837-2 or L53-3 (Gentry 1985). These Shungura horn cores are thought to be the earliest claimed *Syncerus*.

Aff. TRIBE CEPHALOPHINI or BOVINI ?

Brabovus Gentry, 1987

TYPE SPECIES *Brabovus nanincisus* Gentry, 1987

The genus is monospecific; in 1987, the type species was known from the Laetoli holotype skull alone. I now believe that a supposed tragelaphine mandible, LAET 76-4131 (Gentry 1987: pl.10.2), is conspecific and that some other teeth formerly accepted as tragelaphine were misattributed.

Brabovus nanincisus Gentry, 1987

Tragelaphus sp. Gentry, 1987: pl. 10.2.
Brabovus nanincisus Gentry, 1987: p.382, pls.10.4 and 10.5, fig. 10.1.

Holotype

A skull with horn cores, mandibles and atlas vertebra, LAET 78-5376 (Gentry 1987: pls.10.4 and 10.5, fig. 10.1). Original on loan to the National Museum of Kenya, Nairobi; casts in the National Museum of Tanzania, Dar es Salaam and the Natural History Museum, London (M37067).

Type Locality

Laetoli, Tanzania.

Horizon and Range

The holotype came from the Laetolil Beds at Loc. 16 just above Tuff 7. Other remains come from the Upper Laetolil Beds at Locs. 2, 3, 5, 6, 9, 10W, 13, 17, and 22 (1998–2004), and Locs. 1, 3, 4, 5, 6, 8, 10E, 10W, 12, and 16 (1974–1981).

Material

More material of *Brabovus nanincisus* has become available since 1998, and the species is now seen as the lowest ranking among the seven commonest bovids of the Laetolil Beds (Table 15.2). The holotype skull demonstrates the reality and distinctiveness of the species, but it is not easy to differentiate its cheek teeth from Tragelaphini or its horn cores or premolars from Cephalophini. Therefore, a full list of cranial and dental material is given, uncertain though many of the attributions must be.

Fig. 15.2 Horn core of Bovini sp. LAET 75-816 in presumed dorsal view. Scale in mm

- LAET 75-403, Loc. 8. Rt P^2, early wear, 12.7 × 8.3.
- LAET 75-3121, Loc. 12. Horn core (♀?), index of 28.3 × 24.5.
- LAET 75-2879, Loc. 10W. Rt dP^4, unworn, 13.7 × 8.0 × ca.11.5.
- LAET 76-4131, Loc. 12. Lt mandible with P_3–M_3, early middle wear (Gentry 1987: pl.10.2).
- EP 172/98, Loc. 10E. Between Tuffs 5 and 7. Rt dP_4, unworn, 22.9 × 5.6.
- EP 547/98, Loc. 10W. Below Tuff 3. Rt back P_4–broken M_3. M_{1-3} ca. 53.0, M_1 14.6 × 8.6, M_2 17.0 × 9.1.
- EP 833/98, Loc. 10. Below Tuff 3. Lt M_3, ca. 21.9.
- EP 1118/98, Loc. 9. Between Tuffs 6 and 8. Horn core (♀?), index 25.2 × 18.3, total length ca. 50 mm.
- EP 1199/98, Loc. 22. Between Tuffs 5 and 7. Rt M_2, middle wear, 19.4 × 9.5 × ca. 15.5.
- EP 127/99, Loc. 10. Below Tuff 3. Rt M_2, early middle wear, ca.17.0.
- EP 137/99, Loc. 10. Below Tuff 3. Lt M_3, ca. 22.0.
- EP 179/00, Loc. 1. Between Tuffs 6 and 8. Rt upper molar, middle wear, 18.0.
- EP 351/00, Loc. 12. Between Tuffs 5 and 7. Lt P_3–M_2, middle wear. P_3 14.9 × 6.7 × 9.3, P_4 14.2 × 8.0 × 11.3, M_1 15.6 × 9.2, M_2 18.0 × 9.9, ramus depth below M_1 22.4.
- EP 1282/00, Loc. 6. Between Tuffs 5 and 6. Lt M^2 or M^3, middle wear, 16.4 × 11.6 × 11.2.
- EP 1555/00, Loc. 3. Between Tuffs 6 and 8. Rt M^1, middle wear, 16.5 × 12.6 × 10.0.
- EP 1565/00, Loc. 3. Between Tuffs 6 and 8. Lt P_2, 9.6 × 5.2. Might be Hippotragini.
- EP 1716/00, Loc. 2. Between Tuffs 5 and 7. Rt M^2 or M^3, 18.6 × 13.2 × 8.2.
- EP 1891/00, Loc. 5. Between Tuffs 3 and 5. Lt upper molar, middle wear, ca. 21.7 × 17.2 × 17.0.
- EP 1894/00, Loc. 5. Between Tuffs 3 and 5. Rt M^2, middle wear, 18.0 × 14.0 × 8.9.
- EP 1902/00, Loc. 5. Between Tuffs 3 and 5. Lt M^2, middle wear, 19.9 × 16.2 × 6.6.
- EP 1904/00, Loc. 5. Between Tuffs 3 and 5. Lt M^1, middle wear, 18.7 × 17.2 × 9.0.
- EP 1909/00, Loc. 5. Between Tuffs 3 and 5. Rt lower molar frag, middle wear.
- EP 1915/00, Loc. 5. Between Tuffs 3 and 5. Lt and rt mandible pieces and teeth and associated horn cores.
- EP 2069/00, Loc. 13E. Between Tuffs 5 and 8. Horn core (♀?), index 31.2 × 24.5, length ca. 72 mm.
- EP 2103/00, Loc. 13. Between Tuffs 5 and 8. Rt mandible with M_3, middle wear, 23.6 × 8.6.
- EP 2940/00, Loc. 10. Below Tuff 3. Lt lower molar, middle wear, 17.1.
- EP 3198/00, Loc. 10W. Below Tuff 3. Rt mandible with P_3–M_2, late wear.
- EP 3812/00, Loc. 6. Between Tuffs 5 and 6. Horn core (♀?), index, 34.8 × 26.0.
- EP 005/01, Loc. 8. Between Tuffs 5 and 6. Lt M_3, late middle wear.
- EP 085/01, Loc. 17. Between Tuff 7 and Yellow Marker Tuff. Rt mandible piece with M_1, ca. 16.2 long, ramus depth 22.8. Perhaps had erupting teeth behind.
- EP 452/01, Loc. 9. Between Tuffs 6 and 8. Lt P_2.
- EP 1404/01, Loc. 12E. Between Tuffs 5 and 7. Lt M_2 frag., middle wear.
- EP 242/03, Loc. 16. Between Tuffs 7 and 8. Rt lower molar, middle wear.
- EP 359/03, Loc. 5. Between Tuffs 3 and 5. Rt upper molar, middle wear, ca. 17.0 × 12.2.
- EP 1730/03, Loc. 22. Between Tuffs 5 and 7. Lt upper molar, middle wear, damaged, 18.5 long.
- EP 1857/03, Loc. 1. Between Tuffs 6 and 8. Lt upper molar or dP^4, late middle wear, ca. 16.0 × - × 7.6.
- EP 2114/03, Loc. 7. Between Tuffs 5 and 7. Rt M^1, ca. 17–18 mm long. Has a basal pillar.
- EP 098/04, Loc. 22. Between Tuffs 5 and 7. Rt M_3, middle wear, ca. 26.4 × 10.6 × 19.6. Has a basal pillar, lingual walls rounded.
- EP 385/04, Loc. 16. Between Tuffs 7 and just above 8. Rt upper molar, early middle wear, 18.5 × 12.7 × 12.2.
- EP 605/04, Loc. 10W. Below Tuff 3. Rt lower molar, late middle wear, 15.5 × ca. 9.9.
- EP 642/04, Loc. 3. Between Tuffs 6 and 8. Rt M_{1-3}, early middle wear, M_{1-3} ca. 65.6, M_1 17.1 × 9.3, M_2 21.6 × ca. 10.2, M_3 26.9 × – × ca. 24.0, ramus depth below M_3 ca. 26.0.
- EP 1518/04, Loc. 16. Between Tuffs 7 and 8. Rt M_2, early middle wear, ca. 21.6 long.
- EP 1559-61/04, Loc. 12E. Between Tuffs 5 and 7. Lt partial M_3, early middle wear, ca. 21.0 × 8.1 × 17.5; lt M_1 or M_2, middle wear, 15.5 × 8.5 × ca. 12.8; lt P_4, early wear, 14.1 × 7.8 × 14.0.
- EP 1618/04, Loc. 17. Between Tuff 7 and Yellow Marker Tuff. Lt M_1, late middle wear, ca. 16.4 long.
- EP 023/05, Loc. 11. Between Tuffs 7 and 8. Lt upper molar, early middle wear, 18.5 × 16.3 × 13.8.
- EP 088/05, Loc. 8. Between Tuffs 5 and 6. Rt upper molar, middle wear, 17.0 × 14.4 × 9.9.
- EP 094/05, Loc. 8. Between Tuffs 5 and 6. Lt M^1, early middle wear, 16.1 × 12.5 × 7.2; associated lt incisor.
- EP 280/05, Loc. 10. Below Tuff 3. Rt lower molar, unworn, 19.5 × 7.8 × ca. 26.3. Not brachyodont.
- EP 309/05, Loc. 10W. Below Tuff 3. Part lt lower molar, early middle wear.
- EP 516/05, Loc. 12E. Between Tuffs 5 and 7. Lt M^{1-2}, late middle wear, M^1 15.1 × 14.7, M^2 17.2 × 14.9.
- EP 581/05, Loc. 7. Between Tuffs 5 and 7. Rt P_3, early middle wear, ca. 13.6 × 7.1 × 11.4.
- EP 740/05, Loc. 3. Between Tuffs 6 and 8. Lt P_4, early middle wear, 15.0 × 7.0.
- EP 933/05, Loc. 2. Between Tuffs 5 and 7. Lt upper molar, late middle wear, 16.1 × 14.5 × ca. 7.5.

Diagnosis

A medium-sized species. Horn cores short, without any obvious keels, little compression, no flattening of their lateral surface, no transverse ridges, little divergent, inclined backwards in side view, and insertions not wide apart. Moderate sized postcornual fossae, sinuses in the frontals and spreading into the horn pedicels, frontals not raised between the horn bases, dorsal orbital rims projecting laterally, supraorbital pits not visible on the casts and must have been of insignificant size, back of nasals narrow and terminating just behind level of the M^1–M^2 junction, ethmoidal fissure present, preorbital fossa in the form of an extensive shallow area without a clear dorsal border, zygomatic arch not thickened beneath the orbit, infraorbital foramen high above P^2, back of M^3 situated below centre of the orbit. Braincase short or moderately long, its roof straight and little inclined, temporal lines not very prominent, nuchal crests concave upwards on each side of the midline, occipital surface probably with a median vertical ridge, mastoid large, basioccipital not very large, with a wide and shallow central longitudinal groove, and with anterior tuberosities which are small and about the same width apart as the posterior ones, auditory bulla globular but not greatly inflated.

Brachyodont cheek teeth with cusps showing high relief in labial view that may last into later wear. Somewhat rugose enamel. Small basal pillars present on upper molars and moderate to large ones on lower molars. Lingual lobes of upper molars fail to connect centrally with the labial side of the teeth or with each other, and a posterolingual spur may occur in the posterior fossette. Upper molars with a narrow mesostyle remaining well marked to its base, metastyle poor even on M^3s, a moderate-sized rib on the labial wall of the paracone and a variable indication of a labial one on the metacone wall, lingual lobes with pointed tips, and no cingula anterolingually or posterolingually. Lower molars have fairly flat lingual walls and pointed labial lobes, and they are without transverse goat folds anteriorly. M_3 with a small rear (third) lobe. Premolar rows long and P^2 and P^3s relatively large. Paraconid almost fused with metaconid on P_4, labial walls of $P_{3–4}$ passing round anteriorly to a nearly transverse plane, hypoconid not projecting labially on $P_{3–4}$ and without a valley separating it from the protoconid in front, P_2 little reduced, I_1s are not much larger than the other incisors and canine. Mandibular ramus is of shallow depth. (Modified from Gentry 1987).

Description

The collections contain some small horn cores that could be females of this species (Fig. 15.3). EP 1118/98 is very short, tapers rapidly from base to tip, is somewhat compressed, the level of maximum thickness lies centrally, one side surface is less rounded than the other, there is an approach to front and back keels. It is smaller than the horn cores of the holotype, and has a large sinus at the base that makes it unlikely to be a cephalophine. Three other similar horn cores are listed above.

The upper molar EP 1282/00 is moderately hypsodont, does not look like an M^1, has only slight outbowings on its labial walls, no reduncine-like constrictions of its lingual lobes, and no basal pillar. An upper molar, EP 385/04, is shown in Fig. 15.1. The P_2 EP 452/01 is slightly bulbous and has an entoconid separate from the entostylid, the latter better shown than in the slightly larger and slightly higher-crowned *Cephalophus silvicultor*. The incisor EP 094/05, associated with an M^1 supposedly of *Brabovus*, is wider than those on the holotype skull and thereby more similar to most other African bovid species. The P^2 LAET 75-403 (Fig. 15.3) has massive styles and some resemblance to the P^2 of a giraffid, but it is small and does look more like a brachyodont bovid. A maxillary fragment with right M^1 at 17.0×11.5 in middle wear, EP 1166/98 from Loc. 9, was first identified as *Brabovus*, but I have a later note querying whether it might

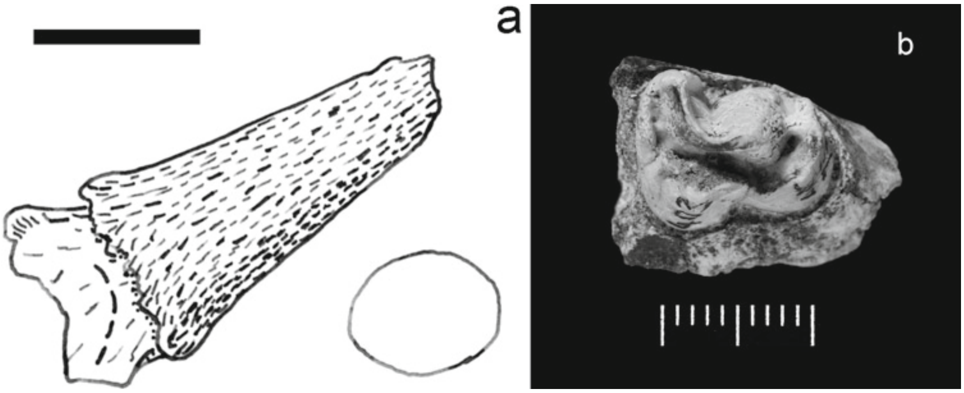

Fig. 15.3 *Brabovus nanincisus*. (**a**) horn core and basal cross section of a possible female EP 2069/00 in unknown orientation. Dashed line indicates likely extent of frontal sinuses; ventral edge of cross section corresponds to the visible surface of the horn core. Scale = 25 mm. (**b**) right P^2 (LAET 75-403) in occlusal view. Scale in mm

be the dP^4 of an alcelaphine. This doubt arose from the convex section of the metacone labial wall and is another example of the uncertainties with identifications.

Discussion

Initially I was impressed by the apparent brachyodonty of this species. The strong and slanted parastyles on M$^{1-2}$ and the high relief of the cusps in labial view (Gentry 1987: pl. 10.5) reinforced the appearance of brachyodonty. This character hindered me from seeing more than "quite a lot of resemblance" between the teeth of the holotype and the mandible LAET 76-4131 from Loc. 12 (Gentry 1987: pl. 10.2), which I had uneasily accepted as the main representative of *Tragelaphus* sp. in the Laetolil Beds. I now prefer to assign the latter to *Brabovus nanincisus*.

As well as having similarities to tragelaphine teeth, *Brabovus* teeth are not dissimilar to some specimens of *Aepyceros dietrichi*, and the two species can occur together, as at Loc. 5 (catalogue numbers around EP 1890/00). Neither species shows any tendency to evolve towards the occlusal complexities seen in modern Bovini, Reduncini, or Hippotragini. The upper molars now assigned to *Brabovus nanincisus* differ from *Aepyceros dietrichi* by being less hypsodont and having no flattening of the labial wall of the metacone.

The small I$_1$s of the holotype (Gentry 1987: fig. 10.1) is a surprising character among African Bovidae. In extant bovids, small central incisors are found in *Bison*, *Pantholops*, and all Caprinae; intermediate-sized incisors are found in Boselaphini, Cephalophini, some Neotragini, *Saiga*, *Pelea*, and Hippotragini; and large ones are found in Tragelaphini, some Neotragini, Antilopini, Reduncini, and Alcelaphini. It looks as though primitively small I$_1$s could have enlarged to a variable extent in most bovids but remained small in Caprinae. (The small ones in *Bison* would presumably be secondary.) Alternatively, pecoran ancestors of bovids already had somewhat enlarged I$_1$s, and all subsequent enlargements and reductions are advanced. Incisors must be used in diverse ways across the range of bovid species, whatever the size of the central pair.

Previously, I classified *Brabovus* as doubtfully Bovini, while Vrba (1987b: 36) took it as a primitive hippotragine and later (Vrba and Gatesy 1994) as not yet hippotragine. Another possibility was to have it as an archaic survivor from near the cephalophine ancestry, and Gentry (1987: 385) noted resemblances of *Brabovus* to the similarly sized *Cephalophus silvicultor* (formerly spelled "*sylvicultor*"). A revised comparison more than 20 years later suggests that the two species agree in horn cores, with little compression and little divergence, slight signs of one or more short keels distally on the horn cores, straight and little-inclined braincase roof, rather small basioccipital, brachyodont cheek teeth, strong paracone ribs on the upper molars, and basal pillars on the lower molars. The system of sinuses within the frontals of *Brabovus* is a major difference, although the same character does not exclude *Menelikia* from being in the Reduncini or *Antidorcas* from being in the Antilopini. The horn cores of *Brabovus* are longer than in *Cephalophus*. The auditory bulla, although globular, is less inflated than in *Cephalophus*. The lower molars of *Brabovus* do not have the outbowed lingual walls of *Cephalophus*, but the small I$_1$ of *Brabovus* is less different from *Cephalophus* than from some other bovids.

Comparisons of Cephalophini with other bovids are awkward to handle, because *Cephalophus* is probably secondarily adapted to forest life and because adaptations for living in forests may involve reacquisition of primitive character states. Moreover, *Sylvicapra*, the other cephalophine genus, has fewer differences from other bovids, such as *Ourebia* or *Tetracerus*, and it is not an inhabitant of forests. The best course is to classify *Brabovus nanincisus* as standing between Cephalophini and Bovinae. Ecologically it may have been a closed-cover species.

SUBFAMILY ANTILOPINAE Gray, 1821

TRIBE CEPHALOPHINI Gray, 1871

Grubb (2001) discussed whether the tribal name should date from Blyth, 1863.

TYPE GENUS *Cephalophus* H. Smith, 1827

Cephalophini, the duikers, are small to medium-sized stocky antelopes feeding by frugivory, selective browsing, and occasional carnivory. *Cephalophus* has many forest-living species across sub-Saharan Africa, while the less specialized *Sylvicapra* has only one species with less-distinctive characters, especially in the teeth, and lives in non-forested areas with cover. Many zoologists have thought that Cephalophini may not be primitively forest dwelling (which would have implied an evolutionary line separate from other bovids since before *Eotragus*), and the debate continues (Kingdon 1982; Heckner-Bisping 2001). The following selection of characters is more strongly expressed in *Cephalophus*. Horn cores are short, not compressed, parallel, inclined backwards, and inserted far postorbitally. Females are hornless and slightly bigger than males. Supraorbital pits in a longitudinally extended line. Frontals shallowly domed longitudinally in front of horn bases, skull width across base of orbits exceeds that across top of orbits. Ethmoidal fissure absent, infraorbital foramen high. Straight and little-inclined braincase roof, small mastoid exposures on the occipital, rather small basioccipital, inflated auditory bulla. Brachyodont cheek teeth with basal pillars on the upper and lower molars, and with rounded labial ribs and correspondingly weak styles on the upper molars. Lower molars have rounded lingual and labial lobes and no stylids, M$_3$ has a small rear (third) lobe. Premolar rows are long and anterior premolars are relatively large. Hypoconid not projecting labially on $P_{3–4}$ and without a valley separating it from the protoconid in front, labial walls of $P_{3–4}$ passing round anteriorly to a nearly transverse plane, I_1s are not much larger than the other incisors and canine.

Cephalophini sp. or spp.

Material

Gentry (1987: 386, pl.10.6) reported and illustrated three cephalophine teeth from the Laetolil Beds: LAET 75-339, Loc. 7; LAET 75-1890, Loc. 10; and LAET 75-3052, Loc. 17. A small number of additional specimens have appeared in the collections dating from 1998–2005, and one new one was noticed in the Leakey collection. The complete list is:

- LAET 75-2957, Loc. 16. Rt M_3, no back lobe, and in earlier wear than 75-339, ca. 19.5 × 7.5 × 15.4.
- EP 758/98, Loc. 10W. Below Tuff 3. Lt upper molar, probably an M^1, early middle wear, 12.4 × 9.1 × 11.2.
- EP 832/98, Loc. 10. Below Tuff 3. Lt mandible with broken M_1 and M_2, then M_3, early middle wear, M_1 11.5 long, M_2 ca. 15.3, M_3 18.1 × 7.4.
- EP 1069/00, Loc. 8. Between Tuffs 5 and 6. Horn core, index 10.5 × 10.8, preserved length 15.4, complete length ca. 24 mm.
- EP 1560/00, Loc. 3. Between Tuffs 6 and 8. Rt mandible frag. with M_1, early middle wear, 12.3 × 6.3 × ca. 7.3, ramus depth under M_1 24.3. The middle (labial) root of a dP_4 can be seen in front of the molar.
- EP 1718/00, Loc. 2. Between Tuffs 5 and 7. Rt M^3, early middle wear, 13.7 × 8.0 × 12.9.
- EP 545/03, Loc. 2. Between Tuffs 5 and 7. Lt lower molar, middle wear, ca. 13.1 × 7.9 × 11.0 (not entered on Fig. 15.5).
- EP 1379/03, Loc. 8. Between Tuffs 5 and 6. Lt dP_4, middle wear, 13.4 × 6.6 × 5.7.
- EP 390/04, Loc. 16. Between Tuffs 7 and 8. Rt M_3, early middle wear, 16.0 × 7.9 × 14.8.
- EP 810/04, Loc. 7E. Above Tuff 8. Rt P_4, early middle wear, 12.5 × 7.9 × 12.0.
- EP 741/05, Loc. 3. Between Tuffs 6 and 8. Lt P_3 or P_4, 8.9 × 4.3.
- EP1331/05, Loc. 22E. Between Tuffs 3 and 8. Rt mandible with broken M_1, 12.8 × 6.5.
- EP1910/00, Loc. 5. Between Tuffs 3 and 5. Rt lower molar, unworn, 13.5 × 5.8 × 8.3. Possibly cephalophine.

Description

The horn core EP 1069/00 could be cephalophine, but it could also be a very young individual of some other antelope. The mandible EP 832/98 is intermediate in size between present-day *C. spadix* and *C. silvicultor*, and the ramus is rather deep. The dP_4 EP 1379/03 is of moderate-small size, has rounded walls of its lingual lobes, and a rounded front lobe labially. It is too small to go with a dP_3 EP 75-3335 of "*Gazella*" *kohllarseni*. The M_3 EP 390/04 is a plump little tooth showing a small third lobe, rounded lingual lobes, only faint stylids in early wear, and no basal pillar. On the P_4 EP 810/04 (Fig. 15.4), the backward-pointing direction of the entostylid, far from parallel to the entoconid crest, suggests a cephalophine identity. It is a less advanced tooth than the P_4s of modern Cephalophini. Quite often, modern duiker P_4s in their short-lasting early wear stage show severance of the entoconid transverse crest so that the fossette behind the metaconid runs past the lingual end of the entoconid (itself joined to the lingual end of the metaconid) and exits to the exterior lingually to the entostylid crest.

Fig. 15.4 Right lower premolars of Cephalophini spp. in occlusal view. Labial sides to the *top*. From the *left*: P_4 EP 810/04, P_3 or P_4 EP 741/05. Scale = 10 mm

The P_3 or P_4 EP 741/05 (Fig. 15.4) is not a deciduous tooth and is without a transverse or diagonally-backwards ridge from its metaconid. A few measurements taken on extant duikers suggested that P_3s are around 90% as long as P_4s, so this specimen is likely to be from a smaller cephalophine species than the other Laetoli specimens even if it is a P_3. The possible cephalophine lower molar EP 1910/00 has outbowed lobes of its lingual walls and crescentic central fossettes. Among modern antelopes, this morphology can be matched in the small *Cephalophus monticola*, in *Sylvicapra grimmia* or in *Ourebia ourebi*.

It is interesting that all but one of the cephalophines at Laetoli seem to be of one species and that it is of a size in between *C. spadix* and *C. silvicultor* (Fig. 15.5). This is large compared with most living species.

Discussion

Cephalophini are rarely found in African fossil localities. They are not common in the Laetolil Beds, but it is exceptional that they should occur at all. A horn core from the KBS (Harris 1991: 228) is the size of a *C. silvicultor* or bigger. A likely cephalophine upper molar from Lukeino (Thomas 1980: 89, fig. 1[2]) would be from a smaller species unless it were an M^1. If *Sylvicapra* were present in the Laetolil Beds, it would be difficult to differentiate from a similarly sized neotragine.

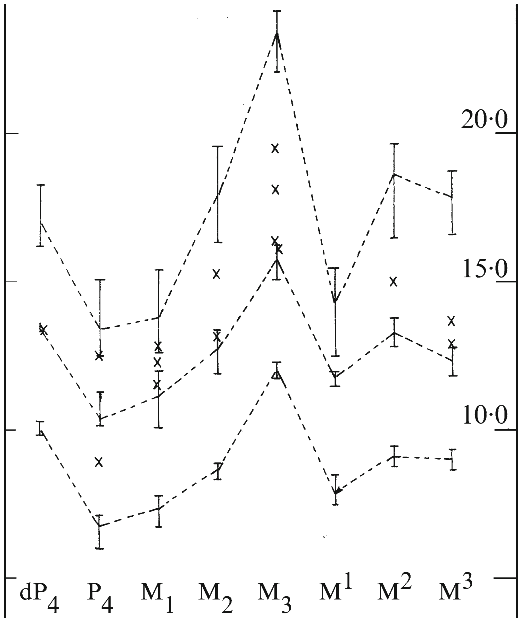

Fig. 15.5 Occlusal lengths of teeth in duikers. Means and ranges are shown for small samples of up to six *Cephalophus silvicultor* (*top*), up to four *C. spadix* (*middle*), and up to three *C. natalensis* (*bottom*). Vertical scale in mm. Readings for fossils from the Laetolil Beds (x) nearly all lie between *C. silvicultor* and *C. spadix*. The lower premolar at 8.9 mm is EP 741/05, which is probably a smaller species and may be a P$_3$

TRIBE NEOTRAGINI Sclater and Thomas, 1894
TYPE GENUS *Neotragus* H. Smith, 1827

African antelopes smaller than *Gazella*. Their horn cores are fairly upright spikes, of small cross-sectional area, set widely apart, and plausibly primitive. There are no basal pillars on the teeth, the lingual walls of lower molars are often straight, central fossettes disappear early in wear, and upper molars have small styles but rarely vertical ribs in between. Many recent classifications suggest that they are not all more closely related to one another than to species outside the Neotragini.

Raphicerus H. Smith, 1827

TYPE SPECIES *Raphicerus campestris* (Thunberg, 1811)

Short to moderately long horn cores having a slightly concave front edge. Back of braincase roof not very strongly curved downwards, temporal lines do not approach closely on the braincase roof. The genus includes the less advanced Cape grysbok (*R. melanotis*) and Sharpe's grysbok (*R. sharpei*), the latter being small and short horned and thereby more like *Madoqua*. *Raphicerus campestris*, the more widespread steinbok, is in many ways the standard or most familiar of the Neotragini, so *Raphicerus* has become a convenient generic name to use for undetermined fossil neotragines larger than *Madoqua*.

?*Raphicerus* sp.

Gazella hennigi (partim) Dietrich, 1950: 25, fig. 13.
?*Raphicerus* sp. indet. Gentry and Gentry, 1978: 425, 62.
?*Raphicerus* sp. Gentry, 1987: 393.

Material

- EP 718/98, Loc. 10W. Below Tuff 3. Horn core 13.3 × ca. 10.0.
- EP 176/98, Loc. 10E. Between Tuffs 5 and 7. Rt M$_3$, early middle wear, 12.0 × 3.8.
- EP 177/98, Loc. 10E. Between Tuffs 5 and 7. Lt M^3, 9.4 × 5.6.
- EP 294/98, Loc. 10E. Between Tuffs 5 and 7. Lt M$_3$, ca. 11.6.
- EP 298/98, Loc. 10E. Between Tuffs 5 and 7. Lt M^1, early middle wear, 9.6 × 5.7 × 8.4.
- EP 310/98, Loc. 10E. Between Tuffs 5 and 7. Lt M$_3$, 9.8.
- EP 838/98, Loc. 10. Below Tuff 3. Lt P$_4$, early middle wear, 7.4.
- EP 1417/98, Loc. 15. Between Tuffs 6 and 7. Lt M^3, middle wear, 8.3 × 6.4.
- EP 1418/98, Loc. 15. Between Tuffs 6 and 7. Rt upper molar, late middle wear, 8.0 × 6.1.
- EP 1542/98, Loc. 10E. Between Tuffs 5 and 7. Lt M^2, late middle wear, 8.9.
- EP 2848/00, Loc. 10E. Between Tuffs 5 and 7. Rt upper molar, middle wear, 8.9 × 6.9.
- EP 2979/00, Loc. 1. Between Tuffs 6 and 8. Lt distal tibia, width 15.5.
- EP 454/01, Loc. 9. Between Tuffs 6 and 8. Rt M$_1$ or M$_2$, middle wear, 9.2 × 4.0 × ca. 10.3.
- EP 839/03, Loc. 10E. Between Tuffs 5 and 7. Rt M$_3$, middle wear, 11.8 × 4.7.
- EP 1375/03, Loc. 8. Between Tuffs 5 and 6. Lt M$_3$, early middle wear, 12.2 × 4.8, ramus depth 12.5.
- EP 1376/03, Loc. 8. Between Tuffs 5 and 6. Rt dP$_4$, early middle wear, 13.0 × 4.2 × 6.6 (height measured as rear valley depth).
- EP 1378/03, Loc. 8. Between Tuffs 5 and 6. Lt M^1, middle wear, 8.7 × 5.9 × 7.5.
- EP 102/04, Loc. 22. Between Tuffs 5 and 7. Lt mandible with M$_2$, middle wear, 9.5 × 5.1.
- EP 1239/04, Loc. 10E. Between Tuffs 5 and 7. Rt P$_{2-3}$, P$_2$ 4.6 long, P$_3$ 7.1 × 2.8.

Description

The horn core EP 718/98 was thought not to be a female gazelle because of strong irregular longitudinal ridges on part of surface. It is also too attenuated to be the tip of a larger species like the "*Gazella*" *kohllarseni* LAET 78-5321. A few other horn cores could belong to this species. The teeth were assigned on the basis of size, being considered as intermediate between *Gazella* and *Madoqua*. They show the characters given above for Neotragini.

Madoqua Ogilby, 1837

Praemadoqua Dietrich, 1950: 34.
TYPE SPECIES *Madoqua saltiana* (Desmarest, 1816)

Generic Diagnosis

See Gentry, 1987: 391.

Remarks

Neotragines substantially smaller than *Raphicerus*, *Oreotragus*, or *Ourebia*. There are several very small species in the Horn of Africa and also *M. kirkii* discontinuously distributed between East and southwestern Africa. Some authors separate the Namibian species as *M. damarensis* on genetic evidence (Bronner et al. 2003).

Madoqua avifluminis (Dietrich, 1950)

Praemadoqua avifluminis Dietrich, 1950: 34, fig. 3, 4, 25, 26.
Madoqua avifluminis (Dietrich) Gentry and Gentry, 1978: 425, 62.
Madoqua avifluminis (Dietrich) Gentry, 1987: 392.

Syntypes

Dietrich (1950: 36) designated as type the left lower and upper dental rows of his figs. 25 and 26. The mandible is composite with the M_3 being from Garusi and in earlier wear than the P_3–M_2, no.690 from Vogel River. An unfossilized P^2 had been added to the maxilla when I saw it early in 1977.

Type Locality

Laetoli, Tanzania.

Horizon and Range

Laetolil Beds.

Material

Abundant in the Laetolil Beds.

Diagnosis

An extinct *Madoqua* about the size of *M. kirkii*. Horn cores are shorter and more thickened basally than in *M. kirkii* and with a concave anteromedial edge, which makes them slightly curved. Back half of M^3 less reduced than in *M. kirkii* and M_1s more frequently with traces of basal pillars. M_3s have a reduced rear or third lobe, but it is not absent as in two of the species in Somalia. Metatarsals are slightly shorter and relatively thicker than in *M. kirkii*.

Discussion

This species was discussed by Gentry (1987). It has a number of character differences from living *Madoqua*, some of which are primitive. *Madoqua* or *Madoqua*-sized neotragines have been claimed or listed back to the Late Miocene of Mpesida and the Adu-Asa Fm. (Thomas 1980: fig. 1[10]; Haile-Selassie et al. 2004).

TRIBE ANTILOPINI Gray, 1821
TYPE GENUS *Antilope* Pallas, 1766

Aepyceros Sundevall, 1847

TYPE SPECIES *Aepyceros melampus* (Lichtenstein, 1812)

Hitherto a majority of recent cladistic studies have placed *Aepyceros* in an unresolved position close to the base of groups (B) and (C) in Table 15.1. (See Table 15.1 caption for references.) In this chapter, and contrary to my own previous opinions, I revert to its traditional placing inside the Antilopini.

Generic Diagnosis

Moderate-sized antelopes. Horn cores long, with the level of maximum transverse thickness lying in an anterior position, and quite a sharp posterolateral edge to the horn core, which does not amount to a keel. Horn cores little compressed, a flattened posterior part of the lateral surface, and often with transverse ridges. They diverge proximally, then change course in their centre and have more or less parallel distal parts, but this lyrated course never becomes strong enough to be spiralled. They curve backwards and insert above the back of the orbits. The postcornual fossa is large, rounded and quite deep. Females hornless. Sinuses in the pedicels and frontals, pedicels short, frontals slightly raised between the horn bases. Small supraorbital pits. Cheek teeth of generally antilopine aspect: quite high crowned, basal pillars absent on upper molars and tiny or absent on lower molars, upper molars with a fairly prominent mesostyle, only a weak rib on the labial wall of the paracone, labial wall of metacone even flatter, M^3 metastyle in the form of a strong flange, lower molars without transverse goat folds anteriorly, premolar rows short in comparison with molar rows, P_2s small, P_4 with paraconid-metaconid fusion to close the anterior part of the lingual wall and with hypoconid tending to project labially.

Remarks

The skull, teeth, and limb bones of the living *Aepyceros melampus* have a number of unique characters, advanced or different from those of any fossil species. The species has been found in the Shungura Fm. back to levels above the top of Mb. G. The preceding impala in Mbs. B–G is *A. shungurae* Gentry, 1985, with more primitive characters (smaller size, frontals less raised between horn bases, supraorbital pits less wide apart, vestige of a preorbital fossa, a shorter face, and others). Likewise, in the Koobi Fora Fm., Harris (1991) found *A. melampus* in the Upper Burgi Mb. and higher levels and *A. shungurae* in the Moiti to Tulu Bor Mbs. An Upper Burgi skull 1657 (Harris 1991: fig. 5.62) appeared to have a mixture of *A. melampus*–like and *A. shungurae*–like characters. Because the holotype skull of *A. shungurae* is from Shungura upper Mb. B, it is possible that later Shungura *A. shungurae* were also changing towards *A. melampus*. *Aepyceros shungurae* was also present in the Usno Fm. and at Kaiso Village (Geraads and Thomas 1994: pl. 3, fig. 3). An earlier *Aepyceros* species in the Mursi and Hadar Fms. and at Karmosit (Gentry 1981, 1985: 183) had more modest lyration of its horn cores. The *Aepyceros* in the Nkondo and Warwire Fms. (Geraads and Thomas 1994) could also belong to this pre–*A. shungurae* species, as could the Lokochot (Koobi Fora Fm.) horn cores attributed to *A. shungurae* (Harris 1991: fig. 5.65, table 5.64), which show the poor lyration and, reportedly, the weak or absent transverse ridges appropriate for this species.

This reasonably straightforward picture has to be extended and modified to take account of (1) the reinterpretation herein of *Aepyceros* in the Laetolil Beds, and (2) the fuller account of the *Aepyceros* at Lothagam in Harris (2003). The latter species, *A. premelampus*, is the commonest bovid at Lothagam, with crania, horn cores, and teeth distributed through the Nawata Fm. and Apak and Kaiyumung members and declining in size in the younger levels. It looks antilopine, but less certainly an *Aepyceros*.

Aepyceros dietrichi **sp. nov.**

Aepycerotinae gen. et sp. indet. Dietrich, 1950: 30, fig. 45.
Gazella kohllarseni (partim) Dietrich, 1950: 25, figs. 16, 49.
?Hippotragini sp. (partim) Gentry and Gentry, 1978: 351, 62.
?Hippotragini sp. nov. (partim) Gentry, 1987: 388, pl. 10.8.
Sp.indet.aff. *Pelea* Gentry, 1987: 394, pl. 10.10.

Holotype

A right horn core and frontal, LAET 76-4077 (Gentry, 1987: pl. 10.8).

Type Locality

Laetoli, Tanzania.

Horizon and Range

The holotype came from the Upper Laetolil Beds at Locality 1. Horn cores are known from Locs. 1, 2, 7, 12, and 20, which are mostly in the vicinity of Tuffs 6 and 7, a relatively rich fossiliferous section of the Laetolil Beds. Teeth are commoner, and some are found at lower levels.

Name

Named for the German paleontologist W. O. Dietrich, whose original opinion on the affinities of this species now seems to have been correct.

Material

Gentry (1987: 388, pl.10.8) listed horn cores of this species and illustrated the future holotype. A few more horn core pieces have come to light in both the Leakey and the 1998–2005 collections:

- LAET 78-5063, Loc. 2. Between Tuffs 5 and 7. Piece of a right horn core in mid-course.
- LAET 81-9, Loc. 2. Between Tuffs 5 and 7. Rt horn core base.
- EP 629/03, Loc. 2. Between Tuffs 5 and 7. Rt horn core base, index 39.4×35.0.

The teeth now regarded as part of this species nearly all exist as isolated finds and are too numerous to be listed as individual fossils. Some fossils with conjoined teeth are:

- EP 843/98, Loc. 10. Below Tuff 3. Lt P^{3-4}, middle wear. P^3 10.2×9.8, P^4 9.8×10.6.
- EP 1092/00, Loc. 8. Between Tuffs 5 and 6. Rt mandible with P_4-M_2, middle wear. P_4 11.8×6.7, M_1 13.1×8.1, M_2 17.1×8.4.
- EP 1728/00, Loc. 2. Between Tuffs 5 and 7. Lt P^{3-4}, late middle wear. P^3 11.4×9.3×9.5, P^4 11.4×10.8×10.0.
- EP 1812/00, Loc. 2. Between Tuffs 5 and 7. Rt M_{1-2}, late middle wear. M_1 13.1×8.1×4.4 high, M_2 15.9×8.9×6.9.
- EP 2100/00, Loc. 13, snake gully. Between Tuffs 6 and 7. Lt mandible with M_{2-3}, middle wear. M_2 14.1×8.9, M_3 20.8×8.4.
- EP 2368/00, Loc. 16. Between Tuffs 7 and 8. Lt M^{1-2}, middle wear. M^1 14.8×12.8×7.8, M^2 17.7×14.4×11.3.
- EP 2603/00, Loc. 2. Between Tuffs 5 and 7. Lt maxilla with M^{2-3}, middle wear. M^2 19.2×ca. 15.6, M^3 ca. 21.7×ca. 15.1.
- EP 2787/00, Loc. 5. Between Tuffs 3 and 5. Rt maxilla with P^4-M^1, middle wear. P^4 11.1×11.2×10.0, M^1 14.3×13.0×7.8.
- EP 4269/00, Loc. 11. Between Tuffs 7 and 8. Rt maxilla with P^4-M^3, middle wear. M^{1-3} 81.8, M^1 16.8×14.7, M^2 18.5×14.0, M^3 18.0×10.0.
- EP 2473/03, Loc. 1NW. Rt mandible with M_{1-3}. M_1 ca. 14.9, M_2 17.1×8.1, M_3 24.0×8.5, ramus depth below M_1 24.7, below M_3 32.4.

A few teeth difficult to identify have also been allocated to this species:

- EP 1402/00, Loc. 1. Between Tuffs 6 and 8. Rt dP^4, middle wear. ca. 14.8×11.0×ca. 7.0. The missing anterolabial piece might make it large enough.
- EP 2614/00, Loc. 2. Between Tuffs 5 and 7. Rt P_4, middle wear. 12.1×7.4.
- EP 238/01, Loc. 5. Between Tuffs 3 and 5. Rt upper molar, middle wear. Occlusal length 16.6.

Diagnosis

A moderate- to large-sized species within *Aepyceros*. Horn cores have well-marked transverse ridges across the anteromedial surface, these ridges becoming more widely spaced distally. The horn cores diverge strongly in their lower parts, show quite a low inclination in side view, long axes of cross-section are set at quite a wide angle to the skull midline, insertions moderately wide apart, and slight anticlockwise torsion on the right side (= heteronymous torsion), which confers a lyrated appearance in anterior view. Cheek teeth differ from those of *Aepyceros melampus* in having a flat or concave labial wall on the metacone and a correspondingly stronger-looking mesostyle, M^3s sometimes with spurs into the central fossettes, lower molars with flat lingual walls reminiscent of modern *Antidorcas* and pointed labial lobes, central fossettes short and straight and disappearing early in wear, and the M_3 has a large rear (third) lobe without a central fossette. The mandibular ramus is fairly deep.

Description

Gentry (1987: 388) designated this species as "?Hippotragini sp. nov." and included teeth now assigned to *Hippotragus*. If the horn cores really are *Aepyceros* or even Antilopinae, the most likely teeth to be conspecific will include many of those Gentry (1987: 394, pl.10.10) described and illustrated as "Sp. indet. aff. *Pelea*." They have the characters given in the diagnosis. Three further dental specimens are illustrated in Fig. 15.6. This constitutes a major round of reidentifications.

The horn cores in the Laetolil Beds overlap and exceed in size those of the modern East African *Aepyceros melampus* and the degree of compression is identical (Fig. 15.7). None are complete. The proximal parts of the horn cores tend to be thicker in proportion to the distance from the base to the point where degree of divergence begins to lessen. A distal part, LAET 75-503 from Loc. 7, shows the transverse ridges to be more widely spaced than they are on proximal parts of the horn cores. The horn core LAET 75-3093 is more compressed than others of this species. The curvature of the horn core LAET 81-9 looks wrong for this species, but perhaps damage and matrix cover have given this impression. The original horn core of Dietrich (1950: pl. 4, fig. 45) is re-illustrated in Fig. 15.8; its index is 50.4×46.0.

The base of a left horn core, EP 3589/00 from Loc. 21 between Tuffs 5 and 8 (Fig. 15.9), is intriguing. Little of it remains, and it has an index of ca. 31×ca. 28. It has little compression, backward curvature, a central or slightly posterior position of the level of maximum transverse diameter, the lateral surface flatter than the medial, perhaps a faint anterior keel, an insertion low over the back of the orbit,

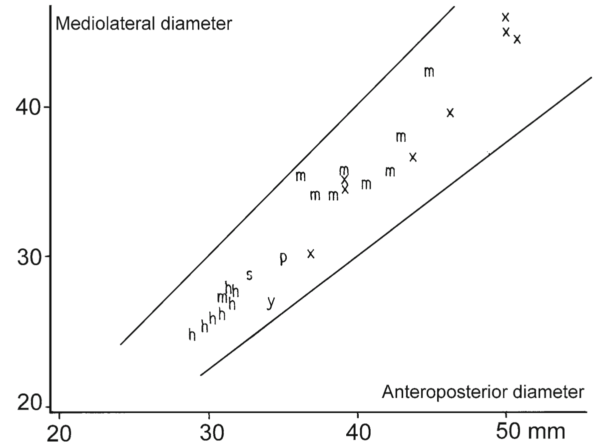

Fig. 15.7 Basal diameters of some *Aepyceros* horn cores. The upper diagonal line is that along which mediolateral diameter is 100% of anteroposterior diameter, the lower line is 75%. h=*Aepyceros* sp. from the Hadar Formation, m=extant *A. melampus*, p=mean of *A. premelampus* (Harris 2003), s=mean of the means of *A. shungurae* from members B-G of the Shungura Formation, x=*Aepyceros dietrichi*, y=*Aepyceros* sp. from the Mursi Formation

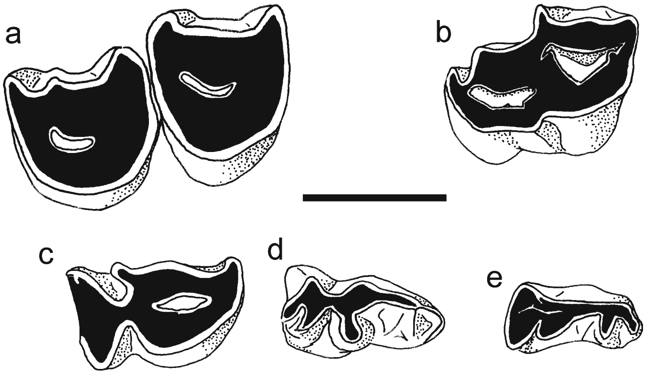

Fig. 15.6 Some premolars of *Aepyceros dietrichi* (**a**–**c**) and "*Gazella*" *kohllarseni* (**d**–**e**) in occlusal view. (**a**) left $P^{3–4}$ EP 843/98. (**b**) left dP^3 LAET 75-2718. (**c**) right P_4 from mandible EP 1092/00. (**d**, **e**) left P_3s LAET 75-3335 and LAET 75-2030. Labial side lowermost in (**c**), uppermost in all others. Scale=10 mm

Fig. 15.8 *Aepyceros dietrichi* left horn core in lateral view. The same specimen and view as in Dietrich 1950: pl. 4, fig. 45. Scale=10 mm

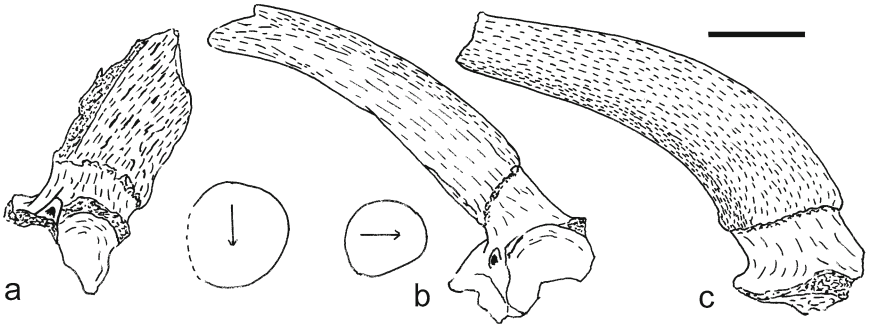

Fig. 15.9 (**a**) left horn core EP 3589/00, possibly of an *Aepyceros* species, from the Laetolil Beds in anterior view. (**b**) right horn core of *Gazella janenschi* LAET 76-445 Loc.18 from the Upper Ndolanya Beds in lateral view. (**c**) left horn core of *Antidorcas recki* EP 243/04 from the Upper Ndolanya Beds in medial view. Cross-sections at base given for (**a**) and (**b**) with arrows pointing anteriorly. Scale = 25 mm

moderate inclination in side view, insertions probably close, and divergence increasing from the base. The pedicel is low, the postcornual fossa is large, no sinuses within the frontals are visible, the frontals between the horn bases are level with dorsal orbital rims, and the supraorbital pit is close below the anterior base of the horn core. The last three characters are closer to a *Gazella* than to *Aepyceros*, but the horn core is bigger than the common *G. janenschi* of the Laetolil Beds. It is about the size of the Shungura and Usno Fm. *Aepyceros shungurae* at 3.0–2.0 Ma or the *Aepyceros* in the Mursi and Hadar Fms. at 4.0–3.0 Ma, so it may be the only representative at Laetoli of a smaller *Aepyceros* than *A. dietrichi*.

Discussion

In my revised opinion, Dietrich's 1950 name "Aepycerotinae gen. et sp. indet." expresses likely affinities of the horn cores of this species. There is too much coincidence between the fossil form and the impala for there not to be a relationship. This is seen in the course of the horn cores, lack of compression, the transverse ridges, the divergence, the short pedicels, and the sinuses, which are well-marked in the pedicels and adjacent parts of the frontals. In fact, horn cores of modern *Aepyceros melampus* could differ only by being longer and often smaller. A probable interpretation of all this could be that a mid-Tertiary large and advanced *Aepyceros* came to evolutionary grief and was outlasted by a smaller relative, which then had the opportunity to develop into the extant species. In this connection, it is interesting that the teeth of *A. dietrichi* are more advanced than those of *A. shungurae*, yet their characters are divergent from *A. melampus* (as set out in the diagnosis). They look a shade smaller than would be expected from the size of the horn cores. The length of the premolar row of the mandibular dentition LAET 75-476 (Gentry 1987: pl.10.10) is 52% of the length of its molar row, a proportion at the long end of the range found in 12 *A. melampus* (43–52%).

Since this chapter was prepared Geraads et al. (2009) have discovered a new *Aepyceros, A. afarensis*, in the Woranso-Mille area of Afar, dating from about 3.75 Ma. It has similarities, but seemingly also some differences, from *A. dietrichi*.

Aepyceros premelampus at Lothagam (presumably conspecific with the Lukeino *Aepyceros* sp. of Thomas, 1980) has a range of dates from 7 Ma or more to around 4 Ma, so its later occurrences would coincide with the time span of the inadequately known *Aepyceros* of the Mursi, Hadar, Nkondo, and Warwire Formations and the Karmosit Beds. It is not certain from the description or illustrations of the Lothagam (Nawata Fm.) holotype and paratype (Harris 2003: figs. 11.19 and 11.20) that the horn cores show the transverse ridges or incipient flattening of the lateral surface to be expected in many *Aepyceros*. Furthermore, they are well inclined, the cranium is wide and rather long for an *Aepyceros*, and the supraorbital pits are large. It is not clear whether this species is better placed in *Aepyceros* or in some other genus – for instance, *Dytikodorcas* Bouvrain and de Bonis (2007), into which the Sahabi *Prostrepsiceros libycus* of Lehmann and Thomas (1987) was placed. Perhaps *Aepyceros* emerged from among the late Miocene antelopes placed in or near *Prostrepsiceros* and is consequently related to *Antilope*. Further studies are needed.

The original state of bovid teeth was probably like the Middle Miocene *Eotragus* and *Tethytragus* of western Eurasia, and Antilopini have developed little from this pattern. Other tribes have sometimes evolved towards occlusal complexity and sometimes towards occlusal simplicity (the Boodontia and Aegodontia of Schlosser (1911) or "millers" and "cutters" of Köhler (1993)). These trends have not been uniform and consistent, so plenty of opportunities for parallelisms have occurred and different tribes now have suites of characters not coinciding with any other tribe. The teeth of *Aepyceros dietrichi* have a morphology like Antilopini but more advanced than *Gazella*. Thus, their morphology approaches but does not coincide with that seen in *Antidorcas* or in Caprini. It is more advanced than that of the smaller teeth of the later *Aepyceros shungurae* at Omo and unlike modern *Aepyceros*. The premolars are about as long as in *Parmularius pandatus*, but the molars are about 15% shorter.

Gazella Blainville, 1816

TYPE SPECIES *Gazella dorcas* (Linnaeus, 1758)

Diagnosis

Small- to moderate-sized bovids. Moderately long to long horn cores, without keels, with a subcircular or variably compressed elliptical cross-section, lateral surface often flatter than the medial, little divergence, some backward curvature, the level of maximum mediolateral width lying at or just behind the anteroposterior midpoint, moderately wide insertions above the back of the orbits, moderately upright insertions, without torsion, strong postcornual fossa, no sinuses within the frontals or a very limited incidence of them, most extant species with horned females, frontals between the horn bases not rising above the level of the dorsal orbital rims, large triangular supraorbital pits around the supraorbital foramina, braincase little shortened and its roof not greatly angled downwards, occipital surface with each half facing partly laterally as well as backwards, moderate to large auditory bullae. Teeth moderately hypsodont, basal pillars present on molars in earlier species. On upper molars the styles are little pronounced. Lower molars have rather flat lingual walls with only gentle low outbowings from the metaconid and entoconid, traces of metastylids on M_2 and M_3, labial lobes fairly pointed but not especially narrow, no goat folds, more or less straight central fossettes which do not disappear in early wear, M_3s often with an enlarged third lobe. P_2s present and small.

Remarks

Gazella has been a widespread genus in both Africa and Eurasia since the Miocene. Some of the 14 or more post-Pleistocene species have been placed in different genera or subgenera on morphological or genetic grounds (Wilson and Reeder 2005). They graze and browse in semiarid and arid, open regions and are well adapted cursorially. Their skulls, horn cores, and dentitions, however, are not notably distinctive, and the history of the contained species is difficult to work out. Their Middle Miocene appearance in Africa and the Siwaliks predates their known Late Miocene appearance in Europe.

Gazella janenschi Dietrich, 1950

Gazella janenschi Dietrich, 1950: 25, figs. 14, 15, and 22.
Gazella janenschi Dietrich Gentry and Gentry, 1978: 442, 62.
Gazella janenschi Dietrich Gentry, 1987: 393, pl.10.9.

Lectotype

Dietrich (1950) founded three species of *Gazella* at Laetoli – *G. hennigi*, *G. janenschi*, and *G. kohllarseni* – diagnosing them at the end of his discussion by a lower level of hypsodonty than in living African gazelles and in increasing order of tooth size. He did not mention type specimens, so all the material available to him at the time of writing became syntypes. I now select as lectotype for *Gazella janenschi* the left horn core of Dietrich (1950: pl.2, fig. 22). It is in the Museum für Naturkunde der Humboldt-Universität, Berlin.

Type Locality

Garusi in the Laetoli area, Tanzania.

Horizon and Range

Dietrich (1950: 48) assigned this species to the oldest of the Laetoli faunas.

Material

This is the common gazelle of the Laetolil Beds. Horn cores have been recovered in good numbers, and some were listed in Gentry (1987). The species appears to have horned females. Some of the latter include:

- EP 773/98, Loc. 10W. Below Tuff 3. Rt index 13.9 × 13.4.
- EP 1547/98, Loc. 10E. BetweenTuffs 5 and 7. Rt index 12.8 × 12.9.
- EP 1121/98, Loc. 9. Between Tuffs 6 and 8. 12.9 × 11.9.
- EP 2045/00, Loc. 13. Between Tuffs 5 and 8. Rt index 12.9 × 13.9.
- EP 1122/98, Loc. 9. Between Tuffs 6 and 8. Rt index 12.8 × 12.6.
- EP 1302/01, Loc. 22. Between Tuffs 5 and 7. Lt index 13.2 × 13.1.
- EP 1204/98, Loc. 22. Between Tuffs 5 and 7. Lt index 16.3 × 13.6.
- EP 1019/04, Loc. 11. Between Tuffs 7 and 8. Rt index 14.8 × 12.8.
- EP 1352/98, Loc. 13. Between Tuffs 5 and 8. Lt index 13.0 × 12.3.

Among the better dental specimens are:

- EP 164/98, Loc. 10E. BetweenTuffs 5 and 7. Lt mandible with P_4-M_3, prob. late middle wear. P_4 ca. 8.7, M_{1-3} ca. 37.3, M_1 ca. 9.4, M_2 11.9, M_3 16.1 × 6.5.
- EP 305/98, Loc. 10E. BetweenTuffs 5 and 7. Lt maxilla with P^2-M^1, middle wear. P^{2-4} 21.7, P^2 8.3 × 6.5 × 7.0, P^3 6.8 × 7.0 × 6.9, P^4 6.9 × 6.7 × 7.3, M^1 11.0 × 8.8 × 7.8.
- EP 456/98, Loc. 10. Below Tuff 3. Lt P^{2-4}, early middle wear. P^{2-4} 22.5, P^2 8.5 × 5.8, P^3 7.6 × 6.7, P^4 7.5 × 6.3.
- EP 35/99, Loc. 10E. BetweenTuffs 5 and 7. Rt M^{2-3}, early middle wear. M^2 12.8 × 9.5, M^3 ca. 13.0 × 8.3.
- EP 497/00, Loc. 21. BetweenTuffs 5 and 8. Rt P^3-M^3, lt P^2-M^3, late middle wear. P^{2-4} 23.5, M^{1-3} 34.7, P^2 7.8 × 6.3, P^3 7.6 × 7.2, P^4 7.5 × 6.9, M^1 10.8 × 8.9, M^2 13.0 × 9.6, M^3 12.3 × 8.3.

- EP 1617/04, Loc. 16. Between Tuffs 7 and 8. Lt mandible with P_{2-3}, M_{1-3}, early middle wear. P_{2-4} 20.2, M_{1-3} 43.2, P_2 4.8×3.1, P_3 8.1×3.9, M_1 11.8×6.4, M_2 14.1×6.4, M_3 17.1×5.8, ramus depth below P_2 13.2, below M_1 17.0, below M_3 22.4.
- EP 204/05, Loc. 9. Between Tuffs 6 and 8. Rt P_{2-4}, early middle wear. P_{2-4} ca. 19.6, P_3 7.6×3.4, P_4 9.2×4.2, ramus depth below P_2 14.7.
- EP 711/05, Loc. 3. Between Tuffs 6 and 8. Lt mandible with P_4-M_3, rt mandible with P_{2-3} early middle wear. P_{2-4} ca. 20.5, M_{1-3} 39.3, P_2 4.7×3.5, P_3 7.3×4.3, P_4 9.3×4.7, M_1 10.9×5.9, M_2 12.0×5.8, M_3 16.4×4.8, ramus depth below P_2 12.0, below M_1 15.2, below M_3 20.8.

Diagnosis

A small gazelle. Horn cores moderately long, with a central position for the level of maximum transverse thickness, little compression, sometimes a flattening of the lateral surface, moderately divergent, quite a low inclination in side view. The postcornual fossa is extensive in area but no more than moderately deep. Females horned. Orbital rims not wide, supraorbital pits narrow. Molars are without basal pillars, M_3 has a large third lobe posteriorly with a central fossette and with its lingual wall not offset. P_3 quite narrow, anterior end of tooth not turned sharply transversely, with only a trace of separation between parastylid and paraconid, metaconid ridge directed more backwards than transversely, entoconid and entostylid combined into one ridge, and with little labial projection of hypoconid.

Description

The horn cores and teeth have been illustrated by Dietrich (1950) and Gentry (1987). The horn cores are usually small compared with those of later African gazelles. One of the larger ones is a right horn core EP 1382/03 from Loc. 8 with index 25.1×23.6, but this was exceeded by LAET 75-690 from Loc. 1 in the Leakey collection, with an index of 28.0×23.1. Not all female horn cores can be identified as right or left; they show little compression and a straight course or a very slight backward curvature (EP 2045/00), a central or anterior position of the level of maximum transverse thickness, slight flattening of the lateral and perhaps of the posteromedial surfaces, a posterolateral keel or intersection, sometimes almost an anterior surface, quite a low inclination in side view, and slight divergence. The postcornual fossa in females can be large, rounded, and shallow.

Discussion

Gazella janenschi horn cores are most like smaller examples of the Late Miocene *G. capricornis* from Pikermi, Greece, which are also little compressed, so it looks like an early or primitive gazelle of the Tertiary period. It is smaller and more primitive than the gazelle at Olduvai. The horn cores are quite similar to the supposed *Gazella* at Fort Ternan (Gentry 1970: pl. 15, figs. 3–5) but are less compressed. They are only as big as the smaller horn cores of the *Gazella* sp. at Langebaanweg but, again, are less compressed. Gazelle teeth (M_{1-3}) at Langebaanweg are appreciably bigger.

Gazella granti Brooke, 1872

In my opinion this species is probably not a member of the bovid fauna of the Laetolil Beds.

Material

- LAET 75-529, Loc. 10E. Rt horn core, index 46.9×29.8.
- LAET 75-1476, Loc. 9. Lt horn core with top of pedicel, index 52.5×28.8.
- LAET 75-2321, Loc. 10. Lt mandible with part M_2 and M_3, middle wear, M_2 18.3×9.2×10.7, M_3 26.3×8.8, ramus depth below M_3 30.0. Height of M_3 would have been ca. 25 mm.
- EP 834/98, Loc. 10. Below Tuff 3. Lt M_3, late middle wear, ca. 25.0×ca. 8.0.
- EP 2030/00, Loc. 13. Between Tuffs 5 and 8, but a few fossils from between Tuffs 3 and 5. Rt M_3, middle wear, occlusal length ca. 23.5.

Description

The East African *Gazella granti* is one of three large extant African gazelles (genus or subgenus *Nanger*) alongside *G. soemmerringi* in the Horn of Africa and *G. dama* in West Africa. It can be recognized by its large size, strongly compressed horn cores, close insertions so that frontals are very narrow between the horn bases, low pedicels, no sinuses in the pedicels, frontals between horn bases not raised above level of dorsal orbital rims, mid-frontal suture complex and ridged. The horn core LAET 75-529 certainly belongs to *Gazella granti*. The lateral surface is flatter than the medial one, the postcornual fossa is quite short and pear shaped, and the pedicel is too short to fit a *Hippotragus*. Part of the orbit is preserved, and the piece has a less-than-fully-fossilized appearance. LAET 75-1476 is very compressed, even for a *G. granti*, and there are no sinuses in the pedicel as would be necessary in a *Hippotragus*. The M_3 2030/00 is intrusive at Loc. 13.

Discussion

Gazella granti still lives at Laetoli. Horn cores of the species are liable to turn up in or on any stratigraphic level in the Laetoli area and Dietrich (1950: 27, pl.1, fig. 6) referred to *G. granti* in younger beds. Those listed here are from the Upper Laetolil Beds, but there is also one in the lower unit and others in the Upper Ndolanya Beds and later deposits. There are also dental remains that look very like *G. granti*. In quite a lot of cases, there is some likelihood that they are intrusive from stratigraphically higher levels, and in some cases they look less fossilized than one would expect. In the M_3 EP 834/98, for example, the enamel is notably white.

Gentry and Gentry (1978: 443) referred to *G. granti* horn cores at Kanjera and a "smaller but similar" one at Kanam, and Harris (1991: fig. 5.75) has claimed *Gazella* aff. *G. granti* from the Okote Mb. of the Koobi Fora Fm. I am loath to accept *Gazella granti* from levels as early as the Upper Ndolanya Beds or older. A fossil form that might more plausibly be related to the living gazelles of the *Nanger* group is *G. vanhoepeni* from Makapansgat Limeworks (Wells and Cooke 1956: 43, figs. 22–24; Wells 1969: 162). It comes from Makapansgat 3 at about 2.6–2.8 Ma and is distinct from any living species. Horn cores of *Gazella* aff. *granti* from Asbole (Geraads et al. 2004: fig. 10[2]) had the much compressed horn cores of *G. granti*, but were a little smaller and with backward curvature like *G. vanhoepeni* or modern *G. soemmerringi*.

TRIBE INDET., ?AFF. ANTILOPINI

Gen. indet., "*Gazella*" *kohllarseni* Dietrich, 1950

Gazella kohllarseni Dietrich, 1950: 25, pl. 1, fig. 7.
?Hippotragini sp. (partim) Gentry and Gentry, 1978: 351, 62.
?Hippotragini sp.nov. (partim) Gentry, 1987: 388.

Lectotype

As noted above under *Gazella janenschi*, Dietrich (1950) founded three species of *Gazella* at Laetoli without mentioning type specimens, so all the material available to him at the time of writing became syntypes. The illustrated P_2–M_3 of *G. kohllarseni* (Dietrich 1950: pl. 2, fig. 16) is a composite specimen assembled from several single specimens. A left horn core labelled "Garussi 2/39" (Dietrich 1950: pl. 1, fig. 7) was referred in the caption to *G. kohllarseni*, but Dietrich (1950: 28) admitted to initial uncertainty about whether it belonged to the second or third of his species and then failed to explain how he had resolved the question. His discussion of the Laetoli gazelles certainly purports to differentiate the species, so I now select the horn core of his pl.1, fig. 7 as the lectotype of *Gazella kohllarseni*. It is in the Museum für Naturkunde der Humboldt-Universität, Berlin, but is not a member of the genus *Gazella*. It is re-illustrated here in Fig. 15.10. This lectotype horn core had been taken by Gentry (1987: 388) to be possibly a female of *Aepyceros dietrichi*, but the species was not otherwise mentioned in that paper.

Type Locality

Garusi in the Laetoli area, Tanzania.

Horizon and Range

Dietrich (1950: 48) assigned this species to the oldest of the Laetoli faunas.

Material

- LAET 75-1597, Loc. 13. Rt horn core, index ca. 33.0×27.0.
- LAET 75-1902, Loc. 2. Lt horn core, index 37.0×30.1.
- LAET 78-5152, Loc. 9S. Below Tuff 1. Rt horn core, index 37.6×25.7.
- LAET 78-5321, Loc. 8. ~ 2 m below Tuff 7. Rt horn core with adjacent skull parts, index 32.7×26.3, preserved length 160 mm, original length ca. 180 mm.
- EP 1124/98, Loc. 9. Between Tuffs 6 and 8. Lt horn core base, frag.
- EP 1423/98, Loc. 15. Between Tuffs 6 and 7. Rt horn core with back of pedicel and part of orbit.
- EP 1105/00, Loc. 8. Between Tuffs 5 and 6. A small-diameter horn core, possibly a distal piece of a "*G*." *kohllarseni*.
- EP 2598/00, Loc. 2. Between Tuffs 5 and 7. Rt horn core pedicel and partial orbit, index ca. 34.0×ca. 27.0.
- EP 3046/00, Loc. 5. Between Tuffs 3 and 5. Rt horn core, index 34.3×27.4.

The teeth are too numerous for individual listing and are not definitely associated with the horn cores. Several interesting or difficult teeth have been allocated as follows:

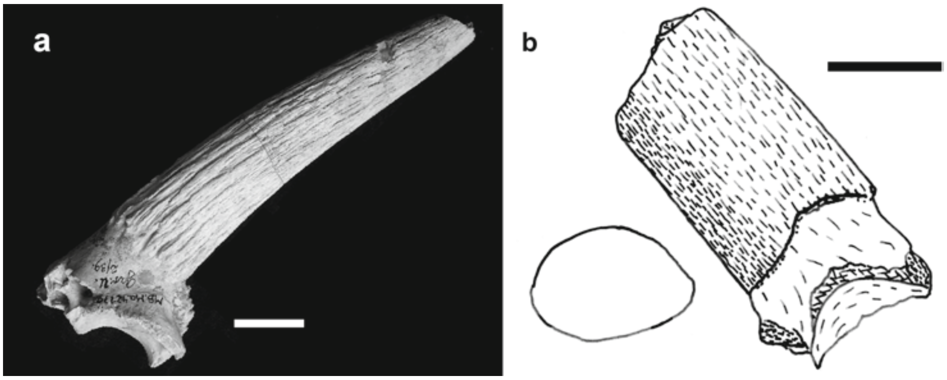

Fig. 15.10 "*Gazella*" *kohllarseni*. (**a**) left horn core, lectotype, in lateral view. The same specimen and view as in Dietrich, 1950: pl.1 fig. 7. Scale = 10 mm. (**b**) base of right horn core, LAET 78-5152 in lateral view and basal cross section. On the cross section anterior is to the *right* and lateral towards the foot of the page. Scale = 25 mm

- LAET 75-848, Loc. 7. Rt P^4, middle wear, 9.8.
- EP 1175/98, Loc. 9. Between Tuffs 6 and 8. Lt and rt P^2-M^3, early middle wear, P^{2-4} 22.8, M^{1-3} 42.9, P^2 7.3×6.0×6.3, P^3 ca. 8.5×–×ca. 9.0, P^4 8.5×8.0×12.3, M^1 ca. 13.8×10.4×12.5, M^2 15.7×10.7, M^3 14.0×8.9×ca. 21.0.
- EP 245/00, Loc. 8. Between Tuffs 5 and 6. Rt dP^4, early wear, 11.0×5.9×7.8. Rear labial wall too flat for *Cephalophus*.
- EP 2209/00, Loc. 7. Between Tuffs 5 and 7. Rt dP^3, middle wear, 8.9×5.6.
- EP 2616/00, Loc. 2. BetweenTuffs 5 and 7. Lt mandible with dP_2 – part dP_4, unworn, dP_2 4.6, dP_3 10.1×4.1.
- EP 546/03, Loc. 2. Between Tuffs 5 and 7, but a few fossils between Tuffs 3 and 5. Rt mandible frag with P_4-M_2, middle wear. P_4 8.9, M_1 11.6×–×c9.3, M_3 13.2.
- EP 101/04, Loc. 22. Between Tuffs 5 and 7. Lt mandible frag with P_{3-4}, early middle wear. P_3 11.5×6.1, P_4 12.6×6.8×12.9.

Diagnosis

This species is not a gazelle. It would be premature at this juncture to found a genus for an enigmatic species having teeth only uncertainly associated with the horn cores. The following diagnosis outlines the main characteristics of "*Gazella*" *kohllarseni* as conceived in this paper.

Fairly small species with short to moderately long horn cores, an anterior position of the level of maximum transverse thickness, an approach to a posterolateral keel, little compression, sometimes a flattening of the lateral surface, no transverse ridges, stronger than normal divergence with the degree of divergence diminishing distally and evenly, quite a low inclination in side view, only slight backward curvature, insertions fairly close together and placed above the back of the orbits. The postcornual fossa is notably large compared with the size of the horn cores, rounded and often deep. An apparently fairly well-developed system of sinuses is present in the pedicels and adjacent parts of the frontals, the frontals between the horn bases are a little raised above the level of the dorsal orbital rims, orbital rims project fairly strongly, supraorbital pits probably small. Hypsodonty probably less than in *Aepyceros dietrichi*. No basal pillars on upper molars, labial wall of metacones not very or at all concave, third lobe of M_3 is small and its lingual wall only slightly offset in later wear, P_4s do not show a closed anterior part of the lingual wall and their hypoconid projects less far labially than in *A. dietrichi*.

Description

Both the Leakey and the 1998–2005 collections contain some mostly poorly preserved and incomplete horn core bases, all or some of which may be conspecific with the lectotype. They are not as consistent in their morphology as could be wished. LAET 75-1902 was listed by Gentry (1987: 388) as "?Hippotragini sp.nov.," but the postcornual fossa is not quite so wide as in *Aepyceros dietrichi*, and the horn core is well inclined. EP 1124/98 is so incomplete that it shows little more than the sinuses and a large postcornual fossa. LAET 78-5152 (Fig. 15.10) is more compressed than other "*G.*" *kohllarseni* horn cores.

The presence of sinuses in the pedicels and nearby parts of the frontals (indicated to the left of the orbit in Dietrich 1950: pl. 1, fig. 7) exclude this species from belonging to *Gazella*. The following characters are not individually decisive, but together they seem too peculiar for a gazelle: the degree of divergence of the horn cores diminishing distally and evenly, the large size of the postcornual fossa in comparison with the size of the horn cores, rounded circumference and depth of the postcornual fossa, the slight raising of the frontals between the horn bases, and the probably small supraorbital pits. One or two of the horn bases may have a slightly swollen pedicel. The anterior position of the level of maximum transverse thickness, approach to a posterolateral keel, strong basal divergence, large postcornual fossa, and sinuses in the frontal are all similarities to *Aepyceros dietrichi*, but other characters differ. Relatively large postcornual fossae are sometimes characteristic of female bovids.

The teeth gathered under the name "*Gazella*" *kohllarseni* are similar in some characters to those assigned to *Aepyceros dietrichi* but are smaller and less specialized (Figs. 15.6, 15.11). They have fewer of the characters whereby the latter species differs from *Gazella*, or they show the presumed advanced states less distinctively. They occupy a size and morphological gap between *A. dietrichi* and *G. janenschi*.

Fig. 15.11 "*Gazella*" *kohllarseni* upper tooth rows EP 1175/98. Anterior to the *right*. Scale in mm

Individual teeth may be difficult to identify. A left M^3, EP 828/98 from Loc. 10, for example, at 16.9 × 10.8 × 12.4, could be either *A. dietrichi* or "*G.*" *kohllarseni* on the basis of size but is more probably the former because of a flat rather than a concave labial wall behind the mesostyle. The P_4 on EP 101/04, listed above, is exceptional for "*G.*" *kohllarseni* in having a closed lingual wall between paraconid and metaconid. A left mandible, EP 2102/00 from Loc. 13, snake gully, has its P_4 in middle wear and is similar to those of "*G.*" *kohllarseni*, but the mandibular ramus is shallow and bulbous in cross-section. It may belong to a different species. Measurements are 11.8 × 5.5, ramus depth below P_4 15.3. The right P^3 EP 162/01 from Loc. 7 shows a shallow and narrow groove on its lingual wall. The premolar row on EP 1175/98 is short in relation to the length of the molar row (53%).

Discussion

This is an extinct species for which, at present, it is hard to suggest a relationship. A link could be sought among other puzzling bovid fossils from sites predating the Laetolil Beds.

SUBFAMILY REDUNCINAE Knottnerus-Meyer, 1907
TRIBE REDUNCINI
TYPE GENUS *Redunca* H. Smith, 1827

Other Genera

Kobus A. Smith, 1840, type species *Kobus ellipsiprymnus* (Ogilby, 1833). Also extinct genera in Africa and the Siwaliks.

The Reduncini originated within or close to Antilopinae and today are moderate- to large-sized grazing antelopes commonly found in habitats near water. Species of *Redunca* are smaller than *Kobus* and less common as fossils. The problematic living *Pelea capreolus*, discussed later in this paper, can be taken as a survivor in South Africa of early Antilopinae close to the origin of Reduncini. One of the most notable features of the bovid faunas of Laetoli is the rarity or probable absence of Reduncini. A high proportion of the few finds give signs of having lived at a late or modern date.

?Reduncini indet.

Material

Dietrich's (1950: 36, fig. 21) horn core of "Reduncini gen. et sp. indet." belongs to the alcelaphine *Parmularius pandatus*, and no finds of Reduncini from the Laetolil Beds were reported by Gentry (1987). Two possible records have been found in the 1998–2005 collections:

- EP 815/03, Loc. 10E. Between Tuffs 5 and 7. Rt upper molar, early middle wear, 22.2 × - × 31.7.
- EP 387/04, Loc. 16. Between Tuffs 7 and 8. Lt upper molar, early middle wear, 16.3 × 12.9 × 10.5.

Description

The upper molar EP 815/03 (Fig. 15.1) is incomplete anterolingually but is the best candidate for being a reduncine. It may not be too hypsodont to fit this tribe and has a tiny basal pillar and a possible constriction of the posterolingual edge of the metaconule lobe. It is not quite too large to fit a reduncine. The second possible reduncine is the upper molar EP 387/04. Its morphology is not overmuch that of a modern species, in that it lacks the localized constrictions or "pinching" of its lingual lobes. It does, however, have a rather large basal pillar. The enamel is not completely white like a modern tooth, but it is lighter than the dentine.

Other apparent reduncine records were rejected. A right mandible piece with broken M_1 to erupting M_3, EP 902/98 from Loc. 9S, is certainly reduncine but has a leached-out appearance and calcrete on its side. The latter feature makes it very likely to have come from Ngaloba Beds at the top of the nearby cliff (Terry Harrison, personal communication), although Loc. 9S is one of the few sites in the Laetolil Beds with evidence of standing water in the form of shallow ponds. The M_2 of EP 902/98 measures 17.1 × 6.2, and the occlusal length of the M_3 is ca. 20.7, so it is a suitable size for a modern kob, *Kobus kob*. EP 1281/00, from Loc. 6, is the lingual part of a right upper molar close in size to EP 815/03. It seems to show a reduncine-like localized constriction of the rear lingual lobe, but this may have arisen from postmortem damage. A right lower molar, EP 244/03 from Loc. 16, has the look of a reduncine but is likely to be an alcelaphine M_1 with an uncharacteristic basal pillar low down.

Discussion

Because Reduncini are otherwise absent in the Laetolil Beds, it is essential to base their occurrence only on definitely identified fossils. The two teeth are not adequate for this purpose. We need a larger sample to be sure of their presence.

SUBFAMILY HIPPOTRAGINAE Sundevall, 1845
TRIBE HIPPOTRAGINI
TYPE GENUS *Hippotragus* Sundevall, 1845

Hippotragini are rather large antelopes with long horns and quite hypsodont teeth and feed mostly by grazing. The long horn cores have no keels or transverse ridges, diverge little, have hollowed pedicels, and are present in both sexes. Despite their sinuses, frontals between the horn bases are substantially raised only in the extant *Hippotragus niger*. Cranial lengths vary among hippotragine species, and more precise analysis is needed to work out their significance for classification, behaviour, and ecology.

The Laetoli Hippotragini have been reorganized. Gentry (1987: pl. 10.7) originally took the horn core LAET 75-3257 from Loc. 18 as belonging to *Praedamalis* (now *Oryx*) *deturi* of Dietrich (1950) and illustrated it as one of the best examples of that species. However, Loc. 18 is in the Upper Ndolanya Beds, so the conspecificity with *P. deturi* in the Laetolil Beds became questionable. Fossils in the 1998–2005 collections showed that most of the Laetolil Beds hippotragine horn cores can be taken as conspecific with EP 941/03, which has preserved much of its total length and is certainly a *Hippotragus*. This *Hippotragus* species is the common hippotragine in the Laetolil Beds, but the *Praedamalis deturi* lectotype horn core in Berlin, a few other horn cores, and a cranium represent a rarer oryx. (Dietrich thought *P. deturi* was an alcelaphine, and the material he assigned to it included alcelaphine teeth.) The hippotragine teeth in the Laetolil Beds have been taken as *Hippotragus*, although a few will surely be of the oryx. They are much more primitive than in living *Hippotragus*, and their strangeness as Hippotragini led me in the past to make too much of a mystery about them. The identity of LAET 75-3257 will be taken up in the account of bovids in the Upper Ndolanya Beds.

Hippotragus Sundevall, 1845

TYPE SPECIES *Hippotragus equinus* (É. Geoffroy Saint-Hilaire, 1803)

Short Diagnosis

The horn cores are long, show lateromedial compression varying between different species, and sometimes flattening of the lateral surface. They are little divergent, with fairly upright insertions, backward curvature, and insertions close together and above the back of the orbits. Well-developed sinuses in the frontals and horn pedicels, females horned, supraorbital pits small and quite close together at the very base of the horn pedicels, little inclination of the cranial roof in lateral view.

Remarks

Opinion 2030 of the International Commission on Zoological Nomenclature (March 2003, *Bulletin of Zoological Nomenclature* 60: 90–91) ruled that *Hippotragus* dates from Sundevall, 1845. The same Opinion also established that the type species by monotypy is *H. equinus* and not, as had been thought for many years, the exterminated bluebuck of South Africa, *H. leucophaeus*.

Hippotragus sp.

Aeotragus garussi (in part) Dietrich 1950: 38, pl.3, figs. 37–40, 42. (These illustrations are of composite specimens.)
Hippotragus sp. Dietrich 1950: 40, pl.1, figs. 11 and 12.
Praedamalis deturi Dietrich. Gentry and Gentry 1978: 351, 62, pl. 22, fig. 3.
?Hippotragini sp.nov. (in part) Gentry, 1987: 388.

Material

Too numerous for complete listing. Specimens with measurable horn cores are:

- LAET 75-2054, Loc.10NE. Horn core, index 39.6×28.4.
- EP 159/98, Loc. 10E. Between Tuffs 5 and 7. Cranial parts including part of occipital, cranial roof and right horn core base. Horn core index 44.7×34.1 (76%), skull width across mastoids ?105–110, occipital height ?40, width across anterior tuberosities of basioccipital 23.6, width across posterior tuberosities of basioccipital 29.8.
- EP 1338/00, Loc. 6. Between Tuffs 5 and 6. Lt horn core, index 40.3×30.2.
- EP 1572/00, Loc. 3. Between Tuffs 6 and 8. Rt horn core, index 37.4×28.9.
- EP 2047/00, Loc. 13. Between Tuffs 5 and 8. Rt horn core, index 41.1×29.5.
- EP 941/03, Loc. 10E. Between Tuffs 5 and 7. Lt horn core with a good proportion of its original length remaining, index 46.7×34.2.
- EP 011/04, Loc. 10E. Between Tuffs 5 and 7. Rt horn core, index 43.8×30.8.
- EP 1166/04, Loc. 13. Between Tuffs 5 and 8. Paired horn core bases, index 45.9×34.6, minimum width across lateral sides of horn pedicels ca. 117.
- EP 1066/05, Loc. 2. Between Tuffs 5 and 7. Frontlet with horn cores, index 47.4×33.1.

Of the supposed "*Praedamalis*" horn cores mentioned in Gentry (1987) it now appears that LAET 74-296 with index 57.6×ca. 42.3 is too large for *Hippotragus* sp., although its degree of compression is suitable, LAET 75-2173 is possibly not hippotragine at all, LAET 75-2217 has an index of ca. 41.3×29.3 (71%) which suits *Hippotragus*, and LAET 75-3257 is the Upper Ndolanya Beds specimen which underlay the reorganization of Laetoli hippotragines.

Some interesting or difficult teeth have been allocated as follows:

- EP 161/98, Loc. 10E. Between Tuffs 5 and 7. Lt mandible with P_2–M_3, early middle wear. P_{2-4} 38.5, P_2 ca. 9.0, P_3 ca. 14.8, M_{1-3} 71.0, M_1 19.7×12.0, M_2 24.2×11.6, M_3 28.5×8.7.
- EP 120/00, Loc. 16. Between Tuffs 7 and 8. Rt P^2, early middle wear, 11.4×8.3×13.3.
- EP 1268/00, Loc. 8. Between Tuffs 5 and 6. Rt P^3–M^3 + lt P^4, early middle wear. M^{1-3} = ca. 67.0, P^3 13.3×11.4×14.0, P^4 12.8×11.5×12.3(left), M^1 19.3×18.0×7.3, M^2 24.3×17.7×10.3, M^3 24.9×16.3×17.5.
- EP 1296/00, Loc. 6. Between Tuffs 5 and 6. Lt mandible with P_4–M_1, middle wear. P_4 15.0×8.8×11.3, M_1 18.0×11.9×7.0.

- EP 1799/00, Loc. 2. Between Tuffs 5 and 7. Rt maxilla with dP$^{3–4}$, middle wear. dP^3 17.7×11.6×6.6, dP^4 18.3×13.1×8.0.
- EP 1901/00, Loc. 5. Between Tuffs 3 and 5. Lt maxilla with M$^{2–3}$, early middle wear. M^2 22.6×15.2, M^3 c19.3×–×22.6.
- EP 2218/00, Loc. 7. Between Tuffs 5 and 7. Rt mandible with M$_1$ in early wear and alveoli of deciduous premolars. dP$_{2–4}$ 48.0, dP$_2$ 8.8, dP$_3$ 16.2, dP$_4$ 20.3, M$_1$ 20.1×8.9.
- EP 2263/00, Loc. 7. Between Tuffs 5 and 7. Lt P^2, 12.8×10.5. Smaller than modern *Hippotragus* and central fossettes less enclosed.
- EP 2264/00, Loc. 7. Between Tuffs 5 and 7. Rt P^3, early middle wear, 14.3×10.6.
- EP 2499/00, Loc. 9. Between Tuffs 6 and 8. Lt P^4–M^2, middle wear. P^4 13.6×12.9, M^1 17.9×18.9, M^2 ca. 22.3×19.5.
- EP 2839/00, Loc. 10E. Between Tuffs 5 and 7. Lt dP$_3$, early middle wear, occlusal length ca. 16.7. Extant ones have lingual end of metaconid more bound into a backward ridge.
- EP 2963/00, Loc.1. Between Tuffs 6 and 8. Rt maxilla frag with M$^{1–2}$, middle wear. M^1 19.1, M^2 ca. 23.0×18.3.
- EP 3337/00, Loc. 15. Between Tuffs 6 and 7. Rt M$^{1–3}$, middle wear. M$^{1–3}$ 64.0, M^1 18.1×16.5, M^2 23.0×18.8, M^3 23.0×16.5.
- EP 3734/00, Loc. 22. Between Tuffs 5 and 7. Rt maxilla with P^4–M^3, early middle wear. P^4 13.2×11.1, M$^{1–3}$ 60.2, M^1 ca. 18.3×17.4×9.2, M^2 21.9×17.6×14.7, M^3 22.8×15.3×19.0.
- EP 4254/00, Loc. 2. Between Tuffs 5 and 7. Rt maxilla with P^3–M^3, late wear. P$^{2–4}$ ca. 38.0, M$^{1–3}$ ca. 60.0, P^3 13.4×12.8, P^4 12.9×15.2, M^1 15.4×ca. 18.8, M^2 20.6×20.2, M^3 ca. 25.2×ca. 17.0.
- EP 482/01, Loc. 13. Between Tuffs 5 and 8. Lt mandible piece with P$_2$–M$_1$, late wear. P$_{2–4}$ 35.5, P$_2$ 9.3×5.9, P$_3$ 12.7×8.1, P$_4$ 14.4×10.6, M$_1$ 15.5×13.8.
- EP 1303/01, Loc. 22. Between Tuffs 5 and 7. Lt mandible frag with P$_{3–4}$, late wear. P$_3$ 12.5×7.9, P$_4$ 15.5×8.8.
- EP 002/03, Loc. 4. Between Tuffs 6 and 8. Lt M$_{1–2}$ + rt M$_1$, late middle wear. M$_1$ 15.9×11.9, M$_2$ 20.4×13.2.
- EP 240/03, Loc. 16. Between Tuffs 7 and just above 8. Lt dP$_3$, middle wear, 14.8×7.4.
- EP 729/03, Loc. 9. Between Tuffs 6 and 8. Rt dP$_3$, early wear, 14.0×5.8×10.3 protoconid height. More brachyodont and weaker metaconid than a P$_3$; front wall is transverse unlike Tragelaphini.
- EP 392/04, Loc. 16. Between Tuffs 7 and 8. Lt dP^3 and dP^4, early middle wear. dP^3 17.4, dP^4 19.4×12.3.
- EP 865/04, Loc. 20. Between Tuffs 6 and 8. Rt P$_2$, 9.5×5.9.
- EP 814/05, Loc. 10E. BetweenTuffs 5 and 7. Rt M$^{1–3}$, late middle wear, M$^{1–3}$ ca. 60.5, M^1 16.1×19.7, M^2 21.9×19.6, M^3 24.2×18.0.

Description

Hippotragus is common in the Laetolil Beds. It has smaller horn cores than in the older and broadly *Hippotragus*-like *Tchadotragus* from Toros-Menalla (Geraads et al. 2008), but the size of the teeth, the premolar/molar row ratio and the degree of hypsodonty may be little different. It is smaller than all later *Hippotragus*, including *H. cookei* Vrba 1987b and (probably) the recently extinct *H. leucophaeus*. The horn cores show mediolateral compression intermediate between extant *H. equinus* and *H. niger*, and sometimes they have flattening of the lateral surface. They are little divergent, with the degree of divergence diminishing very slightly distally, inserted fairly uprightly and curving backwards, close together, and above the back of the orbits. Frontals' sinuses extend into the pedicel and into the rear base of the horn core proper. The postcornual fossae are narrow and shallow. Supraorbital pits are small and lie at the very base of the horn pedicels; they may be slightly lateral to the line of descent of the anteriormost part of the horn core, yet are still quite close together. Cranial roof is somewhat inclined, temporal ridges only moderately wide apart, occipital low, mastoid exposure quite large, no central groove on the basioccipital.

The horn core and cranial parts EP 159/98 (Fig. 15.12) are the only source for information on the cranial or postorbital characters. The sinuses from the frontals extend to the top of the pedicels and about a further 15 mm into the back part of the horn cores. The horn core EP 941/03 is sufficiently complete to show some diminution distally of the degree of divergence. On some horn cores – for example, EP 011/04 – the lack of clear distinction between pedicel and horn core proper leads to the pedicel looking high on its anterior side and thereby acquiring a resemblance to Alcelaphini. On this specimen, as on some others, the supraorbital pit lies slightly

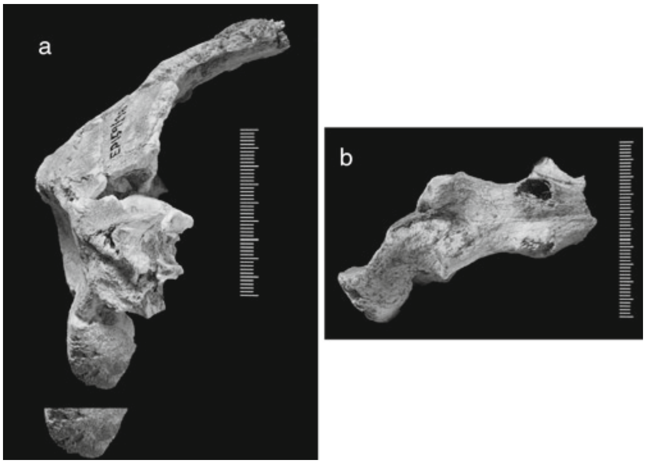

Fig. 15.12 *Hippotragus* sp., EP 159/98. (**a**) partial cranium in right lateral view. (**b**) basioccipital in ventral view. Anterior to the right. Scales in mm

lateral to the line of descent of the anteriormost part of the horn core proper. Other horn cores, like EP 948/98 from Loc. 9S, are difficult to identify as either Hippotragini or Alcelaphini, and this one was eventually taken as *Parmularius pandatus*. A piece of horn core, EP 4084/00 from Loc. 8, shows a hint of transverse ridges on its front surface. The horn core EP 1548/98, from Loc. 10E, has an index of 25.0 × 21.3 and a large sinus in its pedicel; it shows no sign of being juvenile and may be an alcelaphine or perhaps a female of *Hippotragus*.

Because most hippotragine horn cores in the Laetolil Beds belong to *Hippotragus*, the assumption is made that this applies also to the numerous hippotragine teeth. Hippotragine teeth have been described and illustrated by Dietrich (1950) and Gentry and Gentry (1978) under various names. They are unlike the occlusally complex teeth of modern *Hippotragus* and thus are less readily distinguishable in practice from teeth of some other tribes, such as Boselaphini, Miocene Caprinae, or even Tragelaphini. With care, they are distinguishable from teeth of the Laetoli alcelaphines. They are somewhat stoutly built for their mid-Pliocene date, moderately hypsodont, with basal pillars of small to moderate size on the molars. Upper molars have somewhat rounded ribs between their styles, the lingual lobes remaining unjoined or only narrowly joined centrally to one another or to the labial side of the teeth in earlier wear, and there are spurs or localized indentations into the central fossettes. Lower molars have slightly rounded lobes on their lingual walls, labial lobes not very narrowed transversely, and small transverse goat folds are sometimes present anteriorly. Upper premolars may have a vertical groove centrally on their lingual walls, and the anterior ones are relatively large. The metaconid on P_4 is bulbous and projecting lingually, the hypoconid not projecting labially on P_{3-4}.

The mandible EP 161/98 is the only piece from which the relative length of the premolar row can be estimated. The value is 54% of that of the molar row. This is slightly shorter than in the Late Miocene *Tchadotragus*, almost the same as in a *Hippotragus gigas* from Olduvai Gorge, FLKNN I 608 (Gentry and Gentry 1978), about the same as in *Oryx*, but shorter than in the two living *Hippotragus* species.

The hippotragine teeth of the Laetolil Beds can be differentiated from the alcelaphine teeth in the same deposits by having basal pillars, more rugose enamel, stronger styles on the upper molars, weaker or later joining up of the crescentic crests in the centre of the molars, and less-rounded lingual lobes of their lower molars. They have a more squared appearance (Figs. 15.13–15.15) but are less high crowned. Crown height was 95% of occlusal length in an M_3 EP 1381/03 in early wear, whereas the average for six similar examples of *Parmularius pandatus* was 147%.

EP 891-5/01, Loc. 7, are some P_3s and P_4s not of Alcelaphini. The P_4s have a bulbous lingual end of the metaconid crest, which approaches but does not fuse with the paraconid. The metaconid crest in the P_3s is slanted more backwards than transversely. Both P_3 and P_4 are shorter than in other examples of Hippotragini and show no differentiation of paraconid from parastylid. The latter character may, of course, have been present in earlier wear. The P_2 EP 865/04 may be hippotragine on the basis of being too robustly built to be *Brabovus*. The dP^3 and dP^4 EP 392/04 are too low crowned to be alcelaphine, and the dP^4 has a basal pillar.

Discussion

Two fossil species of *Hippotragus* exist in time levels postdating the Laetolil Beds. *Hippotragus gigas* Leakey (1965: 49, pls. 56, 58–61) comes from Olduvai Beds I–III, Makapansgat Limeworks Mb. 5, and Elandsfontein. Its horn cores were less compressed than in either living *Hippotragus* and they reached a very large size in Olduvai Bed II. The braincase was low and wide like roan and not as narrow as in sable. The teeth had a simpler occlusal pattern than in living *Hippotragus*. *Hippotragus cookei* Vrba (1987b: figs. 1 and 2) was a Late Pliocene species of Makapansgat Limeworks Mb. 3 and Sterkfontein Mb. 4. Two horn core specimens are close to the size of the smaller *H. gigas* in Olduvai Bed I, while the teeth may be larger than in Bed I. The horn cores are compressed about as much as in *H. equinus* and their basal divergence is greater than in other *Hippotragus*. The teeth (Vrba 1976: pl. 39 B, E, G, H, K–M) are as advanced as *H. gigas* in their hypsodonty, the squared-off upper molars with nearly parallel front and back walls, and the lower molars with goat

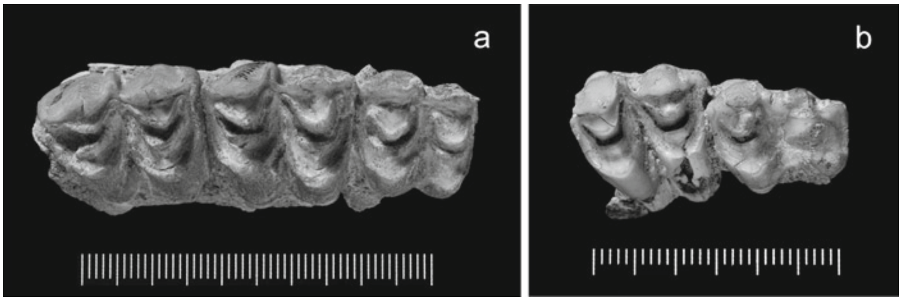

Fig. 15.13 *Hippotragus* sp. (**a**) right M^{1-3} EP 3337/00; (**b**) right dP^{3-4} EP 1799/00. Scales in mm

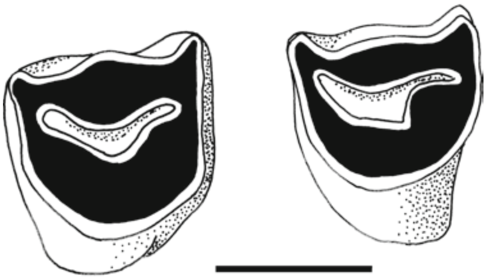

Fig. 15.14 Occlusal views of P^4s, labial sides to the *top*. From the *left*: *Hippotragus* sp. right P^4 EP 2499/00, *Parmularius pandatus* P^4 EP 3340/00 (reversed image of a left P^4). The *Hippotragus* tooth is squarer and with a more outbowed labial wall. Scale = 10 mm

Fig. 15.15 Occlusal views of lower dentitions, anterior to the *right*. *Top*, *Hippotragus* sp., left P_2-M_2, LAET 75-3197; below, *Parmularius pandatus*, right P_2-M_3, LAET 74-55. Scales in mm

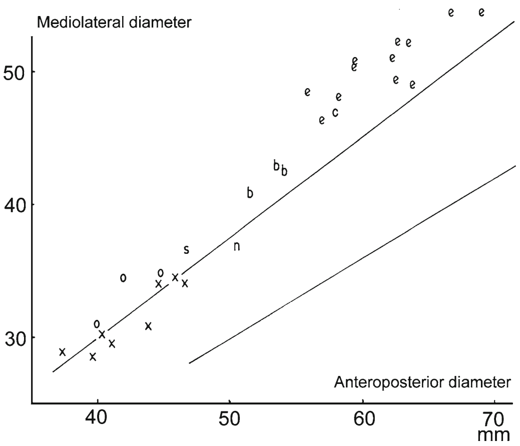

Fig. 15.16 Basal diameters of some hippotragine horn cores. Upper diagonal line = 75%, lower one = 60% as in Fig. 15.7. x = *Hippotragus* sp. from the Laetolil Beds, b = *H. leucophaeus* (Klein 1974), c = *Hippotragus cookei*, e = extant *H. equinus*, n = *Hippotragus* horn core EP 1294/98 from the Ndolanya Beds, o = *Oryx* spp. (the *left* and *middle* ones are *O. deturi* EP 1796/03 and EP 1120/98 from the Laetolil Beds and the one on the *right* is *Oryx* sp. LAET 75-3257 from the Upper Ndolanya Beds), s = *Hippotragus* sp. from Sahabi. Smaller examples of *H. gigas* at Olduvai are the size of *H. equinus* but less compressed, while the three largest attain indices of 87.6 × 73.0, 84.9 × 72.5 and 83.4 × 75.7 (Gentry and Gentry 1978)

folds. The upper molars resemble those of *H. gigas* in having wide bases to the low paracone and metacone labial ribs, and more widely rounded walls of their lingual lobes. These two latter characters are divergent from living *Hippotragus*. It is possible that *H. gigas* is only a localized large variant of *H. cookei* in Olduvai Bed II and that the Makapansgat Mb. 5 and Elandsfontein species continued as *H. cookei*. However, if only one name is required, as supposed by De Ruiter (2003), then *H. gigas* has seniority.

The *Hippotragus* of the Laetolil Beds is more primitive than either *H. cookei* or *H. gigas*. It has smaller horn cores than any later species (Fig. 15.16). Linear dimensions at the base of its horn cores are about two-thirds of those of living *H. equinus*. The teeth are also more primitive, although not smaller than those from Olduvai Bed I or Elandsfontein. They are less massively built and look less hypsodont, and the upper molars fail to show wide ribs and retain correspondingly more obvious styles. Only incipient goat folds are visible on some lower molars. There is no reason why this Laetoli species should not be ancestral to *H. cookei*-*H. gigas*. Presumably, the modern *Hippotragus* species with their lengthened premolar rows and occlusally complicated (boödont or ox-like) molar teeth were a late development in another direction, but their origin is unknown.

Earlier *Hippotragus* are known back into the Late Miocene of Sahabi, Djebel Krechem, and, doubtfully, Lothagam (Lehmann and Thomas 1987: fig. 4a; Geraads 1989: pl. 2, fig. 1, text fig. 3a; Harris 2003, fig. 11.14). Once bovids had evolved longer horn cores than in the Middle Miocene *Eotragus*, then backward curvature appeared, as in *Tethytragus*, *Gazella*, and *Hippotragus*, among others. Early species of these genera have many resemblances. The Laetoli *Hippotragus* continues to be primitive in its teeth as well as its horn cores. It is interesting that it seems to have existed in substantial numbers as a prominent member of the mammal herbivore fauna, a role that is no longer open to the two living *Hippotragus* species.

Aeotragus garussi was described on the basis of composite tooth rows assembled from hippotragine teeth (Dietrich 1950: figs. 37–40, 42) and a rolled or otherwise eroded, incomplete frontlet with the lower part of the left horn core (Dietrich 1950: fig. 43). The frontlet came from Garusi, and the species as a whole was attributed to the oldest beds of the southern Serengeti. The picture of the frontlet is a left lateral view. The horn cores on the frontlet have an index 35.2 × 39.5, are slightly compressed anteroposteriorly, with only a hint of an anterior keel, no transverse ridges, fairly strong divergence, well inclined backwards, no demarcation between pedicel and horn core proper, and with possible sinuses in the pedicel. Dietrich thought it was related to

Addax, but I cannot give a confident opinion (a surface-damaged tragelaphine, a small bovine?). Dietrich did not specify a holotype, so all his cited pieces are syntypes. Selection of a single tooth from one of the illustrated dentitions as a lectotype, after verification of its hippotragine identity, would not make it a suitable species name for the Laetolil Beds *Hippotragus*, because of the possibility of it belonging to the next species below.

Oryx Blainville, 1816

Praedamalis Dietrich 1950: p.30
TYPE SPECIES *Oryx gazella* (Linnaeus, 1758)

Diagnosis

Long horn cores showing little compression, varying between slightly mediolateral and slightly anteroposterior. Horn cores straight or with very slight backward curvature, inserted somewhat widely apart, at a low inclination and behind the orbits (note that a low inclination accentuates the visual impression of a postorbital insertion). Supraorbital pits are small and wide apart in front of the base of the horn pedicels. Cranium lower and wider, and occipital flatter, than in *Hippotragus*. Weaker longitudinal ridges behind the anterior tuberosities of the basioccipital than in *Hippotragus*. Teeth less occlusally complex than in modern *Hippotragus*.

Remarks

As noted above, the horn core LAET 75-3257 was assigned by Gentry (1987: pl.10.7) to *Praedamalis deturi* but was later revealed to have come from the Upper Ndolanya Beds and will be reclassified later in this chapter as *Oryx* sp. This led to a rearrangement of the Laetoli hippotragines, which left *P. deturi* as an uncommon species in the Laetolil Beds and itself better included in *Oryx*. Its moderately-sized, straight or almost straight horn cores of rather small diameter compared with their length would characterize a small-sized *Oryx* differing from the living species only by its less laid-back horns. The little information we have about its cranial anatomy is compatible with *Oryx*.

Oryx deturi (Dietrich, 1950)

Praedamalis deturi Dietrich 1950: 30, pl.2, fig. 23.
Praedamalis deturi Dietrich (in part). Gentry and Gentry, 1978: 351, 62.
Praedamalis deturi Dietrich (in part). Gentry 1987: 387, not pl.10.7.

Lectotype

A right horn core (Dietrich 1950: fig. 23) in the Museum für Naturkunde der Humboldt-Universität, Berlin. Designated by Gentry (1987: 387).

Type Locality

Deturi in the Laetoli area, Tanzania.

Horizon and Range

Dietrich (1950: 30) assigned this species to the oldest of the Laetoli faunas.

Material

- LAET 75-689, Loc. 1. Piece of a straight horn core.
- LAET 75-1801, Loc. 10W. Distal piece of a small, straight and somewhat compressed horn core, ca. 100 mm long. Diameters at its base, not known to be the original base, 19.7 × 13.5.
- LAET 75-2217, Loc. 10E. Lt horn core pedicel, ca. 41.3 × 29.3. The only specimen listed in Gentry (1987) and still accepted as probably this species.
- EP 1120/98, Loc. 9. Between Tuffs 6 and 8. Horn core piece, probably of the left side, ca. 130 mm long. Diameters at its base, not known to be the original base, 42.0 × 34.5.
- EP 565/03, Loc. 2. Between Tuffs 5 and 7. Piece of a straight horn core.
- EP 1796/03, Loc. 22. Between Tuffs 5 and 7. Heavily encrusted cranium with horn cores. Horn core index ca. 40 × 31, minimum width across lateral sides of horn pedicels ca. 115, skull width across orbits ca. 132.
- EP 543/05, Loc. 12. Between Tuffs 5 and 7. Lt P_{2-3}, early middle wear. P_2 ca. 12.2 long, P_3 14.6 × ca. 6.8

Diagnosis

Horn cores are straight and probably with slight mediolateral compression. They are inclined backwards more strongly than in *Hippotragus* but less than in modern *Oryx*. Braincase of short to moderate length.

Description

The compression of the horn cores may be less than suggested by measurements in the list above, because incomplete preservation of some specimens, such as EP 1120/98, leaves doubt about their orientation on the skull top in life. The horn cores of the heavily encrusted EP 1796/03 are somewhat inclined but much less than in modern *Oryx*. They are inserted quite widely apart, and the supraorbital pits too are wide apart, both characters suggestive of *Oryx* rather than *Hippotragus*. The frontals between the horn bases are close to the level of the dorsal orbital rims and not raised. The braincase of EP 1796/03 is not long, the occipital surface faces backwards, the temporal ridges are only moderately wide apart, the occipital is quite low, its edges fairly rounded, mastoids are wide. The short, low braincase befits *Oryx* but would be less easily distinct from the *Hippotragus* sp. than from modern *Hippotragus*. Other horn cores in the list are not very distinctive other than in their straightness (Fig. 15.17).

Fig. 15.17 Horn core of *Oryx* sp. EP 1120/98 in presumed side view. Scale in mm

They have a slight degree of compression, their maximum transverse thickness lies slightly behind the central level of the presumed anteroposterior diameter, the presumed lateral surface is slightly flattened, there is a sharper intersection of the lateral and medial surface at the front than at the back but no development of a keel, there are no transverse ridges. It is known from the lectotype that the pedicel is hollowed internally and that the frontals between the horn bases are at about the same level as the dorsal parts of the orbital rims.

I have not tried to distinguish teeth of this species from those of *Hippotragus* sp. The P_{2-3} EP 543/05 looked hippotragine but rather low crowned and might be a candidate for belonging to *Oryx*.

Discussion

The *Oryx* of the Laetolil Beds differs from contemporaneous *Hippotragus* by having horn cores with almost no backward curvature, slightly greater inclination in side view, and probably with less compression, and supraorbital pits positioned more widely apart. *Oryx deturi* is also present at Hadar, member DD (Gentry 1981).

It is not quite beyond doubt that the Laetolil Beds *Oryx* could be females of *Hippotragus* sp. Such female horn cores, in having smaller diameters, could also have a differently shaped cross-section and so look more widely inserted. If *O. deturi* is a valid species, as still seems likely, then it would be interesting to know what the female horn cores of the *Hippotragus* sp. could be like.

TRIBE ALCELAPHINI Brooke *in* Wallace, 1876, p. 224
TYPE GENUS *Alcelaphus* Blainville, 1816

Alcelaphines are medium to large grazing antelopes of more open country. They are the most numerous bovids in the Laetolil Beds. Alcelaphines have long skulls, horn cores often with transverse ridges, horned females, frontals with extensive internal sinuses and one large sinus reaching up into the base of the horn core. Frontals raised between horn bases. Braincases short and often strongly angled on the long face, supraorbital pits small, ethmoidal fissures absent in adults. Preorbital fossae usually present, with an upper rim, and slightly deeper in males than females. Zygomatic arch deepening anteriorly under the orbits, jugal with two broad anterior lobes, mastoids large, basioccipital with a central longitudinal groove, upper tooth rows set anteriorly and arcades curved so that P^2s and M^3s on opposite sides are closer to one another than are P^4 s or M^1s. Teeth hypsodont (sometimes very hypsodont), central fossettes complicated but without basal pillars, lingual lobes of upper molars and labial lobes of lowers rounded, strong ribs between styles of upper molars, lower molars without goat folds, premolar rows short, P_2s and sometimes P^2s reduced or absent, P_4s with small hypoconid and paraconid-metaconid fusion to close the anterior part of the lingual wall, mandibles deep, limb bones cursorial and specialized to facilitate anteroposterior articulation.

The Laetolil Beds contain an abundant species of *Parmularius* and a rarer larger species possibly of a genus represented in the Hadar Fm. All who have seen the alcelaphine teeth of the Laetolil Beds agree that at least two species are present, a common one with medium-sized teeth (presumably the *Parmularius*) and a rarer larger species that does not attain the size of Plio-Pleistocene *Megalotragus* or *Connochaetes*. There may also be a third, rarer small species.

Parmularius Hopwood, 1934

TYPE SPECIES *Parmularius altidens* Hopwood, 1934: p. 550

Other Species

Other species from Olduvai were added by Leakey (1965) and then by Gentry and Gentry (1978), who gave an expanded generic diagnosis. Since then, more species have been named, and eight names now exist for species other than *P. altidens*. The genus has uncertain morphological boundaries with *Damaliscus*. *Damalops* Pilgrim, 1939, type species *D. palaeindicus* (founded in 1859 by Falconer), of the Late Pliocene Pinjor Fm., India (Lydekker 1886: pl. 4, figs. 4 and 5) and Tadzhikistan (Dmitrieva 1977) may have been in or near *Parmularius*.

Occurrences and Range

Mid-Pliocene to Middle Pleistocene from most regions of Africa.

Diagnosis

Extinct alcelaphines of small-moderate to moderate-large size. Horn cores moderate to long, slightly compressed mediolaterally, without keels, occasionally with transverse ridges, usually little divergent but more so distally, inclinations low (= oblique), insertions close together and above the back of the orbits or postorbital, and often with posteromedial, posterior or posterolateral swellings at the bases.

Horn core pedicels long (partly connected with oblique insertions), and braincase short with steep roof. Supraorbital pits remain relatively close, preorbital fossae small, often a median conical parietal boss centrally on the cranial roof, auditory bullae rather small and not very inflated, and premolar rows short and often without P_2s.

Remarks

The nearly complete and often undistorted alcelaphine fossils at Langebaanweg reveal two species: *Damalacra acalla*, perhaps close to the ancestor of later alcelaphines, and *D. neanica*, more specialized with its postorbital but still uprightly inserted horn cores. Later in the mid-Pliocene, other medium- and medium-large–sized alcelaphines with more advanced teeth appear. One of the former is *Parmularius pandatus*, a good candidate for relationship and even ancestry to later *Parmularius* and *Damaliscus*. *Parmularius* is an extinct genus prominent in the later Pliocene and centred on Olduvai, from where three species have been described. According to Hopwood's original diagnosis, *Parmularius* would differ from *Alcelaphus* in subparallel horn cores, short pedicels, a deeper lachrymal (= preorbital) fossa, less bending of the face and basicranial axes, and a parietal boss. This last character presumably inspired the genus name, being a protective adornment like a small buckler (Latin: *parmula*). Some characters of *Parmularius* must be linked; the low (= oblique) horn core inclinations, postorbital insertions, long pedicels, and short braincases with steep roofs all go together.

Parmularius pandatus Gentry, 1987

Reduncini gen. et sp.indet. Dietrich, 1950: 364, fig. 21.
?Parmularius sp. Gentry and Gentry, 1978: 382, 62, pls.21, 22, fig. 2.
Parmularius pandatus Gentry, 1987: 389.

Holotype

A cranium with horn cores, LIT 1959.277 (Gentry and Gentry 1978: pls.21, 22, fig. 2) on loan to the National Museum of Kenya, Nairobi; cast in the Natural History Museum, London, M35178.

Type Locality

Laetoli, Tanzania.

Horizon and Range

The holotype was probably found at Loc. 10, 10E or 10W, Upper Laetolil Beds.

Material

Parmularius pandatus is the commonest bovid in the Laetolil Beds after *Madoqua*. Gentry (1987: 390–391) listed some of the better material. Much more material, especially of teeth, has been recovered in the 1998–2005 field seasons. The better ones of about 15 new horn cores or their bases are:

- EP 635/00, Loc. 2. Between Tuffs 5 and 7. Rt horn core, index 43.2 × 35.4.
- EP 1336/00, Loc. 6. Between Tuffs 5 and 6. Rt horn core, index 47.5 × 39.0.
- EP 1411/00, Loc. 1. Between Tuffs 6 and 8. Lt horn core, index 43.6 × 33.6.
- EP 2049/00, Loc. 13. Between Tuffs 5 and 8. Paired horn cores, index 39.0 × 31.0, length ca. 225.
- EP 2267/03, Loc. 13. Between Tuffs 5 and 8. Lt horn core, index 41.7 × 33.8 Central sinus only reaches top of pedicel, so identity could be disputed.
- EP 1410/04, Loc. 6. Between Tuffs 5 and 6. Lt horn core, index ca. 46.0 × 33.8.
- EP 542/05, Loc.12. Between Tuffs 5 and 7. Rt horn core.

Some partial tooth rows are:

- EP 163/98, Loc. 10E. Between Tuffs 5 and 7. Lt mandible with P_3–M_3, late middle wear, presence of P_2 in life not ascertainable. P_{3-4} 17.7, M_{1-3} 60.0, P_3 7.9 × 6.0, P_4 9.4 × 8.0, M_1 13.4 × 9.5, M_2 18.6 × 10.2, M_3 27.3 × 9.9 × 19.7.
- EP 546/98, Loc. 10W. Below Tuff 3. Rt P_4–M_3, late wear. P_4 13.0 × 7.8, M_{1-3} ca. 69.0, M_1 16.1 × 12.1, M_2 20.9 × -, M_3 ca. 32.0 × 12.0, ramus depth below M_1 35.7, below M_3 38.7.
- EP 271/00, Loc. 8. Between Tuffs 5 and 6. Rt P^4–M^3, late middle wear. P^4 10.2 × 11.5, M^1 13.1 × 14.5, M^2 19.6 × 15.5, M^3 21.2 × 13.7.
- EP 818/00, Loc. 10. Below Tuff 3. Lt mandible with dP_3–M_1. dP_3 14.2 × 7.6, dP_4 25.1 × 9.0, M_1 22.0 × 8.5.
- EP 1803/00, Loc. 2. Between Tuffs 5 and 7. Lt maxilla with P^2–M^2, rt M^2. P^{2-4} 28.6, P^3 ca. 10.4, P^4 8.9, M^1 13.3 × – × 6.6, M^2 21.2 × 16.8 × 13.9.
- EP 2253/00, Loc. 7. Between Tuffs 5 and 7. Rt maxilla with P^3–M^3, late middle wear. P^{2-4} ca. 30.5, M^{1-3} 70.2, P^3 12.2 × 11.7, P^4 11.9 × 13.7, M^1 18.9 × 17.6, M^2 24.3 × 18.2, M^3 27.4 × 17.0.
- EP 3355/00, Loc. 15. Between Tuffs 6 and 7. Rt mandible with M_{1-3}, early middle wear. M_{1-3} ca. 64.5, M_2 22.2 × 9.8, M_3 27.6 × 8.9 × 31.6. The M_3 itself is in early wear.
- EP 312/01, Loc. 3. Between Tuffs 6 and 8. Lt mandible with P_4–M_2, late middle wear. P_4 11.5 × 6.9 × 9.7, M_1 16.6 × 10.8 × 6.8, M_2 19.8.
- EP 515/01, Loc. 10E. Between Tuffs 5 and 7. Paired mandibles, almost certainly no P_2s in life. P_{3-4} 18.0, M_{1-3} 60.7.
- EP 1267/01, Loc. 9S. Below Tuff 2. Rt dP^3–M^1, lt dP^2–M^1, early middle wear. Lt: dP^2 10.9 × 7.2 × 10.0, dP^3

18.2×10.7×8.0, dP^4 20.9×12.7×10.7, M^1 23.7×13.0×30.0. The M^1 is long, perhaps befitting one in early wear.

- EP 1594/03, Loc. 15. Between Tuffs 6 and 7. Rt M^{1-3}, late wear. M^{1-3} 47.9, M^1 13.0×13.5, M^2 15.5×14.5, M^3 19.6×14.3.
- EP 1723/03, Loc. 22. Between Tuffs 5 and 7. Rt mandible with P_3–M_1, late wear. P_3 9.8×6.5, P_4 ca. 10.6×7.3, M_1 12.3×9.4.
- EP 1724/03, Loc. 22. Between Tuffs 5 and 7. Lt mandible with P_3–M_1, early middle wear. P_{2-4} ca. 26.6, P_3 10.0×6.1, P_4 12.6×7.3.
- EP 2295/03, Loc. 13, snake gully. Between Tuffs 6 and 7. Lt mandible with M_{1-3}, late middle wear. M_{1-3} 60.7, M_1 14.8×10.0, M_2 19.9×10.0, M_3 25.6×9.8.
- EP 2303/03, Loc. 13, snake gully. Between Tuffs 6 and 7. Rt M^{1-3}, late middle wear. M^1 13.5×15.6×7.0, M^2 19.0×17.3×9.9, M^3 22.3×–×7.0.
- EP 299/04, Loc. 8. Between Tuffs 5 and 6. Lt M_3, early wear. 25.0×7.6×41.0.
- EP 647/04, Loc. 3. Between Tuffs 6 and 8. Rt mandible with P_4–M_3, early middle wear. P_4 12.7×7.5, M_{1-3} 60.2, M_1 15.9×10.2, M_2 19.7×9.6, M_3 25.7×8.9.
- EP 1014/05, Loc. 2. Between Tuffs 5 and 7. Rt mandible with P_3–M_3, early middle wear, no P_2 in life. P_{3-4} 21.5, M_{1-3} 63.8, P_3 10.0×5.3, P_4 12.1×5.9, M_1 18.7×8.9, M_2 ca. 21.0×8.7, M_3 ca. 24.6.

Diagnosis

About the size of *P. altidens*. Horn cores with their greatest transverse width lying centrally or slightly behind the central level of the anteroposterior diameter, more compressed than in the Olduvai *P. altidens* or *angusticornis*, without a flattened lateral surface, not very divergent basally but sometimes with a slight lyration in their course, curving backwards, inserted less far behind the back of the orbits and less inclined than in later *Parmularius*, and with posterolateral basal swellings. Frontals between supraorbital pits concave and not swollen, then rising between horn bases to a level above that of the dorsal orbital rims. Braincase still quite long for an alcelaphine and its roof not very inclined. Some indication of a *Parmularius* boss on the braincase roof, temporal lines rather close posteriorly, occipital surface facing partly laterally on each side of its mid-line, basioccipital narrow.

Description

The frontlet LAET 74-245, Loc. 8, shows noteworthy infraspecific differences from the holotype of *Parmularius pandatus* in its larger size, a more pronounced lyration in anterior view, and a less localized bending backwards along the course of the horn cores. The left horn core base EP 1410/04, from Loc. 6, has an irregular transverse ridge on its front surface around 50 mm above the base, just where divergence increases slightly. The horn core EP 542/05 has small diameters at its proximal end of 31.7×26.6, but the actual base of the horn core may not have been preserved. Flattening of the lateral surface and incipient lyration and transverse ridges could all make *Hippotragus* an unlikely identity.

Alcelaphine teeth of the Laetolil Beds have advanced on those of the early alcelaphines of Langebaanweg and Manonga (Gentry 1997: fig. 7) but still retain some scope for occasional confusion with the teeth of other tribes of antelopes. At this evolutionary stage, they are less modernized than teeth in the Shungura Fm. and noticeably less advanced than those of the present day. For example, a left M^3, EP 347/00 from Loc. 12, has wide, little protruding labial ribs, still quite a pointed anterior lingual lobe, and a tiny low basal pillar. The right M_3, EP 3860/00 from Loc. 7, is in early wear and rather low crowned with an occlusal length 23.4 and crown height at ca. 33.5. In early wear, an approach to a goat fold can sometimes be seen on lower molars – for example, the small M_3 EP 1305/00. The P_4 LAET 75-2200 from Loc. 2, shown in Gentry (1987: pl.10.10) as "Sp.indet. aff. *Pelea*," is an alcelaphine. Its measurements are 13.3×7.4×17.0. Lingual contact of paraconid and metaconid on P_4s begins in early wear, and then from just above the mid-wear level they fuse. For example, EP 3862/00 from Loc. 7, a left P_4 in middle wear, has a length of ca. 13.0, a height of 17.8, and the paraconid-metaconid fusion begins at 11.1 above the base. The P_3 on EP 163/98 also shows a close approach of the lingual ends of the paraconid and metaconid. Paired mandibles EP 515/01 from Loc. 10E show that *Parmularius pandatus* could be without P_2s in life. When the tooth was present, it might be small, as in LAET 74-55 (Fig. 15.15).

P^4s are quite asymmetrical in *Parmularius pandatus*, and the upper premolars generally are less square and blocklike than in the contemporaneous Hippotragini (Fig. 15.14). The dP^3 EP 579/05 is the size of an *Alcelaphus buselaphus* and seemingly alcelaphine on the basis of its hypsodonty. The right P^4 EP 3340/00 from Loc. 15 could be confused with *Aepyceros dietrichi* but is more likely to be an alcelaphine. It has measurements of 11.7×11.1×ca. 24.0 and is in middle wear.

In a large collection, such as that from the Laetolil Beds, one quite often finds teeth that look anomalously modern. The left lower molar EP 1905/00 from Loc. 5, with a length of c19.6, looks occlusally modern. It shows strongly rounded lingual lobes and much curvature of the central fossettes, with the rear one in particular having quite a complex outline.

Discussion

Parmularius pandatus differs from *P. altidens* by more upright horn core insertions, posterolateral basal swellings on the horn cores, less shortened braincase, and a lower and less localized boss on the braincase roof. There is no apparent reason why it could not be ancestral to *P. altidens*. The occipital surface of the holotype *P. pandatus* has a median vertical ridge so that the two sides face partly laterally as well as backwards. This seems to be a character of earlier alcelaphines that disappears from around the end of the Pliocene; the state of the holotype *P. altidens* is equivocal because of restoration in the area.

Parmularius pachyceras Geraads et al. (2001: 339, figs. 3O, 5D and E) from the mid-Pliocene of Koro Toro is of similar date to *P. pandatus*. It is larger and has thickened horn cores with a posterior surface towards their base. Such characters may indicate no more than a regionally differentiated species closely related to the Laetoli species and less likely by its specialization to be connected with later species elsewhere. Premolar rows are fairly short as befits a *Parmularius* of the period.

Parmularius braini Vrba (1977: 140, figs. 3–5) from Makapansgat Limeworks Mb. 3 is about 1.0 myrs younger than *P. pandatus*. It is a larger species, the horn cores are well compressed, with posteromedial basal swellings, closely inserted and backwardly curved, the cranial roof slopes steeply and has a parietal boss. *Damaliscus eppsi* Harris (1991: 195, figs. 5.51 and 5.52) looks a little like *P. braini* and is an instructive species to consider. It comes from the Koobi Fora Fm., KBS and Okote Mbs., and therefore postdates *P. braini* and predates and overlaps *Damaliscus niro* further south in Africa. The holotype is very like some Olduvai horn cores included in *D. niro* by Gentry and Gentry (1978) (e.g., Leakey 1965: pl.86, 3rd from left) in having a more localized backwards bend in mid-course and a basal posterolateral swelling. The two species, *D. eppsi* and *D. niro*, appear to be close, and I agree with Harris (1991) that *D. eppsi* is not related to the earlier *Parmularius braini*. All these species combine to suggest that localized backward bends in alcelaphine horn cores can come and go without having much significance for species phylogeny.

The Late Pliocene *P. atlanticus* Geraads and Amani (1998: 198, figs. 1D and E) from Ahl al Oughlam is larger than *P. pandatus*, with long horn cores curving backwards and showing increasing divergence until shortly before the tips. The long axis of the cross-section is oblique to the sagittal plane. It is not much like *P. pandatus*, but could be related to the Siwaliks *Damalops palaeindicus*.

Parmularius ambiguus (Pomel 1894) is a North African Early-Middle Pleistocene species studied by Geraads (1981). It is the commonest bovid at Tighenif and occurs also at Aïn Maarouf (Geraads and Amani 1997). The strong angling of the planes of the frontals behind and in front of the horn bases indicate a steeply inclined cranial roof, and the supraorbital pits are well anterior to the horn bases. Both characters suggest *Parmularius*. The fairly localized backwards bend of the horn cores can be found in earlier *Parmularius*, and the marked thinning of their distal parts recalls the Olduvai *P. angusticornis*, a possible descendant of *P. altidens*. It is a large *Parmularius* and unlikely to be close to *P. pandatus*, but a striking character is that the premolar rows are long for a *Parmularius*. For lower dentitions, this is boosted by the presence of P_2, but the ratios $P_{2–4}/M_{1–3}$ in *P. altidens* and *P. pandatus* are still about 7% shorter than the mean of four *P. ambiguus* cited by Geraads. Once again we have an indication of uncertain generic boundaries between fossil alcelaphines.

Damaliscus ademassui Vrba (1997: 170, fig. 12a) from the Late Pliocene of Gamedah is not greatly different from *P. pandatus* but shows possible relationship to one or another *Damaliscus* in the compression of the horn cores (78%), their increased basal divergence, a flattened lateral surface, and strong and widely spaced transverse ridges on the anterior surfaces. The horn pedicel still looks as long in lateral view as in contemporaneous *Parmularius*, suggesting that the short pedicels of later *Damaliscus* had yet to evolve. On the other hand, *D. ademassui* may have been a local and/or short-lived species and not linked with *Damaliscus.*

Awashia suwai Vrba (1997: 172, figs. 14 and 15) from the Late Pliocene of Matabaietu 3 has quite a wide skull and little compressed horn cores with their maximum basal diameters set rather widely to the anteroposterior line of the skull. The postcornual fossa is deeper and more localized than in most alcelaphines. The nasals are broad and flat. Some of its characters fit *Parmularius*: supraorbital pits close together and rather far in front of the horn core bases, a steeply inclined braincase roof, and perhaps the well inclined horn core insertions. However, the preorbital fossae are very large with marked upper rims, and any parietal boss is unclear.

Gen. indet., Alcelaphini larger sp. indet.

Alcelaphini sp. indet. Gentry and Gentry, 1978: 390, 412, 62, pl. 22, fig. 1.

Genus indeterminate, Alcelaphini sp. indet. Gentry, 1987: 391

Material

- EP 291/98, Loc. 10E. Between Tuffs 5 and 7. Rt mandible frag with $M_{2–3}$. M_2 26.2, M_3 33.3.
- EP 405/98, Loc. 10NE. Lt $M^{2–3}$, M^2 28.3.
- EP 943/98, Loc. 9S. Below Tuff 2. Rt M^2, early middle wear, ca. 26.0×–×30.5.
- EP 242/00, Loc. 8. Between Tuffs 5 and 6. Rt M^2, early middle wear, ca. 25.9×–×35.8.
- EP 474/00, Loc. 21. BetweenTuffs 5 and 8. Lt M_3, early wear, ca. 29.5×8.9×ca. 36.0.
- EP 1130/00, Loc. 8. Between Tuffs 5 and 6. Horn core.
- EP 1270/00, Loc. 8. Between Tuffs 5 and 6. Partial cranium, occipital joined to basioccipital and other fragments. Skull width across mastoids ca. 114.5, occipital

height 43.6, width across anterior tuberosities of basioccipital 25.4, width across posterior tuberosities of basioccipital 36.4.

- EP 352/01, Loc.2. Between Tuffs 5 and 7. Rt M^2, middle wear, ca. 27.3 × 17.0 × 34.5.
- EP 949/03, Loc.10. Below Tuff 3. Rt M$_2$, early wear, 24.9 × 9.8 × ca. 33.0.
- EP 201/05, Loc. 9. Between Tuffs 6 and 8. Broken rt M$_{2-3}$, early middle wear, M$_3$ ca. 29.0 × – × 36.3.

Description

The horn core EP 1130/00 is large and straight and has a sinus at its base. The base of the preserved portion has its greatest and opposing diameters at ca. 42 × ca. 29 mm. The basioccipital of the cranium EP 1270/00 looks alcelaphine and has a central longitudinal valley flanked by ridges behind the anterior tuberosities. The occipital surface faces more definitely backwards than does that of *Parmularius pandatus*. Just above the top of the occipital it looks as if the cranial roof is rising sharply.

The Laetoli alcelaphine cranium LIT 1959.233 in Nairobi (Gentry and Gentry 1978: 390, pl. 22, fig. 1) could be conspecific with the above remains. It is a larger species than *Parmularius pandatus* and also differs by its probable slight forward bending of the horn cores in profile, a flat cranial roof, and supraorbital pits placed more widely apart. Its horn core index is 47.6 × 42.7, slightly larger than even the frontlet LAET 74-245 of a large *P. pandatus*. LIT 1959.233 probably comes from the Laetolil Beds, since the Leakeys primarily collected at the locality 10 complex in both 1935 and 1959 (Leakey and Harris 1987: 3, 5). Fossils from Locs. 10 and 10W come from below Tuff 3, while any from Loc. 10E are most likely to come from between Tuffs 5 and 7.

Some of the remains of larger alcelaphines in the Laetolil Beds are suspect. A curved horn core tip, EP 2048/00 from Loc. 13, is light in weight and could be a modern *Connochaetes* or derived from the Ngaloba Beds. Among examples of larger alcelaphine teeth, EP 1905/00 from Loc. 5 is a lower molar with strongly rounded lingual lobes and the rear central fossette constricted across its centre and with a complicated posterior outline. These features look modern, so the tooth may have come from a small hillock of Ngaloba Beds present at Loc. 5.

The histogram of alcelaphine M$_3$ lengths (Fig. 15.18) is not clear-cut but could be compatible with the presence of more than one alcelaphine species in the Laetolil Beds. Also, the overall means of occlusal lengths for all upper and lower molars in *Hippotragus* sp. and *Parmularius pandatus* (Table 15.4) are 22.5 and 21.1 mm, respectively. Thus, an "average" molar is about 6% longer in *Hippotragus*. Yet the corresponding readings for standard deviations are much bigger in *Parmularius* (2.49 mm compared with 1.8 mm).

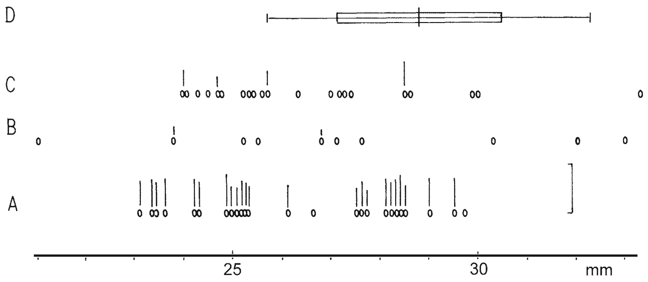

Fig. 15.18 Histogram of occlusal lengths in alcelaphine M$_3$s from the Laetolil Beds. Crown heights are indicated where known. The vertical scale for crown heights measures 50 mm. The occlusal length of bovid M$_3$s increases in later wear, so that in a single species the older M$_3$s would be expected to be longer and to have lower heights. A = earlier (early + early middle) wear, B = later (late middle + late) wear, C = unspecified wear (usually arising from wear state not having been listed or occlusal surface being obscured by matrix). D = mean, standard deviations and range for 49 M$_3$s of *Damalacra* in middle wear from Langebaanweg, where two equally-sized species are present. If the range of *Damalacra* were lengthened to the right to include specimens in late wear it would come close to equalling the range at Laetoli

One explanation could be that the *Parmularius* molars are mixed with those of a slightly larger species and therefore are more variable. Some of the safer examples of an alcelaphine larger than *Parmularius pandatus* have been listed above. Teeth of this species may be present in the proportion of about 10–15%. Gentry (1987) listed some dental pieces of a larger alcelaphine in the Leakey collection.

Discussion

The most likely alcelaphine known from elsewhere to be related to the Laetoli larger alcelaphine is the Hadar Fm. form referred to as "*?Damalops* sp." by Gentry (1981) and informally as *(Damalops)* "*sidihakomae*" by Vrba (1997: 132 [table 2], 135, figs. 2[a and b], 3, 4). The Hadar fossils include a good skull, AL 208-7 from Mb. SH. The species may also occur in the Tulu Bor Mb. and an unknown horizon of the Koobi Fora Fm. (Harris 1991: figs. 5.61 and 5.59), and Vrba (1997) listed additional occurrences at Aramis, Wee-ee, and Maka in the Middle Awash. This hoped-for unitary species differs from earlier *Parmularius* in its larger size, as well as less backward curvature of its horn cores and their distal attenuation and divergence. It does have resemblances to the Siwaliks *Damalops palaeindicus*, as first suggested for the cranium LIT 1959.233 by Gentry and Gentry (1978: 412), but I now believe that the Siwaliks species lies within the large group of *Parmularius-Damaliscus* species and may be closely related to *P. atlanticus* Geraads and Amani (1998: figs. 1D-E) from the Late Pliocene of Ahl al Oughlam.

In summary, the inadequately known larger alcelaphine from the Laetolil Beds and other localities may be conspecific with or related to an alcelaphine in the Hadar Fm. that is larger than *Parmularius pandatus* and not congeneric

Table 15.4 Occlusal lengths (mm) of teeth in Laetolil Beds Bovidae of the 1998–2005 collections. All entries are arranged as in the *top left* corner

		M3																	
		No	Mean	SD															
		Range			M2			M1			P4			P3			P2		
Aepyceros dietrichi	Upper	20	19.4	1.39	18	17.8	0.76	18	15.7	1.51	18	10.3	0.77	7	10.5	–	2	10.9	–
		16.5–21.4			16.5–18.9			13.7–19.1			9.0–11.7			9.5–11.4			10.5–11.3		
	Lower	11	23.2	1.57	10	16.6	1.16	9	14.6	–	6	12.0	–						
		20.7–25.3			14.1–18.1			13.0–16.1			11.4–12.8								
“*Gazella*” *kohllarseni*		16	15.1	0.97	11	14.7	0.82	4	13.7	–	4	8.6	–	5	7.9	–	3	7.7	–
		13.8–16.9			12.9–15.7			13.0–14.2			8.0– 9.6			6.8–8.8			7.3–8.1		
		6	19.8	–	6	14.0	–	3	13.5	–	9	10.6	–	5	10.1	–			
		17.5–21.3			12.2–17.1			11.6–16.1			8.9–12.6			8.2–11.5					
Gazella janenschi		19	13.1	0.87	25	12.3	1.04	18	11.1	1.21	14	7.4	0.41	15	7.6	0.52	10	7.2	–
		11.6–14.9			9.8–14.2			8.9–13.4			6.8– 8.1			6.6– 8.3			5.5– 8.5		
		41	17.1	1.18	41	12.2	0.81	34	10.8	1.09	14	8.5	0.70	6	8.0	–	3	4.9	–
		14.8–19.9			10.0–14.1			8.2–12.4			7.2– 9.3			7.3– 9.9			4.7 – 5.1		
Hippotragus sp.		27	23.5	1.44	37	22.9	1.23	16	19.0	2.29	29	13.2	0.66	19	13.1	0.69	13	12.2	0.82
		19.3–25.9			20.3–24.8			15.1–23.1			11.2–14.8			11.9–14.3			10.4–13.3		
		28	29.5	1.75	22	22.1	1.85	20	17.9	2.22	17	14.7	0.72	14	13.0	0.89	5	10.3	–
		26.3–32.8			18.6–24.8			14.5–23.0			12.9–16.0			11.6–14.4			9.0–13.0		
Parmularius pandatus		98	22.3	2.79	53	21.6	2.32	54	19.0	2.58	17	11.3	1.15	8	10.8		–		
		16.7–28.9			15.5–25.7			13.0–24.1			9.6–13.7			8.6–12.3					
		57	26.2	2.31	42	20.4	1.87	25	17.1	3.09	22	12.3	1.19	6	9.4	–	2	10.9	–
		21.0–33.0			17.2–24.2			12.2–23.1			10.6–15.0			8.7–10.0			10.5–11.3		

with it. The wider taxonomic relationships of the Hadar species are not known but probably do not include *Damalops*.

Gen. indet., Alcelaphini, small sp.?

Material

- EP 378/00, Loc. 12E. Between Tuffs 5 and 7. Rt M^2, early middle wear, 18.2 × 12.8 × 11.5.
- EP 482/00, Loc. 21. BetweenTuffs 5 and 8. Rt M_3, late middle wear, ca. 21.0.
- EP 2539/00, Loc. 4. Between Tuffs 6 and 8. Rt lower molar, middle wear, 16.5 × 8.5 × 9.8.
- EP 354/01, Loc. 2. Between Tuffs 5 and 7. Lt M^2, middle wear, 17.6 × 14.2 × 10.9.

Description

There are a very few alcelaphine teeth in the Laetolil Beds that may be too small to belong to *Parmularius pandatus*, and some of these have been listed above. The lower molar EP 2539/00 has a basal pillar and may not be sufficiently high crowned to be an alcelaphine. The M^2 EP 354/01 may be too short relative to its low height to be a *P. pandatus* M^2. Taken together, these and other records do not lift the small alcelaphine quite out of the reach of uncertainty. It may not exist.

Systematics: Bovidae of the Lower Unit of the Laetolil Beds

In this section, the details of Kakesio fossils collected in 1982 come from an unpublished short report prepared for Mary Leakey in January 1984. More recently, Harrison has restudied the collection in Nairobi. Harris (1987) previously discussed the fauna from this unit. The unit has an age range of about 0.5 myr, dating to 3.8–4.3 Ma (Deino 2011).

Bovini sp.

Material

- EP 089/99, Esere 1. Short piece of a curved and uncompressed horn core. Length ca. 95 mm, diameters at its thickest end are ca. 48 × ca. 44.
- EP 096/99, Esere 1. Metapodial condyle.
- EP 101/99, Esere 1. Proximal radius, total width 78 mm.
- EP 103/99, Esere 1. Left upper molar, early middle wear, occlusal length ca. 32.6
- EP 203/03, Kakesio 8. Distal radius, total width of 76 mm.

The postcranial remains are big enough to be of Bovini, and the piece of horn core EP 089/99 is from quite a small bovine. Harrison (personal communication) also identified several isolated bovine teeth from Kakesio in the Nairobi collections.

?Raphicerus sp.

Material

- KK 82-181. Lt horn core with part of frontal. Index 12.2 × 12.0, length ca. 49 mm.
- KK 82-182. Frag. lt. mandible with broken M_3.

Description

The horn core is too large for *Madoqua* and is about the size and length of living *R. campestris*. It is inserted above the orbit, the pedicel/horn core boundary is not clear, and there are no sinuses in the pedicel. It has little or no compression. The cross-section is not rounded but shows approaches to a mid-medial keel, a mid-lateral or postero-lateral keel, and perhaps even an anterior one. The horn cores would have been almost parallel in anterior view. Characters unlike extant *R. campestris* are the degree of divergence diminishing slightly and evenly from base to tip, the insertion more slanted backwards, and the profile not concave forwards in side view.

Madoqua avifluminis

Material

- KK 82-208, Kakesio. ?Lt horn core. Index 10.7 × 7.6, length 29 mm.
- Harrison (personal communication) considers that the Kakesio *Madoqua* is identical to the Upper Laetolil Beds species.

Aepyceros dietrichi

Material

- KK 82-180, Kakesio. Lt base of a battered horn core, index ca. 36.0 × 32.4.
- KK 82-270c, Kakesio. Horn core fragment that may also belong to this species.
- EP 045/98, Kakesio. Lt upper molar, late middle wear, 17.0 × 13.1 × 13.9.

This species is otherwise known only from the Upper Laetolil Beds.

Gazella janenschi

Material

- KK 82-11, Kakesio. Horn core piece.
- KK 82-23, Kakesio. Frag. lt mandible with M_1 or M_2, ca. 12.0.
- KK 82-52, Kakesio. Lt complete horn core, index 23.3 × 21.7, length ca. 135 mm.

- KK 82-72, Kakesio. Lower part lt horn core, index 25.6×21.3.
- KK 82-284, Kakesio. Lower part lt horn core, index 21.8×19.2.
- EP 1348/03, Kakesio 1-6. Rt mandible, M_{1-3} early middle wear. M_{1-3} 42.8, M_1 12.2×6.6, M_2 13.7×6.8, M_3 ca. 17.9 long, ramus depth under M_1 17.1, under M_3 20.7.

Description

The horn core KK 82-52 (Fig. 15.19) has a small piece missing at the tip but is otherwise complete. It is moderately long, little compressed, the lateral surface is flattened unlike most specimens in the Upper Laetolil Beds, some strong longitudinal grooves lie just medial to the posterolateral extremity, the level of greatest mediolateral width is midway between the front and back of the horn core and there is almost a mid-medial keel, there are no transverse ridges, it is moderately divergent, but the degree of divergence lessens distally, the insertion is inclined backwards, and there is a small triangular supraorbital pit. The horn core KK 72/82 shows no sinuses in the pedicel. The mandible EP 1348/03 appears to be of a completely typical Tertiary (Late Miocene to mid-Pliocene) small gazelle. It shows strong backward entostylids on M_1 and M_2, straight central fossettes, pointed labial lobes, slight outbowings on lingual walls, no goat folds, a large third lobe on M_3, and a tiny basal pillar on M_1. This gazelle is not separable from *Gazella janenschi* in the Upper Laetolil Beds.

Gazella granti

Material

- KK 82-304. Lower part rt. horn core, index 54.0×34.5.

Description

In my 1984 report, I wrote as follows on KK 82-304 (Fig. 15.19):

> "The horn core identified as *Gazella granti* is the problem. I can neither doubt my identification nor believe that it was contemporaneous with the other Kakesio bovids. It is unlike living and fossil Hippotragini in the absence of large sinuses in its pedicel. It is more compressed than any *Hippotragus*."

This view was duly reported by Harris (1987: chapter 14). Harrison (personal communication) confirmed the absence of any sinus in the pedicel, which helps to fit *Gazella granti*. I still do not believe that *G. granti* existed at the date of the Lower Laetolil Beds.

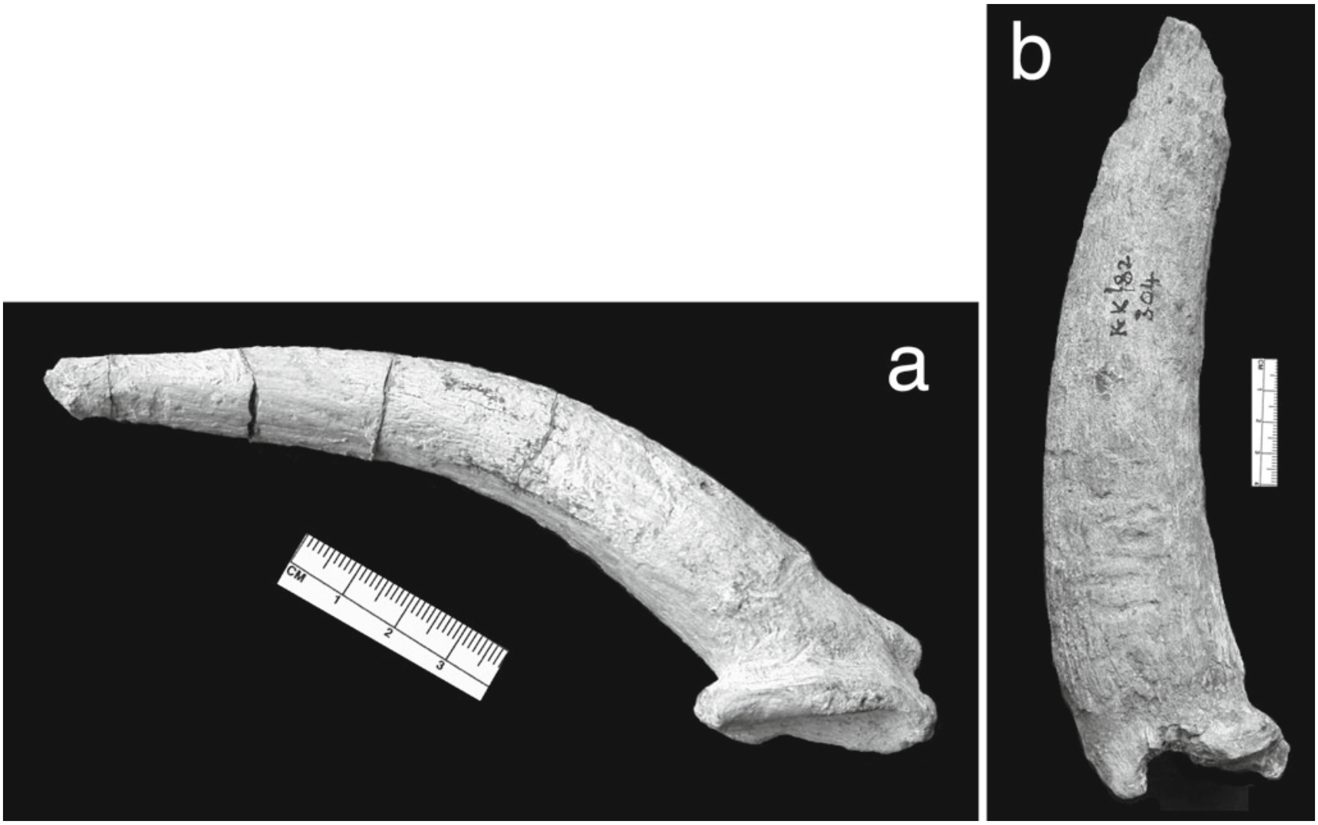

Fig. 15.19 Two horn cores from the lower unit of the Laetolil Beds. (**a**) left horn core of *Gazella janenschi* KK 82-52 in medial view. (**b**) right horn core of *Gazella granti* KK 82-304 in medial view. Scales in mm

Hippotragus sp.

Material

- KK 82-196-198, Kakesio. Part lt mandible, P_4 – broken M_2, middle wear. Occlusal lengths P_4 16.0, M_1 17.1.
- KK 82-262, Kakesio. Rt M_1 or M_2, middle wear, occlusal length 22.0.
- EP 044/98, Kakesio 4. Rt upper molar, late middle wear, occlusal length ca. 17.6.
- EP 1177/01, Kakesio 1-6. Right M^3, early middle wear, 21.6 × 20.4.

Description

The P_4 lacks fusion of paraconid with metaconid on the lingual side.

Parmularius pandatus

Material

- KK 82-9a+b, Kakesio. Paired mandible fragments with M_1 and newly erupted M_2. Occlusal lengths 16.3 and 17.8, ramus depth below M_1 29.0.
- EP 093/98, Kakesio 3. Lt M^{2-3}, middle wear, M^2 18.3 × 13.3 × 11.2, M^3 18.1 × 11.4 × 15.8.
- EP 3646/00, Kakesio 6. Part of a right M_3.
- EP 195/03, Kakesio 8. A right distal humerus.
- EP 518-9/03, Kakesio 10. An upper molar and an M_{1-2}.
- EP 521/03, Kakesio 10. Base of a left horn core and distal parts of the left and right horn cores, index ca. 41.5 × 32.2.
- EP 1340-1/03, Kakesio 1-6. Two right M^3s.

Description

Because the lateral surface of alcelaphine horn cores descends lower than the medial, the base of EP 521/03 can be identified as of the left side. The horn cores were quite long, and no transverse ridges were detectable. The level of maximum transverse diameter lies centrally or posteriorly. The lateral surface becomes flatter distally and, together with the simple backward curvature, gives it a certain resemblance to *Gazella granti*. But the sinus in the pedicel reaching to the top of the pedicel rules out *G. granti*, as does the poor degree of compression, and it is similar to *Parmularius pandatus*. A left horn core, EP 300/99 from Emboremony 1, with a flatter lateral than medial surface and a large sinus at its base, could be conspecific with EP 521/03. Its index is 35.9 × 32.1, so it is less compressed than *Hippotragus* sp. (Fig. 15.16), and it is too small for a modern male or female *H. equinus*. Another horn core, EP 1661/98 from Esere, is definitely a piece of a *Connochaetes* horn core but may have come from the Mbuga Clay.

The upper molars EP 093/98 are good generalized bovid teeth, quite close to the primitive state of Langebaanweg and Manonga alcelaphines, except that the labial rib of the metacone is slightly more pronounced and the styles perhaps more insignificant. Matrix hides the position of any basal pillars that may have survived. They may best be taken as Alcelaphini. Their size is small compared with the *Parmularius pandatus* in the Upper Laetolil Beds.

Discussion

Concerning the morphology of the horn core EP 521/03, it can be said that not all *Parmularius pandatus* horn cores show much in the way of lyration or a sharp backward bending in the middle of their courses. Backwardly curved horn cores with a degree of compression are primitive among bovids and can be found in *Tethytragus* (Middle Miocene), some early gazelles, caprines, *Hippotragus*, and probably others. They would not be surprising in an early mid-Pliocene alcelaphine. Harrison (personal comunication) considered that the smaller alcelaphine species was the commonest taxon in the Lower Laetolil Beds and was indistinguishable from *P. pandatus* in the upper unit.

Alcelaphini, larger sp. indet.

Material

- KK 82-172, Kakesio. Lt upper molar, early middle wear, occlusal length ca. 22.0.
- KK 82-263, Kakesio. Lt P_3 and M_{2-3}, late middle wear, occlusal lengths 9.8, 19.6, 31.4.
- KK 82-271, Kakesio. Rt M_2 and M_3, damaged, middle wear.
- KK 82-273, Kakesio. Rt P^4, middle wear, occlusal length 13.9.

Description

These teeth were thought to belong to a bigger species than *Parmularius pandatus*, but only the M_3 KK 82-263 and the P^4 KK 82-273 are outside the range of that species (Table 15.4). Harrison (personal communication) considered that a large alcelaphine was present but very rare at Kakesio. A cranial vault and horn core in Nairobi (KK 82-270) seems to be identical to the cranium LIT 1959.233 cited above for the Upper Laetolil Beds and included with other material under the name "Alcelaphini larger sp.indet." Indeed, Vrba (1997: 138) has already made the same identification of KK 82-270. In my unpublished 1984 notes, I had wrongly identified KK 82-270c as "?Hippotragini sp." (now = *Aepyceros dietrichi*).

Conclusions

None of the bovids from the Lower Laetolil Beds look very different from those in the Upper Laetolil Beds. The possibility of the two alcelaphine species having smaller teeth cannot be decided until larger samples become available.

Systematics: Bovidae of the Upper Ndolanya Beds

SUBFAMILY BOVINAE
TRIBE TRAGELAPHINI

Tragelaphus* sp. cf. *T. buxtoni

?(*Tragelaphus* sp. cf. *buxtoni* Lydekker, 1910.) Dietrich, 1942: 118, fig. 154.
?(*Tragelaphus* sp. cf. *spekei* or *angasi*) Gentry and Gentry, 1978: 305.
Tragelaphus sp. cf. *buxtoni* Gentry, 1987: 397.

Material

- EP 1245/98, Loc. 22S. Rt dP^3, no wear 18.0×9.5×9.2.
- EP 1247/98, Loc. 22S. Rt upper molar, early middle wear ca. 25.2 long.
- EP 3943/00, Loc. 7E. Lt M^1, early middle wear 22.3×14.9×17.8.
- EP 3949/00, Loc. 7E. Lt P_2, 11.4×6.2×8.6.
- EP 1138-40/03, Loc. 7E. Rt M^3, M^2 and M^1, early middle wear. M^1 19.8×15.4, M^2 23.8×15.4, M^3 23.5×13.0.
- EP 095/04, Loc. 22S. Rt lower molar, unworn.
- EP 1499/04, Loc. 22E. Lt mandible with M_{1-3}, middle wear, M_{1-3} ca. 74.8, M_2 ca. 21.0, M_3 ca. 29.4.

Description

The above list is a selection of the better Ndolanya tragelaphine teeth. Most of them seem to be from a smaller species than the contemporaneous *T. nakuae* of the Shungura Fm., but it is quite likely that more than one species is present. The P_2 EP 3949/00 is probably tragelaphine, since it looks insufficiently shortened to match Hippotragini or Alcelaphini.

Discussion

A fine cranium with horn cores, LAET 75-1686 from Loc. 14, apparently now lost, was described but not illustrated by Gentry (1987), whose verdict was that it most resembled *Tragelaphus buxtoni* among living species but was slightly larger. He noted that a frontlet in Berlin that Dietrich (1942, 1950) had also called *T.* sp. cf. *buxtoni* had more inclined insertions, which gave it more of a resemblance to extant *T. spekei* or *T. angasi*. The Loc. 14 specimen was about the size of *T. strepsiceros* but had lyrated rather than spiralled horn cores, a strong posterolateral keel, and slight anteroposterior compression. The initial divergence increased initially at the horn bases so that the posterolateral edges were concave in anterior view. Divergence then lessened, thereby giving the horn cores their lyrated appearance, which I take to be more primitive than the stronger spiralling of kudus. The teeth listed above could be conspecific with the Loc. 14 cranium.

Dietrich's 1942 frontlet was supposed by him to have come from the "Ältestquartär der südlichen Serengeti," which can usually be taken as the Laetolil Beds of later authors. Leakey et al. (1976) stated that it was "now possible to exclude some genera from the published lists of fauna from the Laetolil Beds, such as *Theropithecus*, *Tragelaphus*, *Equus* and *Phacochoerus*," but this could be an inadvertent contradiction or overlooking of Dietrich (1942) as far as *Tragelaphus* is concerned. They gave no opinion on the provenance of the Berlin frontlet. If from the Laetolil Beds, the frontlet would be an additional species to the one currently recognized earlier in this chapter; if it were really from the Upper Ndolanya Beds, then it is an awkward morphological fit with the Loc. 14 cranium. Despite some anteroposterior compression in the horn cores of both specimens, neither of them matched *Tragelaphus nakuae* of the Shungura Fm. or even the more primitive *T.* aff. *nakuae* (Gentry 1981) in Mb. DD of the Hadar Fm.

LAET 75-1632 from Loc. 14 is a piece of a right mandible having a dP_4 in middle wear and with an occlusal length of 23.2. It was listed near the end of Gentry (1987) with other bovid fossils from Loc. 14 that had been identified in the belief that Loc. 14 was in the Laetolil Beds. Seeing it again in 2004–5, I believed it to be a tragelaphine tooth. By size, it could be conspecific with the teeth listed above.

TRIBE BOVINI

The problems with bovine identifications in the Laetolil Beds continue into the Upper Ndolanya Beds. Quite a lot of possibilities are open. Supposed *Simatherium* was still alive at this period. *Pelorovis* appeared in Africa around 2.5 Ma, perhaps while the beds were being deposited, and probably did not descend from earlier *Simatherium*. It is first known in Shungura D and the upper Burgi Mb. of the Koobi Fora Fm. (Gentry 1985; Harris 1991). It had quite curly horn cores, like the European *Leptobos stenometopon* or *L. elatus*, and already they were inserted well back above the top of the occipital surface (the horn core of Gentry 1985: pl. 4, fig. 2 has a small area of the occipital surface at its base that is not visible in the plane of the published photograph). The Upper Ndolanya Beds would also be of a suitable date to contain a very late *Ugandax* or an early *Syncerus*. Little is known of fossil species of *Syncerus* other than the *S. acoelotus* in Olduvai II–IV (Gentry and Gentry 1978: pl. 2).

Bovini sp. or spp. indet.

Material

- LAET 75-3221, Loc. 7E. Base of a horn core, preserved length about 110 mm.
- LAET 78-4870, Loc. 18. Distal part of a horn core, about 170 mm long.

- EP 3027/00, Loc. 1. Lt M^2, middle wear, 38.8×27.3.
- EP 3029/00, Loc. 1. Base of a horn core, preserved length about 130 mm.
- EP 110/03, Loc. 18. Lt metacarpal, length 257 mm, minimum transverse width of shaft 64 mm.
- EP 1170/04, Loc. 14. Rt upper molar, middle wear.

Description

LAET 75-3221 is the bulky base of a curved horn core. It is probably bovine and unlikely to be giraffine. Its basal diameters are about 110×95, tapering rapidly to about 66×63. It could have had an original length from about 23 cm to somewhere above 45 cm. Gentry (1987) treated it as a Laetolil Beds specimen.

EP 3029/00 is part of a curved horn core with sinuses visible at its base. The diameters at its broken distal end are 116×95, so it is larger than LAET 75-3221. In ventral view, it can be seen to overhang a temporal fossa and so must have been inserted postorbitally. It looks as though its concavely curved edge is the rear one, which would make it a left horn core and with a curvature unlike that of *Pelorovis oldowayensis*. In this orientation, its posteroventral surface is shallowly dished.

The upper molar EP 3027/00 is occlusally complex, more so than in *P. oldowayensis*, but not perhaps more so than in L20-12 in Shungura F (Gentry 1985: 143, pl.3, fig. 2).

The metacarpal EP 110/03 is of much interest because of its great size (Fig. 15.20). It is much encrusted with matrix, so its dimensions quoted above are approximate. Nonetheless, its size exceeds that of an Olduvai *Pelorovis oldowayensis* metacarpal, 1952.277 from the BK site in Upper Bed II, which is 235 mm long and 49 mm wide (Gentry 1967). It is of the same length as metacarpals in a collection of *Bos primigenius* from London (Middle Pleistocene, Ilford) but is somewhat wider. The late Pliocene *Leptobos* metacarpal in Fig. 15.20 shows that, in Europe, the bovine preceding the Pleistocene *Bos* and *Bison* remained considerably more gracile at a period over 0.5 myr later than the Upper Ndolanya Beds. Another left metacarpal in three pieces, EP 1031/00 from Loc. 18, has minimum length and least shaft width of ca. 260 and ca. 60. Other bovine postcranial bones of exceptionally large size came to light in 2005 among bones previously taken as giraffid in the Laetoli 1998–2005 collections, for example:

- EP 1032/00, Loc. 18. Prox. right metacarpal, DAP×TS 56.8×85.7
- EP 3432/00, Loc. 15. Dist. metatarsal, DAP×TS ca. 42.7×80.5
- EP 3433/00, Loc. 15. Prox. left metacarpal
- LAET 78-03, Loc. 18. Prox. left metacarpal, DAP×TS 59.8×96.0

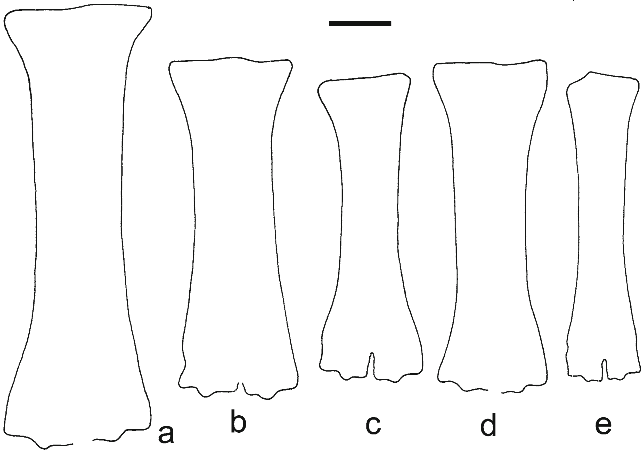

Fig. 15.20 Outline drawings of five metacarpals. (**a**) the giraffid *Sivatherium giganteum* BM 39533 from the Siwaliks, (**b**) the bovine EP 110/03 from the Ndolanya Beds, (**c**) *Pelorovis oldowayensis* 1952 BK II 277 from Olduvai Gorge, (**d**) *Bos primigenius* BM 35008 from Ilford, England, (**e**) *Leptobos etruscus* from Senèze, France. Scale = 50 mm

- EP 1669/03, Loc. 15. Lt cuneiform, DAP×height 48.0×50.0
- EP 201/04, Loc. 15. Lt lunate, DAP×height 56.0×45.2
- EP 203/04, Loc. 15. Rt astragalus, TS×medial height ca. 60.0×75.4
- EP 205/04, Loc. 15. Cervical vertebra.

These very large Bovini come from two Upper Ndolanya Beds localities and cannot be seen as stray or anomalous occurrences of the large long-horned buffalo from the Late Pleistocene. The lunate EP 201/04 was of markedly different appearance from one of an Ilford *Bos primigenius*, so anatomical studies might be fruitful.

Discussion

All these bovines are of uncertain generic attribution and may represent more than one species. The horn cores could turn out to be *Syncerus* if more were known of them, but they fail to resemble either *Simatherium* or *Pelorovis*. Both specimens are smaller and less compressed than *Pelorovis oldowayensis* at Olduvai Gorge or the smaller *P. turkanensis* best known from the KBS and Upper Burgi Mbs. of the Koobi Fora Fm. (Harris 1991: table 5.12). The concave edge of EP 3029/00, large enough to be a *Pelorovis*, looks as if it is posterior and therefore unlike *Pelorovis*. The horn cores are also much smaller than the frontlet from Eyasi or Njarasa (Dietrich 1950: 47, pl. 6, fig. 56), which presumably comes from the Late Pleistocene long-horned buffalo, *Syncerus* (or *Pelorovis*) *antiquus*. The very large limb bones are significant in revealing the existence of such a large bovine early in the late Pliocene but are uninformative about its identity.

SUBFAMILY ANTILOPINAE
TRIBE CEPHALOPHINI

?Cephalophini sp. indet.

A small horn core, EP 3216/00 from Loc. 18, could be of a cephalophine. It was probably short and was slightly curved in one plane, presumably backwards. The cross-section narrows towards the concave (?back) edge. The base is probably present. The index of the horn core is ca. 12.3 × 11.3, and its length was about 40 mm. Another nearly complete horn core, EP 3467/00, Loc. 15, has an index of 11.1 × 10.2 and its length was about 44 mm. It becomes slightly curved towards the tip. It is not certain that these horn cores are cephalophine, but neotragine horn cores are more likely to be straight and to taper less markedly.

TRIBE NEOTRAGINI

?Raphicerus sp.

?Raphicerus sp. Gentry 1987: 400.

A single tooth fragment was recorded in 1987, and there are a few new records – for example, EP 081/03, a right horn core with index 13.5 × 11.2 and a length of 51 mm. A right upper molar, EP 3952/00 from Loc. 7E, in middle wear and with measurements 8.8 × 6.6 × 6.3 high, is of a suitable intermediate size between *Gazella* and *Madoqua*.

Madoqua ?avifluminis

Madoqua ?avifluminis Gentry 1987: 400.

As reported in 1987, the horn cores in the Upper Ndolanya Beds are larger than those of the Laetolil Beds or extant dik dik (Gentry 1987: fig. 10.6). Size increase of horn cores from Loc. 7E to Loc. 18 within the Upper Ndolanya Beds was not taken as evidence of a time span. The fairly pronounced tapering of the horn cores puts them closer to *M. avifluminis* than to the living dik dik, but they may have a straighter course than *M. avifluminis*. The teeth are not larger than those of the Laetolil Beds. A horn core from Mb. KH of the Hadar Fm. was small but thought to agree with Upper Ndolanya Beds specimens. No further observations have been made.

TRIBE ANTILOPINI

Four species of Antilopini, in addition to the ever-problematic *Gazella granti*, occur in the Upper Ndolanya Beds. They can be distinguished on the basis of their horn cores but not with much success on the basis of teeth. One difficulty is that the number of fossils is low. Another is that the teeth of early *Antidorcas*, a new arrival in the record, differ less from *Gazella*, of which there are two species, than did those of *Aepyceros dietrichi* from *Gazella janenschi* in the Laetolil Beds. Teeth known from later extinct *Antidorcas* species differ from *Gazella* in upper molars with strong styles and a flatter and even concave wall between mesostyle and metastyle, lower molars with flat lingual walls, and premolar rows short and often lacking p2s (Gentry and Gentry 1978: 430, text fig. 32). The strong styles and concave rear part of the labial wall of upper molars are also seen in *Aepyceros shungurae*. This did not obstruct identifications while *Antidorcas* was common at Olduvai, *Aepyceros* was common in the Shungura Fm., and *Gazella* was uncommon at both localities. However, a series of antilopine dental fossils, such as EP 232-240/04 at Loc. 18 in the Upper Ndolanya Beds, has to remain unidentified until time allows a thorough study of antilopine teeth in the major east African Plio-Pleistocene localities.

Aepyceros sp.

?Aepyceros melampus Gentry 1987: 400.

Material

- LAET 75-1700, Loc. 14. Rt horn core base, index 41.3 × 38.5.
- LAET 76-341, Loc. 18. Partial lt horn core.
- EP 943/04, Loc. 9. Part of a horn core.

Description

A partial left horn core, LAET 76-341, looking like modern *Aepyceros melampus* was thought by Gentry (1987) to be anomalous in the Ndolanya Beds, but there can be little doubt of its generic identity or stratigraphic level. The horn core base LAET 75-1700 is certainly conspecific with LAET 76-341. An anterolateral sinus in its pedicel could correspond with those of *Aepyceros dietrichi* in the Laetolil Beds, as seen, for example, in EP 629/03. Possibly the large more medial sinus at the base of *A. dietrichi* pedicels does not extend so high as the anterolateral ones. The lateral edge of LAET 75-1700 does not seem to be concave outwards. EP 943/04 is part of another horn core, possibly a middle section of a conspecific piece of the right side. The diameters near the base of the existing piece are ca. 43 × ca. 35. In the Laetolil Beds, EP 943/04 might be taken as part of a right horn core of *Parmularius pandatus*, but in the Upper Ndolanya Beds and with no knowledge of the condition of any sinus at its base, it is not an easy fit with either *Aepyceros dietrichi* or *Parmularius ?altidens*. No antilopine teeth have been found large enough to fit an *Aepyceros* species larger than *A. shungurae*.

Discussion

How these horn core pieces might be related to modern *Aepyceros melampus* or to *A. dietrichi* of the Laetolil Beds is undecided. LAET 76-341 is much like the Laetolil Beds LAET 75-503 but very slightly bigger and perhaps more gradually curved. The Upper Ndolanya Beds specimens are from a species larger than *A. shungurae* of the Shungura and Usno Fms., a species that had existed since around 3.0 Ma. They are also bigger by about a third (33%) in linear dimensions than the impala in the Upper Burgi Mb. of the Koobi Fora Fm. (Harris 1991: table 5.62) regarded by that author as early *A. melampus*. It would be simpler to take them as *A. dietrichi*. This could make them the last known representatives of a fairly large mid-Pliocene *Aepyceros* that was about to disappear, leaving behind the smaller *A. shungurae*. Some years ago, Vrba (1987b) suggested that a small piece of horn core from Makapansgat Limeworks (Wells and Cooke 1956: fig. 19), supposedly of *Aepyceros*, could be conspecific with the Laetolil Beds species. So this could be another lingering *A. dietrichi* and not a too-early *A. melampus*.

Gazella janenschi

Gazella janenschi Gentry 1987: 401.

Description

The horn cores cited in 1987 continue to be acceptable as this species. They have flattened lateral surfaces and greater mediolateral compression than in the Laetolil Beds.

Discussion

It is interesting that minimally changed *Gazella janenschi* is still present in the Upper Ndolanya Beds (Fig. 15.9), where it now exists alongside an early *Antidorcas*. The larger *Gazella praethomsoni* Arambourg 1947 with mediolateral compression of its horn cores is known from Shungura Mb. F onwards and earlier from the Lokochot Mb. of the Koobi Fora Fm. (Harris 1991). By the time of Olduvai Beds I–II, a gazelle more like the living *G. rufifrons* is present in East Africa, perhaps having descended from *G. praethomsoni*.

Gazella sp.

Antilopini sp.1, Gentry and Gentry 1978: 444, pl. 39, fig. 2. Olduvai, Beds I–II. Early Pleistocene.
Antilopini sp.indet. Gentry 1985: 180. Shungura Fm, Mbs K–L. Early Pleistocene.
Gazella praethomsoni (in part, Omo 33 70.2680 + 70.2993) Gentry 1985: 179. Shungura Fm, Mb F. Late Pliocene.
Antilopini "sp.1" Gentry 1987: 401, pl. 10.12. Laetoli, Upper Ndolanya Beds. Late Pliocene.

Material

- LAET 1976-84, Loc. 18. Rt horn core, index ca. 28.0 × 23.5 (Gentry 1987: pl.10.12).
- EP 3219/00, Loc.18. Lt horn core, index 25.3 × 20.7.
- EP 021/03, Silal Artum. Rt horn core, index ca. 25.5 × 20.5.

Description

The horn cores show a central or slightly posterior position of the level of maximum transverse diameter, an approach to an anterior keel, some compression, the lateral surface flatter than the medial, no transverse ridges, divergence increasing rapidly from the base, a fairly upright insertion over the back of the orbit in side view, backward curvature, and insertions probably close. The pedicel is low, the frontals are not raised between the horn bases, and the supraorbital pit is fairly large and triangular. The front edge of EP 021/03 is missing, and it has less of an approach to a posterolateral keel than in LAET 1976-84.

Horn cores like these have also been found in Shungura F–L and at Olduvai from the surface of Bed I to upper Bed II. They are about the size of *Gazella janenschi* but more compressed, and some of the Olduvai ones are bigger. The Shungura ones showed no sign of sinuses within the frontals or pedicels, and one of them looked as if the horn cores might have had a degree of lyration when complete.

An antilopine right maxilla with P^2–M^3 in middle wear, EP 2170/00 from Loc. 7E, may belong to *Gazella*. The tooth measurements on this specimen are as follows: P^{2-4} 20.4, M^{1-3} 38.0, P^2 6.9 × 6.3, P^3 7.5 × 7.2, P^4 6.8 × 7.6, M^1 10.7 × 9.9, M^2 12.9 × 10.9, M^3 15.0 × 9.6. Compared with the *G. janenschi* maxilla EP 497/00 in the Laetolil Beds, the premolar row is much shortened; P^{2-4}/M^{1-3} drops from 68% to 53%. If the maxilla is *Gazella*, it might be of this species.

Discussion

Most of the characters of these horn cores would fit *Gazella*, but the more upright insertions, the strong initial divergence, and perhaps the less pronounced flattening of the lateral surface are not found in *G. janenschi* or the Olduvai *Gazella*. They are about the size of larger *G. praethomsoni* horn cores, and have some overlap with the latter's strong compression (Fig. 15.21). However, no previous treatment of *G. praethomsoni* has suggested that divergence increased from the base upwards or that there was distal lyration.

These horn cores could be another *Gazella* species in East Africa or a development within or from late *G. janenschi*. It is less likely that they could belong to a small antilopine close to *Antilope*. As well as living in India today, *Antilope* has been recorded from Mb. C of the Shungura Fm. (Gentry 1985: pl. 11, fig. 3). Our horn cores differ from the Omo *Antilope* in having less torsion, a flattened lateral surface, an approach to an anterior keel, more upright insertions in side view, and divergence increasing from the base.

Gazella granti

Material

EP 942/04, Loc. 9. Between Tuffs 6 and 8. Left horn core, index 47.7 × 31.5.

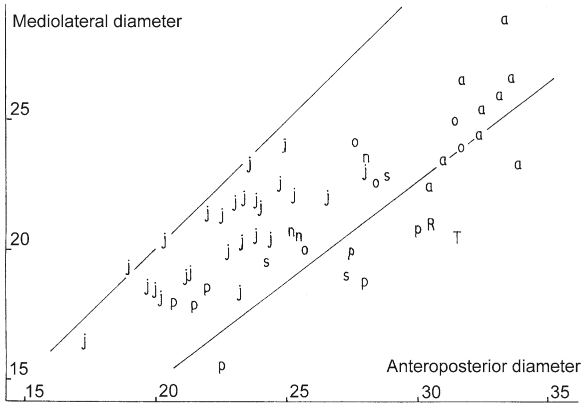

Fig. 15.21 Basal diameters of some antilopine horn cores. a=*Antidorcas recki* from the Ndolanya Beds, j=*Gazella janenschi* from the Laetolil Beds (both Leakey and Harrison collections), n=*Gazella* sp. from the Ndolanya Beds, o=the same from Olduvai Gorge, s=the same from the Shungura Formation, p=*G. praethomsoni* from the Shungura Formation. R and T=means for samples of the extant species *G. rufifrons* and *G. thomsoni*. The lower cluster of three *G. praethomsoni* may be females; the lowest reading of all is the holotype, in poor condition and perhaps subadult. *Upper* diagonal line=100%, *lower* one=75% as in Fig. 15.7

Description

Several horn cores and dental pieces in the lower and upper units of the Laetolil Beds were morphologically satisfactory as the extant *Gazella granti*. EP 942/04 is another such specimen from the Upper Ndolanya Beds. No doubts have been expressed about the stratigraphic derivation of this specimen, but I am reluctant to see a familiar large gazelle of present-day East Africa surviving from so ancient a fauna while so much biotic change took place around it.

Antidorcas Sundevall, 1847

TYPE SPECIES *Antidorcas marsupialis* (Zimmermann, 1780)

Other Species

Antidorcas recki from Olduvai Beds I–IV and other localities in East and southern Africa; *A. bondi* and *A. australis* in the Pleistocene of South Africa. *Antidorcas bondi* has very hypsodont teeth.

Short Diagnosis

Horn cores usually little compressed, sometimes with transverse ridges, bending backwards and diverging from close above the base of their rather upright insertions, often more massive basally in relation to their length than in *Gazella*, sometimes with homonymous (clockwise on the right) torsion. Horned females. Sinuses in the frontals, the frontals raised between the horn core bases, supraorbital pits small, braincase short, lower molars with flat lingual walls, premolar rows short, and p2s often absent.

Remarks

The diagnoses of the genus and the Ndolanya species (below) have been shortened from the versions in Gentry and Gentry (1978). *Antidorcas* is distinguished from *Gazella* by sinuses in the frontals, the frontals raised between the horn core bases, supraorbital pits small, braincase shorter, premolar rows shorter and p2s often absent, and mandibular ramus relatively deeper under the molars than under the premolars. All extinct species are smaller than the extant South African one. The occurrence in the Upper Ndolanya Beds is an early *Antidorcas*, but possible earlier ones come from the Tulu Bor Mb. of the Koobi Fora Fm. and Koro Toro (Harris 1991; Geraads et al. 2001: fig. 5F).

Antidorcas recki (Schwarz, 1932)

Adenota recki Schwarz 1932: 1, pls. 1-2. Olduvai Gorge, Early-Middle Pleistocene.
Phenacotragus recki Schwarz 1937: 53, pl.1, fig. 1.
Gazella hennigi (*partim*) Dietrich 1950: 25, pl.1, figs. 1 and 2. Laetoli.
?Antidorcas sp. Gentry and Gentry 1978: 433, 62.
Antidorcas sp. Gentry 1987: 400.

Material

More horn cores and teeth have been recorded from the Upper Ndolanya Beds since 1987.

- EP 1297/98, Loc. 22S. Lt horn core base, index 32.5×24.4.
- EP 3953/00, Loc. 7E. Frag base of lt horn core.
- EP 3954/00, Loc. 7E. Frag base of rt horn core.
- EP 1505/01, Silal Artum. Rt horn core base, index 31.0×23.4.
- EP 1506/01, Silal Artum. Part of base of lt horn core.
- EP 243/04, Loc. 18. Lt horn core, index 32.7×ca. 25.3.

Diagnosis

Smaller than *Antidorcas marsupialis*, horn cores more mediolaterally compressed and often more sharply bent backwards in their distal parts, upper molars with stronger styles and a flatter and even concave wall between mesostyle and metastyle, P_2 sometimes absent, but often present.

Description

Antidorcas horn cores are bigger, at least at their bases, than in *Gazella janenschi* (Fig. 15.21). Mostly the new ones are uninformative, but EP 243/04 (Fig. 15.9) looks very like *Antidorcas recki*. A right horn core, LAET 78-5047 from Loc.14, index 23.4×18.6, could be a female if it turns out that this species did not have hornless females, but because the dorsal orbital rim is at the same level as the frontals between the horn bases it might be of a gazelle instead.

A right M_3 in middle wear, EP 849/00 from Loc. 18, measuring c15.3×5.9, and a left M^3 in early middle wear, EP 857/00 from Loc. 18, measuring 13.2×9.7 both suggest that the dentitions of *Antidorcas recki* could be larger than in *Gazella janenschi*. The dentition of Dietrich (1950: pl. 2, fig. 13) is a neotragine and not this species.

Discussion

Horn cores of *Antidorcas recki* at Olduvai vary extensively (Gentry and Gentry 1978: 429). Some, such as BK II 1955.71, BMNH M14513 from Bed I and others, are short, taper rapidly to a point from their thick bases, and have no flattened lateral surface or transverse ridges. They agree with four horn cores in Berlin, one of which (45 from Gadjingero = Loc. 18) was illustrated by Dietrich under the name *Gazella hennigi.* Gentry (1987) cited more such horn cores from the Upper Ndolanya Beds. They diverge in their distal parts, unlike *Gazella janenschi*. I choose not to use *G. hennigi* as a separate species name for this Ndolanya early *Antidorcas*, because the variation among the Olduvai horn cores fails to correlate straightforwardly with stratigraphic horizon, and because the Ndolanya horn core EP 243/04 looks more like an Olduvai *A. recki*.

Within East Africa, *Antidorcas recki* is a Middle Pliocene–Early Pleistocene species also found in Mbs. B–H of the Shungura Fm.; the lower Tulu Bor- Okote Mbs. of the Koobi Fora Fm.; and the Lomekwi, Kalachoro, and Kaitio Mbs. of the Nachukui Fm.

SUBFAMILY REDUNCINAE
TRIBE REDUNCINI

Reduncini sp. indet.

Gentry (1987) mentioned two specimens of reduncine lower teeth from Loc. 7E. No further remains have been found from the Upper Ndolanya Beds. A right horn core, LAET 81-28 from Loc. 23, index 34.6×ca. 37.5, looks like a modern *Redunca* of *R. arundinum* size. Most of the fossils at this locality have come from the Ngaloba Beds and LAET 81-28 is likely to be much younger.

SUBFAMILY HIPPOTRAGINAE
TRIBE HIPPOTRAGINI

Hippotragus sp. aff. *cookei?*

Hippotragus cookei Vrba 1987b: 49, figs. 1 and 2.

Type Locality

Makapansgat Limeworks Mb 3. Also at Sterkfontein Mb 4. Late Pliocene.

Hippotragus cookei has already been extensively discussed above. For the present it is possible that any scantily known late Pliocene *Hippotragus* may be of this species. The attribution "*Hippotragus* sp. aff. *cookei?*" also serves to differentiate the *Hippotragus* of the Upper Ndolanya Beds from that in the Laetolil Beds.

Material

- EP 1294/98, Loc. 22S. Lt horn core, index 50.5×36.9.

Description

The horn core EP 1294/98 is larger than the *Hippotragus* sp. of the Laetolil Beds, and its cross-section at the very base is drawn out posteriorly to a posterolateral point. It is insufficiently compressed to match *Gazella granti*.

Five Upper Ndolanya Beds teeth and partial dentitions from Locs. 18 and 7E were identified as hippotragine by Gentry (1987). They were more advanced than the *Hippotragus* of the Laetolil Beds – for example, in the more definite transverse goat folds at the front of lower molars – but remained slightly smaller than the *Hippotragus* of Olduvai Bed I. Another four specimens from Loc. 18 (LAET 76-335, 395, 536, and 541) were held to be the only teeth in the Upper Ndolanya Beds that could resemble the *Hippotragus* of the Laetolil Beds. Three further hippotragines from Loc. 14 can be added to the latter group. They were listed near the end of Gentry (1987) together with other bovid fossils from that locality, which I had thought in 1977 was in the Laetolil Beds and had been identified as *Hippotragus*. They were:

- LAET 75-1638, Loc. 14. Fragmentary lt maxilla with two damaged upper molars.
- LAET 75-1655, Loc. 14. Lt mandible with P_4–M_2, middle wear, occlusal lengths P_4 16.4, M_1 19.2, M_2 23.2.
- LAET 75-1656, Loc. 14. Rt M^3 middle wear, occlusal length 26.0.

Presumably, these teeth will belong to either the *Hippotragus* in the Upper Ndolanya Beds or to the *Oryx* to be described next. Two further hippotragine teeth were identified in the 1998–2005 collections: a left M_1 or M_2 in early wear, EP 931/04 from Loc. 9, 26.0×9.2; a left upper molar in early middle wear, EP 1176/05 from Loc. 14, 33.1×20.3×37.3. The lower molar has a goat fold, an advance on hippotragine teeth in the Laetolil Beds. The upper molar has quite a simple occlusal pattern, perhaps partly because it is still in the earlier part of wear.

Oryx sp.

Praedamalis deturi Dietrich (partim). Gentry 1987: 387, pl.10.7.

Material

- LAET 75-3257, Loc. 18. Rt horn core with part of frontal, index 44.8×35.0, length 285 mm.

Description

LAET 75-3257 is a moderately long horn core showing an anterior position of the level of maximum transverse thickness, no keels or transverse ridges, some compression, no flattening of the lateral or medial surfaces, slight divergence in anterior view with degree of divergence increasing distally, not a low inclination in side view, slight backward curvature, insertions fairly close together and above the back of the orbits. The postcornual fossa is shallow. Sinuses in the pedicels and adjacent parts of the frontals, the frontals between the horn bases are at about the same level as the dorsal orbital rims.

Discussion

As noted in the account of Hippotragini of the Laetolil Beds, the horn core LAET 75-3257 was misidentified by Gentry (1987: pl.10.7) as *Praedamalis deturi* and later turned out to have come from the Upper Ndolanya Beds. It differed from "*Praedamalis*" (now *Oryx*) *deturi* horn cores in having slight backward curvature. This slight backward curvature is like the modern species *O. leucoryx* of Arabia and *O. dammah* of West Africa but is probably insufficient for a female *Hippotragus*. Its inclination is a little greater than in *Hippotragus*, but far from being as swept back as in modern *Oryx* species.

TRIBE ALCELAPHINI

***Megalotragus* Van Hoepen, 1932**

TYPE SPECIES *Megalotragus priscus* (Broom, 1909)

Bubalis priscus Broom 1909; 280, text figure, South Africa, many Middle and Late Pleistocene sites.

Other Species

Megalotragus kattwinkeli (Schwarz 1932), Olduvai Gorge; *M. isaaci* Harris 1991, Koobi Fora Fm.; *M. atopocranion* (Pickford and Thomas 1984), a species of reduced size from the Late Pleistocene or Holocene of Rusinga Island, Kenya.

Occurrence and Range

Late Pliocene to Late Pleistocene or Holocene.

Diagnosis

Large extinct alcelaphines, probably including the largest known. Horn cores diverging, more closely inserted than in *Connochaetes*, inserted postorbitally and at a low inclination. Torsion is homonymous (clockwise on the right side) and variably expressed. All species except *M. priscus* are known to have the nasals and anterior parts of the frontals domed upwards to form an inflated snout. Short premolar rows. Legs long.

Megalotragus kattwinkeli* or *isaaci

Parestigorgon gadjingeri Dietrich 1950: 30, 32, pl.4, fig. 44.
Parestigorgon gadjingeri Dietrich 1950. Gentry 1987: 399.

Holotypes

1. For *Megalotragus kattwinkeli*: a right horn core, VI-1099, from Olduvai Bed IV (Gentry et al., 1995: fig. 2; Opinion 2029 of the ICZN, *Bulletin of Zoological Nomenclature* 60: 88–89, 2003) in the Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich.
2. For *Megalotragus isaaci*: a frontlet with horn cores, KNM-ER 2591, from the KBS Mb. of the Koobi Fora Fm. (Harris 1991: fig. 5.46). Vrba (1997) relegated *M. isaaci* to being a subspecies of *M. kattwinkeli*.

Horizon and Range

Megalotragus kattwinkeli is present in middle Bed II to Bed IV Olduvai Gorge, and perhaps in Bed I as well (Gentry and Gentry 1978: pl.12, fig. 2, pls.13 and 14). *Megalotragus isaaci* is in the Upper Burgi to Okote Mbs. of the Koobi Fora Fm. (Harris 1991: figs. 5.46–5.48) and therefore precedes and overlaps *M. kattwinkeli* in time. *Megalotragus kattwinkeli* or *isaaci* is also present at Bouri 1–2 and Matabaietu 1, Ethiopia (Vrba 1997: figs. 8 and 9), in Mbs. D–G of the Shungura Fm. (Gentry 1985: pl.8, fig. 4), and in Kaiso Village (Geraads and Thomas 1994).

Material

- EP 1485/00, Loc. 7E. Associated partial skeleton including complete left radius and metacarpal. Radius length and minimum transverse width of shaft 356 and 35 mm, metacarpal 291 and 25.6 mm.
- EP 3221/00, Loc. 18. Rt mandibular piece with M_3, middle wear, ca. 40.5 × 15.2.
- EP 532/04, Loc. 1. Rt upper molar, ca. 30.5
- EP 1110/05, Loc. 1. Rt M^3, late middle wear, 32.3 × – × 27.2.

Diagnosis

Horn cores short to moderately long, inserted postorbitally, but not overhanging the occipital surface, sometimes dorsoventrally compressed at their bases, with transverse ridges, moderately divergent but less than in most *Connochaetes*, curving upwards from the base followed by a sharp curve backwards. (Shortened and modified from Gentry and Gentry 1978.)

Description

It is rare to be able to identify contemporaneous alcelaphine teeth below the tribal level on the basis of morphology. Three size categories have previously been seen at Plio-Pleistocene localities from about the time level of Olduvai Bed I or Shungura G onwards: "large-sized," suitable for *Megalotragus* or *Connochaetes;* "medium-sized" for *Damaliscus* or *Parmularius;* and "small-sized," no bigger than in modern South African *Damaliscus dorcas*. The small category means that one or more species or lineage of small alcelaphine was once present in East Africa but is so no longer. Extinct *Beatragus* would probably be in or nearer the large category, although the modern species has only medium-sized teeth, but *Beatragus* has not yet come into question at Laetoli.

The three listed alcelaphine teeth are larger than any in the Laetolil Beds and are among the largest in the Upper Ndolanya Beds. They are large enough to be likely to belong to *Megalotragus*. So is LAET 75-1018 from Loc. 7E, a left mandible (associated with a right maxilla) with P_4–M_3 mentioned in Gentry (l987) under the name *Parestigorgon gadjingeri*. The radius and metacarpal of EP 1485/00 are fully as long as the *M. kattwinkeli* of Olduvai Bed II. They are more gracile than most Olduvai specimens, except for a single metacarpal, JK2 A.1272 from Bed III.

Discussion

The type species *Megalotragus priscus* had long and divergent horn cores overhanging the occipital at their bases and resembling the bovine *Pelorovis oldowayensis* at Olduvai. It seems to have been as big as *M. kattwinkeli*, but no examples of the preorbital part of the skull have been published. *Megalotragus kattwinkeli* was the first described *Megalotragus* in East Africa, and the species differs from *M. isaaci* in having shorter and more curved horn cores, presumably the result of a simple transition. It continued to possess the inflated nasal region of *M. isaaci*. Olduvai material (Gentry and Gentry 1978) demonstrates that the front legs were relatively longer than in *Connochaetes*. The large size of the Ndolanya *Megalotragus* is of interest, as it certainly predates the paired *Megalotragus* horn cores P947-1 in Shungura Mb. G-3 and might also predate Upper Burgi *Megalotragus*. The gracility of its metacarpal goes well with a single post–Bed II *Megalotragus* from Olduvai Gorge. Vrba (1997: 151) did not detect any temporal trend to inceased or decreased body size in East African *Megalotragus*.

The Position of Parestigorgon gadjingeri

Dietrich (1950) described this as a new genus and species of alcelaphine from the Ältestquartär. The syntypes were a horn core, perhaps of the left side (Dietrich 1950: pl. 4, fig. 44), labeled Gadjingero 2/39 and one or more upper molar rows with total occlusal lengths between 69 and 82 mm. The M^{1-3} of pl. 3, fig. 34 is a composite row in which the individual teeth are not from the same animal. The syntype horn core from Gadjingero would have come from the site later known as Loc. 18 in the Upper Ndolanya Beds (Leakey and Harris 1987: 6). Its two basal diameters are 51.0×41.1. Three horn cores were listed by Gentry (1987) for this species: LAET 75-1022, LAET 75-1023, and LAET 75-1043, all from Loc. 7E, while LAET 76-346 from Loc. 18, also mentioned in 1987, now seems to be better taken as of an undetermined species. Two more horn cores are EP 1209/00 from Loc. 22S and EP 199/04 from Loc. 15, a right horn core but only doubtfully conspecific with the others. The orientation of the horn cores is impossible to know in the absence of pedicels and adjacent skull parts, but an unoriented index for EP 1209/00 would be 47.8×36.6. If the syntype horn core is a left one, then Dietrich (1950: fig. 44) has shown it in anterolateral view. In supposed lateral view, its slight curvature would have been backwards. If horn core LAET 75-1022 is of the right side, it too would have a slight backward curvature. LAET 75-1023 may be the left side of the same individual, while LAET 75-1042+3 is the more distal part of a right.

The material is insufficient to sustain *Parestigorgon gadjingeri* as an independent species. Dietrich diagnosed it as a wildebeest-like representative ("Vertreter") in the fauna of that period, seemingly hinting at it not being taxonomically near *Connochaetes*. He mentioned no morphology in his one-line diagnosis. The horn cores would have been moderately long when complete, compressed by about one-fifth in an unknown plane at the bases, one side smoother surfaced than the other, without keels or transverse ridges, with a very slight curvature in one plane, and with a sinus in the pedicel.

Gentry (1987) linked *Parestigorgon gadjingeri* with the cranium LIT 1959.233, which belongs to a species of the Laetolil Beds. The latter species could have lasted into the Upper Ndolanya Beds, but a better solution for *Parestigorgon gadjingeri* may be to link it with *Megalotragus*, in which case the two readings within each basal index given above and in Gentry (1987) would need interchanging. Horn cores of *Megalotragus isaaci* are longer than in *M. kattwinkeli*, and any curvature present in shorter pieces is correspondingly more difficult to detect than in the later species. The slight backward curvature of the Ndolanya horn cores could have become the localized backward bending at the base of *M. isaaci* horn cores that then disappeared in *M. kattwinkeli*. More complete finds may or may not demonstrate the truth of any of this.

***ConZochaetes* Lichtenstein, 1814**

TYPE SPECIES *Connochaetes gnou* (Zimmermann, 1780).
?Connochaetes sp.

Material

- EP 1442/00, Loc. 7E. Lt mandible piece with M_3, middle wear, 31.7×11.4, ramus depth below M_3 56.4.
- EP 3040-1/00, Loc. 1. Two distal metapodials. Maximum transverse width×anteroposterior diameter=45.5×26.6 and 49.2×26.7 respectively.
- EP 3374/00, Loc. 15. Rt mandible with P_4-M_3, late middle wear. M_3 33.9×ca. 12.6.
- EP 3383/00, Loc. 15. Rt. mandible with P_{2-4}, M_{2-3}, middle wear. P_{2-4} 30.2, P_2 5.5×4.2, P_3 10.7×6.1, P_4 14.1×8.2, M_2 23.0×11.7, M_3 ca. 29.5×10.8.
- EP 720/01, Loc. 18. Rt M^2, middle wear, 28.0×20.5×18.8.

- EP 361/05, Loc. 15. Lt M_3, early middle wear, 35.6×12.8×ca. 35.0.
- EP 1111/05, Loc. 1. Rt M^2, early wear, 26.7×14.2×46.0.
- EP 1112/05, Loc. 1. Lt dP^4, early middle wear, 21.9×12.3×19.5.
- EP 1119/05, Silal Artum. Lt mandible with dP_4-M_1, early middle wear, dP_4 26.5×8.6.
- EP 1122/05, Silal Artum. Rt upper molar, middle wear, ca. 28.1×11.4×13.5.

Description

The mandible EP 3383/00 is the size of a modern *Connochaetes* and has occlusally simple molars and a P_4 with a larger rear lobe than in modern alcelaphines. The P_2 is notably small. The second of the two distal metapodials is sufficiently flattened to be a metacarpal, and both could belong to a *Connochaetes*. The remaining mandibular pieces and teeth in the above list are closer in size to inadequately estimated mean occlusal lengths of Olduvai *Connochaetes* than to *Megalotragus* but have not otherwise been identified.

Discussion

Connochaetes is only known from the late Pliocene onwards, and the above occurrences are insufficient to establish a record at Laetoli.

Parmularius ?altidens **Hopwood, 1934**

Parmularius altidens Hopwood 1934: 550. Olduvai Bed I.
Alcelaphini, medium sp. Gentry 1987: 400.

Material

- LAET 75-1654, Loc. 14. Lt horn core, index 43.3×33.3.
- LAET 75-1667, Loc. 14. Part of rt horn core, diameters at its basal end as preserved = 26.3×23.0.
- LAET 75-1709, Loc. 14. Lt horn core, index 44.8×37.1.
- LAET 78-4850, Loc. 18. Rt horn core, index 35.8×30.1.
- EP 1295/98, Loc. 22S. Lt horn core, 38.2×27.2.
- EP 1461/00, Loc. 7E. Frontlet with horn core, index 32.9×29.8.
- EP 2182/00 and EP 819/04, Loc. 7E. Rt horn core base, index 37.0×25.8, and distal part of same horn core.
- EP 3220/00, Loc. 18. Rt horn core, index 29.3×23.8. Rather small.
- EP 3385/00, Loc. 15. Rt horn core, index 39.5×28.3.
- EP 3386/00, Loc. 15. Rt horn core, index 38.6×30.1.
- EP 3389/00, Loc. 15. Lt horn core, index 35.2×28.1.
- EP 3390/00, Loc. 15. Lt horn core, index 36.1×29.2.
- EP 3955/00, Loc. 7E. Rt horn core, index 34.3×26.5.
- EP 819/04. See EP 2182/00 above.

Diagnosis

Parmularius altidens is perhaps a little smaller than extant *Alcelaphus buselaphus*. Slender and moderately long horn cores with somewhat limited divergence. The few horn cores low in Olduvai Gorge Bed I are backwardly curved, but in higher horizons the curvature gradually becomes more distal and then almost absent as the horn cores acquire a straighter profile. Concurrently, their inclination becomes more marked. Localized medial or posteromedial swellings at the horn core bases. Braincase short, its roof strongly sloped and bearing a central boss or protuberance on the parietal. (Shortened and modified from Gentry and Gentry 1978.)

Description

Quite a lot of horn cores can be placed here, showing a considerable range of size. Mostly they are smaller than *Parmularius altidens* at Olduvai. They are moderately long, with a central or posterior position of the level of maximum transverse thickness, without keels or transverse ridges, compressed at the base but less so distally, the lateral surface smoother than the medial and slightly flattened, the anteroposterior diameter thinning markedly shortly above the base, a tendency to a posteromedial basal swelling and to a sharp corner angle at the posterolateral base, divergence increasing slightly just above the base and then diminishing in degree distally, moderately inclined, straight or slightly curved backwards, insertions close together, and inserted above the back of the orbits. A smaller number of the fossils show a moderately large and moderately deep postcornual fossa, frontals between the horn bases raised above the level of the dorsal orbital rims, and cranial roof strongly inclined.

Many of these horn cores – for example, LAET 75-1654 and EP 1461/00 – look very like *Parmularius pandatus* (see Fig. 15.22), and the first three in the list were cited as such in Gentry (1987). They differ slightly in being shorter and smaller, with very little or no backwards curvature, divergence increasing very slightly in their distal part, anteroposterior diameter may become markedly smaller at a level shortly above the base, a tendency to a posteromedial basal swelling. The strong inclination of the cranial roof, visible in EP 3385/00, is different from *P. pandatus*.

The sample of alcelaphine teeth is smaller than in the Laetolil Beds. Many are about the size of *Parmularius pandatus*, but a smaller species is present in the Upper Ndolanya Beds alongside the *P. ?altidens*, and this reduces the reliability of any identifications. The teeth of EP 2145/00 from Loc. 13/14 (parts of associated upper and lower dentitions; lengths M^3 ca. 23.0, P_4 12.0, M_1 15.9, M_2 18.2) may be close to the minimum size possible for *P. ?altidens*.

Discussion

Parmularius altidens differs from *P. pandatus* in its less upright horn core insertions, posteromedial basal swellings on the horn cores, shorter braincase, and more localized boss on the braincase roof. The holotype skull (Leakey, 1965:

Fig. 15.22 Right horn core of *Parmularius ?altidens* LAET 78-4850 in anterior and medial views. Scale in mm

pl. 70) is almost certainly female and shows well the boss on the cranial roof after which the genus was named. The common alcelaphine of the Upper Ndolanya Beds looks as if it must be either a conspecific continuation from *Parmularius pandatus* or an early occurrence of *P. altidens*. Too little is known of it to be aware of any substantive difference from *P. altidens*. Rather than found a new species, it will be provisionally attributed to this species. *Parmularius altidens* is a species of the Late Pliocene. Away from Olduvai Gorge, it occurs in the KBS Mb. of the Koobi Fora Fm. and in Shungura Mbs G–H. The holotype horn core of *Redunca eulmensis* Arambourg (1979: pl. 44, fig. 4) from Aïn Boucherit also looks like a *P. altidens* as noted by Geraads (1981).

Parmularius parvicornis, sp. nov.

Alcelaphini, small sp. Gentry 1987: 400.
?Pelea sp. Gentry 1987: 402.

Holotype

EP 3372/00, Loc. 15. skull (Fig. 15.23); many other skeletal elements comprising atlas and cervical vertebrae, glenoid of scapula, proximal humerus, distal humerus, humeral shaft pieces, distal radius, proximal femur, distal femur, distal tibia, naviculocuboid, rib fragments. Teeth in middle wear. A second atlas of a large bovid has been included with the other material in EP 3372/00. Horn core index 18.7×16.3 (87%), minimum width across lateral sides of horn pedicels 52.4, width across dorsal orbital rims 86.7, length from level of back of horn pedicels to occiput 73.5, length from back of frontals to occiput 60.0, braincase width 73.0, skull width across external auditory meati 74.2, occipital height 24.5, width across anterior tuberosities of basioccipital 15.5, width across posterior tuberosities of basioccipital 24.8, occlusal length M^{1-3} ca. 49.5, occlusal lengths×widths: P^3 9.1×7.2, P^4 8.6×8.5, M^1 14.0×-, M^2 ca. 18.4×12.8, occlusal length M_{1-3} 50.8, occlusal lengths×widths: M_1 ca. 11.5×-, M_2 16.5×8.6, M_3 22.3×7.9, ramus depth below M_1 26.2, ramus depth below M_3 33.1.

Type Locality

Laetoli, Tanzania.

Horizon and Range

Upper Ndolanya Beds. The holotype comes from Loc. 15.

Name

The specific name comes from the Latin “parvus,” small, and “cornu,” horn.

Material

- LAET 75-1682, Loc. 14. Lt horn core with part of the frontal, index 15.6×13.0.
- LAET 75-2573, Loc. 15. Lt mandible with back P_4 – broken M_3, the last in early wear. M_1 14.8×ca. 8.4, M_2 17.8×7.6, M_3 ca. 7.5 high, ramus depth below the M_{2-3} transition 41.0.
- LAET 76-577, Loc. 18. Lt horn core, index 20.9×17.1.
- EP 860/00, Loc. 18. Lt mandible with M_{1-3}, middle wear. M_{1-3} 49.3, M_1 12.9×7.7, M_2 ca. 15.4 long, M_3 ca. 20.7×–×ca. 30.7.
- EP 3444/00, Loc. 15. Rt dP^4 in maxilla, 13.8×8.0×ca. 9.4.
- EP 4030/00, Loc. 15. Lt mandible piece with M_2, middle wear. Length M_2 14.3 mm.
- EP 4036/00, Loc. 15. Horn core, prob. rt, and with a wide orbital rim posterodorsally, index 17.1×15.9.
- EP 1022/01, Loc. 15. Lt mandible piece with dP_4-M_1, dP_4 in middle wear. dP_4 18.2×6.2, M_1 15.7×5.7, ramus depth below M_1 25.7.
- EP 1650/03, Loc. 15. Lt mandible piece with molar, early middle wear 17.6×6.7×ca. 27.5.
- EP 1663/03, Loc. 15. Lt lower molar, 16.0×7.8.
- EP 1123/05, Silal Artum. Rt M_2, early middle wear 15.7×5.7×ca. 29.0.
- EP 1124/05, Silal Artum. Lt mandible with molar, 14.7×7.5.

Diagnosis

A species smaller than extant *Damaliscus dorcas*. The moderately long horn cores are of low diameter, without keels or transverse ridges, a little less compressed mediolaterally than in *Parmularius pandatus*, with a flattened lateral surface, with only a hint of a posterolateral basal swelling, parallel or with little and little-changing divergence along their preserved length, inclined backwards, straight in side view, long axis of basal

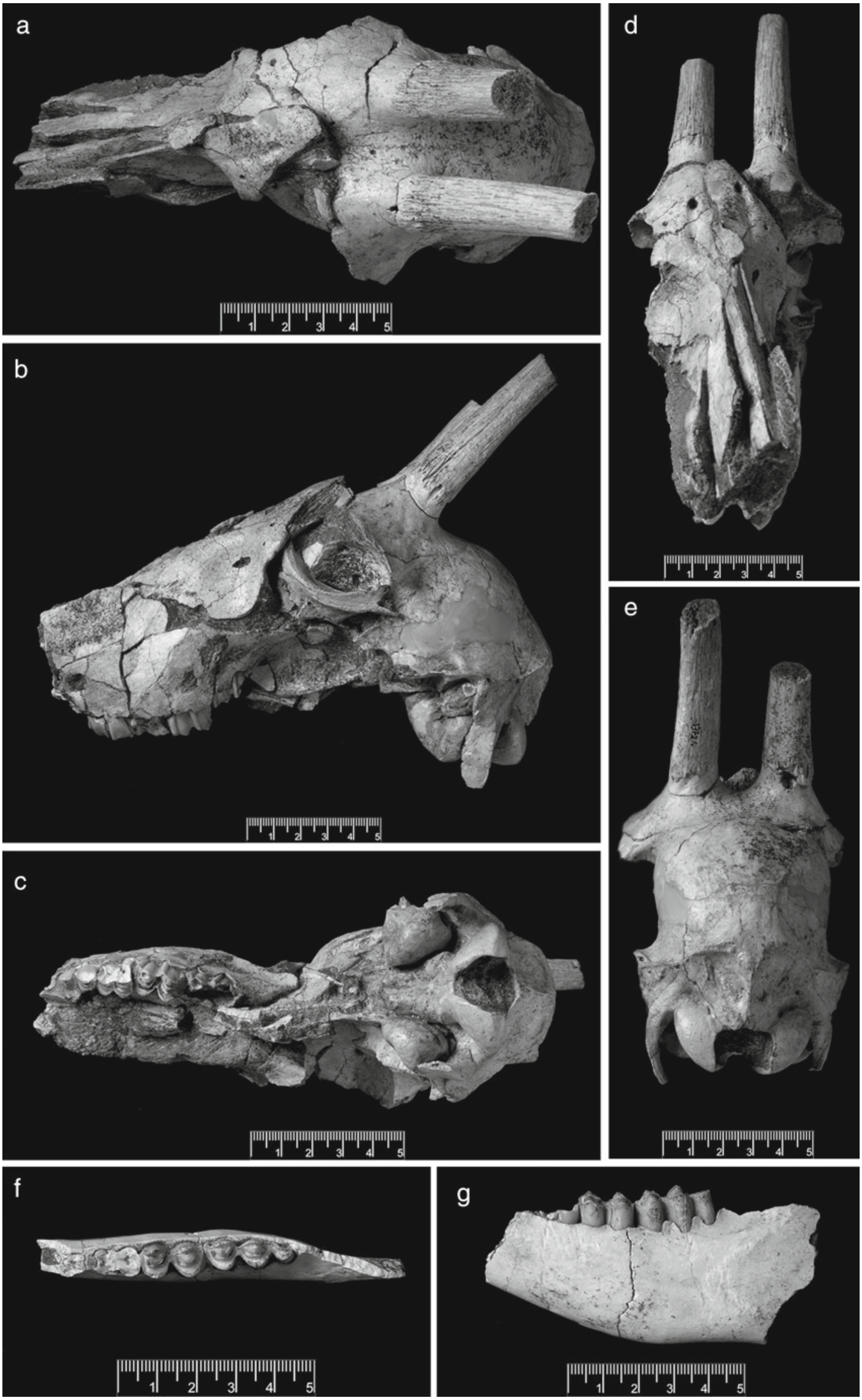

Fig. 15.23 Holotype skull of *Parmularius parvicornis* EP 3372/00 in (**a**) dorsal, (**b**) left lateral, (**c**) palatal, (**d**) anterior and (**e**) posterior views. Mandible in (**f**) occlusal and (**g**) lateral views. Scales in mm

cross-section at the usual slight angle to the midline of the skull, close together as is usual in *Parmularius*, and inserted above or just behind the back rim of the orbits. Horn core pedicels expanding rapidly downwards into the sloping orbital rims. The frontals and pedicels are well hollowed internally, and the frontals between the horn bases are at a level above that of the dorsal orbital rims. The mid-frontals suture is not very complicated. Very small supraorbital pits some distance in front of the horn bases and above the centre of the orbits, nasals long and narrow, ethmoidal fissures would have been narrow or absent, preorbital fossa moderately deep and extensive with an approach to a short upper rim, zygomatic arch not thickened anteriorly beneath the orbit, back of M^3 perhaps level with front rim of orbit, infraorbital foramen high above front edge of P^3. The braincase is little shortened for an alcelaphine, its roof only becomes markedly downturned in its posterior part, and there is no *Parmularius* protuberance on the roof. The temporal ridges approach closely posteriorly. The occipital surface is low, it has two halves each facing partly laterally, and the nuchal crests are concave upwards. The mastoids lie within the occipital, ventral to nuchal crests and widening as they descend. The basioccipital is quadrangular, without a transverse constriction centrally, the anterior tuberosities moderately strong, central longitudinal groove almost present between ridges behind the anterior tuberosities, large foramen ovale in front of level of anterior tuberosities, auditory bullae inflated posterior to the tympanohyal pit. Teeth hypsodont, without basal pillars, short premolar rows, P^2 absent, rounded lingual lobes of upper molars, lingual walls of lower molars with wide rounded ribs and labial walls bluntly pointed, mandible deep below molar row, rear third lobe of M_3s small.

Description

The latter part of the preceding diagnosis is largely an abbreviated description of the skull EP 3372/00 discovered by Chris Robinson and painstakingly prepared by Bill Sanders. It is slightly smaller than the holotypes of *Parmularius pandatus* in the Laetolil Beds or *Damaliscus agelaius* at Olduvai, and certainly smaller than the holotype skulls of *P. altidens* or *P. rugosus* at Olduvai. It is about the same size as or slightly larger than the holotype skulls of *Aepyceros shungurae* from Shungura B and *Antidorcas recki* from Olduvai. It would almost certainly have been bigger than the *Gazella* and *Antidorcas* species alongside it in the Upper Ndolanya Beds.

The small-diameter, straight, and little-divergent horn cores of EP 3372/00 must have been evolutionarily arrested at a stage little past that of a neotragine or have reverted to that condition. They are probably too gracile to match a female of *P. pandatus* or *P. altidens*, but the common *Parmularius* of the Upper Ndolanya Beds is probably a smaller species. As preserved, the horn cores are parallel in anterior view, but slight postmortem displacement of the base of the right horn core suggests that in life they might have diverged very slightly. The slope of the braincase roof is about the same as in *P. pandatus*, which is less than that seen in the Upper Ndolanya Beds horn core EP 3385/00 of *P. ?altidens*. Perhaps the horn core LAET 75-1682 (Fig. 15.24) is a female and EP 3372/00 a male. The frontals are well hollowed immediately anterior to the pedicels, and this hollowing almost certainly extends into the pedicels. The dorsal orbital rims show a long slope down from the high and close insertions of the relatively small horn cores, much as in the holotype skull of *P. altidens*. The braincase is more bulbous than in *Parmularius pandatus*, and this is presumably an allometric effect of the smaller size of EP 3372/00. No complete lower premolar row is known, but the absence of P^2 in EP 3372/00 is a striking specialization.

The Laetoli horn cores LAET 75-1682 and LAET 76-577 had been thought by Gentry (1987: 402) to be of the neotragine or reduncine *Pelea* because of their long, spikelike horn cores of small diameter and a long vertical postcornual fossa. However, they differ in having less uprightly inserted horn cores, a longer pedicel, and frontals between the horn bases almost certainly raised above the level of the dorsal orbital rims. They also have internal hollowing in the frontals and almost certainly in the pedicels, whereas any sinuses in *Pelea* can be only of very limited extent in the vicinity of the supraorbital pits if they exist at all. A left upper molar,

Fig. 15.24 Left horn core of *Parmularius parvicornis* LAET 75-1682 in lateral view. Scale in mm

LAET 75-889 from Loc. 7E, 17.6 × 6.8 × 8.7, was also attributed to "*Pelea* sp." in 1987 but must be of an antilopine.

LAET 75-2573 is an alcelaphine mandible with small teeth and a deep ramus, which becomes markedly shallow anteriorly. It goes well with the rest of the Loc. 15 material of this species. Mary Leakey collected from the Laetolil Beds at Loc. 15 and did not know of or collect from the Upper Ndolanya Beds a short distance away at the same locality. None the less, I take LAET 75-2573 as this species rather than postulate a not-very-common small alcelaphine in both the Ndolanya and Laetolil Beds. Associated partial upper and lower dentitions, EP 2145/00, come from a small alcelaphine. They are of uncertain provenance and possibly younger than the Ndolanya Beds given on the specimen label. They do not look fully fossilized, and neither are they from an extant species.

Discussion

The skull and teeth listed above appear to be of a small alcelaphine, certainly smaller than any species alive today in East Africa. Fossil remains of small alcelaphines have been noted many times at various East African localities. The Olduvai Bed I remains artificially grouped as "Alcelaphini species 4" include slender and curved horn cores (Gentry and Gentry, 1978: pl. 40, figs. 4 and 5) with a hollowed pedicel, as well as short mandibles with rami markedly deeper below the molars than further anteriorly. Similar small mandibles occur in the Shungura Fm. (Arambourg 1947: pl.30, figs. 3 and 3a - "*Antidorcas* sp."). Records from the Katwe Ashes (Gentry, 1990) and from Lukenya Hill and other sites (Marean 1992) indicate an end-Pleistocene extinction for at least one East African small alcelaphine. Very little is known of these antelopes, and not all specimens need be alcelaphine; for example, the illustrated horn cores of "Alcelaphini species 4." The most likely alternative would be membership of the Antilopini, a tribe with smaller-sized species than alcelaphines and in which *Antidorcas* and *Aepyceros* both have frontals with sinuses and smaller supraorbital pits than in *Gazella*, while *Antidorcas* also shows the alcelaphine-like features of frontals raised between the horn bases and shortened premolar rows.

The Laetoli skull EP 3372/00 now allows us to consider this small alcelaphine in more detail. Five questions about it are answered below.

1. It is an alcelaphine. It shows frontals raised between the horn bases and with sinuses, long and narrow nasals, a less pronounced maxillary tuberosity than in Antilopini, temporal ridges approaching closely posteriorly (similar to *Damaliscus* and other *Parmularius* but unlike *Antidorcas* and *Gazella*), a rectangular basioccipital with an approach to a central longitudinal groove, a deep mandible, very short premolar rows, a curved upper tooth arcade with P2s and M3s closer to their partners on the opposite side than are P4s or M1s, outbowed ribs between the styles of upper molars, rounded lingual lobes of upper molars, and similar rounded outlines on the lower molars. The rear lobe of M$_3$ is not enlarged. Not all these characters are advanced or unknown in Antilopini, but the combination of them suggests Alcelaphini. One character differs from other alcelaphines: the absence of thickening of the zygomatic arch beneath the orbit.
2. EP 3372/00 belongs to *Parmularius* not *Damaliscus*. The unanswered background problem is how to distinguish *Damaliscus* from *Parmularius* and to assign all the many named species in the genus. The problem is intensified because *Damaliscus* is still living, whereas *Parmularius* is extinct, but did acquire during its time span numbers of skull characters more advanced than in *Damaliscus*. It is also possible that the lineage of the *Damaliscus* type species, *D. dorcas* of South Africa, may be only one of several evolutions of *Damaliscus*-like antelopes. Concerning EP 3372/00, there is no boss on the roof of the parietal, which is unlike *Parmularius*, but neither is there the localized low swelling seen in many *Damaliscus*. The cranial roof is not shortened (Fig. 15.25) or strongly inclined, both of which make it like many *Damaliscus* and unlike later *Parmularius*. On the other hand, it does resemble the earlier *P. pandatus* in the longer braincase and the downward bend of the posterior part of its roof. The horn cores are not inserted as far back as in later *Parmularius*, but again this is not different from the more primitive condition of the earlier

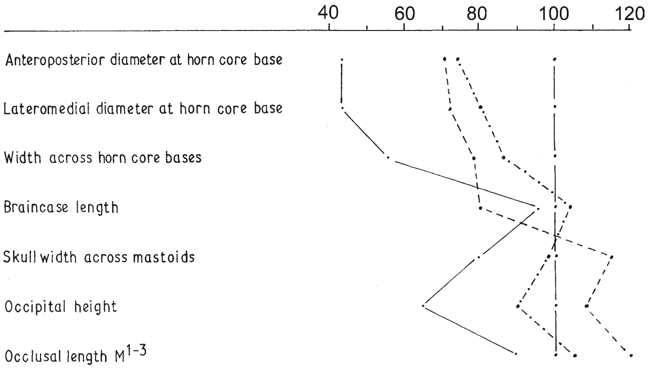

Fig. 15.25 Percentage diagram of some cranial measurements in four alcelaphine holotypes. The standard line at 100% is for *Parmularius pandatus* from the Laetolil Beds. The other continuous line is for *P. parvicornis* from the Ndolanya Beds, the dashed line for *P.altidens* from Olduvai Bed I, and the line with dots and dashes for *Damaliscus agelaius* from Olduvai Beds III-IV. "Width across horn bases" is the minimum distance across the lateral sides of the horn pedicels; "braincase length" is from the back of the frontals to the occipital top (estimated for *P.altidens*). *Parmularius pandatus* is probably male and *P. altidens* and *D. agelaius* probably female, so the *pandatus* readings (especially the *top* three) should be to the *left* for more realistic comparisons. *Parmularius parvicornis* is smaller than the other species and its braincase is proportionately very long – presumably a primitive character. *Parmularius altidens* is wide across the back of the skull and the teeth have enlarged, traits that might have become intensified in the *P. angusticornis* of Olduvai Bed II

P. pandatus. The horn core pedicels look long as in *Parmularius* and not short as in *Damaliscus*, but if the horn cores had been larger, the pedicels would probably have looked shorter. The preorbital fossa is larger than in later *Parmularius* and therefore resembles *Damaliscus agelaius*, but there is a suggestion on the maxilla surface that the fossa is becoming confined to only a small area immediately in front of the orbit as in *Parmularius*. The suggestion from all this is that EP 3372/00 could be a smaller-sized offshoot from an ancestor close to *P. pandatus*, and I am not ready to assert that it is likely to be congeneric with *D. dorcas*.

Damaliscus ademassui from Gamedah, already mentioned in comparison with *Parmularius pandatus*, is close in date to the Upper Ndolanya Beds. The holotype cranium is about the size of a large *D. dorcas* and suspected of being female. It is too large to fit EP 3372/00 and also differs by having larger and more compressed horn cores with a posterolateral edge or keel, quite strong transverse ridges on the anterior surface, and gentle backward curvature.

3. EP 3372/00 is not a female of the common *Parmularius* in the Ndolanya Beds. The latter is likely to be not as large as *P. pandatus* or *altidens*, but the horn cores of EP 3372/00 are still probably too small to fit a female individual. Furthermore, the strongly inclined cranial roof of EP 3385/00, an example of the other Ndolanya Beds *Parmularius*, is different from *P. parvicornis*.
4. EP 3372/00 is not *Parmularius parvus* Vrba 1978. *Parmularius parvus* was founded on associated right lower (P_3–M_3) and upper (P^4–M^3) tooth rows, KA 646A and B from Kromdraai A (Vrba 1978: pls. 2a, 5a and b). Vrba cited other dental and incomplete skull remains from other South African sites, and she also believed that skull 1963.068/5976 from upper Bed IV or the Masek Fm., Olduvai Gorge ("Alcelaphini sp. 1", Gentry and Gentry 1978: pl. 35, fig. 2), belonged to *P. parvus*. The Olduvai skull is about the size of *P. rugosus*, it agrees with that species in the narrow width across its supraorbital pits and in the short braincase with steep cranial roof, and it may now be best to accept it as in *P. rugosus*. Our Laetoli skull is definitely not of *P. rugosus* because of its smaller size, longer braincase with roof downturned posteriorly, anterior end of zygomatic arch not thickened below the orbit, and smaller teeth. Nor is it likely to be the Kromdraai *P. parvus* itself. EP 3372/00 differs by being slightly smaller (than *P. parvus* as well as than *P. rugosus*), the horn cores smaller and more widely separated across their medial sides than in the *P. parvus* skull of Vrba (1978: pl. 6), and the teeth having a less advanced occlusal pattern. The hypsodonty and posterior depth of the mandibular ramus may be less accentuated, but this is uncertain.
5. Resemblances between small alcelaphines and *Antidorcas* make it harder to sustain some of the differences of the tribes Antilopini and Alcelaphini. *Antidorcas bondi* (Cooke and Wells 1951) is a small and very hypsodont *Antidorcas* found at many Pleistocene sites of southern Africa north of the Cape zone and especially numerous at Swartkrans 2 (Vrba 1976) whence comes the only known cranial material. The teeth are so hypsodont that the lower edge of the mandible in almost mature individuals is incompletely ossified. Vrba (1978) noted that *Parmularius parvus* is associated with *A. bondi* at several localities. Furthermore, it resembles *A. bondi* in a high degree of hypsodonty, short premolar rows, and posteriorly deep mandibular ramus. All three characters are bound to be linked, insofar as a shortening of the premolar row allows shortening of the anterior part of the ramus and accentuates the abruptness of shallowing in front of the molars, and any concurrent increase in molar hypsodonty deepens the ramus posteriorly and augments the effect. So we have visually striking resemblances between mandibles in two different tribes. It is also characteristic of *A. bondi* to have lower molars with slight rounding of lingual lobes, and central fossettes slightly constricted transversely, much as in modern *Aepyceros melampus* but also giving the lower molars an alcelaphine aspect. However, *Antidorcas bondi* remains a convincing antilopine because of its shorter nasals, basioccipital like other *Antidorcas*, upper molars with strong styles and flat or concave labial walls of the metacones, and M_3s with an expanded third lobe. *Parmularius parvicornis* shares short premolar rows with *A. bondi*, but it is a larger species and it has less robust horn cores and no other resemblances. It could be an earlier relative of an alcelaphine with short and deep mandibles in the Shungura Fm. (Arambourg, 1947: pl. 30, fig. 3 - "*Antidorcas* sp.") and Olduvai Bed I (Gentry and Gentry 1978 - "Alcelaphini species 4"). However, an unassociated horn core tentatively placed in "Alcelaphini species 4" is definitely unlike *P. parvicornis*.

Gentry (1987) listed three alcelaphine species in the Upper Ndolanya Beds by tooth size. The allocations of individual teeth may well vary according to different investigators and on different occasions, but presumably the categories correspond to *Megalotragus* or *Connochaetes* (large), *Parmularius ?altidens* (medium sized), and *P. parvicornis* (small). Of course, the number of alcelaphine species inhabiting the Laetoli region during the deposition of the Upper Ndolanya Beds may not be limited to three.

A new note on Locality 14

Gentry (1987: 403) listed specimens he had identified from Loc. 14 in the belief that this was a locality in the Laetolil Beds. These specimens, all from the 1975 season (except LAET 75-462), were checked in July 2005 and the following revisions made (fourth column). About half of them have been mentioned above.

? Hippotragini sp. nov.	1700	horn core	*Aepyceros* sp.
? Hippotragini sp. nov. or *Praedamalis deturi*	1632	dP_4	Tragelaphini
"	1638	two upper molars	*Hippotragus* or *Oryx*
"	1655	mandible with P_4–M_2	*Hippotragus* or *Oryx*
"	1656	M^3	*Hippotragus* or *Oryx*
Parmularius pandatus	462	P^3	*?Aepyceros*
"	1631	lower molar	Alcelaphini
"	1654	horn core	*Parmularius ?altidens*
"	1667	horn core	*Parmularius ?altidens*
"	1669	upper molar	Alcelaphini
"	1701	M_{1-2}	Alcelaphini
"	1709	horn core	*Parmularius ?altidens*
Alcelaphini sp. indet.	1664	M_{2-3}	Alcelaphini
"	1672	cranial frags	No determination
Gazella janenschi	1649	horn core	*Gazella janenschi*
"	1663	upper molars	*Antidorcas* or *Gazella*
"	1694	upper molar	*Antidorcas* or *Gazella*

Conclusions

My successive interpretations of the Laetoli bovids have changed at each stage from the base supplied by Dietrich (1950). This is especially true of the present chapter, hence the quotation from Tolstoy's famous novel at its start. It also happens of course that the total fossil sample has increased over this time period, as has information on other East African faunas.

It is worth simply contemplating the bovid faunas contained in the Laetolil and Upper Ndolanya Beds. The Laetolil Beds have 17 or 18 bovid species, depending on whether *Gazella granti* is included. According to the classification used here, they come from at least seven tribes or tribal groupings, which entails a diverse assemblage. *Madoqua avifluminis* is overwhelmingly the most abundant species, but its tiny size marks it off from other bovids. Among these, a single species each of *Gazella*, *Hippotragus*, and *Parmularius* predominate. The aepycerotine and *Brabovus* are the next most common, while Tragelaphini, Bovini, and Cephalophini are rare, although the presence of any cephalophine in a fossil fauna is notable. Reduncini are very rare or absent, and it is unusual for any shortfall in their numbers to be so total. There are no long-horned reduncines more or less resembling modern lechwes or waterbuck (even if unrelated to them), no kob-like species, no *Menelikia*, nor any reedbuck-like species. This could be related to the absence of permanent bodies of water.

This is a bovid fauna substantially different from the well-known and later Plio-Pleistocene faunas in Olduvai and in the Koobi Fora and Shungura Fms. Presumably it is a more developed stage of early Pliocene faunas. The rare tragelaphine has not been identified; one could expect it to be *Tragelaphus kyaloae*, but Laetoli has a good record for yielding surprises. One of the bovines is *Simatherium kohllarseni* without a lot of resemblance to Pliocene *Ugandax* or to Plio-Pleistocene *Syncerus*. It is not certain that the cranium LAET 75-3064 is conspecific, and there is a probable additional and smaller bovine. Perhaps the most interesting of the Laetolil Beds species is *Brabovus nanincisus* with its uncertain tribal affiliation, distinctive incisors, and frontal sinuses. The definite cephalophine belongs to quite a large species. *Aepyceros dietrichi* is another species long gone and not close to modern *A. melampus*, yet specialized in both its horn cores and teeth. Probably *Aepyceros* is a genus of spiral-horned antilopines, and possibly it has a connection, via Sahabi *Dytikodorcas libycus*, back to the Turolian spiral-horned antilopines of Southeast Europe and Southwest Asia. *Gazella janenschi* has few differences in its horn cores and teeth from the Late Miocene gazelles of Eurasia. This makes it unlike later gazelles in Africa but quite plausible as an ancestor. The *Hippotragus* sp. is an abundant species, a position never occupied by the *Hippotragus* species in later faunas. A rarer *Oryx* is also present, but with less inclined horn cores than in modern species. Both hippotragines could be appropriate ancestors for later members of their tribe. *Parmularius pandatus* is well suited to be an early member of its genus, perhaps ancestral to the Olduvai Bed I *P. altidens* and near the base of the extensive radiation of later *Parmularius* and *Damaliscus*. A poorly known larger alcelaphine may be conspecific with or related to an alcelaphine in the Hadar Fm., which is larger than *Parmularius pandatus* and not congeneric with it. Such a species could pre-date the appearance of *Megalotragus* or *Connochaetes*.

The Upper Ndolanya Beds have many fewer specimens than the Laetolil Beds but attain a minimum of 17 species (again excluding *Gazella granti*), many of them given only qualified identifications. One or two look larger and more recent than I would have expected and almost as if they are close or identical to those of Olduvai Beds I and II. Nevertheless, uncertainty prevails. The lost Leakey Collection cranium of *Tragelaphus* sp. cf. *T. buxtoni* looks like a primitive larger species surviving from a time before the appearance of kudus. Some bovine limb bones equal or exceed the size of those of *Pelorovis oldowayensis* in Olduvai Bed II, and perhaps *Simatherium* had attained this size level at this earlier date. There is evidence of an *Aepyceros* larger than *A. shungurae* that had already appeared elsewhere at around 3.0 Ma. If descent of *A. melampus* from *A. shungurae* or a similar species is to be believed, it would be better to take the Ndolanya representative as surviving *A. dietrichi* and to hope for more complete fossils in the future. A slightly changed *Gazella janenschi* survives into the Upper Ndolanya Beds, but *Gazella* sp. and *Antidorcas* are new arrivals, the latter one of the earlier reliable records of the genus in Africa. A slightly changed *Madoqua* is still common, but not in such overwhelming numbers as in the Laetolil Beds. Reduncini have changed their status from rare or absent to rare. There has been a decline in numbers of Hippotragini since the Laetolil Beds. *Hippotragus* sp. aff. *cookei?* is a little advanced on *Hippotragus* sp. but perhaps remains smaller than *H. cookei* at later localities. More material from the Ndolanya Beds and of *H. cookei* in South Africa is needed to ascertain the position. *Megalotragus* has appeared and, like the Ndolanya bovine, is as large as in Olduvai Beds II and III. A possible or probable *Connochaetes* has appeared. The most common alcelaphine is a *Parmularius* changed from *P. pandatus* and seemingly close to *P. altidens* of Olduvai Bed I, but it was passing through a dip in size in the interval between these two species. Apart from the tiny *Madoqua*, the commonest Ndolanya bovids may be *Antidorcas recki* and *Parmularius ?altidens*. No species in the Upper Ndolanya Beds can be seen as unchanged from the Laetolil Beds. The *Aepyceros* is the most likely not to have changed, but we have only a few very incomplete horn core pieces. Some other species are too poorly represented to know if they have changed or not: the *Tragelaphus*, two Bovini, a cephalophine, and a possible *Raphicerus*. The *Antidorcas*, one of the *Gazella* species, the *Megalotragus* (plus *Connochaetes* if it is there), and *Parmularius parvicornis* are all new. The Laetolil Beds species *Brabovus nanincisus* and "*Gazella*" *kohllarseni* are no longer present.

There appears to be a lack of overlap between bovid species of the Upper Ndolanya Beds and those of Shungura C to E at about the same geological age, and this constitutes a major ecological distinction. The two localities are a good way apart geographically, but not an incredibly long distance. The lack of precise identities for so many of the Ndolanya Beds bovids may be masking some similarities. There are 12 "sp." designations out of 17 listed species in the Upper Ndolanya Beds (compared with only six out of 17 in the Laetolil Beds). Nevertheless the commoner species in the Shungura Fm. are *Tragelaphus nakuae*, the early kudu *T. gaudryi*, two or three *Kobus* species, one *Menelikia* species probably replacing another, and a smaller *Aepyceros* than *A. dietrichi*. There are almost no Hippotragini or Alcelaphini. None of the species can be identified as such in the Upper Ndolanya Beds, they may all be absent, and the tribal proportions are very different from in the Upper Ndolanya Beds. Neither the Laetolil nor the Upper Ndolanya Beds contain any Caprinae, such as were found in the Awash localities further north again from the Shungura Fm. (e.g., Vrba 1997).

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Appendix

A catalogue of identified cranio-dental specimens of bovids from Laetoli and other localities on the Eyasi Plateau collected from 1998–2005, arranged by locality and alphabetical order of taxon.

Alan W. Gentry and Denise F. Su.

A. Upper Laetolil Beds

U = upper, L = lower, d = deciduous, M = molar, P = premolar, MAND = mandible, MAX = maxilla, HC = horn core

Locality 1

Specimen #	Side	Element	Tribe	Genus	Species
EP 1402/00	R	Udp4	Antilopini	*Aepyceros*	*dietrichi*
EP 1404/00	R	Udp3	Antilopini	*Aepyceros*	*dietrichi*
EP 177/00	R	UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 182/00	L	UP4	Antilopini	*Aepyceros*	*dietrichi*
EP 1855/03	R	UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 1858/03	R	UP4	Antilopini	*Aepyceros*	*dietrichi*
EP 481/04	R	UP4	Antilopini	*Aepyceros*	*dietrichi*
EP 173/00	R	UM1 or UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 1410/00	R	HC fragment	Alcelaphini	*Parmularius*	*pandatus*
EP 1411/00	L	HC fragment	Alcelaphini	*Parmularius*	*pandatus*

(continued)

Locality 1 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 178/00	L	UM	Alcelaphini		
EP 2960/00	L	MAND fragment (probably M2)	Alcelaphini		
EP 2961/00	R	UM	Alcelaphini		
EP 2962/00	L	UM	Alcelaphini		
EP 2971/00	R	UP3	Alcelaphini		
EP 1105/01	L	UM1	Alcelaphini		
EP 1848/03	L	UM	Alcelaphini		
EP 1856/03	L	UM	Alcelaphini		
EP 1400/00	R	MAND fragment (M1-M2)	Antilopini	*Gazella*	*janenschi*
EP 1114/01		LP4 fragment	Antilopini	*Gazella*	*janenschi*
EP 482/04	L	MAND fragment (P4)	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1438/00	L	UM fragment	Bovini		
EP 3027/00	L	UM2	Bovini		
EP 3029/00		HC fragment	Bovini		
EP 179/00	R	UM fragment	Indet.	*Brabovus*	*nanincisus*
EP 1857/03	L	UM	Indet.	*Brabovus*	*nanincisus*
EP 2963/00	R	MAX fragment (M1-M2)	Hippotragini	*Hippotragus*	
EP 1912/03	R	HC	Hippotragini	*Hippotragus*	
EP 171/00	L	UM3	Hippotragini		
EP 172/00	R	MAND fragment (M3)	Hippotragini		
EP 175/00	R	UM	Hippotragini		
EP 180/00	L	Udp3	Hippotragini		
EP 181/00	R	Udp3	Hippotragini		
EP 1403/00	L	UP3	Hippotragini		
EP 1106/01	L	UM2	Hippotragini		
EP 1108/01	R	LM	Hippotragini		
EP 474/04	R	MAX fragment (M3)	Hippotragini		
EP 1067/05	R	MAX fragment (M)	Hippotragini		
EP 1068/05	L	UM	Hippotragini		
EP 185/00		MAND (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 186/00		MAND (dp4-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 187/00		MAND (P4-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 188/00		MAND (P3-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 189/00		MAND fragment (dp3-dp4)	Neotragini	*Madoqua*	*avifluminis*
EP 190/00		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 191/00		MAND fragment (P2-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 192/00		MAND fragment (P3)	Neotragini	*Madoqua*	*avifluminis*
EP 193/00		MAX fragment (P3-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 194/00		UM1	Neotragini	*Madoqua*	*avifluminis*
EP 195/00		MAX fragment (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 196/00		MAX fragment (P4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 1407/00		UM3	Neotragini	*Madoqua*	*avifluminis*
EP 2964/00		MAND (M)	Neotragini	*Madoqua*	*avifluminis*
EP 2965/00		UP3	Neotragini	*Madoqua*	*avifluminis*
EP 2966/00		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 2967/00		MAND fragment (dp4)	Neotragini	*Madoqua*	*avifluminis*
EP 2968/00		MAND fragment (P4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 2969/00		MAND fragment (P4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 2970/00		MAND fragment (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 2972/00		UM	Neotragini	*Madoqua*	*avifluminis*
EP 2973/00		HC + cranial fragment	Neotragini	*Madoqua*	*avifluminis*
EP 2974/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 1111/01		MAX fragment (dp2-dp3)	Neotragini	*Madoqua*	*avifluminis*
EP 1112/01		UP4	Neotragini	*Madoqua*	*avifluminis*
EP 1113/01		UP2	Neotragini	*Madoqua*	*avifluminis*
EP 1115/01		MAND (P4-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1116/01		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1849/03		MAND fragment (P2-P3)	Neotragini	*Madoqua*	*avifluminis*

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Locality 1 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 1854/03		MAND (P3-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1859/03		MAND (P4-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1860/03		MAND (P2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1861/03		MAND fragment (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1862/03		MAND fragment (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1863/03		UP3	Neotragini	*Madoqua*	*avifluminis*
EP 1864/03		UP3	Neotragini	*Madoqua*	*avifluminis*
EP 1865/03		MAND (M)	Neotragini	*Madoqua*	*avifluminis*
EP 475/04		MAND fragment (M1- M2)	Neotragini	*Madoqua*	*avifluminis*
EP 476/04		MAX fragment (M)	Neotragini	*Madoqua*	*avifluminis*
EP 477/04		MAX fragment (P)	Neotragini	*Madoqua*	*avifluminis*
EP 478/04		UP	Neotragini	*Madoqua*	*avifluminis*
EP 479/04		UP	Neotragini	*Madoqua*	*avifluminis*
EP 480/04		Udp3	Neotragini	*Madoqua*	*avifluminis*
EP 475/04		MAND fragment (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 476/04		MAX fragment (M)	Neotragini	*Madoqua*	*avifluminis*
EP 477/04		MAX fragment (P)	Neotragini	*Madoqua*	*avifluminis*
EP 478/04		UP	Neotragini	*Madoqua*	*avifluminis*
EP 479/04		UP	Neotragini	*Madoqua*	*avifluminis*
EP 480/04		Udp3	Neotragini	*Madoqua*	*avifluminis*
EP 1069/05		MAND fragment (dp2-dp4)	Neotragini	*Madoqua*	*avifluminis*
EP 1070/05		MAND fragment (P4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 1071/05		MAND fragment (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1073/05		MAND fragment (M)	Neotragini	*Madoqua*	*avifluminis*

*Associated material

Laetoli Locality 1NW

Specimen #	Side	Element	Tribe	Genus	Species
EP 2473/03	R	LM1-M3	Antilopini	*Aepyceros*	*dietrichi*
EP 2475/03	L	UM	Antilopini	*Aepyceros*	*dietrichi*
EP 2476/03	L	LM3 fragment	Antilopini	*Gazella*	*janenschi*
EP 2474/03	R	UM3	Hippotragini		
EP 2480/03	L	UP3	Hippotragini		
EP 2479/03		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*

Laetoli Locality 2

Specimen #	Side	Element	Tribe	Genus	Species
EP 627/00	L	UP	Antilopini	*Aepyceros*	*dietrichi*
EP 607/00	L	UM2	Antilopini	*Aepyceros*	*dietrichi*
EP 1808/00	R	MAX fragment (dp3-dp4)	Antilopini	*Aepyceros*	*dietrichi*
EP 1812/00	R	LM1-M2	Antilopini	*Aepyceros*	*dietrichi*
EP 1813/00	L	LP4	Antilopini	*Aepyceros*	*dietrichi*
EP 2603/00	L	MAX fragment (M2-M3)	Antilopini	*Aepyceros*	*dietrichi*
EP 2614/00	R	LP4	Antilopini	*Aepyceros*	*dietrichi*
EP 4189/00	R	UM2	Antilopini	*Aepyceros*	*dietrichi*
EP 355/01	L	UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 629/03	R	HC	Antilopini	*Aepyceros*	*dietrichi*
EP 1721/00	L	UP2	Antilopini	*Aepyceros*	*dietrichi*
EP 1727/00	L	MAND fragment (M)	Antilopini	*Aepyceros*	*dietrichi*
EP 1728/00	L	MAX fragment (P3-P4)	Alcelaphini	*Aepyceros*	*dietrichi*
EP 541/03	R	UM	Antilopini	*Aepyceros*	*dietrichi*

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Laetoli Locality 2 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 544/03	R	UM	Antilopini	*Aepyceros*	*dietrichi*
EP 548/03	R	UP3	Antilopini	*Aepyceros*	*dietrichi*
EP 709/03	L	MAX fragment (P4-M1)	?Alcelaphini		
EP 2608/00	R	LM2	Alcelaphini		
EP 2610/00	R	LM1	Alcelaphini		
EP 605/00	R	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 608/00	L	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 609/00	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 610/00	L	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 611/00	L	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 613/00	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 621/00	L	LM3	Alcelaphini	*Parmularius*	*pandatus*
EP 625/00	L	LM1	Alcelaphini	*Parmularius*	*pandatus*
EP 635/00	R	HC	Alcelaphini	*Parmularius*	*pandatus*
EP 421/04	R	HC fragment	Alcelaphini	*Parmularius*	*pandatus*
EP 614/00	L	UM3	Alcelaphini	*Parmularius*	small sp.
EP 1014/05	R	MAND fragment (P3-M3)	Alcelaphini	*Parmularius*	*pandatus*
EP 1800/00	L	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 1801/00	L	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 1802/00	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 1803/00*	R	MAX (P2-M2)	Alcelaphini	*Parmularius*	*pandatus*
	L	MAX (M2)			
EP 1810/00	L	MAND fragment (M3 fragment)	Alcelaphini	*Parmularius*	*pandatus*
EP 1814/00	R	LM3	Alcelaphini	*Parmularius*	*pandatus*
EP 2597/00	L	HC	Alcelaphini	*Parmularius*	*pandatus*
EP 2600/00	L	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 2605/00	R	LM3	Alcelaphini	*Parmularius*	*pandatus*
EP 2617/00	L	LP4	Alcelaphini	*Parmularius*	*pandatus*
EP 4190/00	L	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 4199/00	R	MAND (P4-M1)	Alcelaphini	*Parmularius*	*pandatus*
EP 4200/00	L	LM3	Alcelaphini	*Parmularius*	*pandatus*
EP 1724/00	L	LM3 fragment	Alcelaphini	*Parmularius*	*pandatus*
EP 612/00	L	UM	Alcelaphini		
EP 615/00	L	LM fragment	Alcelaphini		
EP 617/00	L	LM	Alcelaphini		
EP 622/00	R	LM3	Alcelaphini		
EP 623/00	R	LM3	Alcelaphini		
EP 626/00	R	LM	Alcelaphini		
EP 634/00	L	Ldp4	Alcelaphini		
EP 425/04	R	UM	Alcelaphini		
EP 426/04	L	LM	Alcelaphini		
EP 1673/04	R	MAND fragment (M2- M3)	Alcelaphini		
EP 1674/04	R	MAND fragment (M1- M2)	Alcelaphini		
EP 1676/04	R	UP4	Alcelaphini		
EP 1804/00	R	UM3	Alcelaphini		
EP 1806/00	L	UM3	Alcelaphini		
EP 1818/00	R	MAND (M)	Alcelaphini		
EP 2602/00	L	UM3	Alcelaphini		
EP 2604/00	R	UM1	Alcelaphini		
EP 2606/00	R	LM	Alcelaphini		
EP 2607/00	L	MAND fragment (dp4)	Alcelaphini		
EP 2615/00	R	LP4	Alcelaphini		
EP 4188/00	L	UdP4-M1	Alcelaphini		
EP 4194/00	L	Udp3	Alcelaphini		
EP 351/01	R	UM (probably M2)	Alcelaphini		Larger sp.
EP 353/01	L	UM	Alcelaphini		
EP 620/03	R	UM3	Alcelaphini		

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Laetoli Locality 2 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 717/03	R	UM3	Alcelaphini		
EP 718/03	R	UP4	Alcelaphini		
EP 352/01	R	UM (probably M2)	Alcelaphini		Larger sp.
EP 354/01	L	UM1	Alcelaphini		Small sp.?
EP 1012/05	R	LP4	Alcelaphini		
EP 1725/00	R	MAND fragment (P4-M1)	Alcelaphini		
EP 1731/00	R	UM	Alcelaphini		
EP 539/03	L	UM	Alcelaphini		
EP 540/03	L	UM1	Alcelaphini		
EP 550/03	R	UP4	Alcelaphini		
EP 922/05	L	MAND fragment (M2- M3)	Alcelaphini		
EP 923/05	L	MAX fragment (M2-M3)	Alcelaphini		
EP 924/05	L	UM3	Alcelaphini		
EP 929/05	R	LP4	Alcelaphini		
EP 427/04	R	UM fragment	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 616/00	R	UM1	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 633/00	L	UM3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1805/00	L	UM3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 2598/00	R	HC base	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 2616/00	L	MAND fragment (dP2- dP4)	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 2618/00	R	LP3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 546/03	R	MAND fragment (P4-M2)	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 4192/00	R	UM1	Antilopini		
EP 744/00	R	UM3	Antilopini	*Gazella*	*janenschi*
EP 746/00	R	LP4	Antilopini	*Gazella*	*janenschi*
EP 422/04	L	MAND fragment (M2- M3)	Antilopini	*Gazella*	*janenschi*
EP 423/04		MAND fragment (M2)	Antilopini	*Gazella*	*janenschi*
EP 1807/00	R	UM3	Antilopini	*Gazella*	*janenschi*
EP 2611/00	R	MAND fragment (M3 fragment)	Antilopini	*Gazella*	*janenschi*
EP 2612/00	R	MAND (P4-M3)	Antilopini	*Gazella*	*janenschi*
EP 2613/00	R	MAX fragment (M2-M3)	Antilopini	*Gazella*	*janenschi*
EP 4193/00	L	UM1	Antilopini	*Gazella*	*janenschi*
EP 4197/00	R	MAND (P4-M1)	Antilopini	*Gazella*	*janenschi*
EP 4198/00	R	MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 359/01	R	MAND fragment (M1- M2)	Antilopini	*Gazella*	*janenschi*
EP 1722/00	R	UM	Antilopini	*Gazella*	
EP 1730/00	R	MAND fragment (dp4)	Antilopini	*Gazella*	*janenschi*
EP 1754/00	L	HC	Antilopini	*Gazella*	*janenschi*
EP 320/01	R	UM1	Antilopini	*Gazella*	*janenschi*
EP 324/01		HC fragment	Antilopini	*Gazella*	*janenschi*
EP 496/01	R	MAND (M2-M3)	Antilopini	*Gazella*	*janenschi*
EP 498/01		HC fragment	Antilopini	*Gazella*	*janenschi*
EP 547/03	L	UM	Antilopini	*Gazella*	*janenschi*
EP 743/00	L	UM1	Bovini	*Simatherium*	*kohllarseni*
EP 4202/00		HC fragment	Bovini		
EP 1718/00	R	UM3	Cephalophini		
EP 545/03	L	LM	Cephalophini		
EP 1799/00	R	MAX (dp3-dp4)	Hippotragini	*Hippotragus*	
EP 1819/00		HC	Hippotragini	*Hippotragus*	
EP 4251/00	L	HC + assoc. cranial frags (23)	Hippotragini	*Hippotragus*	
EP 4254/00	R	MAX (P3-M3, P2 roots)	Hippotragini	*Hippotragus*	
EP 1066/05	R + L	Frontlet (HCs	Hippotragini	*Hippotragus*	
EP 564/03	L	HC	Hippotragini	*Hippotragus*	
EP 565/03		HC	Hippotragini	*Oryx*	*deturi*
EP 630/00	L	LP2	?Hippotragini		
EP 602/00	L	UM3	Hippotragini		
EP 603/00	L	UM2	Hippotragini		
EP 606/00	R	UM	Hippotragini		

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Laetoli Locality 2 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 618/00	L	LM2	Hippotragini		
EP 619/00	R	LM1	Hippotragini		
EP 620/00	R	LM3 fragment	Hippotragini		
EP 624/00	L	LM1	Hippotragini		
EP 628/00	R	LP4	Hippotragini		
EP 629/00	R	UP	Hippotragini		
EP 1615/04	R	MAND fragment (M3)	Hippotragini		
EP 1677/04	L	MAX fragment (UM)	Hippotragini		
EP 1809/00	R	MAND fragment (M3)	Hippotragini		
EP 1815/00	R	LM	Hippotragini		
EP 1816/00	R	LP4	Hippotragini		
EP 2599/00	L	UM2	Hippotragini		
EP 2601/00	R	UM	Hippotragini		
EP 2621/00	L	UP4	Hippotragini		
EP 4191/00	L	UM1	Hippotragini		
EP 4201/00	R	LM3 fragment	Hippotragini		
EP 356/01	L	LM3	Hippotragini		
EP 358/01	L	UP	Hippotragini		
EP 621/03	L	MAND fragment (P4)	Hippotragini		
EP 1066/05	R + L	HCs + Frontlet	Hippotragini		
EP 1717/00	L	UM2 fragment	Hippotragini		
EP 1719/00	R	LM fragment	Hippotragini		
EP 1720/00	L	UM	Hippotragini		
EP 319/01	R	UM2	Hippotragini		
EP 321/01	L	MAND fragment (M1)	Hippotragini		
EP 322/01	L	UP2	Hippotragini		
EP 542/03	L	UM	Hippotragini		
EP 543/03	L	UM	Hippotragini		
EP 549/03	L	UP3	Hippotragini		
EP 1716/00	R	UM2 or M3	Indet.	*Brabovus*	*nanincisus*
EP 933/05	L	UM	Indet.	*Brabovus*	*nanincisus*
EP 935/05	L	UM	Neotragini	*?Raphicerus*	*sp.*
EP 636/00		MAND (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 637/00		MAND (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 638/00		MAND (P2-P3)	Neotragini	*Madoqua*	*avifluminis*
EP 639/00		MAX (P4)	Neotragini	*Madoqua*	*avifluminis*
EP 424/04		MAND fragment (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1678/04		MAND fragment (P4)	Neotragini	*Madoqua*	*avifluminis*
EP 1679/04		MAND fragment (P4)	Neotragini	*Madoqua*	*avifluminis*
EP 1680/04		MAX fragment (M)	Neotragini	*Madoqua*	*avifluminis*
EP 1681/04		UM	Neotragini	*Madoqua*	*avifluminis*
EP 1690/04		HC fragment	Neotragini	*Madoqua*	*avifluminis*
EP 424/04		MAND fragment (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1820/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 1821/00		MAND fragment (dp4- M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1822/00		MAND fragment (M1 + M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1823/00		LM fragment	Neotragini	*Madoqua*	*avifluminis*
EP 1824/00		LM1	Neotragini	*Madoqua*	*avifluminis*
EP 1825/00		MAX (P2-P3)	Neotragini	*Madoqua*	*avifluminis*
EP 2619/00		LP4	Neotragini	*Madoqua*	*avifluminis*
EP 2620/00		dp4	Neotragini	*Madoqua*	*avifluminis*
EP 2623/00		UM	Neotragini	*Madoqua*	*avifluminis*
EP 360/01		UM	Neotragini	*Madoqua*	*avifluminis*
EP 361/01		MAND fragment (M)	Neotragini	*Madoqua*	*avifluminis*
EP 1016/05		HC	Neotragini	*Madoqua*	*avifluminis*
EP 622/03		HC fragment	Neotragini	*Madoqua*	*avifluminis*
EP 1733/00		MAX fragment (M1-M3)	Neotragini	*Madoqua*	*avifluminis*

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Laetoli Locality 2 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 1734/00		MAX fragment (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1735/00		MAX fragment (M1 or M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1736/00		MAX fragment (P3-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 1737/00		UM2, UM3 (2)	Neotragini	*Madoqua*	*avifluminis*
EP 1738/00		LM1 or LM2	Neotragini	*Madoqua*	*avifluminis*
EP 1739/00		MAND fragment (P4)	Neotragini	*Madoqua*	*avifluminis*
EP 1740/00		UP2, UP4 (2)	Neotragini	*Madoqua*	*avifluminis*
EP 325/01		MAND fragment (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 326/01		LM3	Neotragini	*Madoqua*	*avifluminis*
EP 551/03		MAX fragment (P2-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 552/03		MAND fragment (M1- M2)	Neotragini	*Madoqua*	*avifluminis*
EP 710/03		HC	Neotragini	*Madoqua*	*avifluminis*
EP 936/05		UM3	Neotragini	*Madoqua*	*avifluminis*
EP 937/05		UM	Neotragini	*Madoqua*	*avifluminis*
EP 938/05		UM3	Neotragini	*Madoqua*	*avifluminis*
EP 939/05		UP	Neotragini	*Madoqua*	*avifluminis*
EP 940/05		UM	Neotragini	*Madoqua*	*avifluminis*
EP 941/05		LM	Neotragini	*Madoqua*	*avifluminis*
EP 942/05		UM	Neotragini	*Madoqua*	*avifluminis*

[a] Associated material

Laetoli Locality 3

Specimen #	Side	Element	Tribe	Genus	Species
EP 1562/00	R	LP4	Antilopini	*Aepyceros*	*dietrichi*
EP 1564/00	L	UP4	Antilopini	*Aepyceros*	*dietrichi*
EP 309/03	R	UM fragment	Antilopini	*Aepyceros*	*dietrichi*
EP 1554/00	L	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 1559/00	R	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 2723/00	L	LM3 fragment	Alcelaphini	*Parmularius*	*pandatus*
EP 312/01	L	MAND (P4-M2)	Alcelaphini	*Parmularius*	*pandatus*
EP 308/03	R	UM1	Alcelaphini		
EP 310/03	R	LM	Alcelaphini		
EP 647/04	R	MAND (P4-M3)	Alcelaphini		
EP 704/05	L	LM	Alcelaphini		
EP 672/04	R	UP4	Alcelaphini		
EP 199/01	R	UM2	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 200/01	R	LP4	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 311/03	L	LP3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1556/00	L	UM3	Antilopini	*Gazella*	*janenschi*
EP 1557/00	R	UM1	Antilopini	*Gazella*	*janenschi*
EP 1561/00	R	LM3	Antilopini	*Gazella*	*janenschi*
EP 443/03	L	MAND (M1-M2)	Antilopini	*Gazella*	*janenschi*
EP 444/03	R	UM	Antilopini	*Gazella*	*janenschi*
EP 711/05*	L R	MAND (P4-M3)MAND (P2-P3)	Antilopini	*Gazella*	*janenschi*
EP 1560/00	R	MAND fragment (M1)	Cephalophini		
EP 741/05	L	LP3 or 4	Cephalophini		
EP 1555/00	R	MAX (M1)	Indet.	*Brabovus*	*nanincisus*
EP 1565/00	L	LP2	Indet.	*Brabovus*	*nanincisus*
EP 642/04	R	MAND fragment (M1-M3)	Indet.	*Brabovus*	*nanincisus*
EP 740/05	L	LP4	Indet.	*Brabovus*	*nanincisus*
EP 442/03	L	MAX (M1)	?Hippotragini		

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Laetoli Locality 3 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 1572/00	R	HC	Hippotragini	*Hippotragus*	
EP 1553/00	R	UM1 or UM2	Hippotragini		
EP 1563/00	L	LM3	Hippotragini		
EP 2236/03	R	UM	Hippotragini		
EP 2721/00	L	UM	Hippotragini		
EP 2722/00	L	LM1	Hippotragini		
EP 493/03	L	UM	Hippotragini		
EP 1566/00		MAND (P4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 1567/00		MAND (M1)	Neotragini	*Madoqua*	*avifluminis*
EP 1568/00		Associated UM1 + UM2	Neotragini	*Madoqua*	*avifluminis*
EP 1569/00		UM	Neotragini	*Madoqua*	*avifluminis*
EP 1570/00		Associated HC + Skull fragment	Neotragini	*Madoqua*	*avifluminis*
EP 1571/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 2735/00		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 305/01		MAND fragment (dp3-dp4)	Neotragini	*Madoqua*	*avifluminis*
EP 445/03		HC	Neotragini	*Madoqua*	*avifluminis*
EP 639/04*	R	MAX fragment (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
	L	MAX fragment (P2-M1)			
EP 640/04		MAND fragment (P2-P3)	Neotragini	*Madoqua*	*avifluminis*
EP 641/04		MAND fragments (P3-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 705/05		UM	Neotragini	*Madoqua*	*avifluminis*
EP 706/05		LP	Neotragini	*Madoqua*	*avifluminis*
EP 494/03	R	UP2	Tragelaphini	*Tragelaphus*	

*Associated material

Laetoli Locality 4

Specimen #	Side	Element	Tribe	Genus	Species
EP 168/03	L	UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 1641/04	R	UM fragment	Antilopini	*Aepyceros*	*dietrichi*
EP 006/00	R	MAND fragment (M3 fragment)	Alcelaphini	*Parmularius*	*pandatus*
EP 007/00	L	LM3	Alcelaphini		
EP 188/03	R	LM3	Alcelaphini		
EP 2539/00	R	LM1	Alcelaphini		Small sp.?
EP 1642/04	R	UM	Antilopini	*Gazella*	*janenschi*
EP 011/00	R	LP2	?Hippotragini		
EP 002/03	L	LM1-M2	Hippotragini	*Hippotragus*	
	R	LM1			
EP 008/00	L	LP4	Hippotragini		
EP 001/03	L	UM	Hippotragini		
EP 167/03	L	UM	Hippotragini		
EP 001/00		MAND fragment (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 002/00		MAND fragment (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 003/00		MAX fragment (dp3-dp4)	Neotragini	*Madoqua*	*avifluminis*
EP 005/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 075/01		HC	Neotragini	*Madoqua*	*avifluminis*
EP 169/03		MAND fragment (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 002/04		UM	Neotragini	*Madoqua*	*avifluminis*
EP 1640/04		Associated P3, M1-M3	Neotragini	*Madoqua*	*avifluminis*
EP 010/00	L	UM2	Tragelaphini	*Tragelaphus*	

Laetoli Locality 5

Specimen #	Side	Element	Tribe	Genus	Species
EP 1672/00	R	UM2	Antilopini	*Aepyceros*	*dietrichi*
EP 1673/00	L	UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 1890/00	L	UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 1892/00	R	UM1 or UM2	Antilopini	*Aepyceros*	*dietrichi*
EP 1893/00	L	UM2	Antilopini	*Aepyceros*	*dietrichi*
EP 1895/00	R	UM2	Antilopini	*Aepyceros*	*dietrichi*
EP 1898/00	L	UM1	Antilopini	*Aepyceros*	*dietrichi*
EP 1899/00	R	UM1	Antilopini	*Aepyceros*	*dietrichi*
EP 1908/00	L	LM fragment	Antilopini	*Aepyceros*	*dietrichi*
EP 1913/00	R	MAND fragment (M)	Antilopini	*Aepyceros*	*dietrichi*
EP 1914/00	R	UP2	Antilopini	*Aepyceros*	*dietrichi*
EP 2787/00	R	MAX fragment (P4, M1)	Antilopini	*Aepyceros*	*dietrichi*
EP 238/01	R	UM	Antilopini	*Aepyceros*	*dietrichi*
EP 239/01	L	UM2	Antilopini	*Aepyceros*	*dietrichi*
EP 240/01	L	MAND fragment (M1)	Antilopini	*Aepyceros*	*dietrichi*
EP 357/03	L	UM1-M2	Antilopini	*Aepyceros*	*dietrichi*
EP 358/03	R	UP3	Antilopini	*Aepyceros*	*dietrichi*
EP 1900/00	L	UM3 fragment	Alcelaphini		
EP 1906/00	R	LM3	Alcelaphini		
EP 3047/00	R	UM3	Alcelaphini		
EP 356/03	L	MAX fragment (M)	Alcelaphini		
EP 1291/04		UM1-M3	Alcelaphini		
EP 1312/04	L	MAND fragment (M3)	Alcelaphini		
EP 1674/00	L	UM2	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1911/00	L	LM2	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 3046/00	R	HC base	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1676/00	R	LM3	Antilopini	*Gazella*	*janenschi*
EP 1684/00		HC	Antilopini	*Gazella*	*janenschi*
EP 1907/00	R	MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 1912/00	R	MAND fragment (M2)	Antilopini	*Gazella*	*janenschi*
EP 1997/00	R + L	Associated HC	Antilopini	*Gazella*	*janenschi*
EP 3056/00	L	LM3 fragment	Antilopini	*Gazella*	*janenschi*
EP 1311/04	L	MAND fragment (M1)	Antilopini	*Gazella*	*janenschi*
EP 1891/00	L	UM	Indet.	*Brabovus*	*nanincisus*
EP 1894/00	R	UM2	Indet.	*Brabovus*	*nanincisus*
EP 1902/00	L	UM2	Indet.	*Brabovus*	*nanincisus*
EP 1904/00	L	UM1	Indet.	*Brabovus*	*nanincisus*
EP 1909/00	R	LM fragment	Indet.	*Brabovus*	*nanincisus*
EP 1915/00*		MAND fragments (P2-M3) HC fragments	Indet.	*Brabovus*	*nanincisus*
EP 359/03	R	UM	Indet.	*Brabovus*	*nanincisus*
EP 1901/00	L	MAX (M2-M3)	Hippotragini	*Hippotragus*	
EP 1675/00	R	M3	Hippotragini		
EP 1910/00	R	LM1	Cephalophini		
EP 1677/00		UM (3)	Neotragini	*Madoqua*	*avifluminis*
EP 1678/00		MAX (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1679/00		MAND (P3-M1 + M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1680/00		MAND (P2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1681/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 1925/00		MAND (P4-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1926/00		MAND fragment (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1927/00		MAND fragment (P4)	Neotragini	*Madoqua*	*avifluminis*
EP 1928/00		MAND fragment (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1929/00		MAND fragment (dp4)	Neotragini	*Madoqua*	*avifluminis*
EP 1930/00		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1931/00		MAX (M2)	Neotragini	*Madoqua*	*avifluminis*

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Laetoli Locality 5 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 1932/00		UM3 (2)	Neotragini	*Madoqua*	*avifluminis*
EP 1933/00		MAX fragment (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1934/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 2027/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 2788/00		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 2789/00		MAND fragment (M1- M3)	Neotragini	*Madoqua*	*avifluminis*
EP 2790/00		MAND fragment (P2- M1)	Neotragini	*Madoqua*	*avifluminis*
EP 2791/00		UM	Neotragini	*Madoqua*	*avifluminis*
EP 2792/00		UP3	Neotragini	*Madoqua*	*avifluminis*
EP 2793/00		LP	Neotragini	*Madoqua*	*avifluminis*
EP 2800/00		HC base	Neotragini	*Madoqua*	*avifluminis*
EP 3052/00		MAND fragment (dp3)	Neotragini	*Madoqua*	*avifluminis*
EP 3053/00		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 3057/00		UP2	Neotragini	*Madoqua*	*avifluminis*
EP 242/01		MAND fragment (M1- M2)	Neotragini	*Madoqua*	*avifluminis*
EP 243/01		MAND fragment (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 244/01		MAND fragment (M1- M2)	Neotragini	*Madoqua*	*avifluminis*
EP 245/01		MAND fragment (M)	Neotragini	*Madoqua*	*avifluminis*
EP 360/03		MAND (P3-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 361/03		UM3	Neotragini	*Madoqua*	*avifluminis*
EP 1292/04		MAX fragment (P2-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 1293/04		MAX fragment (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1294/04		MAX fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1295/04		MAND fragment (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1296/04		HC fragment	Neotragini	*Madoqua*	*avifluminis*
EP 1665/04		UP	Neotragini	*Madoqua*	*avifluminis*
EP 755/05	L	MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 756/06		LI	Neotragini	*Madoqua*	*avifluminis*
EP 757/05		HC base	Neotragini	*Madoqua*	*avifluminis*

*Associated material

Laetoli Locality 6

Specimen #	Side	Element	Tribe	Genus	Species
EP 3797/00	L	LM3 fragment	Antilopini	*Aepyceros*	*dietrichi*
EP 090/01	L	UM1 or UM2	Antilopini	*Aepyceros*	*dietrichi*
EP 1273/00	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 1275/00	R	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 1277/00	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 1284/00	L	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 1285/00	R	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 1286/00	L	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 1292/00	L	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 1302/00	R	MAND fragment (M3)	Alcelaphini	*Parmularius*	*pandatus*
EP 1304/00	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 1309/00	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 1336/00	R	HC	Alcelaphini	*Parmularius*	*pandatus*
EP 1337/00	R	HC	Alcelaphini	*Parmularius*	*pandatus*
EP 3792/00	R	UM fragment	Alcelaphini	*Parmularius*	*pandatus*
EP 3811/00	R	HC fragment	Alcelaphini	*Parmularius*	*pandatus*
EP 1410/04	L	HC	Alcelaphini	*Parmularius*	*pandatus*
EP 1278/00	R	UM3 fragment	Alcelaphini		
EP 1280/00	R	UM	Alcelaphini		
EP 1293/00	L	MAND fragment (M3)	Alcelaphini		
EP 1298/00	L	MAND fragment (M3)	Alcelaphini		
EP 1305/00	L	LM3 fragment	Alcelaphini		

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Laetoli Locality 6 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 1306/00	L	UM3	Alcelaphini		
EP 1308/00	R	Udp4	Alcelaphini		
EP 1310/00	L	UM fragment	Alcelaphini		
EP 3790/00	R	UM2	Alcelaphini		
EP 3795/00	L	UP	Alcelaphini		
EP 3801/00	L	LP4	Alcelaphini		
EP 1990/03	R	UM3	Alcelaphini		
EP 1991/03	L	UM3	Alcelaphini		
EP 1993/03	R	UM fragment	Alcelaphini		
EP 1994/03	R	UM1	Alcelaphini		
EP 1998/03	L	UP4	Alcelaphini		
EP 1999/03	R	LP	Alcelaphini		
EP 1384/04	L	UM1-UM2	Alcelaphini		
EP 1385/04*	L	P3-P4	Alcelaphini		
	R	P3			
EP 1387/04	R	UP3	Alcelaphini		
EP 1389/04	R	LM	Alcelaphini		
EP 1390/04	R	Udp3	Alcelaphini		
EP 632/05	R	UM3	Alcelaphini		
EP 1295/00	R	MAND fragment (M3)	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1995/03	R	UM	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1289/00	L	MAX fragment (M1- M3)	Antilopini	*Gazella*	*janenschi*
EP 1290/00	R	MAX fragment (M2- M3)	Antilopini	*Gazella*	*janenschi*
EP 1299/00	L	MAND (P2-M2)	Antilopini	*Gazella*	*janenschi*
EP 1303/00	L	MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 1311/00	R	LP4	Antilopini	*Gazella*	*janenschi*
EP 1312/00	R	LP3	Antilopini	*Gazella*	*janenschi*
EP 1313/00	R	MAND fragment (dp3-M1)	Antilopini	*Gazella*	*janenschi*
EP 087/01		HC	Antilopini	*Gazella*	*janenschi*
EP 091/01	R	UM1	Antilopini	*Gazella*	*janenschi*
EP 1996/03	R	UM	Antilopini	*Gazella*	*janenschi*
EP 2004/03		MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 1391/04	R	LM1 or LM2	Antilopini	*Gazella*	*janenschi*
EP 1392/04	R	UP2	Antilopini	*Gazella*	*janenschi*
EP 1282/00	L	UM2	Indet.	*Brabovus*	*nanincisus*
EP 3812/00		HC fragment	Indet.	*Brabovus*	*nanincisus*
EP 1272/00	R	UM3	Hippotragini		
EP 1296/00	L	MAND fragment (P4-M1)	Hippotragini	*Hippotragus*	
EP 1338/00	L	HC	Hippotragini	*Hippotragus*	
EP 2296/00		HC fragments	Hippotragini	*Hippotragus*	
EP 089/01	L	UM2	Hippotragini		
EP 1271/00	L	UM3	Hippotragini		
EP 1274/00	R	UM3	Hippotragini		
EP 1276/00	L	UM1	Hippotragini		
EP 1279/00		UM fragment	Hippotragini		
EP 1287/00	R	UM1	Hippotragini		
EP 1288/00	R	UP4	Hippotragini		
EP 1291/00	L	MAX fagment (M1-M2)	Hippotragini		
EP 1294/00	L	MAND fragment (M2)	Hippotragini		
EP 1297/00	L	MAND fragment (M3)	Hippotragini		
EP 1301/00	L	LM3	Hippotragini		
EP 1307/00	L	LP4	Hippotragini		
EP 3791/00	L	UP4	Hippotragini		
EP 3793/00	R	MAX fragment (M2)	Hippotragini		
EP 3802/00	R	UP2	Hippotragini		
EP 1992/03	L	UM	Hippotragini		
EP 1997/03	L	UP4	Hippotragini		
EP 1386/04	R	LM1	Hippotragini		

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Laetoli Locality 6 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 1388/04	R	UP3	Hippotragini		
EP 634/05		UM	Hippotragini		
EP 1314/00		MAND fragment (M2- M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1315/00		MAND (P4-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1316/00		MAND fragment (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1317/00		LM3	Neotragini	*Madoqua*	*avifluminis*
EP 1318/00		LM1	Neotragini	*Madoqua*	*avifluminis*
EP 1339/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 1340/00*	L + R	HC (2)	Neotragini	*Madoqua*	*avifluminis*
EP 3798/00		MAND fragment (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 3799/00		MAX fragment (M2- M3)	Neotragini	*Madoqua*	*avifluminis*
EP 3800/00		MAX fragment (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 3803/00		UP3	Neotragini	*Madoqua*	*avifluminis*
EP 3804/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 092/01		MAND fragment (P4- M2)	Neotragini	*Madoqua*	*avifluminis*
EP 093/01		MAND fragment (M1- M2)	Neotragini	*Madoqua*	*avifluminis*
EP 094/01		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 095/01		MAND fragment (M2- M3)	Neotragini	*Madoqua*	*avifluminis*
EP 096/01		UM (3)	Neotragini	*Madoqua*	*avifluminis*
EP 2000/03		HC	Neotragini	*Madoqua*	*avifluminis*
EP 2001/03		MAX (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 2003/03		UM	Neotragini	*Madoqua*	*avifluminis*
EP 1393/04		MAND fragment (M)	Neotragini	*Madoqua*	*avifluminis*
EP 1394/04		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1395/04		UM3	Neotragini	*Madoqua*	*avifluminis*
EP 1396/04		UM	Neotragini	*Madoqua*	*avifluminis*
EP 1397/04		UM3 Germ	Neotragini	*Madoqua*	*avifluminis*
EP 637/05		UM	Neotragini	*Madoqua*	*avifluminis*
EP 649/05		MAND fragment (M)	Neotragini	*Madoqua*	*avifluminis*
EP 1283/00	R	UM	Tragelaphini	*Tragelaphus*	
EP 088/01	R	UM3	Tragelaphini	*Tragelaphus*	

*Associated material

Laetoli Locality 7

Specimen #	Side	Element	Tribe	Genus	Species
EP 2267/00	L	UM fragment	?Alcelaphini		
EP 2254/00	L	UM2	Antilopini	*Aepyceros*	*dietrichi*
EP 2270/00	L	LM3	Antilopini	*Aepyceros*	*dietrichi*
EP 746/04	R	MAND fragment (P4)	Antilopini	*Aepyceros*	*dietrichi*
EP 2271/00	L	LM2 OR LM1	Alcelaphini	*Parmularius*	*pandatus*
EP 3863/00	L	MAND fragment (M2-M3)	Alcelaphini	*Parmularius*	*pandatus*
EP 857/01	L	UM	Alcelaphini	*Parmularius*	*pandatus*
EP 859/01	L	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 860/01	R	LM3 fragment	Alcelaphini	*Parmularius*	*pandatus*
EP 862/01	L	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 863/01	L	MAND fragment (M3)	Alcelaphini	*Parmularius*	*pandatus*
EP 884/01	R	UM	Alcelaphini	*Parmularius*	*pandatus*
EP 885/01	R	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 889/01	L	LM3 fragment	Alcelaphini	*Parmularius*	*pandatus*
EP 890/01	R	LM3 fragment	Alcelaphini	*Parmularius*	*pandatus*
EP 159/01		MAND fragment (M)	Alcelaphini		Larger sp.
EP 886/01	R	LM1	Alcelaphini		Larger sp.
EP 888/01	L	LM3 fragment	Alcelaphini		Larger sp.
EP 1497/00	L	UP3	Alcelaphini		
EP 2203/00	R	MAX fragment (M2)	Alcelaphini		

(continued)

Laetoli Locality 7 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 2205/00	L	UM	Alcelaphini		
EP 2252/00	R	MAX (P4-M2)	Alcelaphini		
EP 2253/00	R	MAX (P3-M3)	Alcelaphini		
EP 2255/00	R	UM	Alcelaphini		
EP 2260/00	L	UM1 or UM2	Alcelaphini		
EP 2261/00	L	UM	Alcelaphini		
EP 2273/00	L	LM3	Alcelaphini		
EP 3859/00	L	UM2	Alcelaphini		
EP 3860/00	R	LM3	Alcelaphini		
EP 3862/00	L	LP4	Alcelaphini		
EP 880/01	R	UM	Alcelaphini		
EP 1913/03	R	UM	Alcelaphini		
EP 1916/03	L	LM	Alcelaphini		
EP 1919/03	R	LP4-M3	Alcelaphini		
EP 2111/03	R	UM	Alcelaphini		
EP 2112/03	L	LM	Alcelaphini		
EP 2122/03	L	MAND fragment (P4-M1)	Alcelaphini		
EP 2167/03*	R	UM2-M3	Alcelaphini		
	L	UM3			
EP 2171/03	R	LP4	Alcelaphini		
EP 740/04	R	MAX fragment (M)	Alcelaphini		
EP 741/04	L	MAX fragment (M3)	Alcelaphini		
EP 742/04	L	MAX fragment (M)	Alcelaphini		
EP 747/04	L	MAND fragment (P4)	Alcelaphini		
EP 794/04	L	MAX fragment (M)	Alcelaphini		
EP 796/04	R	MAX fragment (P4)	Alcelaphini		
EP 2204/00	R	MAX fragment (M2-M3)	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 2209/00	R	UdP3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 162/01	R	UP3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1914/03	R	UM	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 2165/03	R	UM	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 2168/03	R	LP4	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 2169/03	R	LP3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 2201/00	R	MAND fragment (dp4-M1)	Antilopini	*Gazella*	*janenschi*
EP 2202/00	R	MAND (P4-M2)	Antilopini	*Gazella*	*janenschi*
EP 2212/00	R	HC	Antilopini	*Gazella*	*janenschi*
EP 2262/00	R	UM2	Antilopini	*Gazella*	*janenschi*
EP 877/01	L	MAND (M1-M3)	Antilopini	*Gazella*	*janenschi*
EP 908/01	R	HC base	Antilopini	*Gazella*	*janenschi*
EP 1336/03	L	MAX (P4-M3)	Antilopini	*Gazella*	*janenschi*
EP 1917/03	R	LM3 fragment	Antilopini	*Gazella*	*janenschi*
EP 2110/03	R	MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 2113/03	L	UM	Antilopini	*Gazella*	*janenschi*
EP 743/04	L	MAND fragment (M2-M3 fragments)	Antilopini	*Gazella*	*janenschi*
EP 744/04	L	MAND fragment (M)	Antilopini	*Gazella*	*janenschi*
EP 795/04	L	MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 2114/03	R	UM1	Indet.	*Brabovus*	*nanincisus*
EP 581/05	R	LP3	Indet.	*Brabovus*	*nanincisus*
EP 2257/00	L	MAX (P4-M1)	?Hippotragini		
EP 922/01	L	LP2	?Hippotragini		
EP 2218/00	R	MAND (M1-M2)	Hippotragini	*Hippotragus*	
EP 2263/00	L	UP2	Hippotragini	*Hippotragus*	
EP 2264/00	R	UP3	Hippotragini	*Hippotragus*	
EP 1498/00	R	UP3	Hippotragini		
EP 2200/00	L	LM1	Hippotragini		
EP 2210/00	L	LP4	Hippotragini		
EP 2256/00	L	UM1 or UM2	Hippotragini		
EP 2258/00	R	LM1 or LM2	Hippotragini		
EP 2259/00	L	UM2	Hippotragini		

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Laetoli Locality 7 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 2274/00	R	MAND fragment (M3)	Hippotragini		
EP 3861/00	R	UM1	Hippotragini		
EP 160/01	L	LM2	Hippotragini		
EP 161/01	R	LP3	Hippotragini		
EP 878/01	L	UM2	Hippotragini		
EP 879/01	R	UM	Hippotragini		
EP 881/01	L	UM	Hippotragini		
EP 882/01	R	UM2	Hippotragini		
EP 883/01	L	UM2	Hippotragini		
EP 891/01	L	LP4	Hippotragini		
EP 892/01	L	LP4	Hippotragini		
EP 893/01	L	LP3	Hippotragini		
EP 895/01	L	LP3	Hippotragini		
EP 1918/03	R	UP3	Hippotragini		
EP 2166/03	R	MAX fragment (M2-M3)	Hippotragini		
EP 2170/03	L	LP3	Hippotragini		
EP 739/04	R	UM	Hippotragini		
EP 745/04	L	UP2	Hippotragini		
EP 2206/00		MAND fragment (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 2207/00		MAND fragment (P2-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 2208/00		MAND fragment (P4)	Neotragini	*Madoqua*	*avifluminis*
EP 2213/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 2214/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 2275/00		MAND (P4-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 2276/00		MAND fragment (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 3864/00		MAX fragment (P3-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 3865/00		MAX fragment (dp4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 3866/00		MAND fragment (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 3867/00		MAND fragment (M)	Neotragini	*Madoqua*	*avifluminis*
EP 3868/00		LP4	Neotragini	*Madoqua*	*avifluminis*
EP 163/01		MAND (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 164/01		MAND (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 897/01		MAND (P2-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 898/01		MAND (P4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 899/01		MAND (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 900/01		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 901/01		MAND (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 902/01		LM	Neotragini	*Madoqua*	*avifluminis*
EP 1920/03		MAX fragment (dp4-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1921/03		MAND (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1922/03		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1923/03		LM	Neotragini	*Madoqua*	*avifluminis*
EP 1924/03		LM	Neotragini	*Madoqua*	*avifluminis*
EP 1925/03		UM2	Neotragini	*Madoqua*	*avifluminis*
EP 1926/03		LM	Neotragini	*Madoqua*	*avifluminis*
EP 1927/03		UP2	Neotragini	*Madoqua*	*avifluminis*
EP 1928/03		HC	Neotragini	*Madoqua*	*avifluminis*
EP 2116/03		HC (2)	Neotragini	*Madoqua*	*avifluminis*
EP 2172/03		MAX fragment (M1M2)	Neotragini	*Madoqua*	*avifluminis*
EP 2173/03		UP2	Neotragini	*Madoqua*	*avifluminis*
EP 2174/03		MAND fragment (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 2175/03		LM2	Neotragini	*Madoqua*	*avifluminis*
EP 2176/03		MAND (P4-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 2177/03		MAX fragment (dp3-dp4)	Neotragini	*Madoqua*	*avifluminis*
EP 748/04		MAND (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 749/04		MAX (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 582/05		UM	Neotragini	*Madoqua*	*avifluminis*
EP 583/05		MAND fragment (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 584/05		MAND fragment (M2-M3)	Neotragini	*Madoqua*	*avifluminis*

*Associated material

Laetoli Loc. 7E

Specimen #	Side	Element	Tribe	Genus	Species
EP 810/04		MAND fragment (P4)	Cephalophini		
EP 807/04		MAND fragment (M2- M3)	Neotragini	*Madoqua*	*avifluminis*
EP 808/04		MAND (M)	Neotragini	*Madoqua*	*avifluminis*
EP 809/04		MAND (dp4)	Neotragini	*Madoqua*	*avifluminis*

Laetoli Locality 8

Specimen #	Side	Element	Tribe	Genus	Species
EP 1077/00	L	UM2	Antilopini	*Aepyceros*	*dietrichi*
EP 1081/00	R	UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 1087/00	L	LM or LM2	Antilopini	*Aepyceros*	*dietrichi*
EP 1092/00	R	MAND (P4-M2)	Antilopini	*Aepyceros*	*dietrichi*
EP 007/01	L	UM2	Antilopini	*Aepyceros*	*dietrichi*
EP 1370/03	R	UM	Antilopini	*Aepyceros*	*dietrichi*
EP 1374/03	R	LM	Antilopini	*Aepyceros*	*dietrichi*
EP 1470/03	L	Udp3	Antilopini	*Aepyceros*	*dietrichi*
EP 306/04	L	UP4	Antilopini	*Aepyceros*	*dietrichi*
EP 271/00	R	MAX (P4-M3)	Alcelaphini	*Parmularius*	*pandatus*
EP 273/00	L	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 274/00	L	UM	Alcelaphini	*Parmularius*	*pandatus*
EP 1070/00	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 1071/00	R	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 1072/00	R	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 1073/00	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 1079/00	L	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 1082/00	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 1083/00	R	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 1085/00	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 1088/00	R	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 4065/00	L	MAX (M1-M3)	Alcelaphini	*Parmularius*	*pandatus*
EP 4073/00	R	LP4	Alcelaphini	*Parmularius*	*pandatus*
EP 001/01	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 002/01	R	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 009/01	R	LM3	Alcelaphini	*Parmularius*	*pandatus*
EP 242/00	R	UM2	Alcelaphini		Larger sp.
EP 1075/00	R	UM3	Alcelaphini		Larger sp.
EP 1130/00		HC	Alcelaphini		Larger sp.
EP 1270/00		Partial cranium	Alcelaphini		Larger sp.
EP 4080/00	R	MAND fragment (M1-M2)	Alcelaphini		Larger sp.
EP 243/00	L	UM3	Alcelaphini		
EP 1080/00	L	UM	Alcelaphini		
EP 1089/00	R	LM3 fragment	Alcelaphini		
EP 1093/00	L	MAND (P4-M1)	Alcelaphini		
EP 4068/00	R	MAND (M1)	Alcelaphini		
EP 4074/00	L	UP3	Alcelaphini		
EP 003/01	R	MAX fragment (M2)	Alcelaphini		
EP 1361/03	R	UM	Alcelaphini		
EP 1362/03	L	UM	Alcelaphini		
EP 1363/03	L	UM1	Alcelaphini		
EP 1364/03	L	UM3	Alcelaphini		
EP 1366/03	R	UM	Alcelaphini		
EP 1371/03	R	UM	Alcelaphini		

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Laetoli Locality 8 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 1469/03	R	UM	Alcelaphini		
EP 299/04	L	MAND fragment (M3)	Alcelaphini		
EP 300/04	L	UM, probably UM1	Alcelaphini		
EP 301/04	R	UM3	Alcelaphini		
EP 304/04	R	MAND fragment (M2-M3)	Alcelaphini		
EP 307/04	L	UP3	Alcelaphini		
EP 244/00	L	UM1	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 245/00	R	Udp4	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1084/00	L	UM3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1095/00	L	UM3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1105/00		HC	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1106/00		HC	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 006/01	R	UM3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 010/01	L	LP4 fragment	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1369/03	R	UM3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1387/03	L	LP4	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1386/03	R	UP2	aff. Antilopini?	"*Gazella*"	*kohllarseni or janenschi*
EP 275/00	R	MAND (M2-M3)	Antilopini	*Gazella*	*janenschi*
EP 1076/00	R	MAX (M2-M3)	Antilopini	*Gazella*	*janenschi*
EP 1086/00	R	LM3	Antilopini	*Gazella*	*janenschi*
EP 1090/00	R	UM1 fragment	Antilopini	*Gazella*	*janenschi*
EP 1103/00	L	HC	Antilopini	*Gazella*	*janenschi*
EP 1104/00	L	HC	Antilopini	*Gazella*	*janenschi*
EP 4069/00	L	MAX (M2)	Antilopini	*Gazella*	*janenschi*
EP 004/01	L	UM2	Antilopini	*Gazella*	*janenschi*
EP 015/01	L	HC frag	Antilopini	*Gazella*	*janenschi*
EP 1571/01	R	MAND fragment (M2)	Antilopini	*Gazella*	*janenschi*
EP 1365/03	L	UM	Antilopini	*Gazella*	*janenschi*
EP 1373/03	R	UM	Antilopini	*Gazella*	*janenschi*
EP 1382/03	R	HC	Antilopini	*Gazella*	*janenschi*
EP 303/04	L	MAND fragment (M2)	Antilopini	*Gazella*	*janenschi*
EP 308/04	R	LP4	Antilopini	*Gazella*	*janenschi*
EP 1134/00		LP3-P4	Bovini	*Simatherium*	*kohllarseni*
EP 005/01	L	LM3	Indet.	*Brabovus*	*nanincisus*
EP 088/05	R	RUM	Indet.	*Brabovus*	*nanincisus*
EP 094/05	L	LUM1	Indet.	*Brabovus*	*nanincisus*
EP 1268/00*	R	UP3-M3	Hippotragini	*Hippotragus*	
	L	UP4			
EP 4084/00	R	HC	Hippotragini	*Hippotragus*	
EP 272/00	R	UM3	Hippotragini		
EP 276/00	L	LM2	Hippotragini		
EP 279/00	R	MAND fragment (P4)	Hippotragini		
EP 280/00	R	UP4	Hippotragini		
EP 281/00	L	Udp3	Hippotragini		
EP 1074/00	L	UM3	Hippotragini		
EP 1078/00	L	UM	Hippotragini		
EP 1121/00	R	MAND (P2-M1)	Hippotragini		
EP 4066/00	L	MAND (M2)	Hippotragini		
EP 4067/00	L	UP4-M1	Hippotragini		
EP 4071/00	L	LP3	Hippotragini		
EP 4072/00	R	LP4	Hippotragini		
EP 008/01	R	LM3	Hippotragini		
EP 018/01	R	MAX (dp3-M2)	Hippotragini		
EP 1380/03	R	MAND fragment (M3)	Hippotragini		
EP 1381/03	L	LM3	Hippotragini		
EP 1383/03	L	UP3	Hippotragini		
EP 1384/03	R	UP2	Hippotragini		

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Laetoli Locality 8 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 1385/03	L	Udp2	Hippotragini		
EP 302/04	R	UM	Hippotragini		
EP 305/04	R	UM	Hippotragini		
EP 1069/00		HC	Cephalophini		
EP 1379/03	L	Ldp4	Cephalophini		
EP 257/00		MAND fragment	Neotragini	*Madoqua*	*avifluminis*
EP 284/00		UM3	Neotragini	*Madoqua*	*avifluminis*
EP 285/00		Associated HC fragments (2)	Neotragini	*Madoqua*	*avifluminis*
EP 1058/00		MAND (P2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1059/00		MAND (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1060/00		MAND (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1061/00		LM3	Neotragini	*Madoqua*	*avifluminis*
EP 1062/00		MAND (P2-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 1063/00		MAX (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1064/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 3669/00		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 4086/00		MAX (P3-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 4087/00		MAND (M)	Neotragini	*Madoqua*	*avifluminis*
EP 4088/00		MAX (dp3-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 4089/00		MAX (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 4090/00		MAND (P2-P3)	Neotragini	*Madoqua*	*avifluminis*
EP 4091/00		UM	Neotragini	*Madoqua*	*avifluminis*
EP 4092/00		MAND (dp4)	Neotragini	*Madoqua*	*avifluminis*
EP 4093/00		MAND (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 4094/00		UP2	Neotragini	*Madoqua*	*avifluminis*
EP 4095/00		LP4	Neotragini	*Madoqua*	*avifluminis*
EP 4099/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 013/01		UM	Neotragini	*Madoqua*	*avifluminis*
EP 014/01		LM	Neotragini	*Madoqua*	*avifluminis*
EP 016/01		HC fragment	Neotragini	*Madoqua*	*avifluminis*
EP 017/01		HC	Neotragini	*Madoqua*	*avifluminis*
EP 1377/03		HC	Neotragini	*Madoqua*	*avifluminis*
EP 1493/03B		MAND (erupting dentition)	Neotragini	*Madoqua*	*avifluminis*
EP 1375/03	L	MAND (M3)	Neotragini	*?Raphicerus*	
EP 1376/03	R	Ldp4	Neotragini	*?Raphicerus*	
EP 1378/03	L	UM1	Neotragini	*?Raphicerus*	
EP 1372/03	R	UM	Tragelaphini	*Tragelaphus*	

*Associated material

Laetoli Locality 9

Specimen #	Side	Element	Tribe	Genus	Species
EP 728/03	R	UP4	Antilopini	*Aepyceros*	*dietrichi*
EP 1157/98	R	UM2	Antilopini	*Aepyceros*	*dietrichi*
EP 1163/98		UM1	Antilopini	*Aepyceros*	*dietrichi*
EP 444/01	L	UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 448/01	R	LM3 fragment	Antilopini	*Aepyceros*	*dietrichi*
EP 961/04	L	UM	Antilopini	*Aepyceros*	*dietrichi*
EP 1161/98	L	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 1169/98	L	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 1462/98	R	LP3	Alcelaphini	*Parmularius*	*pandatus*
EP 1463/98	R	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 1466/98	L	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 189/99	L	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 446/01	L	UM2	Alcelaphini	*Parmularius*	*pandatus*

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Laetoli Locality 9 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 449/01	L	MAX fragment (M2-M3)	Alcelaphini	*Parmularius*	*pandatus*
EP 201/05	R	LM2-3 fragments	Alcelaphini		Larger sp.
EP 726/03	R	Ldp4	Alcelaphini		
EP 1168/98	L	MAND fragment (M2)	Alcelaphini		
EP 2502/00	L	LM2	Alcelaphini		
EP 730/03	R	LM or Ldp4	Alcelaphini		
EP 723/03	R	LM	Alcelaphini		
EP 1147/98	L	MAND fragment (M2)	Alcelaphini		
EP 1153/98	L	UM1	Alcelaphini		
EP 1159/98	L	UM	Alcelaphini		
EP 1160/98	L	UM 3	Alcelaphini		
EP 1164/98	L	UM	Alcelaphini		
EP 1167/98	R	UM3	Alcelaphini		
EP 1467/98		UM	Alcelaphini		
EP 1644/98	R	UM	Alcelaphini		
EP 2497/00	R	UM	Alcelaphini		
EP 2500/00	L	LM3	Alcelaphini		
EP 3514/00	R	MAND (P4)	Alcelaphini		
EP 2492/00	R	UM3	Alcelaphini		
EP 2493/00	L	UM3	Alcelaphini		
EP 956/04	L	UM	Alcelaphini		
EP 957/04	R	UM	Alcelaphini		
EP 959/04	R	LM3	Alcelaphini		
EP 960/04	R	UM	Alcelaphini		
EP 202/05	L	MAND fragment (M1- M2)	Alcelaphini		
EP 197/99	R	LP3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 958/04	L	UM1 or UM2	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 722/03	R	UM	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1124/98		Frontlet	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1144/98	L	MAND fragment (M2- M3)	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1171/98		UP3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1175/98*	L+R	MAX (P2-M3)	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 2495/00	R	UM2	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 445/01	L	UM2	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 725/03	R	MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 1121/98		HC	Antilopini	*Gazella*	*janenschi*
EP 1122/98	R	HC	Antilopini	*Gazella*	*janenschi*
EP 1123/98		HC	Antilopini	*Gazella*	*janenschi*
EP 1145/98	L	MAND fragment (M2-M3)	Antilopini	*Gazella*	*janenschi*
EP 1146/98	L	MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 1148/98	R	MAND fragment (dp4-M1)	Antilopini	*Gazella*	*janenschi*
EP 1151/98	L	MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 1468/98	R	UM2	Antilopini	*Gazella*	*janenschi*
EP 1474/98	L	LP	Antilopini	*Gazella*	*janenschi*
EP 1487/98	L	HC fragment	Antilopini	*Gazella*	*janenschi*
EP 191/99	R	MAND fragment (M1)	Antilopini	*Gazella*	*janenschi*
EP 192/99	L	MAND fragment (M1- M2)	Antilopini	*Gazella*	*janenschi*
EP 193/99	L	UM3	Antilopini	*Gazella*	*janenschi*
EP 2490/00	L	HC	Antilopini	*Gazella*	*janenschi*
EP 2496/00	R	UM3	Antilopini	*Gazella*	*janenschi*
EP 2498/00	L	UM1	Antilopini	*Gazella*	*janenschi*
EP 2501/00	R	MAND fragment (M1-2)	Antilopini	*Gazella*	*janenschi*
EP 447/01	R	UP3-P4	Antilopini	*Gazella*	*janenschi*
EP 450/01	L	MAX fragment (M2-M3)	Antilopini	*Gazella*	*janenschi*
EP 451/01	R	UM2	Antilopini	*Gazella*	*janenschi*
EP 456/01	R	LM2	Antilopini	*Gazella*	*janenschi*
EP 963/04	L	UM	Antilopini	*Gazella*	*janenschi*

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Laetoli Locality 9 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 964/04	R	MAND fragment (M2)	Antilopini	*Gazella*	*janenschi*
EP 966/04	R	HC	Antilopini	*Gazella*	*janenschi*
EP 967/04	L	LP4	Antilopini	*Gazella*	*janenschi*
EP 203/05	R	MAND fragment (P3- M1)	Antilopini	*Gazella*	*janenschi*
EP 204/05	R	MAND fragment (P2-P4)	Antilopini	*Gazella*	*janenschi*
EP 1119/98		HC	Bovini		
EP 1166/98	R	MAX fragment (M1-M2)	Indet.	*Brabovus*	*nanincisus*
EP 452/01	L	LP2	Indet.	*Brabovus*	*nanincisus*
EP 1118/98		HC	Indet.	*Brabovus*	*nanincisus*
EP 1648/98		HC fragment	?Hippotragini		
EP 1461/98	R	LM3	Hippotragini		
EP 729/03	R	Ldp3	Hippotragini	*Hippotragus*	
EP 2499/00	L	UP4-M2	Hippotragini	*Hippotragus*	
EP 1471/98	L	UP4	Hippotragini	*Hippotragus*	
EP 1120/98		HC	Hippotragini	*Oryx*	*deturi*
EP 724/03	R	UP	Hippotragini		
EP 721/03	R	UM	Hippotragini		
EP 1143/98	L	MAND fragment (M2- M3)	Hippotragini		
EP 1149/98	L	MAND fragment (M3)	Hippotragini		
EP 1150/98	R	MAND fragment (P4- M3)	Hippotragini		
EP 1152/98	L	UM3	Hippotragini		
EP 1156/98	R	UM2	Hippotragini		
EP 1158/98	L	UM2	Hippotragini		
EP 1162/98	L	UM	Hippotragini		
EP 1165/98		UM fragment	Hippotragini		
EP 1484/98	L	UM3	Hippotragini		
EP 1642/98	R	LP4	Hippotragini		
EP 1643/98	R	LM fragment	Hippotragini		
EP 188/99	L	UM2	Hippotragini		
EP 190/99	L	LM1	Hippotragini		
EP 2491/00	R	UM3	Hippotragini		
EP 2494/00	R	LM	Hippotragini		
EP 2512/00	L	UP2-P3	Hippotragini		
EP 3515/00	R	UM	Hippotragini		
EP 443/01	R	UM3	Hippotragini		
EP 962/04	L	UM	Hippotragini		
205/05	L	UM	Hippotragini		
206/05	L	UM	Hippotragini		
EP 962/04	L	UM	Hippotragini		
EP 731/03		HC	Neotragini	*Madoqua*	*avifluminis*
EP 1172/98		LP4	Neotragini	*Madoqua*	*avifluminis*
EP 1464/98		MAND (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1465/98		LM1 OR LM2	Neotragini	*Madoqua*	*avifluminis*
EP 194/99		MAX (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 195/99		MAX (P2-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 196/99		UP3	Neotragini	*Madoqua*	*avifluminis*
EP 2504/00		MAND (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 2505/00		MAND fragment (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 453/01		UM2	Neotragini	*Madoqua*	*avifluminis*
EP 455/01		MAND fragment (P4)	Neotragini	*Madoqua*	*avifluminis*
EP 457/01		HC	Neotragini	*Madoqua*	*avifluminis*
EP 208/05		UM3	Neotragini	*Madoqua*	*avifluminis*
EP 454/01	R	MAND fragment (M1 or M2)	Neotragini	*?Raphicerus*	
EP 1470/98		UM2	Tragelaphini	*Tragelaphus*	

*Associated material

Laetoli Locality 9 S

Specimen #	Side	Element	Tribe	Genus	Species
EP 906/98	L	MAND fragment (M3)	Antilopini	*Aepyceros*	*dietrichi*
EP 915/98	L	LM1	Antilopini	*Aepyceros*	*dietrichi*
EP 942/98	L	UM2	Antilopini	*Aepyceros*	*dietrichi*
EP 944/98	L	UM2 fragment	Antilopini	*Aepyceros*	*dietrichi*
EP 945/98	L	MAX (P2)	Antilopini	*Aepyceros*	*dietrichi*
EP 947/98	L	UP2	Antilopini	*Aepyceros*	*dietrichi*
EP 2378/03	R	UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 2379/03	L	UM	Antilopini	*Aepyceros*	*dietrichi*
EP 1191/04	L	MAND fragment (M2-M3)	Antilopini	*Aepyceros*	*dietrichi*
EP 1198/04	R	LM1	Antilopini	*Aepyceros*	*dietrichi*
EP 475/05	L	UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 914/98	R	LM3	Alcelaphini	*Parmularius*	*pandatus*
EP 930/98	R	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 933/98	L	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 934/98	L	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 936/98	L	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 938/98	L	LM3	Alcelaphini	*Parmularius*	*pandatus*
EP 941/98	L	UM1 or UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 948/98		HC	Alcelaphini	*Parmularius*	*pandatus*
EP 243/99	R	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 937/98	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 939/98		UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 1042/00	R	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 1195/01	R	LP4	Alcelaphini	*Parmularius*	*pandatus*
EP 1267/01*	L	Udp2-M1	Alcelaphini	*Parmularius*	*pandatus*
	R	Udp3-M1			
EP 943/98	R	UM2	Alcelaphini		Larger sp.
EP 940/98	L	UM3	Alcelaphini		
EP 1191/01	L	LM2	Alcelaphini		
EP 908/98	R	LM	Alcelaphini		
EP 909/98	L	UM1	Alcelaphini		
EP 911/98	R	M fragment	Alcelaphini		
EP 935/98	L	UM1	Alcelaphini		
EP 1002/98	L	UM1	Alcelaphini		
EP 3654/00	R	LM1	Alcelaphini		
EP 1186/01	R	UM3	Alcelaphini		
EP 1188/01	L	UM	Alcelaphini		
EP 1231/01		HC fragment	Alcelaphini		
EP 2373/03	R	UM	Alcelaphini		
EP 2374/03	R	LM3	Alcelaphini		
EP 2375/03	R	UM	Alcelaphini		
EP 567/05	R	LM3	Alcelaphini		
EP 1043/00	R	UM2	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 904/98	L	MAND fragment (M2, M3)	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 910/98	R	LM1	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 931/98		UM1	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 2376/03	R	UM3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1189/01	L	UM	aff. Antilopini?	"*Gazella*"	*kohllarseni or janenschi*
EP 1190/01	R	UM1	aff. Antilopini?	"*Gazella*"	*kohllarseni or janenschi*
EP 1192/01	L	MAND fragment (M2)	aff. Antilopini?	"*Gazella*"	*kohllarseni or janenschi*
EP 1193/01	L	MAND fragment (P4-M1)	aff. Antilopini?	"*Gazella*"	*kohllarseni or janenschi*
EP 1194/01	R	LM3	aff. Antilopini?	"*Gazella*"	*kohllarseni or janenschi*
EP 1196/01	R	LM2	aff. Antilopini?	"*Gazella*"	*kohllarseni or janenschi*
EP 905/98	R	MAND fragment (M1, M3)	Antilopini	*Gazella*	*janenschi*
EP 907/98	L	MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 912/98	L	LM1	Antilopini	*Gazella*	*janenschi*

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Laetoli Locality 9 S (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 917/98	L	LM2	Antilopini	*Gazella*	*janenschi*
EP 932/98	L	UM2	Antilopini	*Gazella*	*janenschi*
EP 1187/01	L	UM2	Antilopini	*Gazella*	*janenschi*
EP 916/98	L	LM3	Hippotragini		
EP 946/98	L	UP2	Hippotragini		
EP 918/98		MAND fragment (M2, M3)	Neotragini	*Madoqua*	*avifluminis*
EP 919/98		MAND (P3-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 920/98		MAND (M1, M2)	Neotragini	*Madoqua*	*avifluminis*
EP 921/98		MAND (dp4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 922/98		MAND (P3, P4)	Neotragini	*Madoqua*	*avifluminis*
EP 923/98		MAND (M2, M3)	Neotragini	*Madoqua*	*avifluminis*
EP 924/98		MAND (M1, M2)	Neotragini	*Madoqua*	*avifluminis*
EP 925/98		MAND (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 926/98*		MAND (M1), UP2-UP4, UM1 or UM2	Neotragini	*Madoqua*	*avifluminis*
EP 927/98		MAX fragment (dp3-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 928/98		MAX (M2, M3)	Neotragini	*Madoqua*	*avifluminis*
EP 929/98		UM3	Neotragini	*Madoqua*	*avifluminis*
EP 949/98		HC	Neotragini	*Madoqua*	*avifluminis*
EP 950/98		HC	Neotragini	*Madoqua*	*avifluminis*
EP 951/98		HC	Neotragini	*Madoqua*	*avifluminis*
EP 244/99		MAND (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 245/99		MAND (M1)	Neotragini	*Madoqua*	*avifluminis*
EP 1044/00		MAND (P3-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 3655/00		UM	Neotragini	*Madoqua*	*avifluminis*
EP 3656/00		LM3	Neotragini	*Madoqua*	*avifluminis*
EP 1197/01		MAND (M)	Neotragini	*Madoqua*	*avifluminis*
EP 1198/01		MAND (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1199/01		MAND (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1200/01		MAND (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1201/01		LM	Neotragini	*Madoqua*	*avifluminis*
EP 1202/01		MAND fragment (dp4)	Neotragini	*Madoqua*	*avifluminis*
EP 1203/01		MAND fragment (P3-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 1204/01		MAX (P4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 1205/01		MAX (P3-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 1206/01		Udp4	Neotragini	*Madoqua*	*avifluminis*
EP 1207/01		Udp3	Neotragini	*Madoqua*	*avifluminis*
EP 1208/01		MAND (P3-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 1209/01		MAND (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1210/01		MAND (P3-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 2380/03		MAND fragment (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 2381/03		MAND fragment (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 2382/03		MAND fragment (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 2383/03		MAND fragment (P4 + M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 2384/03		MAND fragment (M1)	Neotragini	*Madoqua*	*avifluminis*
EP 2385/03		MAND fragment (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 2386/03		LM3	Neotragini	*Madoqua*	*avifluminis*
EP 2387/03		MAND (P3-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 2388/03		MAND (P3-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 2389/03		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 2390/03		HC	Neotragini	*Madoqua*	*avifluminis*
EP 2391/03		HC	Neotragini	*Madoqua*	*avifluminis*
EP 2392/03		HC	Neotragini	*Madoqua*	*avifluminis*
EP 1192/04		MAND (P4-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1193/04		MAND (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1194/04		MAND (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1195/04		MAND (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1196/04		UM	Neotragini	*Madoqua*	*avifluminis*

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Laetoli Locality 9 S (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 1197/04		UM3	Neotragini	*Madoqua*	*avifluminis*
EP 1199/04		HC	Neotragini	*Madoqua*	*avifluminis*
EP 473/05		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 474/05		MAND fragment (P4-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 477/05		HC	Neotragini	*Madoqua*	*avifluminis*
EP 903/98	R	MAND fragment (M3)	Tragelaphini	*Tragelaphus*	

*Associated material

Laetoli Locality 10

Specimen #	Side	Element	Tribe	Genus	Species
EP 448/98	R	UM	?Alcelaphini		
EP 842/98		UM fragment	Antilopini	*Aepyceros*	*dietrichi*
EP 152/99	L	LM1	Antilopini	*Aepyceros*	*dietrichi*
EP 417/98	L	LM1	Antilopini	*Aepyceros*	*dietrichi*
EP 444/98	R	UM2	Antilopini	*Aepyceros*	*dietrichi*
EP 449/98	L	UM	Antilopini	*Aepyceros*	*dietrichi*
EP 843/98	L	MAX fragment (P3-P4)	Antilopini	*Aepyceros*	*dietrichi*
EP 151/99	R	UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 2939/00	R	LM1 or LM2	Antilopini	*Aepyceros*	*dietrichi*
EP 615/01	R	UM2	Antilopini	*Aepyceros*	*dietrichi*
EP 616/01	R	UM2	Antilopini	*Aepyceros*	*dietrichi*
EP 617/01	L	LM fragment	Antilopini	*Aepyceros*	*dietrichi*
EP 942/03	R	UM fragment	Antilopini	*Aepyceros*	*dietrichi*
EP 956/03	L	MAND fragment (M1- M3)	Antilopini	*Aepyceros*	*dietrichi*
EP 830/98	R	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 2938/00	L	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 3105/00	L	LP4	Alcelaphini	*Parmularius*	*pandatus*
EP 949/03	R	LM2	Alcelaphini		Larger sp.
EP 450/98	L	UM	Alcelaphini		
EP 440/98	L	UM1-M2	Alcelaphini		
EP 442/98	L	UM3	Alcelaphini		
EP 443/98	L	UM2	Alcelaphini		
EP 460/98	R	MAND fragment (M2- M3)	Alcelaphini		
EP 470/98	L	LM	Alcelaphini		
EP 514/98	R	UM	Alcelaphini		
EP 825/98	R	LM	Alcelaphini		
EP 829/98	R	UM3 fragment	Alcelaphini		
EP 154/99	R	LM	Alcelaphini		
EP 818/00	L	MAND (dp3-M1)	Alcelaphini		
EP 946/03	R	LM	Alcelaphini		
EP 947/03	R	LM	Alcelaphini		
EP 951/03	R	LM fragment	Alcelaphini		
EP 705/04	R	MAND fragment (M)	Alcelaphini		
EP 706/04	L	UP4	Alcelaphini		
EP 270/05	L	UM3	Alcelaphini		
EP 272/05	R	LM	Alcelaphini		
EP 707/04	L	UP4	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 447/98	R	Probably UM2	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 468/98	R	LP4	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 822/98	L	UM3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 828/98	L	UM3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 155/99	R	UP3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 819/00	L	UM fragment	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 952/03	R	LP4	aff. Antilopini?	"*Gazella*"	*kohllarseni*

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Laetoli Locality 10 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 277/05	R	LM3 fragment	aff. Antilopini?	“*Gazella*”	*kohllarseni*
EP 420/98	R	LM fragment	Bovini	*Simatherium*	*kohllarseni*
EP 456/98	L	MAX fragment (P2-P4)	Antilopini	*Gazella*	*janenschi*
EP 457/98	L	MAX fragment (P4-M2)	Antilopini	*Gazella*	*janenschi*
EP 461/98	R	MAND (M1-M3)	Antilopini	*Gazella*	*janenschi*
EP 462/98	L	MAND (M2-M3)	Antilopini	*Gazella*	*janenschi*
EP 463/98	R	MAND (M2-M3)	Antilopini	*Gazella*	*janenschi*
EP 469/98	R	MAND (M2)	Antilopini	*Gazella*	*janenschi*
EP 827/98	L	UM1	Antilopini	*Gazella*	*janenschi*
EP 866/98		UM2	Antilopini	*Gazella*	*janenschi*
EP 150/99	R	MAND fragment (M1 -M2)	Antilopini	*Gazella*	*janenschi*
EP 153/99	L	LM3	Antilopini	*Gazella*	*janenschi*
EP 2941/00	R	MAND (M1-M2)	Antilopini	*Gazella*	*janenschi*
EP 3103/00	L	HC	Antilopini	*Gazella*	*janenschi*
EP 944/03	L	UP3	Antilopini	*Gazella*	*janenschi*
EP 958/03	R	UP3	Antilopini	*Gazella*	*janenschi*
EP 568/04	L?	HC	Antilopini	*Gazella*	*janenschi*
EP 276/05	R	LM2	Antilopini	*Gazella*	*janenschi*
EP 281/05	L	HC	Antilopini	*Gazella*	*janenschi*
EP 2030/00	R	LM3	Antilopini	*Gazella*	*granti*
EP 833/98	L	MAND fragment (M3)	Indet.	*Brabovus*	*nanincisus*
EP 2940/00	L	L M1 or LM2	Indet.	*Brabovus*	*nanincisus*
EP 280/05	R	LM	Indet.	*Brabovus*	*nanincisus*
EP 959/03		HC fragment	Hippotragini	*Hippotragus*	
EP 851/98		HC fragment	Hippotragini	*Hippotragus*	
EP 824/98		UM3	Hippotragini		
EP 445/98	L	UM2	Hippotragini		
EP 446/98	L	UM2	Hippotragini		
EP 452/98	R	UM	Hippotragini		
EP 831/98	R	LM1	Hippotragini		
EP 841/98	R	UP4	Hippotragini		
EP 3102/00	L	UM2	Hippotragini		
EP 945/03	L	Udp2	Hippotragini		
EP 718/04	L	MAX fragment (M1-M2)	Hippotragini		
EP 832/98	L	MAND fragment (M1- M3)	Cephalophini		
EP 454/98		UM	Neotragini	*Madoqua*	*avifluminis*
EP 455/98	L	MAX fragment (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 458/98		dp4-M2	Neotragini	*Madoqua*	*avifluminis*
EP 459/98		MAX fragment (P2-dp3)	Neotragini	*Madoqua*	*avifluminis*
EP 464/98		MAND (M1)	Neotragini	*Madoqua*	*avifluminis*
EP 465/98		MAND (M2 fragment + M3)	Neotragini	*Madoqua*	*avifluminis*
EP 466/98		MAND (M2 fragment + M3)	Neotragini	*Madoqua*	*avifluminis*
EP 467/98		MAND (P4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 473/98		HC	Neotragini	*Madoqua*	*avifluminis*
EP 823/98		MAX fragment (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 826/98		UM1	Neotragini	*Madoqua*	*avifluminis*
EP 836/98		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 837/98		MAND fragment (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 839/98		Associated P3 + P4	Neotragini	*Madoqua*	*avifluminis*
EP 840/98		UP4	Neotragini	*Madoqua*	*avifluminis*
EP 854/98		HC	Neotragini	*Madoqua*	*avifluminis*
EP 855/98		HC	Neotragini	*Madoqua*	*avifluminis*
EP 856/98		HC	Neotragini	*Madoqua*	*avifluminis*
EP 156/99		MAND (P2-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 157/99		MAND (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 158/99		UM1	Neotragini	*Madoqua*	*avifluminis*
EP 159/99		MAX fragment (P3-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 820/00		UM2	Neotragini	*Madoqua*	*avifluminis*

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Laetoli Locality 10 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 821/00		LM2	Neotragini	*Madoqua*	*avifluminis*
EP 822/00		MAND (P2-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 2942/00		MAND fragment (M)	Neotragini	*Madoqua*	*avifluminis*
EP 2943/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 3110/00		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 3111/00		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 3112/00		UM	Neotragini	*Madoqua*	*avifluminis*
EP 622/01		MAND (P4, M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 623/01		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 624/01		HC fragment	Neotragini	*Madoqua*	*avifluminis*
EP 943/03		MAX fragment (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 953/03		MAND fragment (P2-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 954/03		MAND fragment (dp4- M2)	Neotragini	*Madoqua*	*avifluminis*
EP 955/03		MAND fragment (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 961/03		HC	Neotragini	*Madoqua*	*avifluminis*
EP 962/03		HC	Neotragini	*Madoqua*	*avifluminis*
EP 597/04		MAX (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 708/04		MAX (M)	Neotragini	*Madoqua*	*avifluminis*
EP 709/04		MAX (M)	Neotragini	*Madoqua*	*avifluminis*
EP 838/98	L	MAND fragment (P4)	Neotragini	*?Raphicerus*	

Laetoli Locality 10E

Specimen #	Side	Element	Tribe	Genus	Species
EP 171/98	L	MAND fragment (M3)	Antilopini	*Aepyceros*	*dietrichi*
EP 290/98	L	UM1	Antilopini	*Aepyceros*	*dietrichi*
EP 301/98	R	UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 303/98	L	UM1	Antilopini	*Aepyceros*	*dietrichi*
EP 1539/98	R	LM3 fragment	Antilopini	*Aepyceros*	*dietrichi*
EP 041/99	R	UP3-P4	Antilopini	*Aepyceros*	*dietrichi*
EP 2844/00	R?	UP4	Antilopini	*Aepyceros*	*dietrichi*
EP 837/03	L	LM	Antilopini	*Aepyceros*	*dietrichi*
EP 162/98	R	MAND (M2-M3)	Alcelaphini	*Parmularius*	*pandatus*
EP 163/98	L	MAND (P3-M3)	Alcelaphini	*Parmularius*	*pandatus*
EP 168/98	R	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 169/98	L	UM	Alcelaphini	*Parmularius*	*pandatus*
EP 273/98	L	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 296/98	L	LM3 fragment	Alcelaphini	*Parmularius*	*pandatus*
EP 1533/98	L	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 1534/98	L	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 758/00	L	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 515/01*	R	MAND (P3-M3)	Alcelaphini	*Parmularius*	*pandatus*
	L	MAND (P3-M3)			
EP 516/01	R	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 517/01	L	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 032/99	L	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 291/98	R	MAND fragment (M2-M3)	Alcelaphini		Larger sp.
EP 170/98	R	LM3 fragment	Alcelaphini		
EP 297/98	R	UM	Alcelaphini		
EP 308/98	L	UM3	Alcelaphini		
EP 165/98	R	LM2-M3	Alcelaphini		
EP 275/98	R	LM2	Alcelaphini		
EP 1535/98	L	UM1	Alcelaphini		
EP 2838/00	L	MAND (M2-M3)	Alcelaphini		
EP 2840/00	L	LM2	Alcelaphini		

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Laetoli Locality 10E (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 284100	L	UM3 fragment	Alcelaphini		
EP 2842/00	R	UM1	Alcelaphini		
EP 523/01	R	LM	Alcelaphini		
EP 814/03	L	UM	Alcelaphini		
EP 819/03	R	LM	Alcelaphini		
EP 820/03	R	UM fragment	Alcelaphini		
EP 824/03	R	LM	Alcelaphini		
EP 833/03	R	LM	Alcelaphini		
EP 013/04	R	LM	Alcelaphini		
EP 016/04	L	MAND fragment (P3-P4)	Alcelaphini		
EP 018/04	R	UP	Alcelaphini		
EP 1376/04	L	MAND fragment (M1 fragment)	Alcelaphini		
EP 1377/04	L	LP4	Alcelaphini		
EP 915/05	L	UM3	Alcelaphini		
EP 017/04	L	MAND fragment (M3 fragment)	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 132/98	L	HC base	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 187/98	L	HC	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1541/98	L	UM3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 033/99	R	UM	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 822/03	R	UM	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 036/99	L	MAX fragment (P3-4)	?Antilopini		
EP 131/98	R	HC	Antilopini	*Gazella*	*janenschi*
EP 164/98	L	MAND (P4-M3)	Antilopini	*Gazella*	*janenschi*
EP 166/98	R	MAND (M3)	Antilopini	*Gazella*	*janenschi*
EP 167/98	R	MAND (P2-M3)	Antilopini	*Gazella*	*janenschi*
EP 173/98	R	UM3	Antilopini	*Gazella*	*janenschi*
EP 179/98	R	MAX (P2-P4)	Antilopini	*Gazella*	*janenschi*
EP 180/98	L	UP2	Antilopini	*Gazella*	*janenschi*
EP 293/98	R	UM2	Antilopini	*Gazella*	*janenschi*
EP 295/98	L	HC	Antilopini	*Gazella*	*janenschi*
EP 300/98	R	MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 302/98	R	HC	Antilopini	*Gazella*	*janenschi*
EP 304/98	L	MAND fragment (M1)	Antilopini	*Gazella*	*janenschi*
EP 305/98	L	MAX fragment (P2-M1)	Antilopini	*Gazella*	*janenschi*
EP 307/98	R	UM1	Antilopini	*Gazella*	*janenschi*
EP 309/98	L	MAND fragment (M1-M3)	Antilopini	*Gazella*	*janenschi*
EP 1538/98	L	LM2	Antilopini	*Gazella*	*janenschi*
EP 1547/98	R	HC	Antilopini	*Gazella*	*janenschi*
EP 034/99	L	MAX (P2-M1)	Antilopini	*Gazella*	*janenschi*
EP 035/99	R	MAX (M2-M3)	Antilopini	*Gazella*	*janenschi*
EP 240/00	L	HC	Antilopini	*Gazella*	*janenschi*
EP 757/00*	R	UM2 (2)	Antilopini	*Gazella*	*janenschi*
	L	UM3			
EP 773/00		HC fragment	Antilopini	*Gazella*	*janenschi*
EP 2843/00	L	UM2	Antilopini	*Gazella*	*janenschi*
EP 2846/00	R	MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 2847/00	L	LM1	Antilopini	*Gazella*	*janenschi*
EP 2849/00	R	UP3	Antilopini	*Gazella*	*janenschi*
EP 2866/00	L	HC	Antilopini	*Gazella*	*janenschi*
EP 518/01	L	UM3	Antilopini	*Gazella*	*janenschi*
EP 522/01	R	LM3	Antilopini	*Gazella*	*janenschi*
EP 524/01	R	UP2	Antilopini	*Gazella*	*janenschi*
EP 823/03	R	UM	Antilopini	*Gazella*	*janenschi*
EP 835/03	R	LM	Antilopini	*Gazella*	*janenschi*
EP 836/03	R	LM	Antilopini	*Gazella*	*janenschi*
EP 838/03	R	UM2-M3	Antilopini	*Gazella*	*janenschi*
EP 840/03	R	MAND (M3)	Antilopini	*Gazella*	*janenschi*
EP 012/04	L	HC	Antilopini	*Gazella*	*janenschi*

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Laetoli Locality 10E (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 014/04	R	LM	Antilopini	*Gazella*	*janenschi*
EP 916/05	L	UM3	Antilopini	*Gazella*	*janenschi*
EP 827/05	L	MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 830/03	R	UP	Antilopini	*Gazella*	*janenschi?*
EP 825/03	L	UM fragment	Antilopini	*Gazella*	*janenschi?*
EP 042/99	R	Ldp3	Bovini	*Simatherium*	*kohllarseni*
EP 172/98	R	Ldp4	Indet.	*Brabovus*	*nanincisus*
EP 161/98	L	MAND (P2-M3)	Hippotragini	*Hippotragus*	
EP 2839/00	L	MAND fragment (dp3)	Hippotragini	*Hippotragus*	
EP 941/03	L	HC	Hippotragini	*Hippotragus*	
EP 011/04	R	HC	Hippotragini	*Hippotragus*	
EP 814/05	R	UM1-M3	Hippotragini	*Hippotragus*	
EP 159/98		Partial cranium (occipital, parietal, frontal)	Hippotragini	*Hippotragus*	
EP 1532/98	L	MAND (M2)	Hippotragini	*Hippotragus*	
EP 140/98	L	UM	Hippotragini		
EP 174/98	R	LM fragment	Hippotragini		
EP 222/98	L	MAND fragment (M1- M3)	Hippotragini		
EP 223/98	L	UM	Hippotragini		
EP 224/98	R	UM	Hippotragini		
EP 230/98	L	UP4	Hippotragini		
EP 272/98	R	UM2	Hippotragini		
EP 277/98	R	MAX fragment (P4)	Hippotragini		
EP 279/98	R	UM2	Hippotragini		
EP 299/98	L	UM2	Hippotragini		
EP 229/98	L	UP3	Hippotragini		
EP 231/98	L	UP3	Hippotragini		
EP 232/98	R	LP4	Hippotragini		
EP 280/98	L	MAND fragment (M3)	Hippotragini		
EP 287/98	R	LM3	Hippotragini		
EP 288/98	R	UM2	Hippotragini		
EP 292/98	R	MAND fragment (M2)	Hippotragini		
EP 339/98		UM1 fragment	Hippotragini		
EP 1536/98	R	UM1	Hippotragini		
EP 1537/98	R	UM fragment	Hippotragini		
EP 1561/98	R	UM3	Hippotragini		
EP 030/99	L	MAX fragment (M2-M3)	Hippotragini		
EP 037/99	L	UP4	Hippotragini		
EP 038/99	L	UP3	Hippotragini		
EP 759/00	R	LM3	Hippotragini		
EP 2837/00	R	MAND (P3)	Hippotragini		
EP 2845/00	L	Ldp3	Hippotragini		
EP 519/01	L	MAND fragment (M2)	Hippotragini		
EP 520/01	R	LM	Hippotragini		
EP 521/01	R	LP4	Hippotragini		
EP 816/03	R	UM2-M3	Hippotragini		
EP 817/03	R	UM	Hippotragini		
EP 818/03	R	UM fragment	Hippotragini		
EP 015/04	L	LP3	Hippotragini		
EP 019/04	L	UM2	Hippotragini		
EP 1548/98		HC	Hippotragini or Alcelaphini		
EP 130/98	L	HC	Neotragini	*Madoqua*	*avifluminis*
EP 181/98	R	MAND (P2-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 183/98		UM2	Neotragini	*Madoqua*	*avifluminis*
EP 185/98		MAND fragment (P2 + P3 fragment)	Neotragini	*Madoqua*	*avifluminis*
EP 284/98	R	MAND fragment (P3-M3)	Neotragini	*Madoqua*	*avifluminis*

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Laetoli Locality 10E (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 338/98		LP4	Neotragini	*Madoqua*	*avifluminis*
EP 1540/98		MAND fragment (M1)	Neotragini	*Madoqua*	*avifluminis*
EP 1543/98		Udp3	Neotragini	*Madoqua*	*avifluminis*
EP 1545/98		HC	Neotragini	*Madoqua*	*avifluminis*
EP 1546/98		HC	Neotragini	*Madoqua*	*avifluminis*
EP 043/99		MAND fragment (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 044/99		MAND fragment (P2-P3)	Neotragini	*Madoqua*	*avifluminis*
EP 046/99		HC	Neotragini	*Madoqua*	*avifluminis*
EP 761/00		MAND fragment (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 762/00		MAND fragment (P3-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 763/00		MAND fragment (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 764/00		MAND fragment (erupting M2)	Neotragini	*Madoqua*	*avifluminis*
EP 765/00		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 766/00		MAND fragment (P3)	Neotragini	*Madoqua*	*avifluminis*
EP 767/00		MAND fragment (M)	Neotragini	*Madoqua*	*avifluminis*
EP 768/00		MAND fragment (P4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 769/00		LM3	Neotragini	*Madoqua*	*avifluminis*
EP 770/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 2850/00		MAND fragment (M1- M3)	Neotragini	*Madoqua*	*avifluminis*
EP 2851/00		MAND fragment (P4)	Neotragini	*Madoqua*	*avifluminis*
EP 2852/00		MAND fragment (M1)	Neotragini	*Madoqua*	*avifluminis*
EP 2853/00		MAND fragment (P3-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 2854/00		LM	Neotragini	*Madoqua*	*avifluminis*
EP 525/01		MAND (P4-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 526/01		MAND (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 527/01		MAND (P2-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 826/03		MAX fragment (M)	Neotragini	*Madoqua*	*avifluminis*
EP 827/03		UM	Neotragini	*Madoqua*	*avifluminis*
EP 828/03		UM2	Neotragini	*Madoqua*	*avifluminis*
EP 829/03		MAX fragment (M1 + M2)	Neotragini	*Madoqua*	*avifluminis*
EP 832/03		MAX fragment (P3 + P4)	Neotragini	*Madoqua*	*avifluminis*
EP 841/03		MAND (dp3-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 842/03		MAND (M1 + M2)	Neotragini	*Madoqua*	*avifluminis*
EP 844/03		LM	Neotragini	*Madoqua*	*avifluminis*
EP 020/04		MAND fragment (dp3-dp4 + M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 021/04		MAND fragment (P4-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 022/04		MAND fragment (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 023/04		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 024/04		LM	Neotragini	*Madoqua*	*avifluminis*
EP 025/04		UM3	Neotragini	*Madoqua*	*avifluminis*
EP 026/04		UM3	Neotragini	*Madoqua*	*avifluminis*
EP 027/04		MAX fragment (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 076/04		UM	Neotragini	*Madoqua*	*avifluminis*
EP 077/04		MAX fragment (P3-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 1240/04		MAND fragment (P2-P3)	Neotragini	*Madoqua*	*avifluminis*
EP 1241/04		UM	Neotragini	*Madoqua*	*avifluminis*
EP 1242/04		Ldp4	Neotragini	*Madoqua*	*avifluminis*
EP 076/04		UM	Neotragini	*Madoqua*	*avifluminis*
EP 077/04		MAX fragment (P3-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 020/04		MAND fragment (dp3-dp4 + M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 021/04		MAND fragment (P4-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 022/04		MAND fragment (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 023/04		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 024/04		LM	Neotragini	*Madoqua*	*avifluminis*
EP 025/04		UM3	Neotragini	*Madoqua*	*avifluminis*
EP 026/04		UM3	Neotragini	*Madoqua*	*avifluminis*

(continued)

Laetoli Locality 10E (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 027/04		MAX fragment (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 825/05		UM	Neotragini	*Madoqua*	*avifluminis*
EP 826/05		UM	Neotragini	*Madoqua*	*avifluminis*
EP 828/05		UP	Neotragini	*Madoqua*	*avifluminis*
EP 829/05		MAND fragment (M1)	Neotragini	*Madoqua*	*avifluminis*
EP 830/05		HC	Neotragini	*Madoqua*	*avifluminis*
EP 176/98	R	MAND fragment (M3)	Neotragini	*?Raphicerus*	
EP 177/98	L	UM3	Neotragini	*?Raphicerus*	
EP 294/98	L	MAND fragment (M2-M3)	Neotragini	*?Raphicerus*	
EP 298/98	L	UM1	Neotragini	*?Raphicerus*	
EP 1542/98	L	UM2	Neotragini	*?Raphicerus*	
EP 310/98	L	MAND fragment (M3)	Neotragini	*?Raphicerus*	
EP 2848/00	R	UM	Neotragini	*?Raphicerus*	
EP 834/03	R	LM	Neotragini	*?Raphicerus*	
EP 839/03	R	MAND fragment (M3)	Neotragini	*?Raphicerus*	
EP 1239/04	R	MAND fragment (P2-P3)	Neotragini	*?Raphicerus*	
EP 182/98	L	UP4	Neotragini		
EP 815/03	R	UM	?Reduncini		

*Associated material

Laetoli Locality 10NE

Specimen #	Side	Element	Tribe	Genus	Species
EP 405/98	L	UM2-M3	Alcelaphini		Larger sp.
EP 406/98	R	LP4	Alcelaphini		
EP 408/98		HC	Neotragini	*Madoqua*	*avifluminis*

Laetoli Locality 10W

Specimen #	Side	Element	Tribe	Genus	Species
EP 566/98	L	UM2	Antilopini	*Aepyceros*	*dietrichi*
EP 568/98	L	UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 687/98	L	UM	Antilopini	*Aepyceros*	*dietrichi*
EP 691/98	L	UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 705/98	L	MAND fragment (P4)	Antilopini	*Aepyceros*	*dietrichi*
EP 709/98	R	UP4 fragment	Antilopini	*Aepyceros*	*dietrichi*
EP 761/98	R	LM	Antilopini	*Aepyceros*	*dietrichi*
EP 1593/98	L	LM	Antilopini	*Aepyceros*	*dietrichi*
EP 1594/98	L	UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 1598/98	L	UP4	Antilopini	*Aepyceros*	*dietrichi*
EP 129/99	L	UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 131/99	L	UM	Antilopini	*Aepyceros*	*dietrichi*
EP 670/01	L	UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 671/01	R	UP3	Antilopini	*Aepyceros*	*dietrichi*
EP 562/98	L	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 560/98	L	MAND fragment (M2-M3)	Alcelaphini	*Parmularius*	*pandatus*
EP 677/98	L	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 679/98	R	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 681/98	L	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 682/98	R	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 693/98	R	LM3	Alcelaphini	*Parmularius*	*pandatus*
EP 696/98	R	LM1	Alcelaphini	*Parmularius*	*pandatus*

(continued)

Laetoli Locality 10W (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 697/98	L	LM	Alcelaphini	*Parmularius*	*pandatus*
EP 699/98	L	LM3	Alcelaphini	*Parmularius*	*pandatus*
EP 700/98	L	MAND fragment (M1-M2)	Alcelaphini	*Parmularius*	*pandatus*
EP 701/98	L	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 756/98	L	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 759/98	R	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 768/98	R	LM3	Alcelaphini	*Parmularius*	*pandatus*
EP 1587/98	R	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 1589/98	R	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 1591/98	R	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 130/99	L	LM1	Alcelaphini	*Parmularius*	*pandatus*
EP 663/01	R	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 664/01	L	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 665/01	L	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 666/01	R	MAND fragment (M3)	Alcelaphini	*Parmularius*	*pandatus*
EP 668/01	L	LM1	Alcelaphini	*Parmularius*	*pandatus*
EP 669/01	L	LM3 fragment	Alcelaphini	*Parmularius*	*pandatus*
EP 838/00	L	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 690/98	L	Udp4	Alcelaphini		
EP 546/98	R	MAND fragment (P4-M3)	Alcelaphini		
EP 548/98	R	MAND (P4-M2 crown base)	Alcelaphini		
EP 569/98	R	UM	Alcelaphini		
EP 575/98	R	UM3	Alcelaphini		
EP 576/98	L	UM3	Alcelaphini		
EP 577/98	L	UM	Alcelaphini		
EP 578/98	R	Udp3	Alcelaphini		
EP 675/98	L	UM2	Alcelaphini		
EP 676/98	L	UM1	Alcelaphini		
EP 680/98	R	UM3	Alcelaphini		
EP 683/98	L	UM	Alcelaphini		
EP 684/98	L	UM3	Alcelaphini		
EP 694/98	R	LM3 fragment	Alcelaphini		
EP 702/98	R	LM	Alcelaphini		
EP 703/98	R	MAND fragment (M2-M3)	Alcelaphini		
EP 707/98	L	LP4	Alcelaphini		
EP 763/98	L	LM3	Alcelaphini		
EP 764/98	R	LM	Alcelaphini		
EP 769/98	L	UM3	Alcelaphini		
EP 805/98	L	UM	Alcelaphini		
EP 1583/98	R	MAND fragment (P4-M2)	Alcelaphini		
EP 1585/98	L	LM3	Alcelaphini		
EP 1588/98	R	MAX fragment (M1-M2)	Alcelaphini		
EP 1595/98	R	UM2 fragment	Alcelaphini		
EP 128/99	L	UM3	Alcelaphini		
EP 839/00	L	LP3	Alcelaphini		
EP 3134/00	L	UM1-M2	Alcelaphini		
EP 3144/00	L	MAND (I, M1-M3)	Alcelaphini		
EP 1016/03	R	UM3	Alcelaphini		
EP 1017/03	R	UM3	Alcelaphini		
EP 1018/03	R	UM2-M3	Alcelaphini		
EP 1021/03	R	LM	Alcelaphini		
EP 1022/03	L	UP4	Alcelaphini		
EP 685/04	R	MAND fragment (M3)	Alcelaphini		
EP 1396/05	L	LP4	Alcelaphini		
EP 570/98	L	UM	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 688/98	R	UM	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 573/98	R	LM2	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 692/98	L	LM3	aff. Antilopini?	"*Gazella*"	*kohllarseni*

(continued)

Laetoli Locality 10W (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 706/98	R	LP4	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1020/03	R	UM	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 559/98	R	MAND (P4-M3)	Antilopini	*Gazella*	*janenschi*
EP 567/98	R	UM (?M2)	Antilopini	*Gazella*	*janenschi*
EP 686/98	L	UM3	Antilopini	*Gazella*	*janenschi*
EP 695/98	R	MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 698/98	R	MAND fragment (M1-M2)	Antilopini	*Gazella*	*janenschi*
EP 773/98	R	HC	Antilopini	*Gazella*	*janenschi*
EP 3136/00	L	LM3	Antilopini	*Gazella*	*janenschi*
EP 1019/03	L	UM3	Antilopini	*Gazella*	*janenschi*
EP 1037/03	L	HC	Antilopini	*Gazella*	*janenschi*
EP 686/04	L	UM	Antilopini	*Gazella*	*janenschi*
EP 312/05	L	MAND fragment (P3-M2)	Antilopini	*Gazella*	*janenschi*
EP 547/98	R	MAND fragment (P4-M3)	Indet.	*Brabovus*	*nanincisus*
EP 689/98	L	UM	Indet.	*Brabovus*	*nanincisus*
EP 127/99	R	MAND (M2-M3)	Indet.	*Brabovus*	*nanincisus*
EP 137/99	L	MAND fragment (M2-M3)	Indet.	*Brabovus*	*nanincisus*
EP 3198/00	R	MAND (P3-M2)	Indet.	*Brabovus*	*nanincisus*
EP 605/04	R	LM	Indet.	*Brabovus*	*nanincisus*
EP 309/05	L	LM fragment	Indet.	*Brabovus*	*nanincisus*
EP 662/01	L	UM	Hippotragini		
EP 276/99	L	MAND fragment (erupting P3- P4 + M1)	Hippotragini		
EP 558/98	R	MAND fragment (M2)	Hippotragini		
EP 563/98	R	UM2	Hippotragini		
EP 564/98	R	UM1 or UM2	Hippotragini		
EP 565/98	R	UM1 or UM2	Hippotragini		
EP 572/98	R	LM2	Hippotragini		
EP 685/98	L	UM	Hippotragini		
EP 1590/98	R	UM2	Hippotragini		
EP 667/01	R	LM2 fragment	Hippotragini		
EP 308/05	R	MAND fragment (M3)	Hippotragini		
EP 311/05	R	LM3	Hippotragini		
EP 758/98	L	UM1	Cephalophini		
EP 549/98		MAND (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 550/98		MAND fragment (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 551/98		MAND fragment (M1)	Neotragini	*Madoqua*	*avifluminis*
EP 552/98		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 553/98		MAND fragment (M1 + M3)	Neotragini	*Madoqua*	*avifluminis*
EP 554/98		MAND fragment (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 555/98		MAND fragment (P4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 556/98		MAND fragment (P3-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 557/98		MAND fragment (P2-P3)	Neotragini	*Madoqua*	*avifluminis*
EP 579/98		MAX fragment (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 580/98		UM3	Neotragini	*Madoqua*	*avifluminis*
EP 581/98		HC	Neotragini	*Madoqua*	*avifluminis*
EP 708/98	L	LP4	Neotragini	*Madoqua*	*avifluminis*
EP 719/98		HC	Neotragini	*Madoqua*	*avifluminis*
EP 720/98		HC	Neotragini	*Madoqua*	*avifluminis*
EP 736/98	L	MAND (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 765/98		MAND (P4-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 766/98		MAND (P4-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 767/98	L	MAND (P3-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1584/98		MAND fragment (P2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1592/98		MAND (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1596/98		UM (2)	Neotragini	*Madoqua*	*avifluminis*
EP 1597/98		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1599/98		UM2	Neotragini	*Madoqua*	*avifluminis*

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Laetoli Locality 10W (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 1600/98		UM2	Neotragini	*Madoqua*	*avifluminis*
EP 133/99		MAND fragment (P2-P3)	Neotragini	*Madoqua*	*avifluminis*
EP 134/99		MAND fragment (P4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 135/99		MAND fragment (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 136/99		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 138/99		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 3145/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 3146/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 3147/00		MAND (P2-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 3148/00		MAND (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 3149/00		MAND (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 3150/00		LM	Neotragini	*Madoqua*	*avifluminis*
EP 3151/00		MAX (P2-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 3152/00		UM	Neotragini	*Madoqua*	*avifluminis*
EP 3153/00		UM3	Neotragini	*Madoqua*	*avifluminis*
EP 3154/00		MAND (M2)	Neotragini	*Madoqua*	*avifluminis*
EP 674/01		MAX fragment (P3-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 675/01		UP3-P4	Neotragini	*Madoqua*	*avifluminis*
EP 676/01		MAX fragment (M)	Neotragini	*Madoqua*	*avifluminis*
EP 677/01		MAND fragment (P4-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 678/01		MAND fragment (P4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 679/01		MAND fragment (P4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 1023/03		MAND (P3-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1024/03		MAND (M1- M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1025/03		MAND (M2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1026/03*		UM1 + UM3	Neotragini	*Madoqua*	*avifluminis*
EP 1027/03		UM2	Neotragini	*Madoqua*	*avifluminis*
EP 1028/03		UM	Neotragini	*Madoqua*	*avifluminis*
EP 1029/03		LM1	Neotragini	*Madoqua*	*avifluminis*
EP 1030/03		LM	Neotragini	*Madoqua*	*avifluminis*
EP 1031/03		LM	Neotragini	*Madoqua*	*avifluminis*
EP 1032/03		LI	Neotragini	*Madoqua*	*avifluminis*
EP 1033/03		LP4	Neotragini	*Madoqua*	*avifluminis*
EP 1034/03		UP2-P4	Neotragini	*Madoqua*	*avifluminis*
EP 1035/03		UM	Neotragini	*Madoqua*	*avifluminis*
EP 1036/03		HC	Neotragini	*Madoqua*	*avifluminis*
EP 1651/04	L	MAND (P2-P3)	Neotragini	*Madoqua*	*avifluminis*
EP 616/04		MAND fragment (P4-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 617/04		MAND fragment (P4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 618/04		MAND fragment (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 619/04		MAND fragment (M1)	Neotragini	*Madoqua*	*avifluminis*
EP 688/04		MAX (P4-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 689/04		UM	Neotragini	*Madoqua*	*avifluminis*
EP 313/05		LM	Neotragini	*Madoqua*	*avifluminis*
EP 314/05		HC	Neotragini	*Madoqua*	*avifluminis*
EP 694/05	L	MAND fragment (P4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 718/98		HC fragment, no base	Neotragini	*?Raphicerus*	

*Associated material

Laetoli Locality 11

Specimen #	Side	Element	Tribe	Genus	Species
EP 054/00	L	UM1	Antilopini	*Aepyceros*	*dietrichi*
EP 4269/00	R	MAX (P4-M3)	Antilopini	*Aepyceros*	*dietrichi*
EP 2559/00	R	UM3	Alcelaphini	*Parmularius*	*pandatus*

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Laetoli Locality 11 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 4270/00	L	MAND (M2-M3)	Alcelaphini	*Parmularius*	*pandatus*
EP 053/00	R	UM fragment	Alcelaphini		
EP 2553/00	R	UM3	Alcelaphini		
EP 2554/00	L	UM	Alcelaphini		
EP 2558/00	R	UM1 or UM2	Alcelaphini		
EP 2562/00	L	LP4	Alcelaphini		
EP 4271/00	L	UM3	Alcelaphini		
EP 4272/00	R	UM2	Alcelaphini		
EP 954/01	R	UP4	Alcelaphini		
EP 1268/03	L	MAND fragment (M3)	Alcelaphini		
EP 1020/04	R	UM3	Alcelaphini		
EP 1021/04	R	LM1	Alcelaphini		
EP 1022/04	L	Ldp4	Alcelaphini		
EP 1025/04	R	LP3 fragment	Alcelaphini		
EP 953/01	R	UM fragment			
EP 2561/00	R	MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 951/01	R	UM3	Antilopini	*Gazella*	*janenschi*
EP 952/01	R	UM2	Antilopini	*Gazella*	*janenschi*
EP 2556/00	L	UM3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1018/04	L	MAND (M1-M2)	Antilopini	*Gazella*	*janenschi*
EP 1019/04	R	HC	Antilopini	*Gazella*	*janenschi*
EP 1026/04	L	UP4	Antilopini	*Gazella*	*janenschi*
EP 1269/03	R	UM	Antilopini	*Gazella*	
EP 1271/03		HC	Antilopini	*Gazella*	
EP 1267/03	R	UM3	Antilopini		
EP 023/05	L	UM	Indet.	*Brabovus*	*nanincisus*
EP 048/00	L	UM3	Hippotragini		
EP 049/00	R	MAX (P4-M2)	Hippotragini		
EP 050/00	R	LM2	Hippotragini		
EP 051/00	L	UM	Hippotragini		
EP 052/00	L	MAND fragment (P4)	Hippotragini		
EP 055/00	L	UM2	Hippotragini		
EP 056/00	L	LM	Hippotragini		
EP 057/00	L	UP3	Hippotragini		
EP 059/00	R	UP4	Hippotragini		
EP 2555/00	R	UM1 or UM2	Hippotragini		
EP 2557/00	R	UM2	Hippotragini		
EP 4273/00	R	UP3	Hippotragini		
EP 955/01	R	LM3 fragment	Hippotragini		
EP 1023/04	R	UP2	Hippotragini		
EP 058/00		MAX fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 060/00		MAX (P4-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 2560/00		MAX fragment (P2-P3)	Neotragini	*Madoqua*	*avifluminis*
EP 4288/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 4289/00		MAND (M1)	Neotragini	*Madoqua*	*avifluminis*
EP 4290/00		UP4 fragment	Neotragini	*Madoqua*	*avifluminis*
EP 956/01		MAX (P3-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 957/01		MAND (P3)	Neotragini	*Madoqua*	*avifluminis*
EP 958/01		HC	Neotragini	*Madoqua*	*avifluminis*
EP 959/01		HC	Neotragini	*Madoqua*	*avifluminis*
EP 1270/03		HC (3)	Neotragini	*Madoqua*	*avifluminis*
EP 1272/03		MAND fragment (M1)	Neotragini	*Madoqua*	*avifluminis*
EP 1273/03		MAND fragment (P4)	Neotragini	*Madoqua*	*avifluminis*
EP 1027/04		MAND fragment (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1028/04		UP3-M1	Neotragini	*Madoqua*	*avifluminis*
EP 1029/04		UM2-M3	Neotragini	*Madoqua*	*avifluminis*

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Laetoli Locality 11 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 1030/04		UM	Neotragini	*Madoqua*	*avifluminis*
EP 1031/04		MAND fragment (M)	Neotragini	*Madoqua*	*avifluminis*
EP 1032/04		UP	Neotragini	*Madoqua*	*avifluminis*

Laetoli Locality 12

Specimen #	Side	Element	Tribe	Genus	Species
EP 350/00	L	HC fragment	Alcelaphini	*Parmularius*	*pandatus*
EP 542/05	R	HC	Alcelaphini	*Parmularius*	*pandatus*
EP 347/00	L	UM3	Alcelaphini		
EP 349/00	R	Udp4	Alcelaphini		
EP 352/00	R	MAND fragment (M1- M2)	Alcelaphini		
EP 1576/04	R	MAND (M)	Alcelaphini		
EP 348/00	R	UM3	Antilopini	*Gazella*	*janenschi*
EP 3553/00	R	LM (probably M2)	Bovini	*Simatherium*	*kohllarseni*
EP 351/00	L	MAND (P3-M2)	Indet.	*Brabovus*	*nanincisus*
EP 543/05	L	LP2-P3	Hippotragini	*Oryx*	*deturi*
EP 346/00	L	MAND fragment (M2)	Hippotragini		
EP 1424/01	L	UP4	Hippotragini		
EP 1575/04	L	MAND (P4)	Hippotragini		
EP 1578/04		MAND (M)	Neotragini	*Madoqua*	*avifluminis*
EP 1579/04		MAND (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1580/04		MAND (UM)	Neotragini	*Madoqua*	*avifluminis*
EP 549/05		UM	Neotragini	*Madoqua*	*avifluminis*

Laetoli Locality 12E

Specimen #	Side	Element	Tribe	Genus	Species
EP 380/00	L	LM3	Antilopini	*Aepyceros*	*dietrichi*
EP 378/00	R	UM2	Alcelaphini		?small sp.
EP 376/00	R	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 1403/01	L	UM (probably M1)	Alcelaphini		
EP 1514/03	R	LM	Alcelaphini		
EP 1499/03	R	UM fragment	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 381/00	R	UM2	Antilopini	*Gazella*	*janenschi*
EP 382/00	L	MAX fragment (P3-M1)	Antilopini	*Gazella*	*janenschi*
EP 383/00	L	UM3	Antilopini	*Gazella*	*janenschi*
EP 1404/01	L	LM2 fragment	Indet.	*Brabovus*	*nanincisus*
EP 1559/04	L	LM3 fragment	Indet.	*Brabovus*	*nanincisus*
EP 1560/04	L	LM1 or LM2	Indet.	*Brabovus*	*nanincisus*
EP 1561/04	L	LP4	Indet.	*Brabovus*	*nanincisus*
EP 516/05	L	UM1-M2	Indet.	*Brabovus*	*nanincisus*
EP 379/00	L	UM3	Hippotragini		
EP 384/00	L	UP3	Hippotragini		
EP 3524/00	L	MAND fragment (M)	Hippotragini		
EP 1500/03	R	LM3	Hippotragini		
EP 393/00		MAND (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 394/00		MAND fragment (M3)	Neotragini	*Madoqua*	*avifluminis*
EP 395/00		UM1	Neotragini	*Madoqua*	*avifluminis*
EP 396/00		UM2	Neotragini	*Madoqua*	*avifluminis*
EP 397/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 3522/00		MAND (dp4+M1)	Neotragini	*Madoqua*	*avifluminis*
EP 3523/00		MAND (M1)	Neotragini	*Madoqua*	*avifluminis*

(continued)

Laetoli Locality 12E (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 1405/01		MAND (P3-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1406/01		LM3	Neotragini	*Madoqua*	*avifluminis*
EP 1515/03		MAND (P3-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 517/05		MAX (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 518/05		UM	Neotragini	*Madoqua*	*avifluminis*
EP 519/05		MAND fragment (P4- M1)	Neotragini	*Madoqua*	*avifluminis*
EP 520/05		MAND Fragment (P4- M1)	Neotragini	*Madoqua*	*avifluminis*
EP 521/05		HC	Neotragini	*Madoqua*	*avifluminis*

Laetoli Locality 13

Specimen #	Side	Element	Tribe	Genus	Species
EP 1336/98	R	UM	Antilopini	*Aepyceros*	*dietrichi*
EP 2255/03	R	MAND fragment (M)	Antilopini	*Aepyceros*	*dietrichi*
EP 1112/04	L	UM1	Antilopini	*Aepyceros*	*dietrichi*
EP 1337/98	R	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 1338/98	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 1341/98	R	UM1 or UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 1343/98	L	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 1348/98	L	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 1349/98	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 1351/98	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 2031/00	L	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 2032/00	L	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 2033/00	R	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 2046/00	L	HC	Alcelaphini	*Parmularius*	*pandatus*
EP 2049/00*	L+R	HC (2)	Alcelaphini	*Parmularius*	*pandatus*
EP 2465/00	R	MAND fragment (M3)	Alcelaphini	*Parmularius*	*pandatus*
EP 2466/00		MAND fragment (P4-M2)	Alcelaphini	*Parmularius*	*pandatus*
EP 403/01	R	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 404/01	L	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 406/01	L	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 407/01	L	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 408/01	R	LM2 fragment	Alcelaphini	*Parmularius*	*pandatus*
EP 409/01	R	MAND fragment (M1- M2)	Alcelaphini	*Parmularius*	*pandatus*
EP 410/01	L	MAND fragment (M1-M2)	Alcelaphini	*Parmularius*	*pandatus*
EP 2267/03	L	HC fragment	Alcelaphini	*Parmularius*	*pandatus*
EP 2048/00		HC	Alcelaphini		Larger sp.
EP 1335/98	R	UM	Alcelaphini		
EP 1340/98	R	UM	Alcelaphini		
EP 1344/98	R	LM fragment	Alcelaphini		
EP 1345/98	R	LM	Alcelaphini		
EP 1347/98	L	UM	Alcelaphini		
EP 1350/98	R	UM	Alcelaphini		
EP 2029/00	L	MAND fragment (dp4- M2)	Alcelaphini		
EP 2467/00	L	UM2	Alcelaphini		
EP 2468/00	L	UM3	Alcelaphini		
EP 2470/00	R	UM1	Alcelaphini		
EP 2471/00	L	UM1	Alcelaphini		
EP 2254/03	R	MAND fragment (M)	Alcelaphini		
EP 1108/04	R	UM3	Alcelaphini		
EP 1109/04	L	UM3	Alcelaphini		
EP 1110/04	R	UM3	Alcelaphini		
EP 1111/04	R	UM	Alcelaphini		
EP 1115/04	L	MAND fragment (M3)	Alcelaphini		
EP 1116/04	R	MAND fragment (M1- M2)	Alcelaphini		

(continued)

Laetoli Locality 13 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 1334/98	L	MAX (P2-P3)	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 411/01	L	MAND fragment (M2- M3)	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1352/98	L	HC	Antilopini	*Gazella*	*janenschi*
EP 2044/00	L	MAND (M2)	Antilopini	*Gazella*	*janenschi*
EP 2045/00	R	HC	Antilopini	*Gazella*	*janenschi*
EP 2047/00	R	HC	Hippotragini	*Hippotragus*	
EP 482/01	L	MAND fragment (P2-M1)	Hippotragini	*Hippotragus*	
EP 1166/04*	R+L	HC (2)	Hippotragini	*Hippotragus*	
EP 1339/98	R	UM fragment	Hippotragini		
EP 2257/03	R	UP3-P4	Hippotragini		
EP 2149/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 2259/03		HC	Neotragini	*Madoqua*	*avifluminis*
EP 2260/03		HC	Neotragini	*Madoqua*	*avifluminis*
EP 2261/03		UM	Neotragini	*Madoqua*	*avifluminis*
EP 2262/03		LM1	Neotragini	*Madoqua*	*avifluminis*
EP 1113/04		UM	Neotragini	*Madoqua*	*avifluminis*
EP 1114/04		MAX (P4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 1117/04		HC fragment	Neotragini	*Madoqua*	*avifluminis*
EP 1167/05		MAX (P2-P4+M2 -M3)	Neotragini	*Madoqua*	*avifluminis*

*Associated material

Laetoli Locality 13 "Snake Gully"

Specimen #	Side	Element	Tribe	Genus	Species
EP 2100/00	L	MAND (M2-M3)	Antilopini	*Aepyceros*	*dietrichi*
EP 2104/00	L	MAND (P4-M1)	Alcelaphini	*Parmularius*	*pandatus*
EP 2105/00	L	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 2106/00	L	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 2089/00	R	UM3	Alcelaphini		
EP 2091/00	R	UM	Alcelaphini		
EP 2092/00	R	UM	Alcelaphini		
EP 2094/00	L	UM	Alcelaphini		
EP 2095/00	R	UM3	Alcelaphini		
EP 2101/00	L	MAND (?M2-M3)	Alcelaphini		
EP 2295/03	L	MAND (M1-M3)	Alcelaphini		
EP 2296/03	R	LM3	Alcelaphini		
EP 2299/03	L	UP4	Alcelaphini		
EP 2300/03	L	UP4	Alcelaphini		
EP 2302/03	L	UM3	Alcelaphini		
EP 2303/03	R	UM1-M3	Alcelaphini		
EP 2307/03	L	LP4	Alcelaphini		
EP 2099/00	L	MAND (M1)	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 2301/00	L	UM	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 2297/03	L	MAND fragment (P4)	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 2096/00		UM2	Antilopini	*Gazella*	*janenschi*
EP 2298/03	L	LM	Antilopini	*Gazella*	*janenschi*
EP 2306/03	L	UP2	Antilopini	*Gazella*	*janenschi*
EP 2318/03	L	MAND (M2-M3)	Antilopini	*Gazella*	*janenschi*
EP 2103/00	R	MAND (M3)	Indet.	*Brabovus*	*nanincisus*
EP 2093/00	R	UM fragment	Hippotragini		
EP 2098/00	L	LM2	Hippotragini		
EP 2301/03	R	LM fragment	Hippotragini		
EP 2107/00		MAX (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 2108/00		UM	Neotragini	*Madoqua*	*avifluminis*
EP 2305/03		MAND (P4-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 2308/03		Udp4	Neotragini	*Madoqua*	*avifluminis*

Laetoli Locality 13E

Specimen #	Side	Element	Tribe	Genus	Species
EP 2068/00		HC	Alcelaphini	*?Parmularius*	*?pandatus*
EP 2438/00	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 2064/00	L	UM3	Alcelaphini		Small sp.
EP 2065/00	R	UM	Alcelaphini		
EP 2439/00	L	UM2	Alcelaphini		
EP 2440/00	L	UM1	Alcelaphini		
EP 2441/00	R	UM3	Alcelaphini		
EP 2442/00	L	MAND fragment (dp4)	Alcelaphini		
EP 2353/03	L	LM3	Alcelaphini		
EP 2070/00		HC	Antilopini	*Gazella*	*janenschi*
EP 2443/00	L	MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 1141/05	L	MAND fragment (M)	Antilopini	*Gazella*	*janenschi*
EP 2069/00	R	HC	Indet.	*Brabovus*	*nanincisus*
EP 2063/00	L	MAND (M1-M2)	Hippotragini		
EP1140/05	R	UM	Hippotragini		
EP 2354/03		MAND (M1-M3)	Neotragini	*Madoqua*	*avifluminis*

Laetoli Locality 15

Specimen #	Side	Element	Tribe	Genus	Species
EP 1408/98	R	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 1409/98	L	UM2	Alcelaphini	*Parmularius*	*pandatus*
EP 1411/98	R	UM	Alcelaphini	*Parmularius*	*pandatus*
EP 1412/98	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 1414/98	R	LM	Alcelaphini	*Parmularius*	*pandatus*
EP 3355/00	R	MAND (M1-M3)	Alcelaphini	*Parmularius*	*pandatus*
EP 1410/98	R	LM	Alcelaphini		
EP 3340/00	R	UP4	Alcelaphini		
EP 1079/01	R	LM1 fragment	Alcelaphini		
EP 1594/03	R	UM1-M3	Alcelaphini		
EP 1413/98	L	MAX fragment (P3-P4)	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1423/98	R	HC	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1595/03	R	Udp4	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 1416/98	L	UM	Antilopini	*Gazella*	*janenschi*
EP 3339/00	L	MAND (dp4-M2)	Antilopini	*Gazella*	*janenschi*
EP 1080/01	L	MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 1084/01	L	HC fragment	Antilopini	*Gazella*	*janenschi*
EP 1591/03	R	MAX fragment (M1-M3)	Antilopini	*Gazella*	*janenschi*
EP 1596/03	R	UM1	Antilopini	*Gazella*	*janenschi*
EP 156/04	R	LM	Antilopini	*Gazella*	*janenschi*
EP 1419/98		HC	Antilopini	*Gazella*	
EP 3337/00	R	UM1-M3	Hippotragini	*Hippotragus*	
EP 1415/98	L	UM2	Hippotragini		
EP 3338/00	L	MAND (M1-M2)	Hippotragini		
EP 1593/03	L	LM3	Hippotragini		
EP 1598/03	L	MAND fragment (P4)	Hippotragini		
EP 1420/98		HC	Neotragini	*Madoqua*	*avifluminis*
EP 1597/03		UM3	Neotragini	*Madoqua*	*avifluminis*
EP 1417/98	L	UM3	Neotragini	*?Raphicerus*	
EP 1418/98	R	UM1 or UM2	Neotragini	*?Raphicerus*	
EP 1081/01	R	UP3	Neotragini		

Laetoli Locality 16

Specimen #	Side	Element	Tribe	Genus	Species
EP 112/00	R	UM1	Antilopini	*Aepyceros*	*dietrichi*
EP 113/00	R	UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 2365/00	L	UM2	Antilopini	*Aepyceros*	*dietrichi*
EP 2368/00	L	UM1-M2	Antilopini	*Aepyceros*	*dietrichi*
EP 243/03	L	UP4-M1, UM3	Antilopini	*Aepyceros*	*dietrichi*
EP 1519/04	R	UM1	Antilopini	*Aepyceros*	*dietrichi*
EP 109/00	R	UM1	Alcelaphini	*Parmularius*	*pandatus*
EP 2367/00	L	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 584/01	R	UM3	Alcelaphini	*Parmularius*	*pandatus*
EP 231/03	R	UM	Alcelaphini		
EP 2366/00	R	UM	Alcelaphini		
EP 228/03	R	UM	Alcelaphini		
EP 232/03	L	UM1-M2	Alcelaphini		
EP 235/03	L	MAND fragment (M)	Alcelaphini		
EP 236/03	R	UM fragment	Alcelaphini		
EP 244/03	R	LM	Alcelaphini		
EP 245/03	L	UM	Alcelaphini		
EP 246/03	L	LP3	Alcelaphini		
EP 388/04	L	LM	Alcelaphini		
EP 389/04	R	MAND fragment (M)	Alcelaphini		
EP 1517/04	L	MAND (M3)	Alcelaphini		
EP 160/05	R	UM	Alcelaphini		
EP 155/05	L	MAND fragment (M2)	Alcelaphini		
EP 230/03	R	UM3	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 234/03	R	UM	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 239/03	L	LM	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 117/00	L	MAND (M1+M3)	Antilopini	*Gazella*	*janenschi*
EP 2364/00	L	MAND (P3-M3)	Antilopini	*Gazella*	*janenschi*
EP 2370/00	L	UP4	Antilopini	*Gazella*	*janenschi*
EP 076/01	L	U M1	Antilopini	*Gazella*	*janenschi*
EP 585/01	L	LM1	Antilopini	*Gazella*	*janenschi*
EP 233/03	R	UM2-M3	Antilopini	*Gazella*	*janenschi*
EP 237/03	R	UM	Antilopini	*Gazella*	*janenschi*
EP 241/03	R	UP3-P4	Antilopini	*Gazella*	*janenschi*
EP 1617/04	L	MAND (P2-3, M1-3)	Antilopini	*Gazella*	*janenschi*
EP 2369/00	L	LM3	Antilopini		
EP 242/03	R	LM fragment	Indet.	*Brabovus*	*nanincisus*
EP 385/04		UM	Indet.	*Brabovus*	*nanincisus*
EP 1518/04	R	LM2	Indet.	*Brabovus*	*nanincisus*
EP 259/03	L	LM3	Bovini	*Simatherium*	*kohllarseni*
EP 393/04	R	UM	Bovini	*Simatherium*	*kohllarseni*
EP 120/00	R	UP2	Hippotragini	*Hippotragus*	
EP 240/03	L	Ldp3	Hippotragini	*Hippotragus*	
EP 392/04	L	Udp3-dp4	Hippotragini	*Hippotragus*	
EP 110/00	R	UM2	Hippotragini		
EP 111/00	R	UM3	Hippotragini		
EP 114/00	R	UM fragment	Hippotragini		
EP 116/00	R	LM3 fragment	Hippotragini		
EP 118/00	R	MAND (M)	Hippotragini		
EP 2372/00	R	Ldp3	Hippotragini		
EP 2395/00	R	UM	Hippotragini		
EP 583/01	L	Ldp4	Hippotragini		
EP 229/03	L	UM	Hippotragini		
EP 238/03	L	Ldp4 fragment	Hippotragini		

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Laetoli Locality 16 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 386/04	R	UM	Hippotragini		
EP 391/04	R	UP4	Hippotragini		
EP 1616/04		M	Hippotragini		
EP 156/05	R	MAND fragment (dp4-M1)	Hippotragini		
EP 157/05	L	LM	Hippotragini		
EP 390/04	R	LM3	Cephalophini		
EP 119/00		MAND (P2-P3)	Neotragini	*Madoqua*	*avifluminis*
EP 2374/00		MAND (P2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 2375/00		MAND (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 2376/00		MAND (P4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 2377/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 247/03		LM	Neotragini	*Madoqua*	*avifluminis*
EP 248/03		MAND fragment (P3)	Neotragini	*Madoqua*	*avifluminis*
EP 249/03		MAND fragment (P3-P4)	Neotragini	*Madoqua*	*avifluminis*
EP 250/03		HC	Neotragini	*Madoqua*	*avifluminis*
EP 251/03		HC	Neotragini	*Madoqua*	*avifluminis*
EP 1520/04		MAND (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 159/05		MAX fragment (P4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 161/05		HC	Neotragini	*Madoqua*	*avifluminis*
EP 162/05		HC	Neotragini	*Madoqua*	*avifluminis*
EP 163/05		HC fragment	Neotragini	*Madoqua*	*avifluminis*
EP 387/04	L	UM	?Reduncini		

Laetoli Locality 17

Specimen #	Side	Element	Tribe	Genus	Species
EP 2304/00	R	MAX (dp3)	Antilopini	*Aepyceros*	*dietrichi*
EP 2305/00	R	MAND (M3)	Alcelaphini		
EP 2303/00	R	MAND (M2-M3)	Antilopini	*Gazella*	*janenschi*
EP 2306/00	L	MAND (M1)	Antilopini	*Gazella*	*janenschi*
EP 085/01	R	MAND fragment (M1)	Indet.	*Brabovus*	*nanincisus*
EP 1618/04	L	LM1	Indet.	*Brabovus*	*nanincisus*
EP 2302/00	R	UM2 fragment	Hippotragini		
EP 1636/04	R	UM	Hippotragini		
EP 2315/00		UM3	Neotragini	*Madoqua*	*avifluminis*
EP 2316/00		LM	Neotragini	*Madoqua*	*avifluminis*
EP 2317/00		MAND (P2-M2)	Neotragini	*Madoqua*	*avifluminis*

Laetoli Locality 19

Specimen #	Side	Element	Tribe	Genus	Species
EP 1539/03	L	UM	Alcelaphini		
EP 1601/04	R	UM2	Alcelaphini		
EP 1602/04	L	MAND (P4)	Alcelaphini		
EP 564/05	L	LM	Hippotragini		
EP 1540/03		UP2	Neotragini	*Madoqua*	*avifluminis*
EP 1603/04		MAND (M)	Neotragini	*Madoqua*	*avifluminis*

Laetoli Locality 20

Specimen #	Side	Element	Tribe	Genus	Species
EP 443/00	L	UM1	Antilopini	*Aepyceros*	*dietrichi*
EP 445/00	L	UM3	Alcelaphini		
EP 446/00	R	MAND fragment (M3)	Alcelaphini		
EP 864/04	L	MAND fragment (P3)	Antilopini	*Gazella*	*janenschi*
EP 447/00		HC	Hippotragini	*Hippotragus*	
EP 865/04	R	LP2	Hippotragini	*Hippotragus*	
EP 444/00	R	UM1	Hippotragini		
EP 862/04	R	MAND fragment (M3)	Hippotragini		
EP 863/04	L	MAND fragment (M1-M2)	Hippotragini		
EP 452/00		MAND (dp3-dp4 + M1)	Neotragini	*Madoqua*	*avifluminis*
EP 453/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 3563/00		MAND (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 3564/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 866/04		UP	Neotragini	*Madoqua*	*avifluminis*

Laetoli Locality 21

Specimen #	Side	Element	Tribe	Genus	Species
EP 3675/00	L	UM	Antilopini	*Aepyceros*	*dietrichi*
EP 885/04	R	UM	Antilopini	*Aepyceros*	*dietrichi*
EP 3589/00	L	HC base	Antilopini	*?Aepyceros*	
EP 474/00	L	LM3	Alcelaphini		Larger sp.
EP 482/00	R	LM3	Alcelaphini		Small sp.?
EP 477/00	R	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 480/00	R	UM2-M3	Alcelaphini	*Parmularius*	*pandatus*
EP 490/00	L	HC	Alcelaphini	*Parmularius*	*pandatus*
EP 3679/00	R	HC	Alcelaphini	*Parmularius*	*pandatus*
EP 473/00	R	MAND fragment (M3)	Alcelaphini		
EP 478/00	L	UM	Alcelaphini		
EP 3578/00	L	UM3	Alcelaphini		
EP 3579/00	R	MAND fragment (M)	Alcelaphini		
EP 3580/00	L	MAND fragment (probably M2)	Alcelaphini		
EP 3585/00	R	UM2	Alcelaphini		
EP 3677/00	L	UM2	Alcelaphini		
EP 1559/03	L	MAND fragment (M3)	Alcelaphini		
EP 1560/03	R	LM3 fragment	Alcelaphini		
EP 1561/03	R	MAND fragment (M)	Alcelaphini		
EP 1563/03	L	UM	Alcelaphini		
EP 880/04	R	UM2	Alcelaphini		
EP 881/04	L	LM2	Alcelaphini		
EP 887/04	R	UP4	Alcelaphini		
EP 3586/00	L	UM1 or UM2	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 3587/00	R	UM1 or UM2	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 3582/00	R	UM2	Antilopini	*Gazella*	*janenschi*
EP 3680/00		HC fragment	Antilopini	*Gazella*	*janenschi*
EP 497/00*	R	MAX (P3-M3)	Antilopini	*Gazella*	*janenschi*
	L	MAX (P2-M3)			
		LM fragment			
EP 1435/01	L	HC	Antilopini	*Gazella*	*janenschi*
EP 1555/03	L	MAND fragment (P4-M3)	Antilopini	*Gazella*	*janenschi*
EP 1556/03	L	MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 1565/03	R	HC	Antilopini	*Gazella*	*janenschi*
EP 882/04	R	UM	Antilopini	*Gazella*	*janenschi*

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Laetoli Locality 21 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 883/04	L	UM1	Antilopini	*Gazella*	*janenschi*
EP 886/04	R	UM2	Antilopini	*Gazella*	*janenschi*
EP 888/04	L	UP3	Antilopini	*Gazella*	*janenschi*
EP 3683/00	L	LP4	Bovini	*Simatherium*	*kohllarseni*
EP 3588/00		HC	Hippotragini	*Hippotragus*	
EP 475/00	R	MAND fragment (M3)	Hippotragini		
EP 476/00	R	MAND fragment (M3)	Hippotragini		
EP 481/00*	L	UP2, UM (2)	Hippotragini		
	R	UM, LM3			
EP 3581/00	L	MAND fragment (M2-3)	Hippotragini		
EP 3583/00	L	UP2	Hippotragini		
EP 3584/00	L	UM2	Hippotragini		
EP 3676/00	R	LM3	Hippotragini		
EP 3678/00	R	MAND fragment (M3)	Hippotragini		
EP 1562/03		LM	Hippotragini		
EP 889/04	L	UP4	Hippotragini		
EP 492/00		MAND (M1-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1436/01		HC	Neotragini	*Madoqua*	*avifluminis*
EP 1557/03		MAND (P4-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1558/03		MAND (P2-P3)	Neotragini	*Madoqua*	*avifluminis*
EP 884/04		UM	Neotragini	*Madoqua*	*avifluminis*
EP 890/04		MAND fragment (dp4-M1)	Neotragini	*Madoqua*	*avifluminis*
EP 891/04		MAND fragment (P2)	Neotragini	*Madoqua*	*avifluminis*

*Associated material

Laetoli Locality 22

Specimen #	Side	Element	Tribe	Genus	Species
EP 3720/00	L	MAND fragment (M3)	Antilopini	*Aepyceros*	*dietrichi*
EP 1304/01	R	MAND fragment (M2)	Antilopini	*Aepyceros*	*dietrichi*
EP 1729/03	L	UM	Antilopini	*Aepyceros*	*dietrichi*
EP 106/04		LM fragment	Antilopini	*Aepyceros*	*dietrichi*
EP 107/04	R	UP4	Antilopini	*Aepyceros*	*dietrichi*
EP 538/00	L	LP4	Alcelaphini	*Parmularius*	*pandatus*
EP 3718/00	L	LM2	Alcelaphini	*Parmularius*	*pandatus*
EP 1732/03	R	HC	Alcelaphini	*Parmularius*	*pandatus*
EP 109/04	R	HC	Alcelaphini	*Parmularius*	*pandatus*
EP 1201/98	R	UM3	Alcelaphini		
EP 535/00	L + R	UM (3)	Alcelaphini		
EP 537/00	R	LP4	Alcelaphini		
EP 545/00		HC	Alcelaphini		
EP 1722/03	R	MAND (M2-M3)	Alcelaphini		
EP 1723/03	R	MAND (P3-M1)	Alcelaphini		
EP 1724/03	L	MAND (P3-M1)	Alcelaphini		
EP 1727/03	L	UM	Alcelaphini		
EP 1731/03	R	LM	Alcelaphini		
EP 1760/03	L	UM	Alcelaphini		
EP 099/04	R	UM	Alcelaphini		
EP 100/04	L	MAND fragment (M2-M3)	Alcelaphini		
EP 101/04	L	MAND (P3-P4)	aff. Antilopini?	"*Gazella*"	*kohllarseni*
EP 3721/00	R	MAND (M2-M3)	Antilopini	*Gazella*	*janenschi*
EP 3723/00	R	HC fragment	Antilopini	*Gazella*	*janenschi*
EP 3724/00	R	U M fragment	Antilopini	*Gazella*	*janenschi*

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Laetoli Locality 22 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 534/00	R	MAND fragment (M3)	Antilopini	*Gazella*	*janenschi*
EP 542/00	L	HC	Antilopini	*Gazella*	*janenschi*
EP 1302/01	L	HC	Antilopini	*Gazella*	*janenschi*
EP 1725/03	R	MAND (M2)	Antilopini	*Gazella*	*janenschi*
EP 1733/03	L	HC	Antilopini	*Gazella*	*janenschi*
EP 1734/03	R	HC	Antilopini	*Gazella*	*janenschi*
EP 104/04	R	UM	Antilopini	*Gazella*	*janenschi*
EP 1204/98	L	HC	Antilopini	*Gazella*	*janenschi*
EP 098/04	R	LM3	Indet.	*Brabovus*	*nanincisus*
EP 1199/98	R	MAND (M2)	Indet.	*Brabovus*	*nanincisus*
EP 1730/03	L	UM	Indet.	*Brabovus*	*nanincisus*
EP 1202/98	L	LM3 fragment	Bovini	*Simatherium*	*kohllarseni*
EP 3734/00	R	MAX (P4-M3)	Hippotragini	*Hippotragus*	
EP 1303/01	L	MAND (P3-P4)	Hippotragini	*Hippotragus*	
EP 1796/03		Neurocranium with HCs	Hippotragini	*Oryx*	*deturi*
EP 3722/00	L	MAND (dp3 and dp4 fragment)	Hippotragini		
EP 533/00	R	LM fragment	Hippotragini		
EP 536/00	L	LP4	Hippotragini		
EP 1305/01	L	Udp4	Hippotragini		
EP 1726/03	L	LM	Hippotragini		
EP 1728/03	L	UM	Hippotragini		
EP 105/04	L	UP2	Hippotragini		
EP 540/00		MAX (P2-P3)	Neotragini	*Madoqua*	*avifluminis*
EP 543/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 544/00		HC	Neotragini	*Madoqua*	*avifluminis*
EP 3725/00		MAX (P3-P4?)	Neotragini	*Madoqua*	*avifluminis*
EP 3726/00		MAND (P4-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 1332/01		MAND (P2-M3)	Neotragini	*Madoqua*	*avifluminis*
EP 1735/03		HC	Neotragini	*Madoqua*	*avifluminis*
EP 108/04		MAND fragment (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 108/04		MAND fragment (M1-M2)	Neotragini	*Madoqua*	*avifluminis*
EP 539/00		MAND (M2-M3)	Neotragini	*?Raphicerus*	
EP 102/04	L	L. MAND (M2)	Neotragini	*?Raphicerus*	

Laetoli Locality 22E

Specimen #	Side	Element	Tribe	Genus	Species
EP 1334/01	L	UM3	Alcelaphini		
EP 581/00	L	MAND fragment (M1-M2)	Hippotragini		
EP 583/00	R	LM	Hippotragini		
EP 584/00	R	UP4 fragment	Hippotragini		
EP 589/00	L	LM1-M3	Hippotragini		
EP 1333/01	R	MAND (P3-P4)	Hippotragini		
EP 1331/05	R	MAND (M1)	Cephalophini		
EP 1335/01		UM	Neotragini	*Madoqua*	*avifluminis*

Laetoli Locality 24

Specimen #	Side	Element	Tribe	Genus	Species
EP 1632/98	R	LM (2)	Antilopini	*Aepyceros*	*dietrichi*

B. Upper Ndolanya Beds

U = upper, L = lower, d = deciduous, M = molar, P = premolar, MAND = mandible, MAX = maxilla, HC = horn core

Laetoli Locality 1

Specimen #	Side	Element	Tribe	Genus	Species
EP 1111/05	R	UM2	Alcelaphini		large sp.
EP 1112/05	L	Udp4	Alcelaphini	*?Connochaetes*	
EP 532/04	R	UM	Alcelaphini	*Megalotragus*	*kattwinkeli or isaaci*
EP 1110/05	R	UM3	Alcelaphini	*Megalotragus*	*kattwinkeli or isaaci*
EP 1833/03	R	MAND (M1-M3)	Alcelaphini		
EP 1843/03	R	UM3	Alcelaphini		
EP 1109/05	L	UM	Alcelaphini		
EP 3027/00	L	UM2	Bovini		
EP 3029/00		HC	Bovini		
EP 1831/03	R	UM	Bovini		
EP 1832/03	L	UM3	Bovini		
EP 1844/03	R	MAND (M2)	Tragelaphini		

Laetoli Locality 7E

Specimen #	Side	Element	Tribe	Genus	Species
EP 1442/00	L	MAND (M3)	Alcelaphini	*Connochaetes*	
EP 2182/00	R	HC	Alcelaphini	*Parmularius*	*?altidens*
EP 3955/00	R	HC	Alcelaphini	*Parmularius*	*?altidens*
EP 1461/00		Frontlet	Alcelaphini	*Parmularius*	*?altidens*
EP 1485/00*		LI (3), M fragments (2), Partial Skeleton	Alcelaphini	*Megalotragus*	*kattwinkeli or isaaci*
EP 2165/00	L	UM2	Alcelaphini		
EP 2171/00	L	MAX (dp3-dp4)	Alcelaphini		
EP 3938/00	L	UM1	Alcelaphini		
EP 3939/00	L	UM3	Alcelaphini		
EP 3940/00	R	UM	Alcelaphini		
EP 3941/00	L	LM	Alcelaphini		
EP 3942/00	R	UM3	Alcelaphini		
EP 3946/00		LM fragment	Alcelaphini		
EP 3947/00		LM fragment	Alcelaphini		
EP 827/01	L	UM3	Alcelaphini		
EP 828/01	R	UM3	Alcelaphini		
EP 829/01	L	LM2	Alcelaphini		
EP 830/01	L	UM fragment	Alcelaphini		
EP 1136/03	R	MAX (dp3-dp4)	Alcelaphini		
EP 1137/03	R	MAX fragment (?dp4)	Alcelaphini		
EP 1443/00		MAND (dp4-M1)	Alcelaphini		
EP 1445/00		LM3	Alcelaphini		
EP 1446/00		UM3	Alcelaphini		
EP 1448/00		UM	Alcelaphini		
EP 1449/00		UM	Alcelaphini		
EP 1450/00		UM3	Alcelaphini		
EP 1451/00		UM fragment	Alcelaphini		
EP 1452/00		MAX (dp4-M1)	Alcelaphini		
EP 1455/00		UM3	Alcelaphini		

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Laetoli Locality 7E (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 1146/03		UP4 or UP3	?Alcelaphini		
EP 1147/03	L	UP4 or UP3	?Alcelaphini		
EP 1151/03	R	LM fragment	?Alcelaphini		
EP 3953/00	L	HC	Antilopini	*Antidorcas*	*recki*
EP 3954/00	R	HC	Antilopini	*Antidorcas*	*recki*
EP 1157/03	L	HC	Antilopini	*Antidorcas*	*recki*
EP 1158/03	L	HC	Antilopini	*Antidorcas*	*recki*
EP 1460/00		HC	Antilopini	*Antidorcas*	*recki*
EP 1459/00		HC	Antilopini	*Antidorcas*	*recki*
EP 831/01	R	UM2	Antilopini	*Antidorcas or Gazella*	
EP 1462/00		Cranial fragment	Antilopini	*Antidorcas or Gazella*	
EP 1143/03	R	UM	Antilopini	*Antidorcas or Gazella*	
EP 1155/03	L	MAND fragment (M3 roots)	Antilopini	*Antidorcas or Gazella*	
EP 2164/00	R	UM1	Antilopini	*Antidorcas or Gazella*	
EP 2167/00	R	MAND fragment (M2)	Antilopini	*Antidorcas or Gazella*	
EP 2168/00	R	UM1 OR UM2	Antilopini	*Antidorcas or Gazella*	
EP 2169/00	R	UM1 fragment	Antilopini	*Antidorcas or Gazella*	
EP 2170/00	R	MAX (P2-M3)	Antilopini	*Antidorcas or Gazella*	
EP 3944/00	L	LM3 fragment	Antilopini	*Antidorcas or Gazella*	
EP 3945/00	L	UM3	Antilopini	*Antidorcas or Gazella*	
EP 3948/00	R	UP4	Antilopini	*Antidorcas or Gazella*	
EP 1453/00		MAX (M1-M2)	Antilopini	*Gazella*	*janenschi*
EP 1145/03	R	UM	Antilopini		
EP 1156/03	R	MAND fragment (M3)	Antilopini		
EP 1144/03	R	UM	?Antilopini		
EP 3951/00	L	MAND (M1-M2)	Hippotragini		
EP 1489/00		LM2	Hippotragini		
EP 2172/00		MAND (M2-M3)	Neotragini	*Madoqua*	*?avifluminis*
EP 1152/03		MAND fragment (M2-M3)	Neotragini	*Madoqua*	*?avifluminis*
EP 1153/03		UM	Neotragini	*Madoqua*	*?avifluminis*
EP 1154/03		UM fragment	Neotragini	*Madoqua*	*?avifluminis*
EP 1159/03		HC	Neotragini	*Madoqua*	*?avifluminis*
EP 1457/00		MAND (M2-M3)	Neotragini	*Madoqua*	*?avifluminis*
EP 3957/00		HC	Neotragini	*Madoqua*	*?avifluminis*
EP 3952/00	R	UM	Neotragini	*?Raphicerus*	
EP 3956/00		HC	Neotragini	*?Raphicerus*	
EP 1142/03	R	UM1?	?Tragelaphini		
EP 3949/00	L	LP	Tragelaphini		
EP 1141/03	R	UM3	Tragelaphini		
EP 1444/00		MAND (M1)	Tragelaphini	*?Tragelaphus*	
EP 3943/00	L	UM1	Tragelaphini	*Tragelaphus*	cf. *T. buxtoni*
EP 1138/03	R	UM3	Tragelaphini		
EP 1139/03	R	UM (probably M2)	Tragelaphini		
EP 1140/03	R	UM1	Tragelaphini		

Laetoli Locality 9

Specimen #	Side	Element	Tribe	Genus	Species
EP 932/04	R	UM	Alcelaphini		
EP 933/04	L	UM2	Alcelaphini		
EP 934/04	L	UP (probably P4)	Alcelaphini		
EP 1641/98	R	LM3	Antilopini	*Antidorcas or Gazella*	
EP 942/04	L	HC	Antilopini	*Gazella*	*granti*
EP 944/04	R	HC fragment	Antilopini	*Gazella*	*granti*
EP 943/04		HC fragment	Antilopini	*?Aepyceros*	
EP 931/04	L	LM	Hippotragini		

Laetoli Locality 14

Specimen #	Side	Element	Tribe	Genus	Species
EP 2348/03	L	UM	Alcelaphini		
EP 695/03	L	UM	Alcelaphini		
EP 1168/04	L	UM3	Alcelaphini		
EP 1169/04	R	U M1 or UM2	Alcelaphini		
EP 1175/05	L	UM3	Alcelaphini		
EP 1179/05	R	UP4	Alcelaphini		
EP 696/03	L	UP	Bovini		
EP 1170/04	R	UM	Bovini		

Laetoli Locality 15

Specimen #	Side	Element	Tribe	Genus	Species
EP 3383/00	R	MAND (P2-P4, M2-M3)	Alcelaphini	*?Connochaetes*	
EP 199/04	R	HC	Alcelaphini	*?Megalotragus*	
EP 3385/00	R	HC	Alcelaphini	*Parmularius*	*?altidens*
EP 3386/00	R	HC	Alcelaphini	*Parmularius*	*?altidens*
EP 3389/00	L	HC	Alcelaphini	*Parmularius*	*?altidens*
EP 3390/00	L	HC	Alcelaphini	*Parmularius*	*?altidens*
EP 3372/00§		Cranium + Partial Skeleton	Alcelaphini	*Parmularius*	*parvicornis*
EP 3444/00	R	MAX fragment (dp4)	Alcelaphini	*Parmularius*	*parvicornis*
EP 4030/00	L	MAND fragment (M2)	Alcelaphini	*Parmularius*	*parvicornis*
EP 4036/00	?R	HC	Alcelaphini	*Parmularius*	*parvicornis*
EP 1022/01	L	MAND fragment (dp4-M1)	Alcelaphini	*Parmularius*	*parvicornis*
EP 1650/03	L	MAND fragment (M)	Alcelaphini	*Parmularius*	*parvicornis*
EP 1663/03	L	LM	Alcelaphini	*Parmularius*	*parvicornis*
EP 3374/00	R	MAND (P4-M3)	Alcelaphini		Large sp.
EP 3446/00	R	UM1 or UM2	Alcelaphini		Large sp.
EP 1012/01	L	Udp4	Alcelaphini		Large sp.
EP 361/05	L	LM3	Alcelaphini		Large sp.
EP 3378/00	R	LM2	Alcelaphini		Small sp.
EP 177/04	L	MAND fragment (M1-M2)	Alcelaphini		Small sp.
EP 1017/01		LM fragment	Alcelaphini		Small sp.
EP 1020/01	L	MAND fragment (M3 fragment)	Alcelaphini		Small sp.
EP 3375/00	R	MAND (dp2- erupting M1)	Alcelaphini		
EP 3377/00	L	LM1	Alcelaphini		
EP 3379/00	R	UM3	Alcelaphini		
EP 3381/00	R	UP4-M2	Alcelaphini		
EP 3442/00	L	MAND (dp3-M1)	Alcelaphini		
EP 3448/00	R	UM1	Alcelaphini		
EP 3449/00	R	UM3	Alcelaphini		

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Laetoli Locality 15 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 3450/00	R	LM1 or LM2	Alcelaphini		
EP 4031/00		MAND fragment (M)	Alcelaphini		
EP 4062/00	L	LM3	Alcelaphini		
EP 1010/01	R	UM2	Alcelaphini		
EP 1014/01	R	UM3	Alcelaphini		
EP 1015/01	R	UM	Alcelaphini		
EP 1649/03	R	MAND fragment (M3)	Alcelaphini		
EP 1651/03	R	LM3	Alcelaphini		
EP 1654/03	L	MAX (M1-M2)	Alcelaphini		
EP 1678/03		HC base	Alcelaphini		
EP 180/04	R	LP2	Alcelaphini		
EP 355/05	L	MAX fragment (UM1)	Alcelaphini		
EP 3384/00	R	MAND fragment	?Alcelaphini		
EP 176/04	R	MAND fragment (M3)	Antilopini	*Antidorcas*	*recki*
EP 357/05	R	MAND (M1-M2)	Antilopini	*Antidorcas*	*recki*
EP 358/05	R	MAND (M2-M3)	Antilopini	*Antidorcas*	*recki*
EP 3373/00	L	MAX (M1-M3)	Antilopini	*Antidorcas or Gazella*	
EP 3376/00	R	MAND (M3)	Antilopini	*Antidorcas or Gazella*	
EP 3380/00	R	UM1	Antilopini	*Antidorcas or Gazella*	
EP 4033/00	L	UM1	Antilopini	*Antidorcas or Gazella*	
EP 1013/01	R	UM3	Antilopini	*Antidorcas or Gazella*	
EP 1018/01	L	MAX fragment (dp3-dp4)	Antilopini	*Antidorcas or Gazella*	
EP 1021/01	L	MAND fragment (M1)	Antilopini	*Antidorcas or Gazella*	
EP 1023/01	?L	HC fragment	Antilopini	*Antidorcas or Gazella*	
EP 1024/01		HC fragment	Antilopini	*Antidorcas or Gazella*	
EP 1648/03	R	MAND fragment (M1-M2)	Antilopini	*Antidorcas or Gazella*	
EP 3443/00	R	MAND (M3)	Antilopini	*Antidorcas or Gazella*	
EP 3445/00	R	MAND (M1-M2)	Antilopini	*Antidorcas or Gazella*	
EP 3447/00	L	UM2	Antilopini	*Antidorcas or Gazella*	
EP 4037/00	L	HC base	Antilopini		
EP 1652/03	L	MAND (M2-M3)	Antilopini		
EP 1662/03		Udp4	Antilopini		
EP 178/04	L	MAND fragment	?Antilopini		
EP 3467/00		HC	Cephalophini		
EP 4034/00		LP4	Neotragini	*Madoqua*	*?avifluminis*

§Holotype

Laetoli Locality 18

Specimen #	Side	Element	Tribe	Genus	Species
EP 856/00	L	MAND fragment (M2)	Alcelaphini		Large sp.
EP 720/01	R	UM2	Alcelaphini		Large sp.
EP 854/00		LM2 fragment	Alcelaphini		Large sp.
EP 3221/00	R	MAND (M3)	Alcelaphini	*Megalotragus*	*kattwinkeli or isaaci*
EP 3220/00	R	HC	Alcelaphini	*Parmularius*	*?altidens*
EP 860/00	L	MAND fragment (M1-M3)	Alcelaphini	*Parmularius*	*parvicornis*
EP 848/00	L	UM3	Alcelaphini		
EP 851/00	L	UM1	Alcelaphini		
EP 852/00	R	UM3	Alcelaphini		
EP 858/00	R	MAND fragment (M2)	Alcelaphini		
EP 859/00	L	MAND fragment (M3)	Alcelaphini		
EP 861/00		LM3 fragment	Alcelaphini		
EP 862/00	L	MAX fragment (M1)	Alcelaphini		
EP 863/00	L	MAND fragment (M3)	Alcelaphini		
EP 864/00	R	MAND fragment (M2)	Alcelaphini		

(continued)

Laetoli Locality 18 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 865/00	R	MAND fragment (P4)	Alcelaphini		
EP 867/00	R	UM3	Alcelaphini		
EP 868/00	L	MAND fragment (M1 + erupting M2)	Alcelaphini		
EP 869/00	L	UM	Alcelaphini		
EP 871/00	L	UP3	Alcelaphini		
EP 874/00	R	UP4	Alcelaphini		
EP 876/00	R	UM3	Alcelaphini		
EP 877/00	L	UM	Alcelaphini		
EP 878/00	L	MAX fragment (M2-M3)	Alcelaphini		
EP 1024/00	R	UM1 or UM2	Alcelaphini		
EP 3201/00	R	MAX (dp3-M1)	Alcelaphini		
EP 3202/00	L	LM3 fragment	Alcelaphini		
EP 3204/00	L	UM3	Alcelaphini		
EP 3207/00	L	UM	Alcelaphini		
EP 721/01	R	UM1	Alcelaphini		
EP 725/01	R	MAND (dp4-M1)	Alcelaphini		
EP 041/03	L	UM	Alcelaphini		
EP 042/03	R	MAND fragment (M3)	Alcelaphini		
EP 043/03	R	LM fragment	Alcelaphini		
EP 044/03	L	MAND fragment (M1-M2)	Alcelaphini		
EP 103/03	L	MAND fragment (M3)	Alcelaphini		
EP 109/03	R	UM	Alcelaphini		
EP 112/03	R	UM	Alcelaphini		
EP 389/05	R	MAX (P3-M1)	Alcelaphini		
EP 051/03	R	UP2	?Alcelaphini		
EP 391/05	R	UM	?Alcelaphini		
EP 875/00		UM2 fragment	Antilopini		
EP 3203/00	L	MAX (M1-M2)	Antilopini	*Antidorcas*	*recki*
EP 3218/00	R	HC	Antilopini	*Antidorcas*	*recki*
EP 243/04	L	HC	Antilopini	*Antidorcas*	*recki*
EP 849/00	R	MAND fragment (M3)	Antilopini	*Antidorcas or Gazella*	
EP 857/00	L	UM3	Antilopini	*Antidorcas or Gazella*	
EP 872/00	L	MAND fragment (M1-M2)	Antilopini	*Antidorcas or Gazella*	
EP 882/00	R	HC fragment	Antilopini	*Antidorcas or Gazella*	
EP 2337/00	L	MAND (M2)	Antilopini	*Antidorcas or Gazella*	
EP 2338/00	L	MAND (P4?)	Antilopini	*Antidorcas or Gazella*	
EP 2339/00	R	UM1	Antilopini	*Antidorcas or Gazella*	
EP 3209/00	L	MAND (dp4)	Antilopini	*Antidorcas or Gazella*	
EP 3217/00	R	HC	Antilopini	*Antidorcas or Gazella*	
EP 046/03	L	UM	Antilopini	*Antidorcas or Gazella*	
EP 047/03	L	UM	Antilopini	*Antidorcas or Gazella*	
EP 114/03	L	UM	Antilopini	*Antidorcas or Gazella*	
EP 390/05	R	UM2	Antilopini	*Antidorcas or Gazella*	
EP 392/05	R	MAX fragment (M1-M2)	Antilopini	*Antidorcas or Gazella*	
EP 393/05	R	UM	Antilopini	*Antidorcas or Gazella*	
EP 394/05	L	UM3	Antilopini	*Antidorcas or Gazella*	
EP 730/01		HC fragment	Antilopini	*Gazella*	*?janenschi*
EP 722/01	R	UM1	Antilopini	*Gazella*	
EP 724/01	L	MAND (P4-M2)	Antilopini	*Gazella*	
EP 048/03	L	LM	Antilopini	*Gazella*	
EP 3219/00	L	HC	Antilopini	*Gazella*	
EP 855/00	L	MAND fragment (M2)	Bovini		
EP 3216/00		HC	?Cephalophini		
EP 879/00		MAND fragment (P3)	Neotragini	*Madoqua*	*?avifluminis*
EP 880/00*	R L	MAND (M1-M3) MAND (P2-M3)	Neotragini	*Madoqua*	*?avifluminis*
EP 881/00		MAND (M3)	Neotragini	*Madoqua*	*?avifluminis*

(continued)

Laetoli Locality 18 (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 884/00		HC (4)	Neotragini	*Madoqua*	*?avifluminis*
EP 2340/00		MAND (P4-M2)	Neotragini	*Madoqua*	*?avifluminis*
EP 2341/00		MAX (M3)	Neotragini	*Madoqua*	*?avifluminis*
EP 3208/00		MAND (P4-M2)	Neotragini	*Madoqua*	*?avifluminis*
EP 3210/00		MAX (P2-M1)	Neotragini	*Madoqua*	*?avifluminis*
EP 3211/00		MAND (M2)	Neotragini	*Madoqua*	*?avifluminis*
EP 3212/00		MAX fragment (P2)	Neotragini	*Madoqua*	*?avifluminis*
EP 3213/00		MAND fragment (dp2)	Neotragini	*Madoqua*	*?avifluminis*
EP 3214/00		HC fragment	Neotragini	*Madoqua*	*?avifluminis*
EP 3215/00		HC fragment	Neotragini	*Madoqua*	*?avifluminis*
EP 726/01		MAND fragment (M)	Neotragini	*Madoqua*	*?avifluminis*
EP 727/01		MAND (M2-M3)	Neotragini	*Madoqua*	*?avifluminis*
EP 728/01		MAX fragment (P3)	Neotragini	*Madoqua*	*?avifluminis*
EP 729/01		MAX fragment (P)	Neotragini	*Madoqua*	*?avifluminis*
EP 049/03		MAND fragment (M)	Neotragini	*Madoqua*	*?avifluminis*
EP 050/03		MAND fragment (P4-M2)	Neotragini	*Madoqua*	*?avifluminis*
EP 080/03		HC	Neotragini	*Madoqua*	*?avifluminis*
EP 113/03		MAX (M1-M3)	Neotragini	*Madoqua*	*?avifluminis*
EP 241/04		MAND fragment (M2-M3)	Neotragini	*Madoqua*	*?avifluminis*
EP 242/04		MAND fragment	Neotragini	*Madoqua*	*?avifluminis*
396/05		MAND (P2-P3 + M1)	Neotragini	*Madoqua*	*?avifluminis*
397/05		MAX (P2-M1)	Neotragini	*Madoqua*	*?avifluminis*
EP 081/03	R	HC	Neotragini	*?Raphicerus*	
EP 850/00	L	UM2	Tragelaphini		
EP 853/00		UM1 or UM2 fragment	Tragelaphini		
EP 866/00	L	MAND fragment (P4)	Tragelaphini		
EP 873/00		UM fragment	Tragelaphini		

*Associated material

Laetoli Locality 22E

Specimen #	Side	Element	Tribe	Genus	Species
EP 1468/04	L	MAX (M2 or M3)	Alcelaphini		
EP 1469/04	R	MAX (M3)	Alcelaphini		
EP 1470/04	R	MAND (M)	Alcelaphini		
EP 1488/04	L	MAND (P4)	Alcelaphini		
EP 1471/04	R	HC	Antilopini	*?Antidorcas*	
EP 1499/04	L	MAND (M1-M3)	Tragelaphini		

Laetoli Locality 22S

Specimen #	Side	Element	Tribe	Genus	Species
EP 1241/98	R	MAND (M)	Alcelaphini		Large sp.
EP 1187/00	R	Udp3	Alcelaphini		Large sp.
EP 1185/00	L	UM2	Alcelaphini		Large sp.
EP 1295/98	L	HC	Alcelaphini	*Parmularius*	*?altidens*
EP 1209/00		HC fragment	Alcelaphini	*?Megalotragus*	
EP 1242/98	R	MAND (M1)	Alcelaphini		
EP 1244/98	R	Ldp4	Alcelaphini		
EP 1249/98	L	UM1	Alcelaphini		
EP 1250/98	R	UM fragment	Alcelaphini		
EP 3752/00		M fragment	Alcelaphini		
EP 1797/03	L	LM fragment	Alcelaphini		

(continued)

Laetoli Locality 22S (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 1243/98	R	MAND (M1-M2)	Antilopini	*Antidorcas*	*recki*
EP 1297/98	L	HC	Antilopini	*Antidorcas*	*recki*
EP 1246/98	R	UM	Antilopini	*Antidorcas or Gazella*	
EP 1190/00	R	UM1	Antilopini	*Antidorcas or Gazella*	
EP 3750/00	R	MAND fragment (M3)	Antilopini	*Antidorcas or Gazella*	
EP 1253/98	R	M fragment	Antilopini		
EP 1186/00	?	UM3?	Antilopini		
EP 1294/98	L	HC	Hippotragini	*Hippotragus*	
EP 3748/00	L	UP2	Hippotragini		
EP 1251/98		MAX (dp4-M2)	Neotragini	*Madoqua*	*?avifluminis*
EP 1298/98		HC	Neotragini	*Madoqua*	*?avifluminis*
EP 1236/00		MAX fragment (P4-M1)	Neotragini	*Madoqua*	*?avifluminis*
EP 3751/00		MAND fragment (dp4)	Neotragini	*Madoqua*	*?avifluminis*
EP 1799/03		MAND fragment (M2-M3)	Neotragini	*Madoqua*	*?avifluminis*
EP 1245/98	R	Udp3	Tragelaphini		
EP 1247/98	R	UM	Tragelaphini		
EP 095/04	R	LM	Tragelaphini		
EP 1248/98	L	UM	?Tragelaphini		
EP 1188/00	L	Udp3	?Tragelaphini		
EP 1189/00	R	UP2	?Tragelaphini		

Silal Artum

Specimen #	Side	Element	Tribe	Genus	Species
EP 544/04	R	UM3	Antilopini	*Aepyceros*	
EP 1455/01	R	MAX fragment (M2)	Alcelaphini		Large sp.
EP 1463/01		UM fragment	Alcelaphini		Large sp.
EP 014/03	R	MAX fragment (P4-M2)	Alcelaphini		Small sp.
EP 015/03	R	MAND fragment (M3)	Alcelaphini		Small sp.
EP 1451/01	L	MAND fragment (M3)	Alcelaphini		Small sp.
EP 1124/05	L	MAND	Alcelaphini	*Parmularius*	*parvicornis*
EP 1123/05	R	LM2	Alcelaphini	*Parmularius*	*parvicornis*
EP 1448/01	L	MAND (M1-M3)	Alcelaphini		
EP 1453/01	R	MAND (M1)	Alcelaphini		
EP 1454/01	L	MAND (M2)	Alcelaphini		
EP 1458/01	R	LM3	Alcelaphini		
EP 1459/01		UM	Alcelaphini		
EP 1460/01	L	UM (probably M2)	Alcelaphini		
EP 1461/01	R	UM3	Alcelaphini		
EP 1462/01	L	LM3 fragment	Alcelaphini		
EP 1464/01	L	LM3 fragment	Alcelaphini		
EP 1466/01	L	LP3	Alcelaphini		
EP 013/03	L	UM	Alcelaphini		
EP 016/03	R	UM	Alcelaphini		
EP 017/03	L	UP	Alcelaphini		
EP 018/03*	R	UM1-M3	Alcelaphini		
	L	UM3			
EP 019/03	R	MAND fragment (P4)	Alcelaphini		
EP 2508/03	R	UM3	Alcelaphini		
EP 2509/03	L	MAND fragment (M1-M2)	?Alcelaphini		
EP 1119/05	L	Ldp4	Alcelaphini	*?Connochaetes*	
EP 1122/05	R	UM	Alcelaphini	*?Connochaetes*	
EP 1471/04	R	HC	Antilopini	*Antidorcas*	*recki*
EP 1456/01	R	LM3 fragment	Antilopini	*Antidorcas*	*recki*
EP 1465/01	L	UM3	Antilopini	*Antidorcas*	*recki*

(continued)

Silal Artum (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 1505/01	R	HC	Antilopini	*Antidorcas*	*recki*
EP 1506/01	L	HC	Antilopini	*Antidorcas*	*recki*
EP 541/04	R	UM	Antilopini	*Antidorcas or Gazella*	
EP 542/04	L	UM	Antilopini	*Antidorcas or Gazella*	
EP 1450/01	L	MAX (M1-M3)	Antilopini	*Gazella*	
EP 1452/01	R	MAND fragment (M1)	Antilopini	*Gazella*	
EP 021/03	R	HC fragment	Antilopini	*Gazella*	
EP 1457/01	L	MAX (M1-M2)	Antilopini		
EP 1467/01		UP4	Antilopini		
EP 2507/03	L	UM	Antilopini		
EP 538/04	R	MAND fragment (M3)	Antilopini		
EP 539/04	R	MAND fragment (dp4-M1)	Antilopini		
EP 540/04	L	LM	Antilopini		
EP 012/03	L	LM3	Bovini		
EP 543/04	R	UM	Hippotragini	*Oryx*	*deturi*
EP 1449/01	R	MAND (M3)	Tragelaphini		

*Associated material

C. Lower Laetolil Beds

U = upper, L = lower, d = deciduous, M = molar, P = premolar, MAND = mandible, MAX = maxilla, HC = horn core

Kakesio

Specimen #	Side	Element	Tribe	Genus	Species
EP 1340/03	R	UM3	Alcelaphini		Small sp.
EP 1341/03	R	UM3	Alcelaphini		Small sp.
EP 518/03	L	UM1 or UM2	Alcelaphini		Small sp.
EP 519/03	L	MAND fragment (M1-M2)	Alcelaphini		Small sp.
EP 045/98	L	UM	Antilopini	*Aepyceros*	*dietrichi*
EP 004/98	R	MAND fragment (M2)	Alcelaphini		
EP 026/98*	R	LM2 AND LM3 fragment	Alcelaphini		
EP 521/03*	L + R	HC (2)	Alcelaphini	*Parmularius*	*pandatus*
EP 093/98	L	UM2-3	Alcelaphini		
EP 003/99	R	UM fragment	Alcelaphini		
EP 004/99	R	UM fragment	Alcelaphini		
EP 019/98	L	MAND fragment (M3 fragment)	Antilopini	*Gazella*	*janenschi*
EP 025/98	L	HC	Antilopini	*Gazella*	*janenschi*
EP 1348/03	R	MAND fragment (M1-M3)	Antilopini	*Gazella*	*janenschi*
EP 092/98	R	UP2	Hippotragini		
EP 044/98	R	UM1	Hippotragini		
EP 046/98	L	UM fragment	Hippotragini		
EP 047/98	R	LM3 fragment	Hippotragini		
EP 084/98*	L	LP2-P4 + LM2-M3	Hippotragini		
EP 002/99	R	UM1 or UM2	Hippotragini		
EP 3646/00	R	LM3	Alcelaphini		
EP 1177/01	R	UM	Hippotragini		
EP 028/98	L	MAND (M1-M2)	Neotragini	*Madoqua*	*?avifluminis*
EP 029/98	L	MAND (P4-M1)	Neotragini	*Madoqua*	*?avifluminis*
EP 030/98	R	MAND (M2)	Neotragini	*Madoqua*	*?avifluminis*
EP 1047/05		HC	Neotragini	*Madoqua*	*?avifluminis*
EP 107/98		MAND fragment (P3-M1)	Neotragini	*Madoqua*	*?avifluminis*

*Associated material

Esere

Specimen #	Side	Element	Tribe	Genus	Species
EP 1661/98	L	HC	Alcelaphini	*Connochaetes*	*taurinus*
EP 094/99	R	LM fragment	Alcelaphini		Large sp.
EP 090/99	R	LM3	Alcelaphini		
EP 091/99	L	UM	Alcelaphini		
EP 092/99	L	UM	Alcelaphini		
EP 093/99	L	UM3	Alcelaphini		
EP 095/99	R	LM1	Alcelaphini		
EP 089/99		HC	Bovini		
EP 103/99	L	UM	Bovini		

Emboremony

Specimen #	Side	Element	Tribe	Genus	Species
EP 300/99	L	HC	Alcelaphini	*Parmularius*	*pandatus*
EP 1368/01	L	UM3	Alcelaphini		Small sp.
EP 303/99	R	UM	Alcelaphini		
EP 306/99	R	UM	Alcelaphini		
EP 308/99	L	UM3	Alcelaphini		
EP 309/99	R	LM	Alcelaphini		
EP 2071/03	L	LM	Alcelaphini		
EP 355/99	L	LM fragment	Alcelaphini		
EP 374/99	L	UM3	Alcelaphini		
EP 1521/00	L	UM2	Alcelaphini		
EP 1537/00	L	UM1 fragment	Alcelaphini		
EP 1391/01	L	UM	Alcelaphini		
EP 1392/01	R	UM	Alcelaphini		
EP 349/99	L	UM	?Alcelaphini		
EP 1369/01	L	MAND fragment (dp4)	Tragelaphini		

D. Ngaloba Beds

U = upper, L = lower, d = deciduous, M = molar, P = premolar, MAND = mandible, MAX = maxilla, HC = horn core

Emboremony

Specimen #	Side	Element	Tribe	Genus	Species
EP 284/99	L	UM2	Alcelaphini	*Connochaetes*	*taurinus*
EP 354/99	R	UM1-M2	Alcelaphini	*Connochaetes*	*taurinus*
EP 2098/03		HC	Alcelaphini	*Connochaetes*	*taurinus*
EP 285/99	R	UM	Alcelaphini		Large sp.
EP 289/99	L	UM1	Alcelaphini		Large sp.
EP 304/99	L	UM1	Alcelaphini		
EP 305/99	L	UM1	Alcelaphini		
EP 307/99	L	UM	Alcelaphini		
EP 350/99	L	UM3	Alcelaphini		
EP 1367/01	L	UM	Alcelaphini		
EP 2087/03	L	UM (2)	Alcelaphini		

(continued)

Emboremony (continued)

Specimen #	Side	Element	Tribe	Genus	Species
EP 2088/03	R	UM3 (2)	Alcelaphini		
EP 2089/03	R	LM3	Alcelaphini		
EP 1390/01	R	UM	Alcelaphini		
EP 298/99*	L + R	HC (2) + Cranial fragments (5)	Antilopini	*Gazella*	*granti*
EP 1530/00		HC	Antilopini	*Gazella*	*granti*
EP 2093/03		HC tip	Antilopini	*Gazella*	*granti*
EP 1393/01		HC	Antilopini	*Gazella*	*granti*
EP 357/99*	L + R	HC (2)	Antilopini	*Gazella*	*granti*
EP 302/99	L	UM2	Hippotragini		
EP 1520/00	L	UM	Hippotragini		

*Associated material

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Chapter 16
Amphibia and Squamata

Jean-Claude Rage and Salvador Bailon

Abstract The Pliocene of Laetoli (Tanzania) has produced a taxonomically unbalanced fauna of amphibians and squamate reptiles. Amphibians are represented by only two specimens belonging to indeterminate anurans. Similarly, lizards are comprised of two specimens that are referred to an indeterminate acrodontan and an indeterminate scincomorphan. Snakes are more numerous (more than 150 specimens) and taxonomically diverse. They include a boid (*Python sebae* or *P. natalensis*), at least three colubrids (cf. *Thelotornis*, cf. *Rhamphiophis*, one indeterminate colubrid, and another indeterminate taxon that might be a modern specimen), an elapid (*Naja robusta*), a possible distinct elapid, and a viperid (*Bitis olduvaiensis* or a new species of *Bitis*). The latter taxon represents the most common snake. The paleoecological implications of the fauna are not readily apparent because the most useful indicator taxa are distributed in different beds. Based on the entire fauna it may be concluded that the Laetoli area was neither a desert nor covered by forest. Bodies of water were periodically present, at least during the period of deposition of the Upper Laetolil Beds. An unusual feature of the Laetoli snake community, but similar to a few other Neogene faunas from sub-Saharan Africa, is the fact that colubrids are not the dominant taxon.

Keywords Anurans • Lizards • Snakes • Laetoli • Pliocene • Africa

Introduction

The Pliocene beds of Laetoli have produced a rather small, but relatively taxonomically diverse assemblage of amphibians and squamates (lizards and snakes). They are represented by what are generally well-preserved and mostly disarticulated bones. All the fossils come from the Laetolil Beds and Upper Ndolanya Beds. The Laetolil Beds are subdivided into Lower and Upper Units, dated from more than 4.4 to 3.85 Ma and from 3.85 to 3.6 Ma respectively (Ditchfield and Harrison 2011; Deino 2011). The Upper Ndolanya Beds are dated to 2.66 Ma (Ndessokia 1990; Deino 2011).

Amphibians and lizards are rare, but snakes are fairly numerous and diverse. Previously, amphibians and lizards have not been recorded, but Meylan (1987) published a brief account of a small collection of fossil snakes made by Mary Leakey's expeditions (1974–1982). Since that time, the number of fossils has increased significantly through collections made by teams led by Terry Harrison (1998–2005). The new finds add to our knowledge of taxa already reported on by Meylan (1987) and to the overall diversity of the fauna.

Students of fossil amphibians and squamates from the Tertiary of Africa face a difficult problem. The fossil record of these taxa is poor and few paleontological studies have been published. Partly as a consequence of this state of affairs, few skeletons of extant African species have been prepared for comparisons, especially those of colubrid and elapid snakes. Since it may be presumed that fossils from the Neogene mostly belong to extant genera and species or taxa closely related to them, as is the case on other continents, the lack of skeletons of living forms seriously hinders the study of Neogene amphibians and squamates from Africa. For this reason, the present work cannot be regarded as a comprehensive study providing definitive identifications.

The vertebral terminology follows Auffenberg (1963), Rage (1984), and Szyndlar (1984).

Systematic Account

Amphibia

Amphibians are extremely rare at Laetoli, being represented by only two anuran vertebrae.

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Anura

Family indeterminate

Referred Material

EP 276/01, vertebra from Loc. 5; EP 1111/03, vertebra from Loc. 10W. Both specimens come from the Upper Laetolil Beds.

Description and Discussion

The two vertebrae come from the presacral region. They are procoelous, with depressed condyles and cotyles. The cross section of the centrum is broad compared to the size of the vertebra; consequently, the neural canal is relatively small. These shared features suggest that the two specimens belong to the same family, perhaps even to the same species. Hard matrix obscures the neural arch of EP 276/01, but it may be inferred to have been short. The transverse processes of this specimen are strong, directed transversely and slightly ventrally. This vertebra occupied a more anterior position in the vertebral column than EP 1111/03. The latter differs from EP 276/01 in having a longer centrum and a longer neural arch. The transverse processes are apparently more slender and directed horizontally and slightly posteriorly. The overall morphology of these two vertebrae is reminiscent of that of Bufonidae, but such an identification cannot be confirmed on the basis of this material alone.

Reptilia

Squamata
Lacertilia
Lizards are represented by only two specimens.

Acrodonta

Family indeterminate

Referred Material

EP 806/05, fragment of bone bearing teeth from Loc. 5, Upper Laetolil Beds.

Description

This specimen is probably a fragment of maxilla, but this cannot be confirmed with certainty. Five teeth are preserved; they show a characteristic morphology. They are triangular in lateral aspect, labiolingually compressed without anterior or posterior developed flange, and they are fused to the apical edge of the bone. They have sharp edges and pointed tips. Such teeth are known in acrodontan lizards and in sphenodontians. Wear facets occur on the lingual face of teeth, but they do not extend onto the bone. Two teeth, probably the posterior ones in the series, appear as compressed cones, whereas the others are more blade-like. The long-axes of the teeth are not oblique with regard to the edge of the bone. The bases of the teeth are in contact, but they do not overlap. Apparently, the tooth bases extended slightly onto the lingual face of the bone. Despite this lingual extension, such an implantation is classically labelled acrodont (Estes et al. 1988; Augé 1997). The morphology of the subdental shelf and the presence of a *sulcus dentalis* cannot be determined.

Discussion

The Acrodonta includes the Chamaeleonidae and the traditional, probably paraphyletic Agamidae (i.e., Agaminae plus Leiolepidinae *sensu* Frost and Etheridge 1989). They are mainly characterized by their acrodontan dentition.

The fragment of bone suggests that the teeth do not come from the anterior portion of the tooth row. The blade-like teeth may belong to the hatchling dentition, whereas the two others possibly represent the first mature teeth (Cooper et al. 1970), but this cannot be definitely ascertained. However, assuming this is correct, the fact that the horizontal long-axis of the additional teeth is not oblique and that the tooth bases apparently extend lingually permits us to discount sphenodontians. Moreover, the latter taxon may be ruled out on geographic and stratigraphic grounds, although such considerations should be avoided in making taxonomic assignments. The youngest confirmed African sphenodontian comes from the earliest Cretaceous (Evans and Sigogneau-Russell 1997), but a tooth from the late Paleocene of Morocco might belong to this taxon (Augé and Rage 2006). Therefore, EP 806/05 is referred to the Acrodonta. Unfortunately, anterior teeth that provide unquestionable distinguishing characteristics between chamaeleonids and agamids (Moody and Rocek 1980) are lacking. According to Evans et al. (2002), the absence of interstices between tooth bases and the lingual extension of the latter would suggest referral to agamids. However, interstices appear to occur in some agamids (Moody 1980), while tooth bases would extend lingually also in chamaeleonids (Augé 1997). Consequently, this specimen cannot be precisely assigned below the acrodontan taxonomic level.

Scincomorpha

Family indeterminate

Referred Material

EP 1297/01, incomplete left maxilla from Loc. 22S, Upper Ndolanya Beds.

Description and Discussion

The tooth row is incomplete, the two extremities of the row being broken off. The teeth are elongate, deeply pleurodont, slightly compressed anteroposteriorly, and closely spaced. The apices of the teeth are somewhat blunt, never pointed, and they lack accessory cusps. The parapet is deep, so only a short part of each tooth projects beyond it.

The close-packed condition of the teeth may suggest referral to Gekkonidae. However, gekkonid teeth are cylindrical and slender, not compressed. This specimen is probably referable to the enormously diverse scincomorphan assemblage, but it does not appear possible to narrow the identification beyond this.

Serpentes

More than 150 useful remains (i.e., skull bones and vertebrae) are referred to snakes. In addition, fragments of ribs are also available. At least six genera belonging to four families are represented.

Boidae

At Laetoli, only a few trunk vertebrae of Boidae are represented. Vertebrae of this family are easily identified by the following characters: vertebrae short, wide, and massive; prezygapophyseal process small; paradiapophyses weakly subdivided into para- and diapophyseal surfaces; true, spine-like hypapophyses lacking on mid- and posterior trunk vertebrae, replaced by haemal keels (Szyndlar and Böhme 1996; Rage 2001). These vertebrae from Laetoli were previously studied by Meylan (1987), who referred them to the extant species *Python sebae*. Subsequently, Broadley (1999) recognized the subspecies *P. sebae natalensis* as a distinct species, *P. natalensis* Smith, 1840. *Python sebae* as construed by Meylan (1987) included both *P. sebae*, as currently understood, and *P. natalensis*. Unfortunately, osteological differences between *P. sebae* and *P. natalensis* are still undocumented, assuming that such differences exist. In museum collections, some of the skeletons labelled *P. sebae* may actually belong to *P. natalensis*. This would not be surprising since the observed specimens of *P. sebae* show marked variation of vertebral morphology, mainly affecting the neural spine. In paleontological samples, it will be impossible to discriminate between these two species until a detailed study of the osteology of *P. natalensis* is undertaken.

Python sebae Gmelin, 1789 or *Python natalensis* Smith, 1840

Referred Material

LAET 75-2129A-D, four trunk vertebrae; LAET 76-4037A-F, six trunk vertebrae, including two pairs of articulated vertebrae. All from Loc. 2, Upper Laetolil Beds.

Description

Vertebrae LAET 76-4037A-F come from the mid-trunk region, whereas vertebrae LAET 75-2129A-D occupied a slightly more anterior position. The latter probably came from the transition between the anterior and mid-trunk regions, as indicated by the slightly more ventrally deflected posterior part of the haemal keel. Aside from this difference, their morphology is very uniform.

The vertebrae show the characters of the Boidae mentioned above (see Fig. 16.1). Moreover, they display features that are characteristic of the pythonines (Scanlon and Mackness 2001): zygapophyseal facets weakly inclined relative to the horizontal, anterior border of neural spine steep, posterior border of neural spine overhanging posteriorly, paracotylar foramina absent, haemal keel of mid- and posterior trunk vertebrae delimited laterally by subcentral grooves that reach the cotylar rim, and haemal keel projecting below the centrum only in the posterior part of each vertebra. In addition to these characters, the marked doming of the neural arch above the zygantrum appears to be also a pythonine feature. Aside from these features, in anterior view the zygosphene is narrow and thick; its concave anterior face bears a small median tubercle that originates from its ventral border and protrudes anteriorly. The zygosphenal roof is flat. The cotyle is nearly circular; its width is similar to that of the zygosphene. In dorsal aspect, the zygapophyses project strongly laterally, the major axis of their articular facets being at about 90° to the sagittal plane. Consequently, the interzygapophyseal constriction is deep. On either side, the bottom of the constriction is formed by the interzygapophyseal ridge, which juts out strongly laterally; the interzygapophyseal ridge is nearly straight and slightly oblique, the deepest part of the constriction being shifted posteriorly against the postzygapophyses. In lateral view, the paradiapophyses are elongate dorsoventrally. The diapophyseal part bulges, while the parapophyseal area remains almost flat, but there is no clear demarcation between these two articular areas. The neural spine is damaged on every specimen. Anteriorly, it originates on the posterior part of the zygosphene or slightly more posteriorly. The neural spine was high, as shown by LAET 76-4037A (Fig. 16.1c), but its full height cannot be evaluated because the dorsal edge is not preserved in any of this material. In ventral view, the short ventral face of the centrum widens anteriorly, and is limited laterally by strong but blunt subcentral ridges. The haemal keel is well-developed, with a blunt ventral border. In posterior view, the neural arch is strongly vaulted and, as mentioned above, it bulges above the zygantrum. The roof of the zygantrum is thick. In the largest vertebrae, the maximum length from pre- to postzygapophysis (PR-PO, *sensu* Auffenberg 1963) is about 14 mm, the maximum width across the prezygapophyses (PR-PR) is 24.2 mm, and the centrum length (CL) reaches about 11.5 mm.

Fig. 16.1 *Python sebae* or *P. natalensis*, trunk vertebra LAET 76-4037A in (**a**) anterior, (**b**) dorsal, and (**c**) left lateral views. Scale bar represents 1 cm

Discussion

In the Old World, *Python* is the only pythonine genus that inhabits Africa and Asia today, and this taxon occurred in Europe during the Miocene (Szyndlar and Rage 2003). Other pythonine genera are restricted to Australasia. Four extant species of pythons are known from Africa: *Python sebae*, *P. natalensis*, *P. regius*, and *P. anchietae*. In addition, an extinct species, *P. maurus* Rage, 1976, has been described from the Middle Miocene of Morocco.

Python anchietae is a very rare, small species whose osteology is unknown. However, on the basis of its large size it may be inferred that the python from Laetoli does not belong to this species. In *P. regius* the anterior border of the neural spine originates almost at the anterior border of the zygosphene; in *P. sebae*, the neural spine is more posteriorly placed, with its anterior border arising from about the posterior limit of the zygosphene. Moreover, the paradiapophyses of *P. regius* are more massive than those of *P. sebae*; they extend more anteriorly and their diapophyseal part is comparatively larger. In the vertebrae of *P. maurus*, the base of the anterior border of the neural spine occupies a position similar to that of *P. sebae*, whereas the paradiapophyses are rather similar to those of *P. regius* (Rage 1976). In addition, in anterior view, the paradiapophyses of *P. maurus* are clearly more inclined ventrally than those of the other species, including the python from Laetoli.

In Africa, almost all extinct boid snakes that do not belong to the subfamily Erycinae have been assigned to *Python* (Rage, in progress). The only exceptions are two snakes from the early Miocene of Namibia that may be referred to *Python* only with reservation (Rage, in progress) and a boid from the early Pliocene of Sahabi in Libya that was regarded as an indeterminate member of the Boidae by Hecht (1987). However, Szyndlar and Rage (2003) suggested that the latter might belong to *Python*. In addition, an incomplete vertebra from the late Paleocene of Morocco probably belongs to Boidae, although this assignment cannot be definitely accepted (Augé and Rage 2006). Most extinct African *Python* were referred to *P. sebae*, tentatively referred to this species as 'cf. *P. sebae*', or regarded as a form close to this species as '*P.* aff. *sebae*' (Rage 1973) or '*P.* gr. *sebae*' (Delfino et al. 2004). Aside from *P. maurus* and the boid from Sahabi, all other extinct African pythons have been referred to as *Python* sp. Extinct pythons related to *P. sebae* range from the Early Miocene of Arrisdrift, Namibia (*Python* cf. *P. sebae*: Rage 2003) to the Middle Pleistocene of Olduvai Bed IV, Tanzania (*P. sebae*: Rage 1973). Among these pythons, a snake from Olduvai Bed I (earliest Pleistocene) is distinguished from typical *P. sebae* as *Python* aff. *sebae* (Rage 1973). On each side of the neural spine of the fossil from Olduvai Bed I, a prominent, sharp ridge prolongs the posterior border of the neural arch and reaches the top of the spine. In the living specimens of *P. sebae*, a ridge is present, but it is never so pronounced. The significance of this feature is unknown. Among the fossils from Laetoli, the neural spine of only one specimen (LAET 76-4037A) is relatively well-preserved, and it apparently shows that the ridges did not extend dorsally to the uppermost part of the spine. Therefore, no character distinguishes the Laetoli vertebrae from those of the extant specimens of the *P. sebae* (*P. natalensis* included?) examined. The size of the vertebrae indicates that this python reached 4 m or slightly longer.

P. sebae is widespread is sub-Saharan Africa from Senegal-Eritrea southward to Namibia and Tanzania. The distribution of *P. natalensis* occurs mostly to the south of the range of *P. sebae*, but the two species overlap extensively from southern Angola to Tanzania (Pitman 1974; Uetz et al. 2006). These snakes are both terrestrial and aquatic.

Colubridae

cf. *Thelotornis* Smith, 1849

Referred Material

EP 3548/00, two articulated fragmentary vertebrae from Loc. 12E; EP 906/05, vertebra from Loc. 10E. All from the Upper Laetolil Beds.

Description

The vertebrae are elongate, slightly depressed, and their centrum is poorly limited by faint subcentral ridges. The haemal keel is wide, very shallow and its ventral surface is nearly flat. In EP 3548/00, the haemal keel is hardly demarcated from the centrum. None of the vertebrae preserves the neural spine or prezygapophyseal processes. The length of the centrum in the largest vertebra is greater than 8.3 mm (the precise length cannot be measured because the vertebra is still articulated).

Discussion

The overall morphology of the vertebrae is reminiscent of *Thelotornis*. More specifically, the centrum and haemal keel of the fossils are similar to those of the recent genus. However, the vertebrae are incomplete, so no detailed comparisons can be made. In addition, the fossil is clearly larger than living representatives of *Thelotornis*. The size of the largest vertebra indicates that the total length of this snake was possibly about 2.5 m, while extant *Thelotornis* reaches only 1.7 m. Referral to *Thelotornis* cannot be accepted without reservation. *Thelotornis* is an arboreal, highly venomous colubrid ('opisthoglyphous') that inhabits sub-Saharan Africa.

cf. *Rhamphiophis* Peters, 1854

Referred Material

EP 4172/00, vertebra from Loc. 8; EP 612/03, vertebra from Loc. 2; LAET 75-2397, vertebra from Loc. 10E; EP 649/01a, vertebra from Loc. 10. All from Upper Laetolil Beds.

Description

In contrast to those of cf. *Thelotornis*, the vertebrae of this snake are neither elongate nor depressed. Their neural arch is vaulted and their prezygapophyseal processes are rather long, but not pointed. Subcentral ridges are well-marked, although not salient, and define a narrow centrum that bears a thin and relatively deep haemal keel. The largest vertebra has a centrum length of 7.1 mm.

Discussion

Meylan (1987) referred one of these vertebrae (LAET 75-2397) to cf. *Rhamphiophis*. He correctly noted that the specimen displays the overall morphology of racers, but that it lacks some of the typical features of these snakes. According to Meylan (1987), this colubrid from Laetoli has a less elongate centrum and shorter epizygapophyseal spines. However, as far as the length of the centrum is concerned, Meylan's observation appears to be partly erroneous because the centrum of the fossil is as long as that of the racer *Hierophis*. Nevertheless, assignment to a taxon close to *Rhamphiophis* is reasonable. The new collections include three vertebrae that should be referred to the same taxon. Unfortunately, they do not provide any new information. Aside from Laetoli, *Rhamphiophis* has never been reported as a fossil. Today, it is a terrestrial, more or less fossorial, dweller of arid savannas in sub-Saharan Africa (Pitman 1974).

Colubridae indeterminate A

Referred Material

EP 506/05, vertebra from Loc. 9S, Upper Laetolil Beds.

Description and Comments

This vertebra is approximately as elongate as those referred to above as cf. *Thelotornis*, but it is wider, more depressed, and its haemal keel is markedly narrower and better defined. The vertebra differs from those of cf. *Rhamphiophis* in being more elongate, more depressed, and in having a more vaulted neural arch. This colubrid cannot be identified.

Colubridae indeterminate B

Referred Material

EP 1323/01, vertebra from Loc. 22, Upper Laetolil Beds.

Description and Comments

A single, small vertebra is somewhat similar to those of Natricinae, a group of colubrids that represent a very small proportion of the snake diversity of Africa. Its natricine features include the presence of a laterally flattened hypapophysis, well-developed parapophyseal processes, wide and vaulted neural arch, and anteriorly overhanging neural spine. However, the vertebra is relatively short and its centrum clearly widens anteriorly, which casts some doubts on its natricine affinities. In conclusion, this vertebra cannot be referred to a precise group within the Colubridae. It should be noted that this specimen is well-preserved and only slightly mineralized or not mineralized at all. It may be a modern vertebra collected along with fossils, but this cannot be demonstrated with certainty.

Unidentifiable Colubridae

Referred Material

EP 1110/03, a broken vertebra from Loc. 10W, Upper Laetolil Beds.

A heavily damaged vertebra appears to belong to the Colubridae. However, it cannot be identified below the family level.

Elapidae

Five vertebrae found in association belong to an elapid snake. Meylan (1987) designated them as the holotype of a new species, *Naja robusta*. Vertebrae of the Elapidae do not markedly differ from those of various colubrids; distinctions may even be difficult to identify between elapids and colubrids of the natricine type. Vertebrae of elapids are usually more massively built, shorter, and wider as a whole than those of colubrids. Their neural arch is never markedly vaulted. The neural spine is comparatively low and long. Marked subcentral ridges clearly delimit the ventral face of the centrum, and the latter widens anteriorly. Parapophyseal processes are present. The neck of the condyle is not elongate, and the zygosphene is never very thick. Furthermore, in contrast to most colubrids, elapids have hypapophyses throughout the trunk region. The hypapophyses are always compressed laterally, they tend to extend posteriorly rather than ventrally, and their anterior borders are straight or weakly sigmoid (Bailon 1989; Scanlon et al. 2003).

Naja robusta Meylan, 1987

Referred Material

LAET 75-3016, Holotype, five trunk vertebrae (likely from the posterior trunk region) from Loc. 10W, Upper Laetolil Beds.

Description and Comments

The five vertebrae are represented by three specimens (two pairs of articulated vertebrae and one isolated vertebra). But since they were found in association, they may be accepted as a holotype. None of these vertebrae is complete and Meylan (1987) figured a reconstruction made from several of the specimens. The present study provides an opportunity to further illustrate these specimens (Fig. 16.2a–e). According to Meylan, these vertebrae come from the 'mid-body', but the presence of well-marked, although not deep, subcentral grooves suggests that they come from the posterior trunk region (but not from the posteriormost trunk). It should be noted that in Meylan's figure 3.12 the subcentral grooves appear to be deeper than they really are on the actual specimens.

The vertebrae exhibit the overall morphology of elapids (see above). In addition to these characters, the vertebrae from Laetoli display a suite of features that support their referral to the *Naja* group (e.g., *Pseudohaje*, *Hemachatus*, ?*Paranaja*): interzygapophyseal constriction slight; zygapophyseal facets small with regard to the size of the vertebrae; strong, blunt and relatively short prezygapophyseal processes ('accessory processes' of Meylan); cotyle and condyle large; centrum triangular and relatively wide anteriorly; and subcentral ridges not sharp, but well-marked. More specifically, the ventral face of the centrum, hollowed out by shallow subcentral grooves, appears to be typical of posterior trunk vertebrae of the *Naja* group. Unfortunately, the shape of the neural spine and that of the zygosphene cannot be reconstructed. As far as the neural spine is concerned, it may only be indicated that its base is long. Anteriorly, it reaches the zygosphenal roof, i.e., it is longer than in Meylan's illustrations (1987: Fig. 3.12). The centrum length of the largest vertebra is 6.7 mm.

Discussion

Based on the morphology of the subcentral ridges, Meylan suggested that *N. robusta* is related to the living African species *N. nigricollis* and *N. mossambica*. Based on our present knowledge, this inference appears to be correct, and may be accepted pending an osteological survey of all species of *Naja*. Today, the range of *N. nigricollis* extends from sub-Sahara to southernmost Africa. *Naja mossambica* has a more restricted range, from southern Tanzania and southern Angola, south to Natal Province and northern Namibia (Golay et al. 1993). *Naja robusta* is still known only from the holotype. Taking into account that the available vertebrae probably come from the posterior trunk region, the total length of this cobra is estimated at about 1.7 m. However, if these vertebrae come from the mid-trunk, as inferred by Meylan (1987), then the total length was about 1.4 m.

? Elapidae. Unidentified genus and species

Referred Material

EP 1637/03, posterior trunk vertebra from Loc. 15; EP 800/05, nine associated mid-trunk vertebrae (including EP 800/05a, two articulated trunk vertebrae) from Loc 5. All from the Upper Laetolil Beds.

Description

This snake displays the features that characterize elapids (see above). It differs from *Naja robusta* in being smaller (centrum length of largest vertebra = 4.6 mm), in having a deeper interzygapophyseal constriction, a wider and slightly more vaulted neural arch, clearly smaller cotyle and condyle, narrower and more inclined paradiapophyses (in lateral view), more pointed prezygapophyseal processes, and the ventral face of centrum expanding less anteriorly (Fig. 16.2f–h). Moreover, on the available posterior trunk vertebra, the subcentral grooves are deeper.

Discussion

The most striking feature of these vertebrae is the relative width of the neural arch. This is unusual in terrestrial elapids, but does occur in marine forms, i.e., Hydrophiinae. However, the snake from Laetoli does not show adaptations to aquatic life.

The width of the neural arch, the marked interzygapophyseal constriction, and the small size of the cotyle and condyle demonstrate that this fossil does not belong to a genus of the *Naja* group. It also differs from African elapids, such as *Dendroaspis* and *Elapsoidea*, whose vertebrae are more elongated. Unfortunately, the vertebral morphology of all Elapidae, and even of all African Elapidae, remains unknown. Therefore, the referral of this snake at the genus level cannot be determined. In addition, it should be kept in mind that, although all other features argue for assignment to the Elapidae, the width of the neural arch casts doubts on referral to this family. On the other hand, African colubrids are so numerous and their osteology so poorly known that it cannot be ruled out that this vertebral morphology occurs among them. Consequently, this snake is only tentatively referred to the Elapidae.

Viperidae

Viperids are represented only by one species that clearly outnumbers other snakes. It belongs to the genus *Bitis*. Meylan (1987) referred this species to '*Bitis arietans* Merrem, 1820 or *Bitis olduvaiensis* Rage, 1973'. Subsequent collections at Laetoli have substantially increased the material belonging to this taxon. This allows better comparisons with living forms, but not with the extinct *B. olduvaiensis*. Consequently, the identification of the viper from Laetoli remains uncertain.

Skeletons of all of the 13–16 recognized extant species (Golay et al. 1993; Uetz et al. 2006) are not available for comparisons. However, the fossil from Laetoli is a large species whose size is consistent with that of the living *Bitis arietans*, *B. gabonica*, and *B. nasicornis*, and the extinct *B. olduvaiensis*. Therefore, comparisons have been made with these four species only.

Bitis Gray, 1842

Bitis nov. sp. (unnamed) or *Bitis olduvaiensis* Rage, 1973

Referred Material

LAET 76-7E-51, venom fang from Loc. 7E; LAET 76-18-436, vertebra from Loc. 18; EP 1013/00, two vertebrae from

Loc. 18; EP 3325/00, vertebra from Loc. 18; EP 818/01, vertebra from Loc. 18; EP 819/01, vertebra from Loc. 18; EP 1296/01, vertebra from Loc. 22 S; EP 1256/03a, vertebra from Loc 7E; EP 1256/03, seven vertebrae from Loc 7E; EP 1257/03, two vertebrae from Loc 7E. All from the Upper Ndolanya Beds.

EP 2144/00, skull bones, vertebrae, and ribs likely belonging to a single individual from Loc. 13 [EP 2144/00a, braincase; EP 2144/00b, articulated parts of right frontal and prefrontal; EP 2144/00c, right frontal; EP 2144/00d, fragmentary right compound bone; EP 2144/00e, trunk vertebra; EP 2144/00 undifferentiated, about 62 vertebrae and fragments of vertebrae and ribs]; EP 438/01, fragmentary compound bone, vertebrae and fragments of ribs from Loc. 13 (may belong to the same individual as EP 2144/00, T. Harrison, personal communication) [EP 438/01a, fragment of left compound bone; EP 438/01 undifferentiated, 23 vertebrae and fragments of ribs)]; EP 505/05, vertebra from Loc. 9; LAET 75-1973, vertebra from Loc. 10E; EP 428/03, vertebra from Loc. 5; LAET 75-536, vertebra from Loc. 10; EP 2954/00, vertebra from Loc. 10; EP 819/98, vertebra from Loc. 10W; EP 1109/03, vertebra from Loc. 10W. All from the Upper Laetolil Beds.

EP 018/99, vertebra from Kakesio 6; EP 1060/05, two vertebrae from Kakesio 8. Both from the Lower Laetolil Beds.

Remarks

Among the specimens that likely belong to a single individual (EP 2144/00 and perhaps EP 438/01) were found, as intestine contents, bones of an immature *Serengetilagus praecapensis* (lagomorph) (T. Harrison, personal communication).

Description

EP 2144/00a is a braincase that includes the complete parietal, supraoccipital, both prootics, and both exoccipitals, nearly complete basioccipital and basiparasphenoid, and the posterior part of the left frontal (Figs. 16.3a, b and 16.4a, b). Hard matrix covers parts of the specimen, mainly the lateral and ventral faces. The braincase is wide and depressed. The parietal forms an almost flat table that lacks any crest. However, posteriorly it contributes to the rising anterior limit of the sagittal crest of the supraoccipital. The dorsolateral borders of the

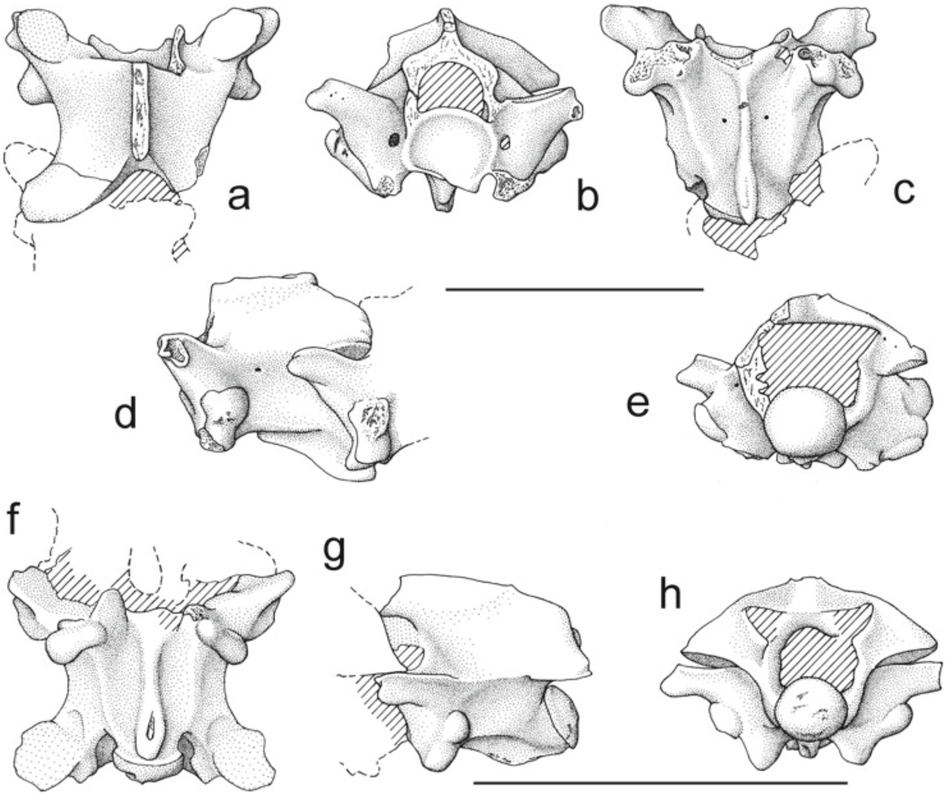

Fig. 16.2 Elapidae. (**a**–**e**) *Naja robusta*, two trunk vertebrae (likely from the posterior trunk region) belonging to the holotype; (a–d) LAET 75-3016A in (**a**) dorsal, (**b**) anterior, (**c**) ventral, and (**d**) left lateral views; (**e**) LAET 75-3016B in posterior view. (**f**–**h**)? Elapidae, mid-trunk vertebra, part of EP 800/05a, in (**f**) ventral, (**g**) left lateral, and (**h**) posterior views. Hatched areas: matrix. Scale bars represent 1 cm

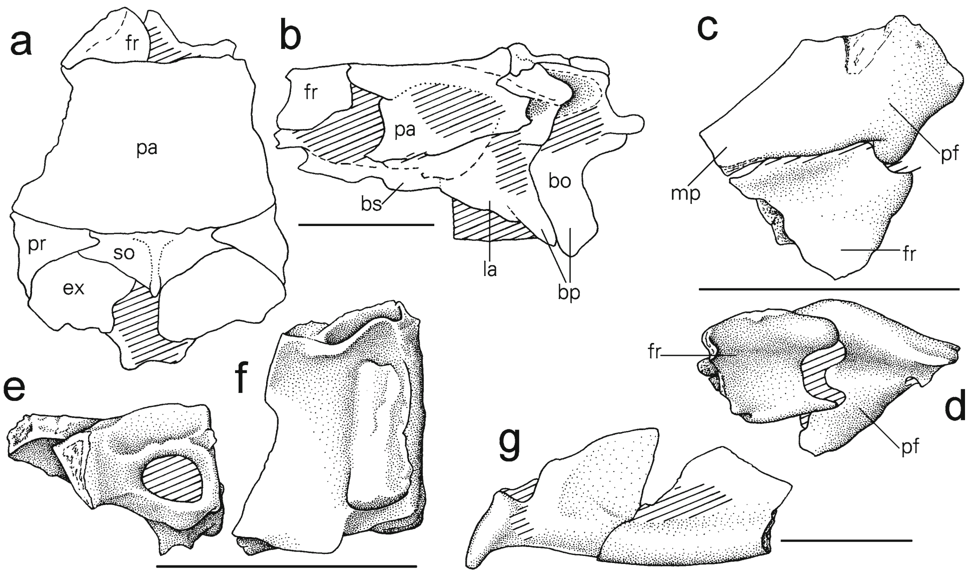

Fig. 16.3 *Bitis* sp. nov. or *Bitis olduvaiensis*. (**a**–**b**) EP 2144/00a, braincase in (**a**) dorsal and (**b**) left lateral views; (**c**–**d**) EP 2144/00b, right incomplete frontal and prefrontal in (**c**) dorsal and (**d**) lateral views; (**e**–**f**) EP 2144/00c, right frontal in (**e**) anterior and (**f**) ventral views; (**g**) EP 2144/00d, incomplete right compound bone in medial view. (*bo* basioccipital, *bp* basioccipital process, *bs* basiparasphenoid, *ex* exoccipital, *fr* frontal, *la* ventral lamina of basiparasphenoid, *mp* medial process of prefrontal, *pa* parietal, *pf* prefrontal, *pr* prootic, *so* supraoccipital). Hatched areas: matrix. Scale bars represent 1 cm

parietal (i.e., the supraorbital flanges) appear to be largely broken off; consequently, the width of the parietal cannot be estimated. Nevertheless, the length/width ratio of the bone appears higher in EP 2144/00a than in the living species. Dorsally, the parietal forms relatively narrow posterolateral projections; only the left one is preserved. A sagittal crest is present on the triangular supraoccipital. The posterodorsal surface of the exoccipital is concave. The sutural line between the prootic on the one hand, and the supraoccipital and exoccipital on the other hand, protrudes dorsally as a ridge. On either side, the dorso-lateral border, formed by the exoccipital, prootic and parietal, projects laterally as an acute lamina. The lateral faces of the braincase are largely covered by matrix. The basioccipital bears a very strong basioccipital process that is directed posteroventrally. The base of the process occupies more than half the length of the basioccipital; its distal part is broken, but it may be inferred that the process was long. The basiparasphenoid is wide and concave ventrally. Posteriorly, its lateral borders extend slightly ventrolaterally as thin lamellae. The anterior process and the suborbital flanges of the bone are broken, but the remaining base of one of the flanges shows that it was well-developed and directed anterolaterally. Posteriorly, the basiparasphenoid forms the anterodorsal part of the basioccipital process that is mainly formed by the basioccipital. A rather deep lamina (la: Fig. 16.3b) prolongs the process anteriorly and runs onto the basiparasphenoid. All cranial foramina are obscured by matrix.

EP 2144/00b is comprised of the anterolateral fragment of a right frontal and articulated part of prefrontal (Fig. 16.3c, d). Both bones are incomplete, but the medial process of the prefrontal affords useful information (see below). EP 2144/00c is a right frontal whose posterior and anterolateral parts are damaged (Fig. 16.3e, f). It is broad but its length cannot be precisely estimated; however, it was certainly short. Its depressed shape and well-developed supraorbital flange are consistent with *Bitis*. EP 2144/00d and EP 438/01a are two posterior parts of compound bones, i.e., the posterior component of the mandible. EP 2144/00d, a right compound bone, is the most complete (Fig. 16.3g). The partially preserved retroarticular process is strong and directed posteromedially. As is typical for *Bitis*, the medial flange (‘prearticular’ flange) is well-developed and high, whereas the vestigial lateral flange (‘surangular’ flange) is almost absent.

The vertebrae display the usual features of the Viperidae (Fig. 16.4c–f): presence of a hypapophysis on all trunk vertebrae; hypapophysis straight (not sigmoid); centrum short; neural arch depressed; cotyle and condyle large; prezygapophyseal processes small; and parapophyseal processes strong. In addition, several characters demonstrate that these vertebrae belong to *Bitis*: vertebra short and wide; interzygapophyseal constriction not deep; neural arch strongly depressed, its dorsal surface slightly concave; posterior median notch shallow; zygosphene comparatively narrow; neural spine long anteroposteriorly and high (Szyndlar 1988; Bailon 2000). Unfortunately, none of the largest vertebrae is well-preserved. Only the width across postzygapophyses (PO-PO *sensu* Auffenberg 1963) and the length of the centrum can be measured on a few vertebrae. Moreover, it is not

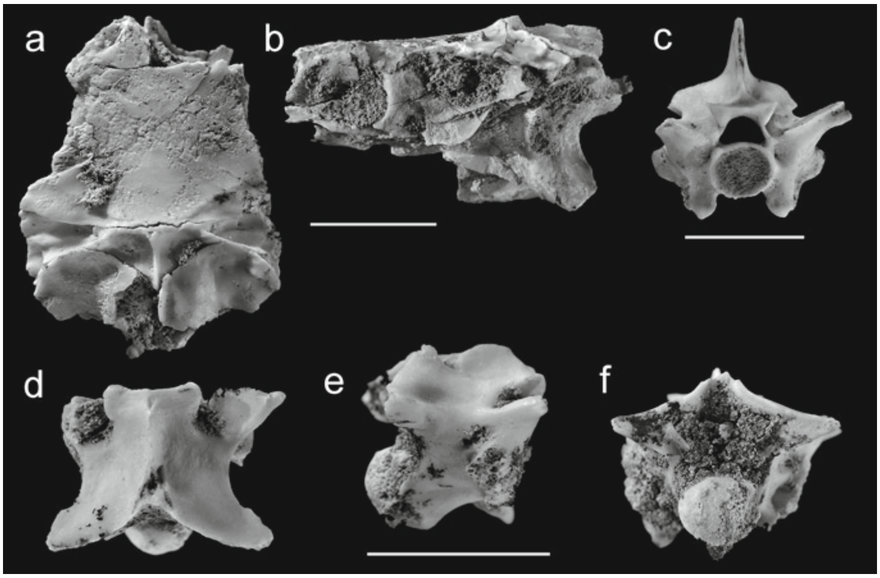

Fig. 16.4 *Bitis* sp. nov. or *Bitis olduvaiensis*. (**a–b**) EP 2144/00a, braincase in (**a**) dorsal and (**b**) left lateral views; (**c**) EP 2144/00e, mid trunk vertebra in anterior view; (**d–f**) EP 1256/03a, mid trunk vertebra in (**d**) dorsal, (**e**) right lateral, and (**f**) posterior views. Scale bars represent 1 cm

possible to take these two measurements on any one single vertebra. The width across the postzygapophyses reaches at least 19 mm in one vertebra, while the centrum length is 10.4 mm in another vertebra.

Discussion

The described specimens may be securely referred to the genus *Bitis*, but the identification of the species is problematic. The specimens of *Bitis* from Laetoli cannot be compared profitably with *Bitis olduvaiensis* from the early Pleistocene of Olduvai. *Bitis olduvaiensis*, the only named extinct species of the genus, is known by maxillae that bear all diagnostic characters of the species, a fragmentary pterygoid, fangs, vertebrae, and ribs (Rage 1973). Therefore, only vertebrae, ribs, and fangs are available for comparison for both snakes (i.e., *B. olduvaiensis* and *Bitis* from Laetoli). But ribs and fangs provide no useful information. On the other hand, the vertebral morphology is very uniform within the genus and it does not allow useful comparisons at the species level. The vertebrae from Laetoli do not differ from those of *B. olduvaiensis*, but this does not mean that the fossil from Laetoli belongs to the latter species.

Comparisons of the skull bones from Laetoli with those of the large extant species of *Bitis* show that the fossil snake may be readily distinguished from them. *Bitis* from Laetoli differs from *Bitis arietans*, *B. gabonica*, and *B. nasicornis* mainly by the shape of the posterolateral projections of the parietal, the shape of the anterior border of the supraoccipital, and likely the length of the parietal. The preserved posterolateral projection of the parietal is narrower and less rounded than in the three living species. It is morphologically closest to that of *B. arietans*. In *B. gabonica* and *B. nasicornis* the projection is regularly rounded. Moreover, in *B. nasicornis*, it is only weakly protruding. In the fossil from Laetoli, the anterior border of the supraoccipital appears as a long, transverse line. In *B. arietans* this border is not very different, but the transverse part is clearly shorter than in the fossil. In *B. gabonica* the anterior border forms a median point that fits a notch in the parietal. In *B. nasicornis* the border is concave anteriorly. Although the width of the parietal cannot be estimated in the fossil, this bone appears to be more elongate than in the three living species.

One additional feature distinguishes the Laetoli species from both *B. arietans* and *B. gabonica*. On the compound bone, ventrolateral to the articular facet, the medial surface is regularly convex in EP 2144/00d (the area is lacking in EP 438/01a) and in *B. nasicornis,* whereas a strong, sharp, and anteroposteriorly elongate ridge runs on this surface in specimens of *B. arietans* and *B. gabonica*.

The fossil from Laetoli is also distinguished from *B. gabonica* and *B. nasicornis* by the shape of the posterior part of the supraoccipital. In the fossil and *B. arietans*, the supraoccipital is triangular posteriorly and it inserts between the two exoccipitals. In *B. gabonica*, the posterior part of the bone is weakly convex, while in *B. nasicornis* the border is similar to that of *B. gabonica* with the addition of a small posterior sagittal point

The medial process of the prefrontal of EP 2144/00b is lacking its medial extremity, but it still provides significant information. It allows the fossil to be distinguished from *B. arietans* and *B. nasicornis*. In EP 2144/00b the medial process is stronger than that of *B. arietans*. Moreover, its posterior border forms a sinuous suture, whereas that of *B. arietans* is straight. The medial process of the prefrontal of *B. nasicornis* appears to be as strong as that of the fossil, but its posterior border is straight as in *B. arietans*. In the fossil, the preserved part of this process matches *B. gabonica*.

The fossil clearly differs from *B. arietans* in having a strong, deep lamina produced by the anterior border of the basioccipital process and that runs anteriorly onto the basiparasphenoid. Such a lamina does not exist in specimens of *B. arietans* of similar size to EP 2144/00a. The lamina does occur in small individuals of *B. arietans*, but it is shallower and less developed than in the fossil. *Bitis gabonica* has a lamina similar to that of the fossil. In the only specimen of *B. nasicornis* examined, the lamina is present, but it is slightly shorter anteroposteriorly than that of the fossil and *B. gabonica*.

In summary, the viper from Laetoli differs from the extant species of similar size (i.e., *B. arietans*, *B. gabonica*, and *B. nasicornis*). The other living species are clearly smaller, and it can be presumed that the fossil *Bitis* from Laetoli represents an extinct species. Unfortunately, the only diagnostic element of the extinct *B. olduvaiensis* (i.e., the maxilla) is unknown in *Bitis* from Laetoli, making direct comparisons impossible. The viper from Laetoli may belong to *B. olduvaiensis*, but on the basis of the available material this cannot be demonstrated. Consequently, no clear conclusion may be drawn. *Bitis* from Laetoli belongs either to a new species that cannot be diagnosed or to *B. olduvaiensis*. Based on the size of the largest vertebrae, *Bitis* from Laetoli had a total length of about 1.4–1.5 m.

Indeterminate snakes

Referred Material

EP 2144/00f, left frontal from Loc. 13; LAET 75-1978, incomplete vertebra of a boid or viperid from Loc. 10E; EP 1069/01, incomplete vertebra of a boid or viperid from Loc. 15; EP 649/01b, centrum with hypapophysis of a boid or viperid from Loc. 10. All from the Upper Laetolil Beds.

Discussion and Conclusions

The fossil taxa from Laetoli that may be identified to at least the genus level belong either to living taxa (*Python*, *Naja*, *Bitis*) or perhaps to extinct forms close to living genera (cf. *Thelotornis*, cf. *Rhamphiophis*). Extinct species are present (*Naja robusta* and the indeterminate species of *Bitis*), but at least one extant species occurs (either *Python sebae* or *P. natalensis,* which at this time cannot be distinguished from their osteological features).

The fauna is very unbalanced since anuran amphibians and lizards are represented by two bones each, while snakes consist of more than 150 bones. The rarity of amphibians in African Neogene localities is common, but lizards are generally well-represented and their low number at Laetoli cannot be explained. The assemblage of snakes also is strongly unbalanced, since the viperid *Bitis* represents more than 78% of the snakes. The fact that a large part of one individual of *Bitis* (EP 2144/00 and perhaps EP 438/01) is preserved, likely skews the number of specimens of this taxon towards overrepresentation (each disarticulated bone of this individual has been counted as a specimen).

The fauna shows a typical African, sub-Saharan pattern. *Python*, whatever the species, is a sub-Saharan taxon. The living *Rhamphiophis* and *Thelotornis* are also inhabitants of sub-Saharan Africa; assuming the approximate identifications are correct, it may be presumed that the geographical ranges of cf. *Rhamphiophis* and cf. *Thelotornis* were similar to those of the living genera. In addition, *Naja* and *Bitis*, that reach North Africa, are by far more frequent and more taxonomically diverse south of the Sahara. The fauna does not include elements living today only north of sub-Saharan Africa. Such taxa are known from the Miocene of Namibia (Rage 2003, in progress). The only marked difference between the assemblage from the Pliocene of Laetoli and the extant fauna of sub-Saharan Africa is the relative rarity of colubrid snakes. Meylan (1987) already noted that colubrids were rare in the sample that he studied. He suggested that this was the result of either preservation bias or limited sampling, or a combination of the two factors. The new collections have increased the number and diversity of colubrids at Laetoli, but this group still remains remarkably poorly represented (only about 5% of the snake specimens). Usually, from the Middle Miocene onwards, the colubrids have outnumbered other snakes (except probably in South America before the Great American Interchange). In North Africa, colubrids dominate in the Middle Miocene and Late Pliocene of Morocco (Rage 1976; Bailon 2000). However, in the Neogene of Uganda (Bailon and Rage 1994) and the Miocene of Namibia (Rage 2003, in progress), colubrids do not dominate the snake fauna. Therefore, the small number of colubrids at Laetoli may be a true reflection of the original diversity, and this might be characteristic of much of Africa during the Neogene.

Only *Bitis* occurs in all the main fossiliferous beds at Laetoli, including the Lower and Upper Laetolil Beds, and the Upper Ndolanya Beds. All other fossils are restricted to parts of the Upper Laetolil Beds. Since they are present in few localities at Laetoli and/or their identification is only approximate or tentative, we cannot regard them as significant from a biostratigraphical point of view.

The ecological requirements of some taxa can be considered. Unfortunately, *Bitis*, the dominant taxon, is not identified at the species level. The living species of *Bitis*, as a whole, do not provide useful ecological information; it may be only concluded that the area was not an extreme desert. The presence of anurans is of interest. With few exceptions, frogs need water, at least at the time of breeding, although temporary ponds may be sufficient. In addition, the presence of frogs may suggest a non-arid environment out of the breeding period. Frogs have only been recovered from Loc. 10W, derived from the base of the Upper Unit of Laetolil Beds (below Tuff 3), where waterworked tuffs are relatively common. However, it cannot be excluded that such small vertebrate may have been introduced to the locality as birds pellets. Only one other taxon, *Python*, has aquatic tendencies. However, it occurs higher in the stratigraphic sequence (Loc. 2, Upper Laetolil Beds between Tuffs 5 and 7). The species of *Python* at Laetoli, either *P. sebae* or *P. natalensis*, lives today in savanna, marshes, and habitats close to the edges of forests, but not in forests. These species of *Python* avoid large deserts and are generally near water that they often enter. cf. *Thelotornis* was arboreal, as demonstrated by its markedly elongate vertebrae. This does not necessarily imply that trees were present, because shrubs and bushes would provide suitable substrates. In conclusion, no clear paleoenvironmental picture emerges. This results partly from the fact that significant taxa do not occur in the same horizons. Based on the amphibian and snake fauna it may be inferred that the area was not a true desert, was likely not forested, and that water (ponds?) was periodically present during the time of deposition of the Upper Laetolil Beds.

As far as snakes are concerned, Laetoli has yielded one of the richest and most diverse faunas from the Plio-Pleistocene of Africa, along with Ahl al Oughlam in Morocco (Bailon 2000) and Olduvai Bed I in Tanzania (Rage 1973). Such faunas remain very poorly known in Africa.

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Chapter 17
Tortoises (Chelonii, Testudinidae)

Terry Harrison

Abstract Two species of tortoises are known from Pliocene sites on the Eyasi Plateau, including Laetoli. The most common species is a medium-sized tortoise, *Stigmochelys brachygularis*, which is well represented in the Laetolil Beds (~3.6–4.4 Ma) and Upper Ndolanya Beds (~2.66 Ma). The giant tortoise, *“Geochelone” laetoliensis*, is known only from the Laetolil Beds, and is much less common than *S. brachygularis*. *Stigmochelys brachygularis* is represented by a number of relatively complete and partial shells, as well as numerous isolated and associated shell fragments, some postcranial remains and eggs. It is generally similar in size and overall morphology to the extant leopard tortoise, *S. pardalis*, but a number of features serve to distinguish the two species. *Stigmochelys brachygularis* and *S. pardalis* are inferred to be closely related, and are most likely sister taxa that represent time-successive species of a single lineage. The age structure of the fossil sample, in conjunction with evidence of carnivore damage on the shells, indicates that *S. brachygularis* was subject to relatively high levels of predation in comparison with modern-day *S. pardalis*. If *S. brachygularis* is presumed to have been ecologically similar to modern *S. pardalis*, it would have been capable of living in a wide range of habitats from semi-desert and savanna to open woodland. The material attributed to “*Geochelone*” *laetoliensis* is more fragmentary, and as a consequence it is not possible to determine its precise phylogenetic or taxonomic relationships. However, it likely represents a distinct genus, possibly with affinities to *Astrochelys* from Madagascar. A more thorough assessment of the relationships of “*G.*” *laetoliensis* with Miocene and Pliocene giant tortoises from Africa and with extant genera will have to await the recovery of more complete material from Laetoli. Giant tortoises, such as “*G.*” *laetoliensis*, became extinct on mainland Africa during the late Pliocene, possibly associated with the appearance of early *Homo* and stone tool using behaviors at 2.6 Ma.

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Introduction

Meylan and Auffenberg (1987) recognized three different species of land tortoises (Testudinidae) from the sequence at Laetoli, all referred to the genus *Geochelone*. Two of the species, *Geochelone brachygularis* and *G. laetoliensis*, were newly recognized and recorded only from the Upper Laetolil Beds (~3.5–3.8 Ma). The third species, referred to the extant leopard tortoise, *G. pardalis*, was recorded from the younger Upper Ndolanya Beds (~2.6–2.7 Ma). *Geochelone brachygularis*, a medium-sized tortoise, was represented by 14 specimens, including eight almost complete shells. The specimens were recovered from throughout the Upper Laetolil Beds (between Tuffs 2 and 8). A nearly complete shell collected in 1935 (BMNH R.6849) is of uncertain provenance (Leakey 1935), but clearly derived from the Upper Laetolil Beds. Meylan and Auffenberg (1987) also indicated that KNM-X 6404 and KNM-X 6405 are shells of unknown provenance. However, reference to the Mary Leakey field catalogue shows that both specimens are from the Upper Ndolanya Beds at Loc. 18, and that their correct identification numbers should be LAET 79-6404 and LAET 79-6405. A small collection of undescribed fossil tortoise specimens from Laetoli, made by Kohl-Larsen in the late 1930s, includes a relatively complete shell of *G. brachygularis* (MB. R.2909) housed in the Museum für Naturkunde der Humboldt-Universität in Berlin.

Geochelone laetoliensis is a giant tortoise, with an estimated carapace length exceeding 1 m. Meylan and Auffenberg (1987) referred this species to the subgenus *Aldabrachelys*, which includes the extant giant tortoise from Aldabra, as well as closely related extinct forms from the late Pleistocene and Holocene of Madagascar and the Seychelles (Austin et al. 2003). *Geochelone laetoliensis* is much less common than *G. brachygularis*, and was represented by six specimens

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only, all of which consist of fragmentary remains of the carapace and plastron. The material was recovered from the Laetolil Beds between Tuffs 3 and 8, although an additional specimen examined in the field at Loc. 10W, but not collected, was found just below Tuff 3.

A partial shell (LAET 79-5497) from the Upper Ndolanya Beds at Loc. 7E was illustrated by Meylan and Auffenberg (1987) and referred to *G. pardalis*, but not described in detail.

Renewed investigations at Laetoli and at neighboring localities on the Eyasi Plateau since 1998 have yielded additional finds of fossil tortoises. These include several additional entire and partial shells, as well as more fragmentary remains that provide further useful information about the morphology and the spatio-temporal distribution of the fossil tortoises at Laetoli (see Tables 17.1–17.4). The aim of this paper is to provide a brief descriptive account of these new finds, as well to refine our understanding of the anatomy, paleobiology, and systematics of the species represented.

The taxonomy of tortoises previously included in the genus *Geochelone* (e.g., Iverson 1992) has recently undergone major taxonomic revision, principally because of the recognition that it is paraphyletic (Bour 1980, 1984, 1985; Crumly 1982, 1984; Gaffney and Meylan 1988; Caccone et al. 1999; Gerlach 2001; Palkovacs et al. 2002; Le et al. 2006; Fritz and Bininda-Emonds 2007). To alleviate this problem, Bour (1980) and Fritz and Bininda-Emonds (2007) recognize five extant genera for the extant tortoises previously included in *Geochelone* (see also Lapparent de Broin 2000). The taxonomic scheme proposed by Fritz and Bininda-Emonds (2007) is followed here.

The two extant species of sub-Saharan Africa tortoises previously included in *Geochelone* are now referred to *Stigmochelys pardalis*, the leopard tortoise, and *Centrochelys sulcata*, the African spurred tortoise. *Stigmochelys pardalis* is a medium-sized tortoise, with a straight carapace length (SCL) in adults of 30–70 cm (Spawls et al. 2001; although exceptional individuals can reach 90 cm, Lapparent de Broin 2003). In East Africa, the species is somewhat smaller, reaching a maximum SCL of 45 cm (Branch 2008). It is common and widely distributed in semi-desert, savanna, bush, and woodland habitats extending from southern Sudan, Ethiopia and Somalia through East Africa, Zambia and Angola, to Botswana, Namibia, Zimbabwe, Mozambique, and South Africa (Loveridge and Williams 1957; Spawls et al. 2001). The eastern leopard tortoise, *G. pardalis babcocki* (Loveridge 1935) occurs today throughout the Serengeti region (Kabigumila 2001a), and is frequently encountered at Laetoli and elsewhere in the southern Serengeti. *Centrochelys sulcata* is the largest of the mainland African tortoises, with a SCL that can attain 80–100 cm (Lapparent de Broin 2003). Its distribution extends as fragmented populations along the southern margin of the Sahara, in arid scrubland and savanna of the Sahel, from Senegal and Mauritania to Sudan, Ethiopia and Eritrea (Iverson 1992; Branch 2008).

Only two species of fossil tortoises are now recognized in the collections from Laetoli–*Stigmochelys brachygularis* and “*Geochelone*” *laetoliensis*. The specimen from the Upper Ndolanya Beds, previously recognized as belonging to the extant *Stigmochelys pardalis* by Meylan and Auffenberg (1987), is here considered to be morphologically indistinguishable from *S. brachygularis*, and included in the same species as material from the Laetolil Beds (see below). The taxonomic and phylogenetic affinities of the giant tortoise from Laetoli are difficult to establish based on the limited material available, so it is provisionally retained as a separate species within “*Geochelone*”, until its relationships to other African fossil and extant tortoises can be better ascertained.

Material

Chelonian remains are relatively common at the major collecting localities at Laetoli and at neighboring sites on the Eyasi Plateau. All of the chelonian material recovered consists of tortoises (Testudinidae). Uniquely for East African Plio-Pleistocene localities, no remains of turtles have been found (except for a fragmentary and poorly preserved shell of *Pelusios sinuatus* [MB. R. 2869], from the Late Pleistocene Lemagrut Korongo, recovered by Kohl-Larsen in 1939). This is consistent with sedimentological evidence that indicates that deposition at Laetoli was primarily subaerial, and that permanent sources of water, such as rivers or lakes, were absent (Ditchfield and Harrison 2011).

Over 500 specimens have now been recovered, including 18 relatively complete or partial shells. A list of the identifiable shell and postcranial material is presented in Tables 17.1–17.4. A number of fossil tortoise eggs ($n=44$) have also been recovered, and these are described here for the first time.

The most important new finds of *S. brachygularis* include: (1) EP 468/00 (Loc. 20), 14 associated shell fragments, comprising much of the right plastron and the anterior part of the left plastron, and a number of associated costals and peripherals (Fig. 17.1). (2) EP 2472/03 (Loc. 9 S) an almost complete shell of a large adult male (Fig. 17.2). The plastron is crushed and slightly depressed. This is the largest known specimen of *S. brachygularis*. (3) EP 1285/04 (Loc. 10E) a relatively complete, but badly crushed shell (Fig. 17.3). The plastron is complete, but depressed into the carapace, especially posteriorly. The carapace is largely complete, but is missing right peripherals I-III, right costal I, and left costal I-X, and the left costals lack their ventral margins. (4) EP 1347/05 (Loc. 22E) comprising slightly more than the anterior half of the shell (Fig. 17.4). The carapace is preserved to

Table 17.1 Better preserved specimens of *Stigmochelys brachygularis* from the Eyasi Plateau, including Laetoli

Catalogue number[a]	Locality	Horizon[b]	Description	Remarks and reference
MB R.2909	Marambu (= Loc. 1)	ULB	Partial shell consisting of much of the carapace and complete plastron	
LAET 75-397	5	ULB, between Tuffs 3 & 5	Entire shell	Paratype - Meylan and Auffenberg 1987
LAET 79-5490	22	ULB, 30 cm above Tuff 3	Partial carapace and plastron	Paratype - Meylan and Auffenberg 1987
LAET 79-5491	10	ULB, 60 cm above Tuff 7	Entire shell	Allotype - Meylan and Auffenberg 1987
LAET 79-5492	5	ULB, Tuff 4	Partial shell, reconstructed	Paratype - Meylan and Auffenberg 1987
LAET 79-5493	2	ULB, Tuff 6	Entire shell	Holotype - Meylan and Auffenberg 1987
LAET 79-5494	9S	ULB, Tuff 3	Shell missing anterior one-third of carapace	Paratype - Meylan and Auffenberg 1987
LAET 79-5496	10W	ULB, 60-90 cm below Tuff 3	Associated shell fragments comprising: left and right epiplastron; left and right xiphiplastron; right peripherals I, II, IX, X, XI; left peripherals IX, X, XI; neurals II, IV, V; pygal	Meylan and Auffenberg 1987
LAET 79-5497	7E	UNB	Entire shell, but crushed	Attributed to *S. pardalis* by Meylan and Auffenberg 1987
LAET 79-6404	18	UNB	Entire shell, but crushed	Listed as KNM-X 6404 by Meylan and Auffenberg 1987
LAET 79-6405	18	UNB	Almost entire shell, but sheared obliquely into two sections. Crushed and weathered.	Listed as KNM-X 6405 by Meylan and Auffenberg 1987
BMNH R6849	Unknown	Probably ULB	Almost entire shell	Paratype - Meylan and Auffenberg 1987
KK 82-22	Kakesio	LLB	Partial shell comprising: fragmentary plastron; right peripherals VII–XI; left peripheral XI; right costal II–VI fragments; suprapygal I–II	
KK 82-66	Kakesio	LLB	Almost entire shell, but badly crushed	
KK 82-452	Kakesio	LLB	Portion of shell consisting of complete plastron and posterior two-thirds of carapace	
EP 2472/03	9S	ULB between Tuffs 1 & 2	Almost entire shell	
EP 1285/04	10E	ULB, between Tuffs 5 & 7	Relatively complete, but badly crushed shell	
EP 1347/05	22E	ULB, between Tuffs 5 & 7	Anterior portion of shell, comprising slightly more than half	

[a] *BMNH*, Louis and Mary Leakey collections, 1935, The Natural History Museum, London; *EP*, Eyasi Plateau expeditions directed by Terry Harrison, 1998–2005, National Museum of Tanzania; *KK*, Mary Leakey collections from Kakesio, 1982, currently housed in the Kenya National Museum; *LAET*, Mary Leakey collections, 1974–1981, currently housed in the Kenya National Museum; *MB*, Kohl-Larsen collection, 1938–1939, Museum für Naturkunde der Humboldt-Universität in Berlin

[b] *LLB* Lower Laetolil Beds; *ULB* Upper Laetolil Beds; *UNB* Upper Ndolanya Beds; *YMT* Yellow Marker Tuff

the anterior portion of neural III. There is a large circular depression on the dorsal aspect of the carapace on the right hand side, probably caused by the weight of the sediment at the time of burial (see Table 17.1).

In addition, several previously undescribed specimens of *S. brachygularis* are included in the present study: (1) KK 82-22 (Kakesio) a partial shell (Fig. 17.5); (2) KK 82-66 (Kakesio) an almost entire shell, but crushed flat dorsoventrally (Fig. 17.6); (3) KK 82-452 (Kakesio) a partial shell consisting of a complete plastron and the posterior two-thirds of the carapace (Fig. 17.7); (4) MB.R. 2909 (Marambu = Loc. 1) a partial shell with complete plastron and much of the carapace intact (Fig. 17.8). All of the peripherals are present, except for portions of peripherals

Table 17.2 List of isolated and associated shell elements of *Stigmochelys brachygularis* from the Eyasi Plateau, including Laetoli

Catalogue number[a]	Locality	Horizon[b]	Description and remarks
MB. R.2491	Garussi	ULB	Unassociated right costal II, left partial xiphiplastron, peripheral ?VI, 10 shell fragments
MB. R.2492	Marambu, Garussi and Deturi	ULB	Unassociated epiplastron and partial entoplastron, right peripheral VII, carapace fragment, plastron fragment
MB. R.2493	Garussi	ULB	Unassociated pygal and suprapygal II, left peripheral XI, right peripheral VIII, left epiplastron fragment, right peripheral II and fragmentary peripheral. Associated left peripheral VIII, left peripheral IX, right peripheral IX and right peripheral X
LAET 78-5438	6	ULB, 3 m below Tuff 7	Epiplastra, entoplastron, parts of hypoplastra
LAET 79-5489	8	ULB, between Tuffs 6 & 7	Right xiphiplastron
LAET 79-5495	8	ULB, 60 cm above Tuff 7	Entoplastron
LAET 79-5496	10W	ULB, 60–90 cm below Tuff 3	Left and right epiplastron, right peripherals I–II, IX–XI, left peripherals IX–XI, right and left xiphiplastron, neurals II, IV, V, pygal
LAET 79-5498	8	ULB, Tuff 5	Right epiplastron
KK 82-60	Kakesio	LLB	Right epliplastron
EP 005/98	Kakesio 1	LLB	Suprapygal
EP 039/98	Kakesio 3	LLB	Right peripherals I, II
EP 040/98	Kakesio 3	LLB	Right perpheral III (possibly same individual as above)
EP 112/98	Kakesio South	LLB	Epiplastra, entoplastron
EP 890/98	10	ULB, below Tuff 3	Neural scute V
EP 1328/98	22S	UNB	Left peripheral XI
EP 1373/98	13	ULB, between Tuffs 5 & 8	Nuchal bone
EP 234/00	1	ULB, between Tuffs 6 & 8	Right Peripheral XI, left peripheral VIII
EP 336/00	8	ULB, between Tuffs 5 & 7	Fragment of nuchal bone
EP 468/00	20	ULB, between Tuffs 6 & 8	14 associated shell fragments, comprising: partial plastron; right peripherals I–IV, VIII and IX; 8 carapace fragments (mostly costals)
EP 736/00	2	ULB, between Tuffs 5 & 7	Right epiplastron, right peripheral II
EP 1177/00	8	ULB, between Tuffs 5 & 7	Unassociated fragment of nuchal bone, left xiphiplastron
EP 1376/00	6	ULB, between Tuffs 5 & 7	Neural VI fragment
EP 1659/00	3	ULB, between Tuffs 7 & 8	11 associated shell fragments comprising: fragment of nuchal bone; right epiplastron; right peripheral I, VIII–XI; left peripheral II, XI; costal; scute fragment indet.
EP 1711/00	5	ULB, between Tuffs 3 & 5	Right peripheral II
EP 1795/00	2	ULB, between Tuffs 6 & 8	Left epiplastron
EP 2016/00	5	ULB, between Tuffs 3 & 5	Right Peripheral III fragment
EP 2085/00	13	ULB, between Tuffs 5 & 8	Left peripheral I fragment
EP 2242/00	7	ULB, between Tuffs 5 & 8	Left peripheral I
EP 2462/00	12E	ULB, between Tuffs 5 & 7	Neural V
EP 2702/00	2	ULB, between Tuffs 5 & 7	Fragment of nuchal bone, right epiplastron
EP 2771/00	3	ULB, between Tuffs 7 & 8	Unassociated right and left anal scute
EP 2828/00	5	ULB, between Tuffs 3 & 5	Pygal
EP 154/01	6	ULB, between Tuffs 5 & 7	Left epiplastron
EP 576/01	10E	ULB, between Tuffs 5 & 7	Entoplastron
EP 482/03	3	ULB between Tuffs 7 & 8	Right peripheral VIII
EP 528/03	Kakesio 10	LLB	10 unassociated shell fragments, including: 2 right epiplastra
EP 805/03	2	ULB, between Tuffs 5 & 7	Entoplastron
EP 1255/03	7E	UNB	Left peripheral II
EP 1904/03	1	ULB, between Tuffs 6 & 8	Left epiplastron
EP 2231/03	7	ULB, between Tuffs 5 & 8	Right epiplastron, entoplastron
EP 2289/03	13	ULB, between Tuffs 5 & 8	Right peripheral XI

(continued)

Table 17.2 (continued)

Catalogue number[a]	Locality	Horizon[b]	Description and remarks
EP 2464/03	9S	ULB, below Tuff 2	Six associated shell fragments comprising: right epiplastron; right peripheral XI; four scute fragments indet.
EP 455/04	2	ULB, between Tuffs 5 & 7	Pygal
EP 784/04	7	ULB, between Tuffs 5 & 8	Left Xiphiplastron fragment
EP 803/04	7	ULB, between Tuffs 5 & 8	Nuchal bone fragment
EP 856/04	Kakesio 8	LLB	Right peripheral III
EP 1098/04	11	ULB, between Tuffs 7 & 8	Nuchal bone
EP 1358/04	5	ULB, between Tuffs 3 & 5	Left epiplastron
EP 1744/04	2	ULB, between Tuffs 5 & 7	Right peripheral I
EP 072/05	11	ULB, between Tuffs 7 & 8	Unassociated 2 left epiplastrons
EP 267/05	17	ULB, between Tuff 7 and YMT	Right peripheral I

[a] *EP*, Eyasi Plateau expeditions directed by Terry Harrison, 1998–2005, National Museum of Tanzania; *KK*, Mary Leakey collections from Kakesio, 1982, currently housed in the Kenya National Museum; *LAET*, Mary Leakey collections, 1974–1981, currently housed in the Kenya National Museum; *MB*, Kohl-Larsen collection, 1938–1939, Museum für Naturkunde der Humboldt-Universität in Berlin

[b] *LLB* Lower Laetolil Beds; *ULB* Upper Laetolil Beds; *UNB* Upper Ndolanya Beds; *YMT* Yellow Marker Tuff

Table 17.3 List of specimens of *"Geochelone" laetoliensis* from the Eyasi Plateau, including Laetoli

Catalogue number[a]	Locality	Horizon[b]	Description	Remarks and reference
LAET 75-578	5	ULB, between Tuffs 3 & 5	Right epiplastron, left xiphiplastron fragment	Holotype - Meylan and Auffenberg (1987)
LAET 76-4208	22	ULB, between Tuffs 3 & 7	Costals I, II or IV, V, VI; neural II, peripheral	Meylan and Auffenberg (1987)
LAET 78-5439	6	ULB, 5 m below Tuff 6	Right epiplastron, right hypoplastron, parts of 7 costals and peripherals	Meylan and Auffenberg (1987)
LAET 78-5440	2	ULB, 0.5 m below Tuff 6	Nuchal, parts of anterior carapace	Paratype - Meylan and Auffenberg (1987)
LAET 79-5499	7	ULB, between Tuffs 6 & 8	Left peripherals III and VII; carapace fragments	Meylan and Auffenberg (1987)
LAET 79-5500	5	ULB, Tuff 3	Right costals I–III	Meylan and Auffenberg (1987)
KK 82-67	Kakesio	LLB	Pygal; nuchal; right epiplastron; partial entoplastron; partial suprapygal; right peripheral I; right peripheral XI, costal fragments	Same individual as EP 012/98
EP 012/98	Kakesio 2	LLB	Neural; left peripheral X, right peripheral X; 3 pelvic fragments	Same individual as KK 82-67
EP 212/03	Kakesio 8	LLB	Epiplastron	
EP 527/03	Kakesio 10	LLB	Ilium, pubis, femur shaft, proximal tibia, humerus shaft	

[a] *EP*, Eyasi Plateau expeditions directed by Terry Harrison, 1998–2005, National Museum of Tanzania; *KK*, Mary Leakey collections from Kakesio, 1982, currently housed in the Kenya National Museum; *LAET*, Mary Leakey collections, 1974–1981, currently housed in the Kenya National Museum

[b] *LLB* Lower Laetolil Beds; *ULB* Upper Laetolil Beds; *UNB* Upper Ndolanya Beds; *YMT* Yellow Marker Tuff

III and IV on the left side. The costals and neurals are incomplete (see Table 17.1). The first three specimens were recovered by Mary Leakey's expedition in 1982, and the last one was collected by Kohl-Larsen in 1939 (see Table 17.1).

All of the new finds of *"G." laetoliensis* are fragmentary. The best-preserved material consists of several associated carapace and postcranial elements (EP 012/98) recovered in 1998 from near the base of the Lower Laetolil Beds at Kakesio, which belongs to the same individual as undescribed material collected by Mary Leakey's team in 1982 (KK 82-67) (see Table 17.3).

The specimens described here are housed in the Natural History Museum in London (BMNH. R, 1935 Leakey collection); Humboldt-Universität Museum für Naturkunde in Berlin (MB. R., 1938–1939 Kohl-Larsen collection); Kenya National Museum in Nairobi (LAET and KK, 1974–1982 Leakey collections on loan from Tanzania); and National

Table 17.4 List of isolated postcranial remains of testudinids from the Eyasi Plateau, including Laetoli

Catalogue number[a]	Locality	Horizon[b]	Description	Taxonomic attribution
EP 435/00	12E	ULB, between Tuffs 5 & 7	Shaft of humerus	*S. brachygularis*
EP 1010/00	18	UNB	Distal humerus	*S. brachygularis*
EP 1255/00	22S	UNB	Proximal phalanx	*S. brachygularis*
EP 1509/00	Kakesio 2–4	LLB	Proximal humerus	*S. brachygularis*
EP 1516/00	Kakesio 6	LLB	Humerus shaft fragment	*S. brachygularis*
EP 3020/00	1	ULB, between Tuffs 6 & 8	Pubic bone fragment	*S. brachygularis*
EP 3327/00	18	UNB	Proximal humerus	*S. brachygularis*
EP 4263/00	2	ULB, between Tuffs 5 & 7	Distal end of phalanx	*S. brachygularis*
EP 194/01	5	ULB, between Tuffs 3 & 5	Middle phalanx	*S. brachygularis*
EP 853/01	7E	UNB	Proximal femur	*S. brachygularis*
EP 525/03	Kakesio 10	LLB	Proximal radius	*S. brachygularis*
EP 526/03	Kakesio 10	LLB	Proximal femur	*S. brachygularis*
EP 527/03	Kakesio 10	LLB	Ilium, publis, femur shaft, proximal tibia, humeral shaft	*"G." laetoliensis*
EP 1258/03	7E	UNB	Shaft and distal end of phalanx	*S. brachygularis*

[a] *EP*, Eyasi Plateau expeditions directed by Terry Harrison, 1998–2005, National Museum of Tanzania

[b] *LLB* Lower Laetolil Beds; *ULB* Upper Laetolil Beds; *UNB* Upper Ndolanya Beds; *YMT* Yellow Marker Tuff

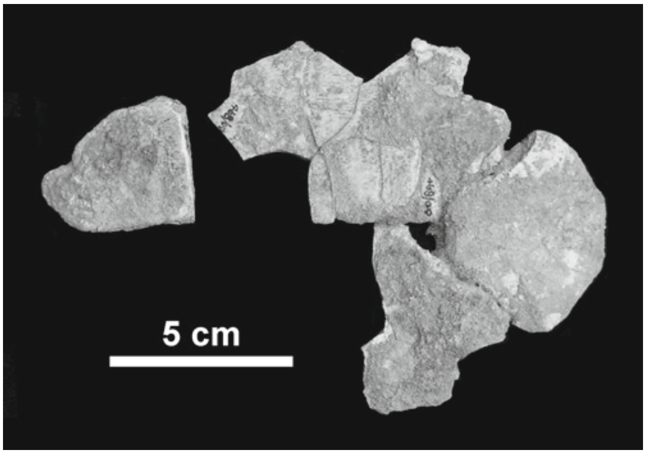

Fig. 17.1 EP 468/00. Partial plastron of *Stigmochelys brachygularis* from Loc. 20 (Upper Laetolil Beds). Ventral view

Museum of Tanzania in Dar es Salaam (EP, Eyasi Plateau expedition, 1998–2005 Harrison collection). Comparisons with extant and fossil tortoises were carried out at the Kenya National Museum and National Museum of Tanzania.

Of the 418 skeletal specimens recovered by the Eyasi Plateau expedition in 1998–2005, 15.3% are from the Lower Laetolil Beds, 78.0% are from the Upper Laetolil Beds, and 6.7% are from the Upper Ndolanya Beds. Tortoises from the Upper Laetolil Beds are recorded from all of the collecting localities, with the exception of Locs. 10NE, 19, 23 and 24 (which have all produced only very small samples of fossil vertebrates), and they are found throughout the entire stratigraphic unit. Evidently, tortoises were common and ubiquitous at Laetoli during deposition of the Upper Laetolil Beds. They appear to be somewhat more rare in the Upper Ndolanya Beds, but are represented at all of the major localities, including Locs. 7E, 14, 15, 18, 22S and Silal Artum. Skeletal remains of tortoises are comparatively common in the Lower Laetolil Beds at Kakesio, and fossil eggs have been recovered from Kakesio, Lobileita, Esere and Emboremony (see Harrison and Kweka 2011). Of the eggs recovered from the Laetoli area, 73% have come from the Lower Laetolil Beds, perhaps implying an important taphonomic difference between the stratigraphic units at localities on the Eyasi Plateau. Tortoise eggs were first recorded at Laetoli by Kent (1941) who noted the discovery in 1935 of a nest containing 11 eggs.

Stigmochelys brachygularis is much more common than *"G." laetoliensis*, and represents more than 98% of the entire sample of fossil tortoises collected since 1998. The former species is found throughout the sequence at Laetoli, from the Lower Laetolil Beds (~3.8–4.3 Ma) to the Upper Ndolanya Beds (~2.6–2.7 Ma), and there is no apparent morphological or metrical change through time. *"Geochelone" laetoliensis* is known only from the Lower and Upper Laetolil Beds, and is not yet recorded from the Upper Ndolanya Beds.

Systematics and Description

Order Chelonii Latreille, 1800
Suborder Cryptodira Cope, 1868
Family Testudinidae Batsch, 1788
Genus *Stigmochelys* Gray, 1873

***Stigmochelys brachygularis* (Meylan and Auffenberg 1987)**

A medium-sized tortoise with a SCL of up to 500 mm (being somewhat smaller than the extant leopard tortoise, *S. pardalis*, with a maximum SCL of ~700 mm) (Figs. 17.9–17.14;

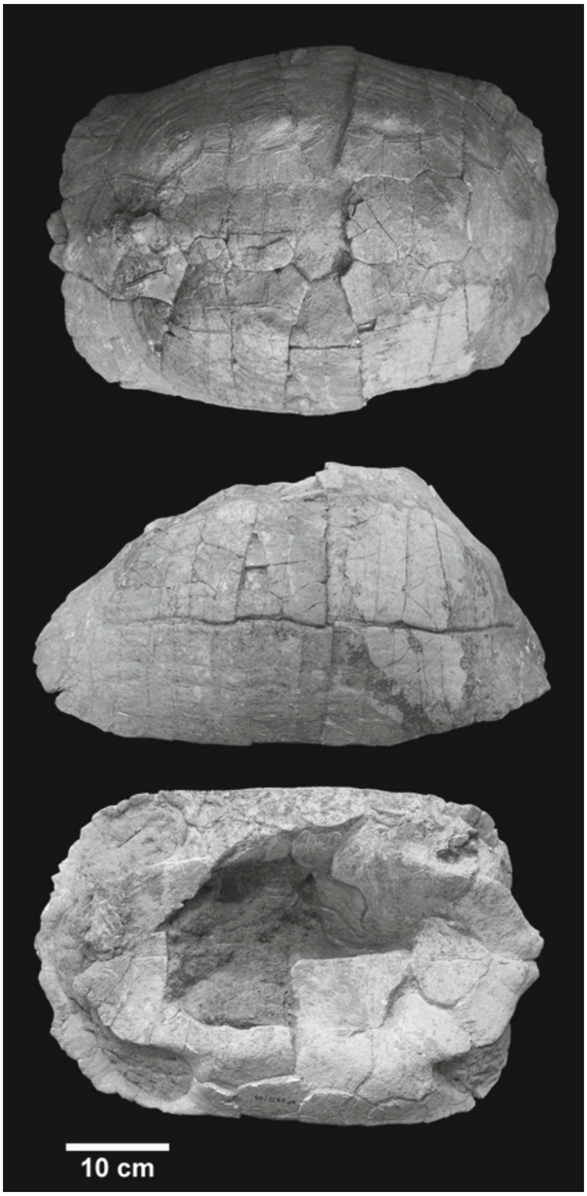

Fig. 17.2 EP 2472/03. Almost complete shell of *Stigmochelys brachygularis* from Loc. 9S (Upper Laetolil Beds). *Top*, dorsal view. *Middle*, lateral view. *Bottom*, ventral view

Fig. 17.3 EP 1285/04. Relatively complete, but crushed shell of *Stigmochelys brachygularis* from Loc. 10E (Upper Laetolil Beds). *Top*, dorsal view. *Bottom*, ventral view

Tables 17.5–17.6). Previously the largest recorded specimen of *S. brachygularis* was LAET 79-5490 with a plastron length (PL) of 395.3, but a new specimen recovered in 2003 (EP 2472/03) has a PL of 426.4 mm and SCL of 490 mm (see Fig. 17.2). The carapace is high-domed with steep sides rather than bulbous. Meylan and Auffenberg (1987) contend that females have a greater doming of the carapace more posteriorly than in males, but the present author could find no significant difference between specimens in this regard. In females of *S. pardalis* the posterior face of the carapace is more vertical, which may facilitate mating (Archer 1948). The base of the carapace, from the ventral margin to the lateral marginal crest, is relatively shallower in *S. brachygularis* than in *S. pardalis*.

The cervical scute is absent, as in all extant representatives of *Geochelone sensu lato* (except *Aldabrachelys*, in which the cervical is lost dorsally, but retained ventrally) (Loveridge and Williams 1957). The anterior notch of the nuchal bone is relatively shallow or indistinct (but generally better developed than in *S. pardalis*). Superiorly, the nuchal bone is slightly convex mediolaterally, but there is no indication of the low boss present in *S. pardalis*. The nuchal bone is relatively shorter than it is in *S. pardalis*. In *S. brachygularis* the mean length of the nuchal bone is 71.1% of its breadth.

There are typically eight neurals, and less commonly seven. The first five neurals consist of alternating quadrilateral and octagonal scutes; the last two or three are more variable. This is the typical pattern for Testudininae (Loveridge and Williams 1957), and the same pattern occurs in *S. pardalis* (with some variants of the first neural being hexagonal). Neural VI is most commonly 8-sided (but varies from octagonal to hexagonal), while neurals VII and VIII are either 6-, 5- or 4-sided. The most common neural formula is

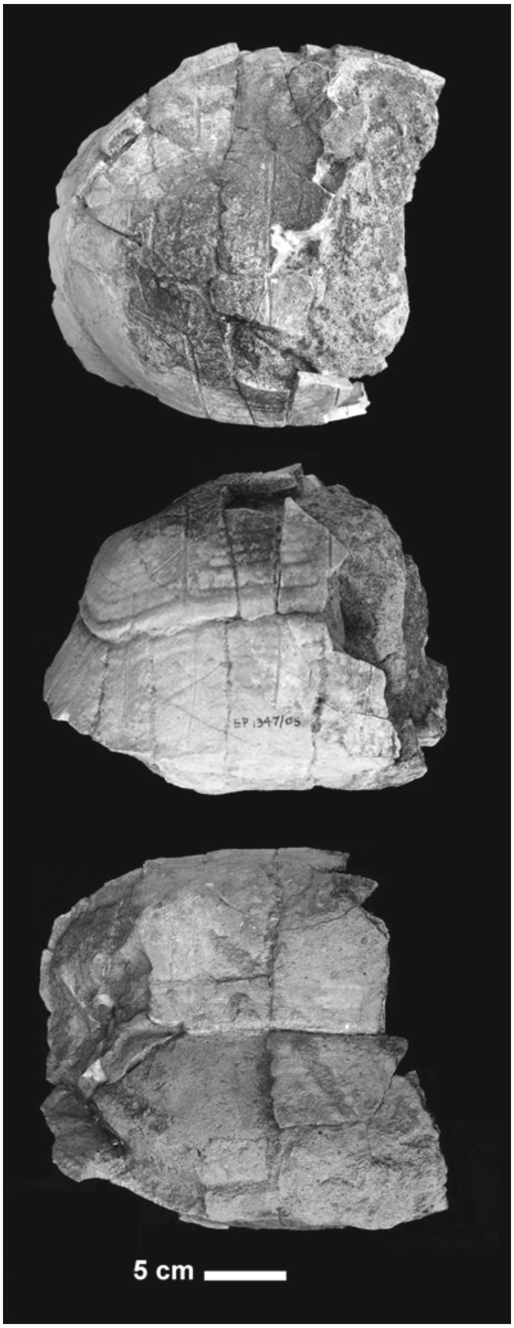

Fig. 17.4 EP 1347/05. Anterior portion of shell of *Stigmochelys brachygularis* from Loc. 22E (Upper Laetolil Beds). *Top*, dorsal view. *Middle*, lateral view. *Bottom*, ventral view

4-8-4-8-4-8-(4 or 6)-(4 or 6), which is typical of testudinines. Neural bosses are moderately to poorly developed, and are likely to be sexually dimorphic, with males having better developed bosses. However, neural bossing is much less pronounced in *S. brachygularis* than it is in *S. pardalis*.

The suprapygal series is relatively short and narrow compared with that in *S. pardalis* (Meylan and Auffenberg 1987). Suprapygal I is much broader than suprapygal II, and it bifurcates posteriorly around the anterior margin of the latter. This means that suprapygal II is completely surrounded by suprapygal I and pygal, and it does not make contact with the posteriormost peripheral (as it does in *S. pardalis*). Suprapygal II is lozenge-shaped, and is transected by the posterior sulcus of the fifth vertebral scute. The pygal is relatively short and narrow compared with *S. pardalis*. In *S. brachygularis* the mean ratio between pygal length and ventral breadth is 1.34 ± 0.45 ($N = 10$) compared with 1.55 ± 0.26 in *S. pardalis* ($n = 18$; data from Meylan and Auffenberg 1987 and this study). The pygal is also much less mediolaterally convex than the strongly domed pygal in *S. pardalis*.

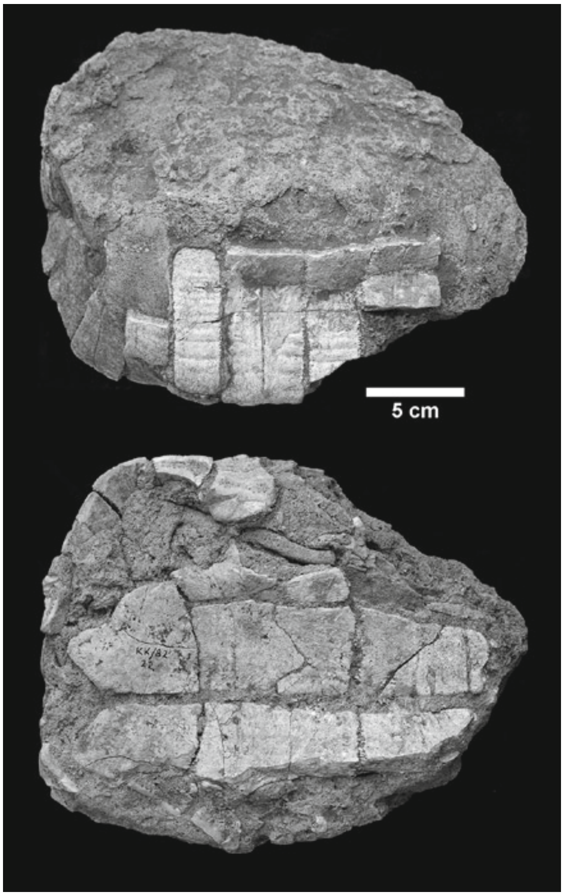

Fig. 17.5 KK 82-22. Partial shell of *Stigmochelys brachygularis* from Kakesio (Lower Laetolil Beds). *Top*, dorsal view. *Bottom*, ventral view

There are eight costals, with low bosses occurring at the dorsal edge of each costal. The latter are much less developed that those of *S. pardalis*. The costals are alternately narrow and wide proximally along the length of the carapace. Typically, there are 11 peripherals, but 10 may occur as an occasional variant (e.g., LAET 79-5492). The peripherals are relatively straight, rather than recurved (as in *S. pardalis*), producing a more vertical sided carapace. Peripherals I-III usually bear distinct denticulations at the ventral termination of the sulci. Peripheral XI has a small angular notch on the ventral margin (not seen in *S. pardalis*). The bridge

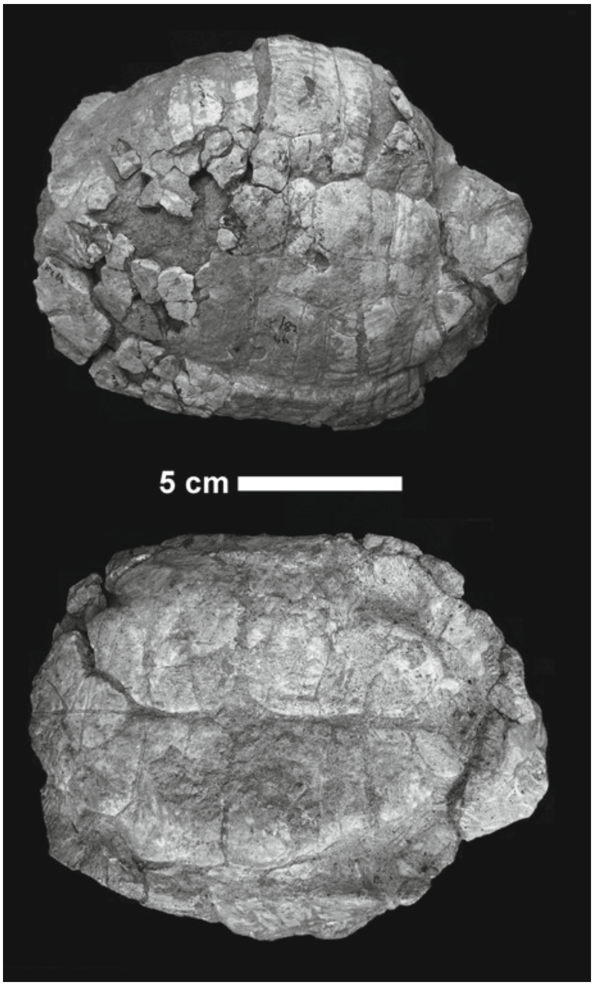

Fig. 17.6 KK 82-66. Almost entire, but badly crushed shell of *Stigmochelys brachygularis* from Kakesio (Lower Laetolil Beds). *Top*, dorsal view. *Bottom*, ventral view. Note the carnivore tooth marks on the dorsal surface of the carapace (see text for discussion)

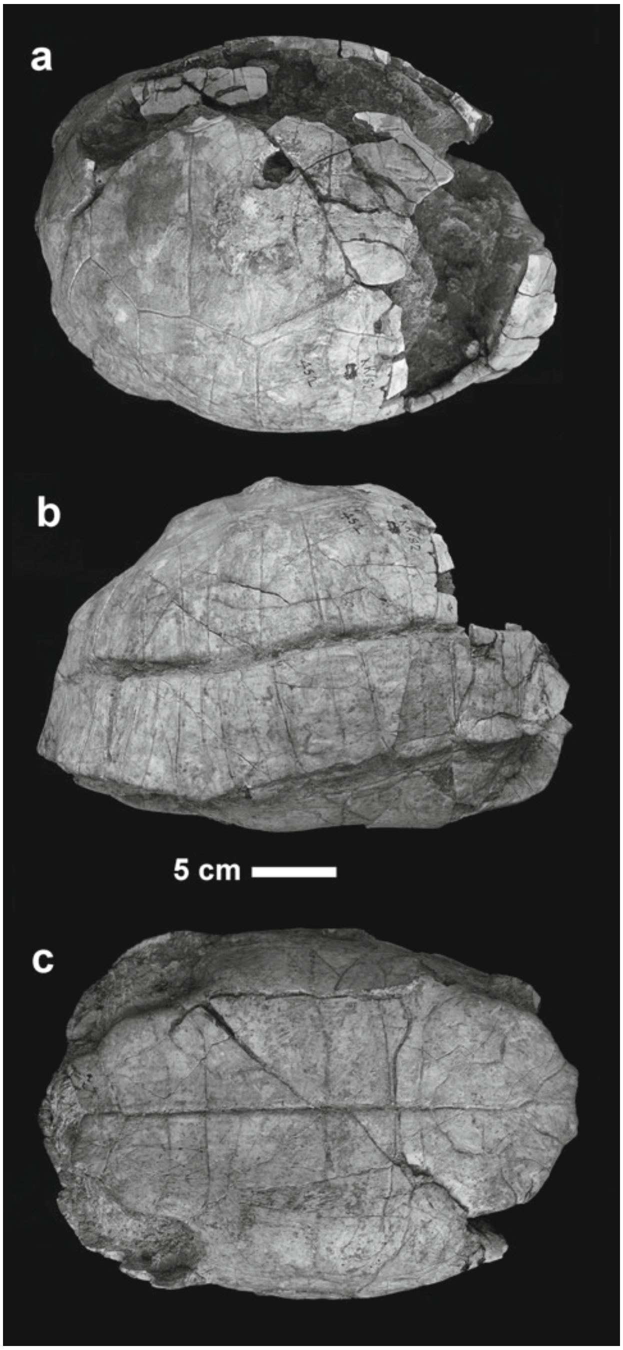

Fig. 17.7 KK 82-452. Partial shell of *Stigmochelys brachygularis* from Kakesio (Lower Laetolil Beds). *Top*, dorsal view. *Middle*, lateral view. *Bottom*, ventral view. Note the carnivore tooth marks on the dorsal surface of the carapace (see text for discussion)

extends between peripherals III to VIII, as in *S. pardalis*. It is relatively long (with a bridge length to plastron length ratio of 0.54 ± 0.02, $N = 11$), being slightly longer than in *S. pardalis*.

On the plastron, the epiplastron bears paired gular scutes. These are moderately long, and they quite commonly overlap with the entoplastron. Meylan and Auffenberg (1987) demonstrated that the frequency of overlap in *S. brachygularis* was only 38% (5 out of 13) compared with 95% in *S. pardalis* (20 out of 21). The new collections from Laetoli (as well as undescribed specimens in Berlin) provide an additional 20 epiplastra, of which 9 overlap the entoplastron, giving a revised frequency of 42.4% (14 out of 33). However, in most of the specimens that do not overlap, the gulars reach as far as the anterior margin of the entoplastron. An index relating gular scute length to midline epiplastron length (Meylan and Auffenberg 1987) gives a mean value of 1.06 ± 0.18 ($n = 25$) for *S. brachygularis*, compared with 1.35 ± 0.22 ($n = 21$) for *S. pardalis*. This indicates a significantly shorter gular scute in *S. brachygularis* (hence the species name). However, it should be noted that only four specimens of the *S. brachygularis* sample actually fall outside the 95% confidence limits of the range of *S. pardalis*, so there is a good deal of overlap in their ranges (Fig. 17.14). Moreover, none of the extant specimens of *S. pardalis* that the author has collected from the Laetoli region

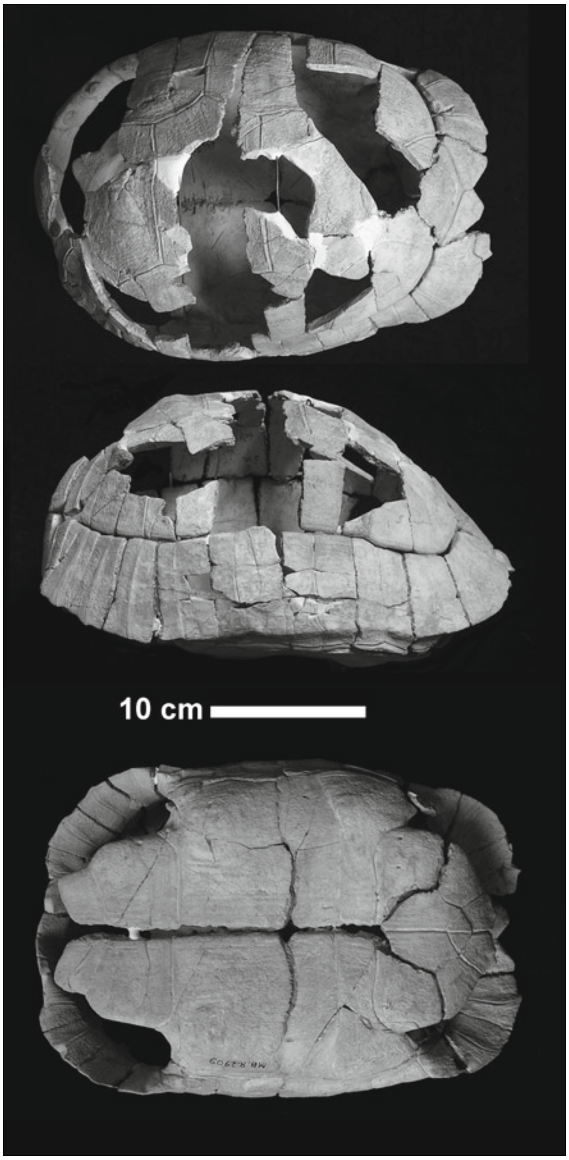

Fig. 17.8 MB R.2909. Partial shell of *Stigmochelys brachygularis* from Marambu (Loc. 1), Upper Laetolil Beds. *Top*, dorsal view. *Middle*, lateral view. *Bottom*, ventral view

($n=6$) has gular scutes overlapping with the entoplastron, and, in this respect, they cannot be distinguished from *S. brachygularis*. In addition, overlap of the gular scute with the entoplastron varies ontogenetically, with a higher incidence of overlap occurring in older individuals (Crumly, personal communication). Since many of the *S. brachygularis* individuals are juveniles, this could account for the discrepancy between the fossil sample and the extant species. Overlap of the gular and entoplastron may eventually turn out to be not such a useful feature for taxonomic separation of these species when larger samples of *S. pardalis* are examined and intraspecific variation is taken into account.

Fig. 17.9 LAET 79-5493. Entire shell of *Stigmochelys brachygularis* (holotype) from Loc. 2 (Upper Laetolil Beds). *Top*, dorsal view. *Middle*, lateral view. *Bottom*, ventral view

The inferred trend towards lengthening of the gular scute through the stratigraphic succession at Laetoli, noted by Meylan and Auffenberg (1987), is not supported by additional data (Fig. 17.14). The length of the gular scute does not differ significantly throughout the Laetolil Beds and Upper Ndolanya Beds. The relatively long gular scute (index = 1.63) in LAET 79-5497, previously the only specimen identified as being from the Upper Ndolanya Beds, does not seem to be typical of the species at this time, when LAET 79-6404 (index = 84.2) and LAET 79-6405 (index = 100.0) from the same stratigraphic horizon are included in the analysis (see Fig. 17.14). Finding that the Upper Ndolanya Beds sample is not distinguishable from that from the Upper Laetolil Beds in

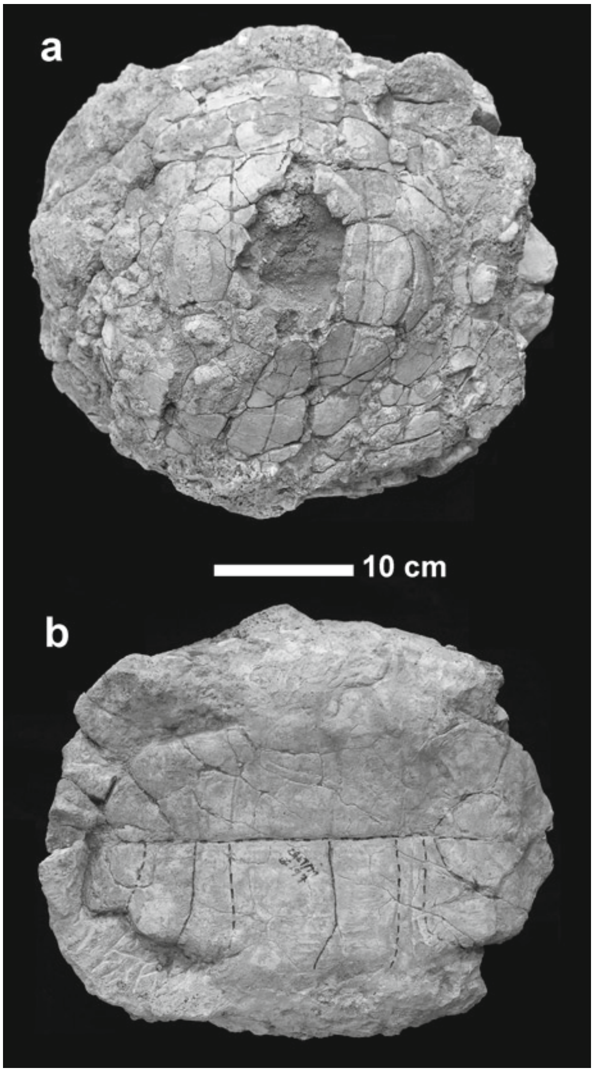

Fig. 17.10 LAET 79-5497. Almost complete, but badly crushed shell of *Stigmochelys brachygularis* from Loc 7E (Upper Ndolanya Beds). *Top*, dorsal view. *Bottom*, ventral view

relative length of the gular scute removes one of the main reasons for excluding the former from *S. brachygularis*.

The gulars extend anteriorly beyond the lateral margins of the epiplastron to form a short, stout tongue-like protuberance, which occasionally bears paired or multiple denticulations. In comparison, these are much less pronounced in *S. pardalis*. However, this is a feature that occurs commonly in juvenile individuals of testudinines, including *S. pardalis* (Lapparent de Broin, personal communication), so its appearance in *S. brachygularis* may be reflective of ontogenetic variation. The dorsal aspect of the epiplastron bears a deeply excavated surface posteriorly for the insertion of the deltoid and sternocleidomastoid muscles. This is a typical feature of extant *Geochelone sensu lato* (and other testudinines), but is apparently absent in several tortoise lineages (Meylan and Auffenberg 1987), including *"G". laetoliensis* (see below).

Fig. 17.11 LAET 79-5491. Almost entire shell of *Stigmochelys brachygularis* from Loc. 10 (Upper Laetolil Beds). *Top*, dorsal view. *Bottom*, lateral view

The entoplastron is elliptical to sub-circular or lozenge-shaped in outline, and the humero-pectoral sulcus passes posterior to it, instead of transecting it (as in *S. pardalis*). In terms of its proportions, the entoplastron is generally slightly wider than long, with a mean length-width ratio of 0.92±0.15 ($n=19$).

The xiphiplastron is relatively narrower than it is *S. pardalis*, with a shorter anal scute. The anal notch is usually narrow and V-shaped (it tends to be broad and U-shaped in *S. pardalis*), relatively quite deep (the depth of the notch expressed as a percentage of the midline xiphiplastron length provides a mean value of 31.3±5.5, $n=8$), with a rounded posterior margin (it is much more sharply pointed in *S. pardalis*). The more restricted anal notch and the less domed pygal of the carapace in *S. brachygularis* (see above) result in a much more restricted, triangular anal aperture than seen in *S. pardalis*. There is a tendency for the anal notch to increase in depth with increasing overall size in *S. brachygularis* as noted previously by Meylan and Auffenberg (1987).

The relative proportions of the different elements that comprise the plastron are very similar to those of *S. pardalis*. The mean midline length ratio of epiplastron:entoplastron:

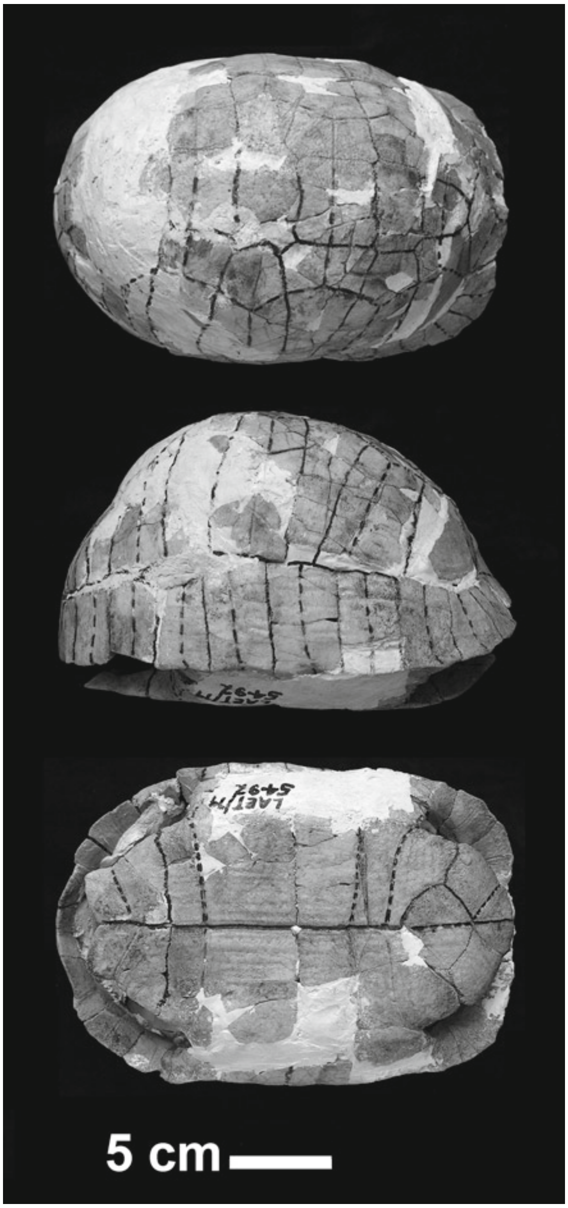

Fig. 17.12 LAET 79-5492. Almost complete shell of *Stigmochelys brachygularis* from Loc. 5 (Upper Laetolil Beds). *Top*, dorsal view. *Middle*, lateral view. *Bottom*, ventral view

hyoplastron:hypoplastron:xiphiplastron is 13:18:24:29:17 in *S. brachygularis* ($n = 14$) compared with 12:20:22:28:18 in *S. pardalis* ($n = 21$).

A few isolated and associated postcranials can be attributed to *S. brachygularis* (Table 17.4). These appear to be metrically and morphologically very similar to those of *S. pardalis*.

Comments

Given the close morphological similarity between *S. brachygularis* from Laetoli and extant *S. pardalis* there can be little doubt that the two species are closely related. They are almost certainly each other's closest sister taxon, and they probably represent time-successive members of a single lineage. In fact, a reasonable argument could be made to attribute them to a single species, especially if the full range of variation of *S. pardalis* across its extensive geographical range is taken into consideration. Moreover, some of the differences might be interpreted as being due to the juvenile

Fig. 17.13 LAET 79-5494. Partial shell of *Stigmochelys brachygularis*, lacking the anterior one-third of the carapace, from Loc. 9S (Upper Laetolil Beds). *Top*, dorsal view. *Middle*, lateral view. *Bottom*, ventral view

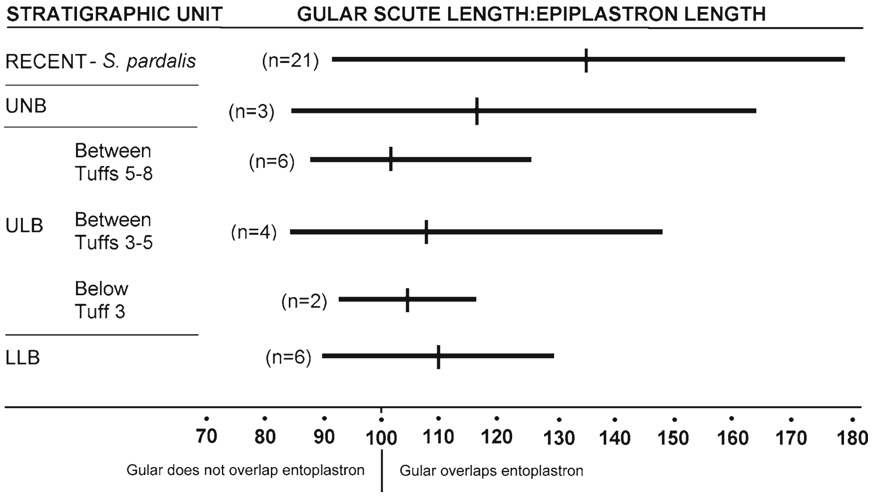

Fig. 17.14 Index of gular scute length relative to the length of the epiplastron in *Stigmochelys brachygularis* specimens from the Lower Laetolil Beds (LLB), Upper Laetolil Beds (ULB) and Upper Ndolanya Beds (UNB) and recent *S. pardalis*. Samples sizes (n) are in parentheses. The *horizontal* bars represent the range of variation and the short vertical bars represent the mean values. Index values greater than 100 imply a gular scute that overlaps the entoplastron. Data from Meylan and Auffenberg (1987) and Harrison (unpublished). See text for discussion

Table 17.5 Dimensions (mm) of carapace of *Stigmochelys brachygularis*

Catalogue number	CL	CH	NBL	NBW	SP1W	SP1L	SP2W	SP2L	PYL	PYW	Reference
MB. R.2909	–	125.0	42.3	56.9	–	22.3	32.3	20.8	28.1	38.2	
LAET 75-397	–	–	61.0	92.8	31.0	57.0	53.0	23.0	–	11.5	M & A 1987
LAET 78-5438	–	–	–	–	–	–	–	–	–	–	M & A 1987
LAET 79-5489	–	–	–	–	–	–	–	–	–	–	M & A 1987
LAET 79-5490	–	–	–	–	–	–	–	–	–	–	M & A 1987
LAET 79-5491	183.0	123.0	38.0	52.0	17.0	33.0	31.6	18.0	22.0	29.2	M & A 1987
LAET 79-5492	–	–	37.5	–	16.5	19.3	35.0	14.4	23.6	19.0	M & A 1987
LAET 79-5493	189.0	112.5	44.4	51.0	13.0	32.4	26.5	17.4	28.0	20.5	M & A 1987
LAET 79-5494	–	181.7	–	–	20.0	43.5	50.0	28.0	54.0	27.0	M & A 1987
LAET 79-5495	–	–	–	–	–	–	–	–	–	–	M & A 1987
LAET 79-5496	–	–	–	–	–	–	–	–	57.5	27.5	M & A 1987
LAET 79-5497	353.5	–	–	–	–	–	–	–	–	–	
LAET 79-5498	–	–	–	–	–	–	–	–	–	–	M & A 1987
LAET 79-6404	381.0	–	67.0	96.6	–	40.6	62.0	39.8	–	–	M & A 1987
LAET 79-6405	–	–	79.0	110.0	36.0	60.0	–	–	–	–	M & A 1987
BMNH R6849	161.0	–	31.0	36.0	14.0	27.0	25.4	14.7	21.5	17.3	M & A 1987
EP 1285/04	170.7	–	30.1	51.1	–	–	–	–	24.2	15.2	
EP 1347/05	–	–	46.4	64.1	–	–	–	–	–	–	
EP 2472/03	490.0	–	79.0	109.0	38.3	50.1	67.5	43.0	46.2	51.2	
KK 82-452	–	–	–	–	–	29.1	–	22.9	33.6	22.5	

Dimensions: CL, carapace length; CH, carapace height; NBL, nuchal bone length; NBW, nuchal bone widthSP1W, suprapygal I width anteriorly; SP1L, suprapygal I length; SP2W, suprapygal II width; SP2L, syprapygal II length

PYL, pygal length; PYW, pygal width posteriorly

Reference: M & A 1987 = Meylan and Auffenberg (1987)

status of many of the *S. brachygularis* sample, although their occurrence in the newly discovered adult male individual (EP 2472/03) demonstrates that the differences in *S. brachygularis* do persist into adulthood. However, the fossil taxon can be distinguished from *S. pardalis* by a suite of features: pygal relatively shorter and less domed; suprapygal II enclosed by pygal and suprapygal I (*S. pardalis* has a broader suprapygal II that contacts the posterior peripheral); suprapygal I shorter in the midline, and relatively narrower; neural bosses much less pronounced; nuchal bone relatively shorter; bossing on costals less pronounced; peripherals less convex (i.e., carapace more steep-sided); gular scutes with prominent anterior

Table 17.6 Dimensions (mm) of plastron of *Stigmochelys brachygularis*

Specimen	PL	EpL	EntL	EntW	GL	HyL	HypL	XiL	AL	BrL	Reference
MB. R.2909	213.5	21.8	42.7	38.5	32.1	42.5	67.0	39.5	19.5	114.0	
LAET 75-397	298.0	41.0	49.0	61.0	41.0	75.0	80.0	52.5	23.0	157.5	M & A 1987
LAET 78-5438	–	26.5	35.0	42.0	33.0	–	–	–	–	–	M & A 1987
LAET 79-5489	–	–	–	–	–	–	–	–	21.0	–	M & A 1987
LAET 79-5490	395.3	60.0	–	82.0	51.0	74.0	112.0	74.5	29.0	–	M & A 1987
LAET 79-5491	167.3	26.0	24.7	32.0	25.3	34.8	47.8	32.0	14.4	92.0	M & A 1987
LAET 79-5492	156.9	22.6	27.0	30.0	22.6	37.8	44.0	26.0	15.0	82.0	M & A 1987
LAET 79-5493	167.5	17.0	32.0	33.6	25.0	39.0	53.0	25.5	11.0	95.6	M & A 1987
LAET 79-5494	262.6	42.0	48.0	57.2	38.9	56.0	74.0	44.0	17.0	146.6	M & A 1987
LAET 79-5495	–	–	23.5	20.6	–	–	–	–	–	–	M & A 1987
LAET 79-5496	–	–	47.9	–	42.0	–	–	57.0	–	–	M & A 1987
LAET 79-5497	319.2	33.3	66.5	62.3	54.4	69.6	90.2	52.7	17.2	–	
LAET 79-5498	–	30.5	–	–	26.5	–	–	–	27.0	–	M & A 1987
LAET 79-6404	335.1	53.0	45.0	64.0	53.0	82.0	100.7	53.7	23.6	166.1	M & A 1987
LAET 79-6405	317.8	48.3	44.3	63.1	48.3	82.8	90.8	49.2	17.6	–	M & A 1987
BMNH R6849	143.0	16.5	29.5	–	23.5	31.0	42.5	23.5	11.0	77.0	M & A 1987
EP 468/00	–	23.7	29.7	45.2	24.4	32.3	–	36.7	7.3	–	
EP 1285/04	166.0	22.0	27.8	27.6	18.3	39.0	48.6	28.6	8.0	93.9	
EP 1347/05	–	–	–	–	–	–	57.9	–	–	–	
EP 2472/03	426.4	58.5	79.1	83.5	68.1	109.5	113.3	66.0	31.6	227.4	
KK 82-22	–	29.7	37.5	38.9	38.4	–	62.6	40.6	13.3	–	
KK 82-66	124.5	15.7	21.7	21.0	17.6	30.2	35.1	21.8	8.3	–	
KK 82-452	245.2	27.2	50.5	42.8	34.3	63.2	76.4	45.6	22.8	134.3	

Dimensions: PL, plastron length; EpL, epiplastron length; EntL, entoplastron length; EntW, entoplastron widthGL, gular scute length; HyL, hyoplastron length; HypL, hypoplastron length; XiL, xiphiplastron length

AL, anal scute length; BrL, bridge length. All length dimensions taken in the midline, except for BrL

Reference: M & A 1987 = Meylan and Auffenberg (1987)

denticulations; a lower incidence of gular scutes overlapping with entoplastron (42% *versus* 95% in *S. pardalis*); narrower epiplastron, with longer epiplastral lip; entoplastron relatively shorter, and subcircular in outline; anal scute of xiphiplastron relatively much shorter; anal notch V-shaped (more U-shaped in *S. pardalis*); and narrow anal notch and flatter pygal, producing a smaller and more triangular aperture (larger, more circular aperture in *S. pardalis*) (Fig. 17.15). These are considered sufficient grounds to maintain a species distinction between *S. brachygularis* and *S. pardalis*

Family Testudinidae Batsch, 1788
Genus indeterminate

"*Geochelone*" *laetoliensis* Meylan and Auffenberg, 1987

A giant tortoise with an estimated SCL greater than 1 m (see Table 17.7 for dimensions). The epiplastron is relatively thick and bulbous, with a broadly rounded anterior margin (Figs. 17.16 and 17.17). It lacks a deep posterior excavation on the dorsal surface, which accommodates the deltoid and sternomastoid muscles. Although this latter feature is present in some extant giant tortoises (see Auffenberg 1964; Meylan and Auffenberg 1987), it is generally associated with a specialized reduction of the mass of the plastron in island endemics. In LAET 75-578 and KK 82-67, the anterior margin of the epiplastron is slightly convex, and bears no protuberant beak or denticulations (unlike *S. brachygularis*). However, in EP 212/03 the epiplastron has well developed gular projections (Fig. 17.16), suggesting that the epiplastra of *"Geochelone" laetoliensis* may have been sexually dimorphism in this regard, as in *Centrochelys sulcata* (Meylan, personal communication). The configuration of protruding gulars, in combination with the absence of the dorsal excavation of the epilastron, resembles the condition in *Astrochelys radiata* from southern Madagascar. The gular scute occasionally overlaps the entoplastron (in LAET 75-578 it does not overlap, whereas in LAET 78-5437 and KK 82-67 is does overlap). The entoplastron is lozenge-shaped, and is much wider than long (Fig. 17.17).

In the carapace, there is no cervical scute. The nuchal bone is longer than wide, with a concave or V-shaped anterior margin. Isolated and fragmentary neurals indicate that they were alternately quadrangular and octagonal. The anterior neurals lack distinct bosses. Neural VI is broader than long and octagonal, with a low, but well-developed boss. The neural formula can be reconstructed as 4-8-4-8-4-8-(?). The costals are wedge shaped, alternately narrowing ventrally and dorsally in adjacent costals. They bear a thickened antero-posterior buttress running along the lateral side of the shell approximately midway between the ventral and dorsal margins, in place of the low bosses seen in *S. pardalis*.

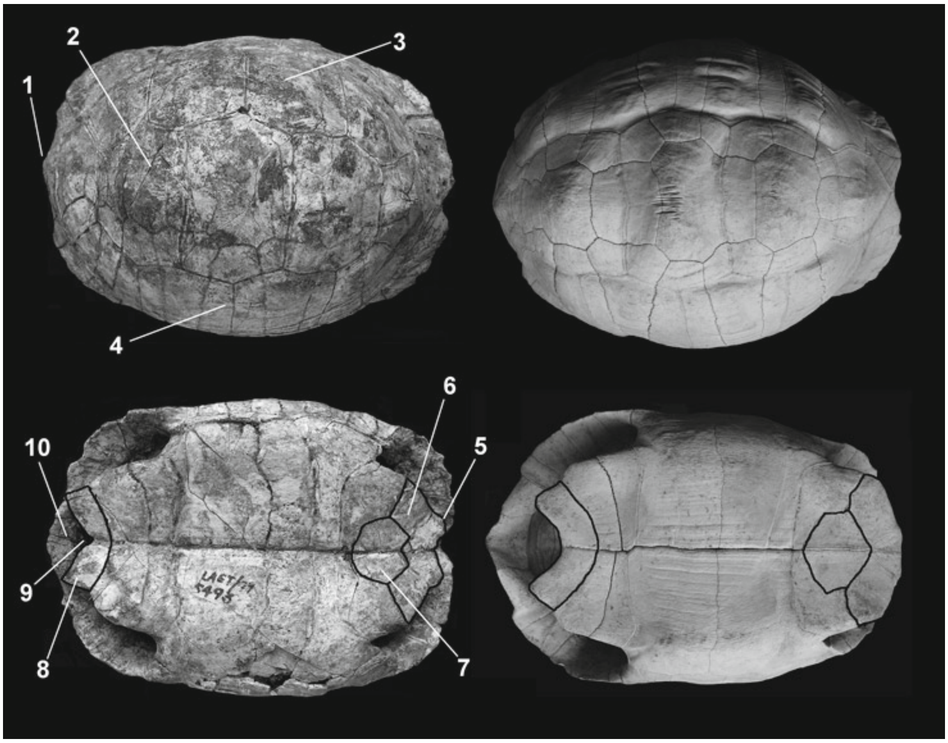

Fig. 17.15 Comparison of *Stigmochelys brachygularis* (LAET 79-5493, holotype) (*left*) and *S. pardalis* (modern specimen from Laetoli) (*right*). *Top*, dorsal views. *Bottom*, ventral views. Note the following distinctive features of *S. brachygularis*: (1) pygal relatively shorter and less domed; (2) neural bosses much less pronounced; (3) bossing on costals less pronounced; (4) peripherals less convex; (5) gular scutes with prominent anterior denticulations; (6) narrower epiplastron; (7) entoplastron relatively shorter, and subcircular in outline; (8) anal scute of xiphiplastron relatively much shorter; (9) anal notch V-shaped (rather than U-shaped in *S. pardalis*); and (10) narrow anal notch and flatter pygal, producing a smaller and more triangular aperture (larger, more circular aperture in *S. pardalis*). See text for further details

Table 17.7 Dimensions of carapace and plastron elements of *"Geochelone" laetoliensis*

Specimen	Element	Dimensions (mm)
LAET 75-578	Epiplastron	Epiplastron length = 100.0[a]
EP 212/03	Epiplastron	Epiplastron length = 114.1
LAET 78-5440	Nuchal bone	Nuchal bone length = 292.0[a]
		Nuchal bone width = ~270 (estimated)[a]
KK 82-67	Pygal	Pygal length = 127.3
		Pygal breadth = ~150 (estimated)
	Nuchal	Nuchal bone length = 140.5
		Nuchal bone width = ~165 (estimated)
	Entoplastron	Entoplastron length = ~121 (estimated)
		Entoplastron width = ~155 (estimated)
	Suprapygal I	Suprapygal I length = 93.6
		Suprapygal I width anteriorly = 48.7

[a] Dimensions from Meylan and Auffenberg (1987)

The pygal is U-shaped, with a bluntly rounded ventral margin. The external surface is evenly convex, rather than strongly domed as in *S. pardalis*. The dorsal margin is convex, rather than V-shaped as in *S. pardalis*. The dorso-lateral angle of the pygal is not preserved, but it seems likely, given the degree of convergence of the lateral and dorsal margins that peripheral XI and suprapygal II made contact with each other (in contrast to *S. brachygularis*). Suprapygal I is a chevron-shaped bone, with a V-shaped ventral notch. It bears a low rounded boss dorsally. The bone is longer and narrower than in *S. pardalis* and *S. brachygularis*, and it has less divergent ventro-lateral arms. Peripheral XI is a broad triangular plate with a deep ventral notch and a strongly projecting lateral flange (Figs. 17.18 and 17.19).

A few fragmentary postcranial remains can be attributed to *"G." laetoliensis* on the basis of their large size and the greater robusticity of the limb bones compared to *S. pardalis* (Table 17.4).

Comments

Meylan and Auffenberg (1987) referred the giant tortoise from Laetoli to a new species *Geochelone (Aldabrachelys) laetoliensis*. Assignment to *Aldabrachelys* was based mainly

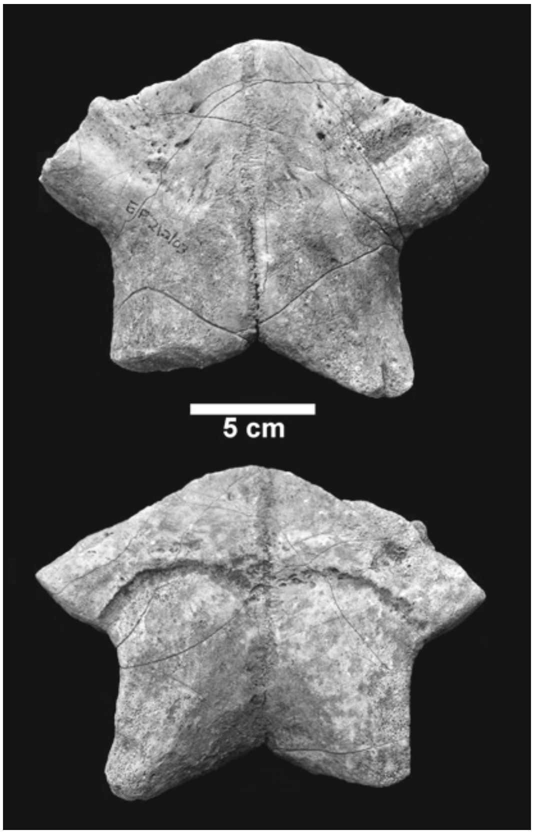

Fig. 17.16 EP 212/03. Epiplastron of *"Geochelone" laetoliensis* from Kakesio 8. *Top*, dorsal view. *Bottom*, ventral view

on the occurrence of thickened epiplastra that lacked deep posterior excavations. However, absence of a posterior excavation in the epiplastron is known to occur independently in a number of lineages (Meylan and Auffenberg 1987). In addition, extant species of *Aldabrachelys* all differ from the Laetoli taxon in retaining a cervical scute (occasionally absent ventrally in *A. gigantea*). The justification for referring the giant tortoise from Laetoli to *Aldabrachelys* is not strongly supported, especially given the fragmentary nature of the available material. Alternatively, Lapparent de Broin (2000) contends that the giant tortoise from Laetoli probably represents a member of the *Stigmochelys* group, and refers to the taxon as ?aff. *Stigmochelys* sp. However, the morphological differences between the large species at Laetoli and *S. brachygularis* and *S. pardalis*, especially in the configuration of the epiplastron, are of sufficient magnitude to argue against it being included in the same genus. The *"G." laetoliensis* material differs from *S. brachygularis* in the following respects: epiplastron thick and robust, and lacking a deep posterior excavation; the gular scute is sexually dimorphic, with a long gular projection in presumed males; pygal with convex dorsal margin; suprapygal II probably made contact with peripheral XI; suprapygal I is relatively longer and narrower; and the limb bones are relatively much stouter. Given the current evidence, it seems unlikely that the Laetoli giant tortoise is phylogenetically closely related to *Stigmochelys*. The distinctive morphology of the epiplastron in "*G.*" *laetoliensis*, with a strong gular projection in males and the absence of an excavated dorsal lip would rule out such a relationship. However, a similar configuration of the epiplastron is seen in the extant *Astrochelys*, presently restricted to Madagascar, and this taxon could plausibly be the closest living relative of the Laetoli giant tortoise. Additional fossil material from Laetoli and more detailed comparisons with *Astrochelys* will be needed to confirm such a relationship.

Giant tortoises of similar age have been recovered from the Denen Dora and Sidi Hakoma Members, Hadar, Ethiopia (3.2–3.4 Ma), Omo Shungura Members B-D, Ethiopia (2.5–3.5 Ma) and Bahr el Ghazal, Chad (3.0–3.5 Ma). These have provisionally been referred to aff. *Stigmochelys* sp. or ?*Centrochelys* sp. (Broin 1979; Lapparent de Broin, 2000), but the material has not yet been described. Until more complete specimens are available from Laetoli, and pending a comprehensive description and taxonomic revision of the fossil giant tortoises from the Miocene and Pliocene of Africa, the generic affinities of the giant tortoise from Laetoli cannot be easily resolved. It is very likely that the giant tortoise from Laetoli represents a new genus, possibly with affinities to *Astrochelys* from Madagascar, but better fossil material and more detailed comparisons are needed. As a consequence, it is referred to here as *"Geochelone"*, not to imply any relationship to *Geochelone sensu stricto* from South Asia, but as a form genus, until such time as its taxonomic and phylogenetic relationships can be better established.

Paleobiology and Paleoecology

Age Structure and Mortality in Stigmochelys brachygularis

Only a few specimens from Laetoli are complete enough to measure their carapace length, but it is possible to provide an approximation of overall size using PL and the relative dimensions of isolated shell fragments. Using this method it is possible to estimate the size of 50 individuals of *S. brachygularis*, and thereby examine their size distribution and age profile. Kabigumila (2000) used three sizes classes corresponding to juveniles (SCL < 150), subadults (SCL 150-300) and adults (≥300) of modern leopard tortoises. Comparable ranges probably also apply to *S. brachygularis*, since carapacial and plastral fenestrae still occur in individuals (i.e., subadult individuals) with estimated SCL of ~280 mm. Using these size classes for *S. brachygularis*, most of the specimens ($n = 37$, 74%) fall into the subadult category.

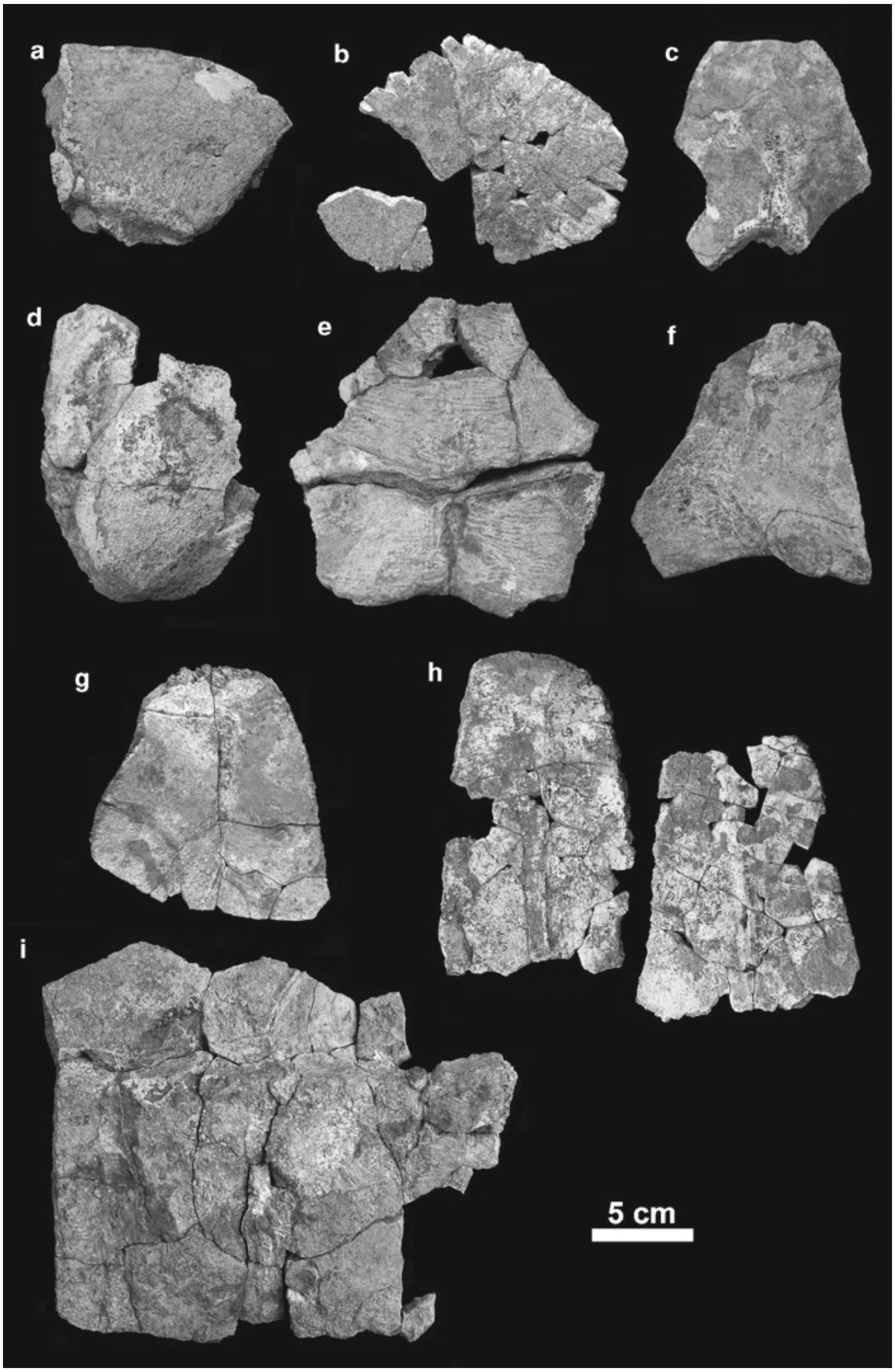

Fig. 17.17 KK 82-67. Associated carapace and plastron fragments of *"Geochelone" laetoliensis* from Kakesio (Lower Laetolil Beds). (**a**) right epiplastron; (**b**) partial entoplastron; (**c**) partial suprapygal I; (**d**) pygal; (**e**) nuchal bone; (**f**) right peripheral XI; (**g**) right peripheral I; (**h**) two partial costals; and (**i**) carapace fragment

Only two specimens (4%) are juveniles, whereas 11 specimens (22%) fall into the adult age category. This is quite different from the mortality profiles of *S. pardalis* in northern Tanzania today, where the estimated age distribution of carcasses ($n=38$) shows a predominance of adults (60.5%) compared with subadults (28.9%) and juveniles (10.5%) (Kabigumila 2001b).

Hatchlings and young leopard tortoises are preyed upon by monitor lizards, snakes, predatory birds, small carnivores, hyenas, and large felids (Loveridge and Williams 1957; Wilson 1968; Spawls et al. 2001; Kabigumila 2001b). However, once they reach 200 mm in length they are generally considered safe from most predators (Spawls et al. 2001).

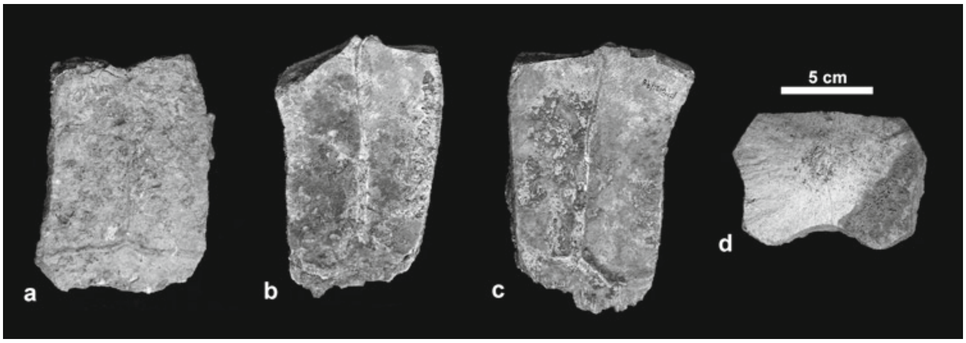

Fig. 17.18 EP 012/98. Associated peripherals (**a–c**) and neural (**d**) of *"Geochelone" laetoliensis* from Kakesio 2 (Lower Laetolil Beds). Same individual as KK 82-67 (see Fig. 17.16)

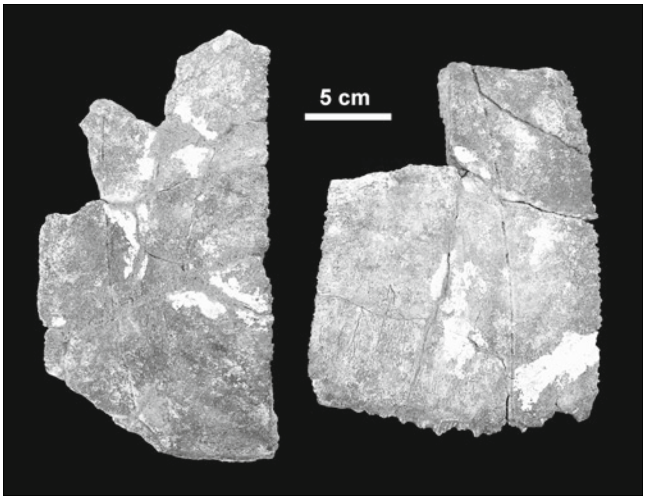

Fig. 17.19 LAET 75-5500. Right costals I–III of *"Geochelone" laetoliensis* from Loc. 5 (Upper Laetolil Beds)

Kubigumila (2001b) studied the incidence of injury and mortality in leopard tortoises in northern Tanzania, and showed that injury and fatalities were due to fire, humans (including road kills), carnivores, and predatory birds. Only 3.7% of the tortoises surveyed showed evidence of injury by carnivores. By comparison, predation rates are much higher in the smaller African hingeback tortoise (*Kinixys spekii*), with a maximum carapace length of less than 20 cm, in which 77–89% of dead tortoises show evidence of predator damage (Coulson and Hailey 2001).

The mortality profile of *S. brachygularis* may provide evidence that, relative to *S. pardalis*, it suffered a higher rate of predation, since a much higher percentage of individuals died before they reached adulthood. Of course, this could also be attributed to taphonomic factors or adverse environmental conditions, such as drought or volcanic eruption. As noted by Meylan and Auffenberg (1987), one would expect to find fewer entire shells of larger individuals (and species) because a greater depth of sediment would be required to bury them completely before natural disarticulation could occur. In this case, however, one would expect to find a higher incidence of juvenile shells and fragments of adult shells in the Laetoli collections. The evidence suggests that juveniles that died tended to be completely destroyed and that the majority of subadult individuals died before reaching adulthood. This is consistent with an inference of high levels of predation at Laetoli.

Support for this comes from several lines of evidence. First, of the 18 partial or complete shells of *S. brachygularis* known from Laetoli, only two (LAET 79-6404 and LAET 79-5494) are associated with cranial or postcranial elements. The majority of shells were buried after the animals had decomposed and the postcranium disarticulated and either eaten or otherwise dissociated from the shell. Scavenging carnivores may have played an important role in disarticulating the carcasses. Second, several of the shells show evidence of having been attacked by a large carnivore; although in no cases can it be demonstrated with certainty that this was the cause of death. For example, KK 82-22 bears a pair of puncture marks in the carapace that were evidently made by the right and left canines of a large felid. Judging from the size of the marks (10.7 × 6.7 mm) and the distance between them (29.9 mm), they were made by an animal about the size of a leopard (*Panthera pardus*). KK 82-452 has a large elliptical puncture mark (14.5 × 11.6 mm) on the left neural III that penetrated the carapacial cavity, as well as numerous score marks on the nuchal bone, anterior peripherals and neurals, and epiplastron made by the teeth of a large carnivore about the size of a lion (*Panthera leo*). LAET 79-6404 has five elliptical to circular perforations on the carapace, in the region of the neurals (maximum size 13.9 × 9.4 mm) made by a felid the size of a lion (Fig. 17.20). Interestingly, the latter is one of the few specimens from Laetoli that preserves limb bones inside the shell, suggesting that the carnivore was unable to kill and consume the tortoise at the time of the attack. Since at least 3 of the 18 (= 16.7%) relatively complete shells from Laetoli show evidence of carnivore damage, this is significantly higher than the frequency seen in *S. pardalis* populations in the Serengeti today (= 3.7%) (Kabigumila 2001b). The age structure and the incidence of carnivore damage suggest that *S. brachygularis* was subject

Fig. 17.20 LAET 79-6404. Relatively complete, but crushed shell of *Stigmochelys brachygularis* from Loc. 18 (Upper Ndolanya Beds). *Top*, dorsal view. *Bottom*, ventral view. Note the carnivore tooth marks on the dorsal surface of the carapace (see text for discussion)

to relatively high levels of predation compared with modern-day *S. pardalis* in East Africa. The high taxonomic diversity of large felids and hyaenids at Laetoli, compared to modern-day East African carnivore communities, may account for this (Werdelin and Dehghani 2011).

Fossil Eggs

A number of fossil reptile eggs ($n=44$) from localities at Laetoli and neighboring sites are consistent in morphology with those of testudinines. In addition, tortoises are by far the most common reptiles found at Laetoli, with turtles and crocodiles entirely absent. Although there is variation in overall size and shape, these eggs are probably all referable to a single species (with the exception of EP 1059/05) (Fig. 17.21). The average length of the eggs is 35.1 mm, with a range of 26.8–50.2 mm. This is approximately 10% smaller on average than eggs of *S. pardalis babcocki* (38.7 mm; Loveridge and Williams 1957; Wilson 1968; Highfield 1990), and, therefore, consistent in size with those of *S. brachygularis*. Only one fossil egg is possibly large enough to have belonged to "*G*". *laetoliensis*; EP 1059/05 from the Lower Laetolil Beds at Kakesio 8, which has an estimated length of ~52 mm. The eggs are elongated in shape, without discernable tapering along their length. The maximum breadth is much shorter than its length, with a mean length-breadth ratio of 1.59 ± 0.08 ($n=20$). The eggs of *S. brachygularis* were apparently relatively more elongated than those of *S. pardalis* (=1.00–1.12), *Astrochelys radiata* (=1.06), *Chelonoidis carbonaria* (=1.07), *Chelonoidis denticulate* (1.06) and *Chelonoidis nigra* (=1.04), but closer in shape to those of *Geochelone elegans* (= 1.36–1.42) (Wilson 1968; Preston 1969; Rodriguez Bayona and Rylander 1984; Highfield 1990). However, some tortoises typically have relatively elongated eggs, including *Kinixys belliana* (=1.26–1.31), *Homopus signatus* (=1.39), *Testudo horsfieldii* (=1.38–1.40), *Testudo hermanni boettgeri* (= 1.38), *Gopherus polyphemus* (=1.42) and *Malacochersus tornieri* (=1.52) (Preston 1969; Highfield 1990; Morris 1994; Wallis et al. 1999; Bergmann 2001; Loehr et al. 2004). Egg width in tortoises is positively correlated with body size (Congdon and Tinkle 1982; Congdon and Gibbons 1985; Hailey and Loumbourdis 1988), and appears to be constrained by the diameter of the pelvic canal. Smaller individuals within species, and smaller species of tortoises, tend to produce more elongated eggs. In this way, eggs of larger volume can be produced despite the limitations imposed on them by the size of the pelvic canal. It is, perhaps, of some significance that the elongated eggs in *S. brachygularis* are apparently associated with a restricted anal aperture of the shell (see above).

The eggs are not perfectly circular in cross section, showing variable degree of flattening. This is partly due to preservational factors, since the weight of the sediments may have compressed the eggs and exaggerated the degree of flattening prior to fossilization. A number of eggs (37.5%) are subcircular in section, with a perpendicular height that is 85–100% of the maximum breadth. This probably represents a close approximation to the original shape of the eggs. The remaining eggs exhibit varying degrees of compression, some having a perpendicular height that is just over half the maximum breadth. Since the majority of eggs were broken at one end, suggesting that they had hatched or were partially consumed by predators, these empty shells might have been more prone to a greater degree of compression than entire shells. This is supported by metrical data from modern-day hatched eggs of *S. pardalis* collected by the author in the vicinity of Laetoli ($n=5$), which show that they are relatively more elongated and more compressed than unhatched eggs (the mean dimensions are $40 \times 23 \times 15$ mm).

Fossil eggs of giant tortoises have been recovered from volcaniclastic sediments on the Canary Islands dated to the Late Miocene and Plio-Pleistocene (Macau-Vilar 1958;

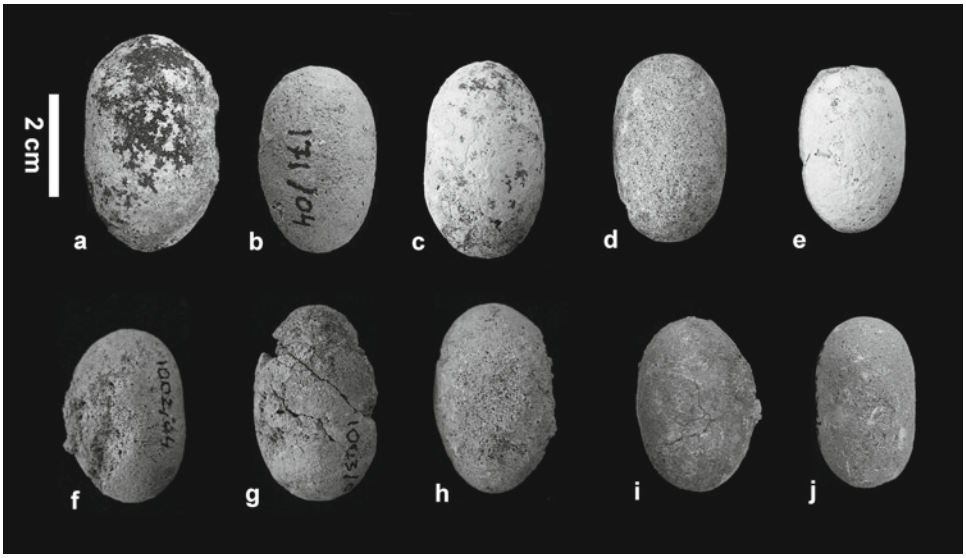

Fig. 17.21 A representative sample of fossil tortoise eggs from the Laetolil Beds assigned to *Stigmochelys brachygularis*. (**a**) EP 070/04 (Loc. 10E, Upper Laetolil Beds); (**b**) EP 171/04 (Loc. 15, Upper Laetolil Beds); (**c–e**) EP 845/04 (Kakesio 1-6, Lower Laetolil Beds); (**f**) EP 1002/04 (Loc. 9, Upper Laetolil Beds); (**g**) EP 1003/04 (Loc. 9, Upper Laetolil Beds); (**h**) EP 1002/04 (Loc. 9, Upper Laetolil Beds); (**i–j**) EP 2079/03 (Emboremony 1, Lower Laetolil Beds)

Hirsch and Lopez-Jurado 1987; Rothe and Klemmer 1991; Hutterer et al. 1997). These are much larger (the maximum length is 70% greater) and more spherical (length:breadth ratio = 1.16) than the eggs of *S. brachygularis* from Laetoli, being closely comparable in size to those of extant *Chelonoidis nigra*, the giant tortoise from the Galapagos Islands, which can attain a SCL in excess of 1 m. Similar reports of fossil and subfossil eggs from the Seychelles have been published (Fryer 1911; Honegger 1966; Burleigh and Arnold 1979). Pliocene-aged fossil tortoise eggs from African localities have also been recorded from the Lower Kada Hadar and Sidi Hakoma Members of the Hadar Formation in Ethiopia (Hirsch 1983) dated to 3.2–3.4 Ma. Again, these are much larger than the eggs from Laetoli, and evidently belonged to a species of giant tortoise.

Paleoecological Considerations

Tortoises today occur in a wide variety of ecological settings ranging from tropical rainforests in Africa, Asia, and South America to semi-deserts in the Sahel and South Africa (Iverson 1992). The modern leopard tortoise, *Stigmochelys pardalis*, probably the closest relative to *S. brachygularis* from Laetoli, is geographically widespread and ecologically adaptable. It lives in a diversity of habitats, ranging from semi-desert, savanna, and coastal woodland, and climatic zones, ranging from sea level to 2,000 m, with an annual rainfall of 100–1,400 mm (Grieg and Burdett 1976; Spawls et al. 2001). Today, *S. pardalis* is common at Laetoli where it inhabits open woodlands and scrub, with a diverse herbaceous understory that includes succulents. Growth rings on the scutes of *S. brachygularis* are identical to those of extant *S. pardalis*, and suggest a seasonal environment with a single wet and dry season annually (Meylan and Auffenberg 1987).

Giant tortoises, such as *"G." laetoliensis*, are now extinct on mainland Africa. They apparently disappeared during the late Pliocene, sometime before 2.0 Ma. Broin (1979) has noted the absence of giant tortoises after Member D_3 (~2.5 Ma) in the Shungura Formation of the Omo. Based on these observations, it is tempting to infer a direct relationship between the extinction of giant tortoises in Africa with the appearance of early *Homo* and stone tool using behaviors (~ 2.3–2.6 Ma) (Kimbel et al. 1996; Semaw et al. 2003). During the Miocene and early Pliocene, large size in tortoises would have been an effective strategy to counter predation by carnivores, but, by the Late Pliocene, with the appearance of *Homo* and behaviors associated with the use of lithic technologies (and possibly also greater use of fire and wider ranging behavior), natural selection would operate against large size in favor of smaller, wider ranging, faster reproducing, and more cryptic species of tortoises. Even relatively low levels of human exploitation and human-induced mortality can lead to precipitous declines in population levels and extirpation of modern-day giant tortoises (Márquez et al. 2007).

Other Fossil Tortoises from Africa

The earliest fossil tortoises in Afro-Arabia are known from the Late Eocene of the Fayum of Egypt (Andrews and Beadnell 1903; Andrews 1906) and the Early Oligocene of

Oman (Thomas et al. 1989; Lapparent de Broin 2000). Apparently, tortoises first colonized Afro-Arabia from Eurasia during the late Eocene (Claude and Tong 2004). The three species originally recognized from the Fayum were initially included in the genus *Testudo* (i.e., *T. ammon, T. beadnelli,* and *T. isis*) by Andrews (1906). These were later transferred to *Geochelone* (Auffenberg 1974), but most recently they have been included in a separate genus, *Gigantochersina* Chkhikvadze, 1989. Recently, de Broin et al. (1999), Lapparent de Broin (2000), and Holroyd and Parham (2003) have included all of the giant tortoises from the Fayum, and probably also those from Oman, in a single species, *Gigantochersina ammon* (Andrews 1903).

Several genera of tortoises are known from Early Miocene localities in Africa and the Arabian Peninsular. *Stigmochelys* and *Centrochelys* are well-represented (Lapparent de Broin 2000), confirming that both lineages had diverged by the Early Miocene. From Kachuku near Karungu in southwestern Kenya (~18 Ma), Andrews (1914) described the giant tortoise, *Testudo crassa*, which was subsequently transferred to the genus *Geochelone*. However, Lapparent de Broin (2000) has suggested that this species might be better referred to the *Stigmochelys* group. The same taxon has been reported from the Pliocene locality of Kanapoi (4.0–4.1 Ma) in Kenya (Meylan and Auffenberg 1986; Harris et al. 2003). The extant genus *Kinixys* is reported from Songhor in Kenya and Napak in Uganda dated at ~19–20 Ma (Meylan and Auffenberg 1986). *Impregnochelys pachytectis* is a specialized robust form from Rusinga Island, Kenya (Meylan and Auffenberg 1986), dated at ~18 Ma, which may be closely related to *Kinixys*. *Namibchersus namaquensis* (Stromer 1926) is known from the Early Miocene localities of Elisabethfeld and Auchus in Namibia, dated at ~18–20 Ma, but material referable to the same genus continues into the Middle to Late Miocene (~8–14 Ma) (Auffenberg 1974; Meylan and Auffenberg 1986; Lapparant de Broin 2003, 2008). *Mesochersus orangeus* a medium-sized tortoise (SCL = 16–20 cm), is known from the late Early Miocene locality of Arrisdrift (~17.0–17.5 Ma) in Namibia (Lapparent de Broin 2003, 2008). All of these Miocene tortoises possess a suite of primitive features, including the retention of a cervical, that readily distinguish them from extant and fossil *Stigmochelys* (Lapparent de Broin 2003, 2008).

A number of Early Miocene to Late Pliocene sites in northern Africa and the Arabian Peninsula, dating from ~18 Ma, have yielded remains that are likely attributable to *Centrochelys* (Thomas et al. 1984, 1982, 1978; Arambourg 1979; Wood 1987; Geraads 1989; Raynal et al. 1990; Roger et al. 1994; Lapparent de Broin and van Dijk 1999; Lapparent de Broin 2000). A large form of *Centrochelys* is known from Bahr el Ghazal in Chad (3.0–3.5 Ma) and Jebel Krechem el Artsouma, Tunisia (Broin 1979; Lapparent de Broin and van Dijk 1999; Lapparent de Broin 2000).

Stigmochelys sp. is well-represented at Pliocene localities in East and South Africa, including Kanapoi (4.0–4.1 Ma), Omo Shungura (Members B-D, 2.5–3.5 Ma), Hadar (Denen Dora and Sidi Hakoma, 3.2–3.4 Ma), Makapansgat (2.6–3.0 Ma), Sterkfontein (2.5–2.8 Ma), and Kromdraai (1.5–1.8 Ma) (Arambourg 1947; Auffenberg 1974; Broadley 1962, 1997; Lapparent de Broin and van Dijk 1999; Lapparent de Broin 2000; Harris et al. 2003). In most cases these specimens have been referred to *S. pardalis*, although no comparisons have yet been made to determine their affinities to *S. brachygularis*. A small to medium-sized tortoise is also known from the Lukeino Formation in Kenya (~5.7–6.0 Ma) in which the absence of a dorsal epiplastral excavation indicates affinities with "*Geochelone*" *stromeri* from the Early Pliocene (~4.0–4.5 Ma) locality of Langebaanweg, South Africa. The latter taxon is readily distinguished from *S. brachygularis* by the presence of a cervical scute, the absence of a dorsal epiplastral concavity, and its smaller size (Meylan and Auffenberg 1986). Lapparent de Broin (2000) recognizes the Langebaanweg tortoise as a distinctive species, but defers assigning it to a known genus.

Somewhat younger localities in East Africa have yielded material that can be more definitively identified as belonging to extant *S. pardalis*, including material from the Pleistocene localities of Olduvai Gorge and Mumba Cave in Tanzania, and Rawi and Kanjera in Kenya (Leakey 1965; Lehmann 1957; Broin 1979; Auffenberg 1981). Fragmentary material from Lower Bed I and Upper Bed II at Olduvai, Tanzania (~1.9 and 1.3–1.5 Ma) has been described by Auffenberg (1981) who referred them to *Stigmochelys pardalis*.

At present, *S. brachygularis* is definitively known only from sites on the Eyasi Plateau, although further comparisons with specimens referred to *Stigmochelys* from other African Pliocene localities might eventually prove that the taxon was more widely distributed. A suite of features distinguishes *S. brachygularis* and *S. pardalis* as separate species, but they are close enough in morphology to be included in the same genus and it is likely that they are one another's sister species.

Giant tortoises, similar in size to "*Geochelone*" *laetoliensis*, with carapaces exceeding 1 m in length, do occur at other late Miocene and Pliocene sites in eastern Africa, including Ngorora (~11.7 Ma), Lothagam (~4.2–8.0 Ma), Kanapoi (4.0–4.1 Ma), Koobi Fora (~3.3 Ma) and Kaiso Beds (~2.0–2.3 Ma) (Lapparent de Broin 2000; Wood 2003; Harris et al. 2003). Of these, the Kanapoi specimens have been referred to *Geochelone crassa* (Harris et al. 2003; Meylan and Auffenberg 1986), which is also known from the Early Miocene locality of Karungu in Kenya. Fragmentary specimens of a large tortoise from Middle Bed I, Olduvai (~1.8 Ma) is referred to *Geochelone* sp. B by Auffenberg

(1981) and to Testudininei indet. sp. B by Lapparent de Broin (2000). Meylan and Auffenberg (1987) suggested that the giant tortoise from Laetoli may be closely related to *Aldabrachelys*, the extant giant tortoises from the Indian Ocean, but the evidence is not compelling. In contrast, Lapparent de Broin (2000) regards the Laetoli giant tortoise as a possible member of the *Stigmochelys* group. However, the marked differences separating it from *S. brachygularis* and *S. pardalis*, especially in the morphology of the epiplastron, provide confirmation that the Laetoli giant tortoise is not closely related to *Stigmochelys*. Instead, it likely represents a separate genus, possibly with affinities to *Astrochelys* from Madagascar, although additional material is needed to allow a more definitive assessment of the taxonomy and phylogeny of *"G". laetoliensis*.

Conclusions

Two species of fossil tortoises are known from Pliocene localities on the Eyasi Plateau - *Stigmochelys brachygularis* and *"Geochelone" laetoliensis*. Both taxa are represented in the Lower Laetolil and Upper Laetolil Beds, ranging in age from ~4.4 to 3.6 Ma. A partial shell from the younger Upper Ndolanya Beds (~2.66 Ma) has previously been referred to the extant *Stigmochelys pardalis* (Meylan and Auffenberg 1987), but additional specimens from these beds and further comparisons indicate that the material is indistinguishable from *S. brachygularis* from the Laetolil Beds, and that they should all be included in a single species. The giant tortoise *"Geochelone" laetoliensis* is much less common than *S. brachygularis* in the Laetolil Beds (comprising less than 2% of all of the fossil tortoise material collected since 1998), and it has not yet been recorded from the Upper Ndolanya Beds.

Stigmochelys brachygularis is well represented at localities in the Laetoli area, where it is known from 18 relatively complete and partial shells, as well as more than 400 isolated and associated shell fragments. A number of new and previously undescribed specimens are included in this study, including a complete shell of an adult male individual (EP 2472/03) that represents the largest recorded specimen of *S. brachygularis*. In addition to shells and shell fragments, a number of postcranial remains and eggs can be referred to this species. The latter are especially common in the Lower Laetolil Beds.

Stigmochelys brachygularis is a medium-sized tortoise with a carapace length less than 50 cm. It is similar in size or slightly smaller than *S. pardalis* (the extant leopard tortoise, which is common in the area today) and is generally comparable in morphology, but differs in a number of key features that serve to distinguish it at the species level. Nevertheless, the two species do appear to be closely related, and it is reasonable to infer that they are sister taxa.

A number of inferences about the paleobiology and paleoecology of *S. brachygularis* are possible from the evidence available. The age structure of the fossil sample at Laetoli and the incidence of carnivore damage on the shells indicate that the species was subject to relatively high levels of predation compared with extant *S. pardalis*. This is consistent with the high diversity of large felids and hyaenids in the Laetoli carnivore fauna compared with modern-day East African communities. If *S. brachygularis* were ecologically similar to modern *S. pardalis*, it would have been capable of living in a wide array of habitats ranging from semi-desert and savanna to open woodland, but there is nothing about the anatomy of the fossil species that would dictate a close correspondence in habit. Growth rings on the scutes of *S. brachygularis* indicate a seasonal environment with a single wet and dry season annually (Meylan and Auffenberg 1987).

All of the remains attributed to the giant tortoise, *"Geochelone" laetoliensis*, are fragmentary, including those recovered since 1998. The best finds include a number of associated shell fragments (EP 012/98) that belong to the same individual as undescribed material from Mary Leakey's collection (KK 82-67) recovered from Kakesio 16 years earlier. Unfortunately, *"G." laetoliensis* is not well enough known to determine its taxonomic and phylogenetic relationships, but it may have affinities with *Astrochelys* from Madagascar based on the distinctive morphology of the epiplastron. Until more complete material is available from Laetoli, and the taxonomy and phylogenetic relationships of the fossil giant tortoises from Africa have been critically reexamined, the affinities of *"G." laetoliensis* will remain uncertain. Giant tortoises became extinct on mainland Africa during the late Pliocene, possibly associated with the appearance of early *Homo* and stone tool using behaviors at 2.6 Ma. With the appearance of hominins that had the technology and behavioral sophistication to locate, kill and butcher tortoises of large size, natural selection would undoubtedly have favored smaller, wider ranging, faster reproducing, and more cryptic species of tortoises.

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Chapter 18
Aves

Antoine Louchart

Abstract The study of the entire fossil bird collection from Laetoli, including the specimens collected by Mary Leakey (1974–1981) and the recent ones collected by the Eyasi Plateau Paleontological Expedition (1998–2005), is presented here. The 247 bird fossils allow the identification of 21 different taxa in 11 families (and eight orders). One fossil is from the Lower Laetolil Beds, 229 from the Upper Laetolil Beds, and 17 from the Upper Ndolanya Beds. The large majority of the fossils belong to francolins (Phasianidae) and guineafowl (Numididae), followed in decreasing order of abundance by Columbidae, Accipitridae, Strigidae, Passeriformes, Coliidae, and – one fossil each – Ardeidae, Falconidae, Scolopacidae and Tytonidae. Some genera or species constitute the earliest known representatives of modern lineages, among which are the falcon *Falco* cf. *eleonorae*, the Vulturine Guineafowl *Acryllium vulturinum*, a dove *Streptopelia* sp. and the eagle-owl *Bubo* cf. *lacteus*. *Acryllium vulturinum*, from the Upper Laetolil Beds, indicates semi-open or open country habitats in the paleoenvironment. A heron, *Ardea* sp. (Upper Ndolanya Beds) and a calidrine wader (Upper Laetolil Beds) imply aquatic settings. Most other birds, including most Galliformes, the Columbidae and the Coliidae (mousebirds) indicate a minimal cover of at least scattered trees or bushes. The fossil birds yield additional information regarding biogeography, differences between stratigraphic units, environment, new perspectives on the study of bird prints and eggs from diverse localities at Laetoli, and finally some clues about the probable status of some birds (i.e., breeding, passage or wintering migrant).

Keywords Ardeiformes • Charadriiformes • Coliiformes • Columbiformes • Falconiformes • Galliformes • Passeriformes • Pliocene • Strigiformes • Tanzania

Introduction

Recent fieldwork (1998–2005) by the Eyasi Plateau Paleontological Expedition has yielded a number of bird fossils, considerably increasing the number of specimens available from the different localities and stratigraphic units at Laetoli. In addition, new fossil eggshells of ostriches (Harrison and Msuya 2005) and eggs of other birds (Harrison 2005) have already been described. Prints and trails of birds at Laetoli were described earlier (Leakey 1987). The present study focuses on the avian fossil skeletal remains. The fossils studied by Watson (1987) – labels beginning with LAET (total 37 fossils) – were re-examined and are included here in addition to the more numerous fossils from the recent fieldwork – labels beginning with EP (total 210 fossils). The former were re-evaluated in the light of the latter specimens, as well as the use of more extensive modern comparative samples. The total individual bird fossils studied here are 247. They provide new evolutionary and biogeographical information on the past avifaunas of eastern Africa, as well as some important insights into the paleoecology at Laetoli.

Material and Methods

The systematic arrangement follows Del Hoyo et al. (1992, 1994, 1996, 1997, 1999) and BirdLife International (2004), except in some cases (e.g., in the Galliformes and the Strigiformes, as well as the Ardeidae, the Accipitridae and the Passeriformes) where more comprehensive and up-to-date published phylogenetic analyses provide better-resolved and more reliable systematic arrangements. The osteological nomenclature is that of Baumel and Witmer (1993) unless stated otherwise. All the measurements are in millimeters unless stated otherwise, and unlike the definitions used by several other authors, width refers here to a measurement orthogonal to the long axis of the postcranial bone, and in the following direction for every element: medio-lateral for

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coracoids, dorso-ventral for humeri, ulnae and radii, orthogonal to dorso-ventral (i.e., in the plane of flatness of the bone) for carpometacarpals, and medio-lateral for femora, tibiotarsi, tarsometatarsi and pedal phalanges; depth refers here to the measurement orthogonal to the width and to the long axis of the bone unless stated otherwise. For some of the families concerned, drawings of how the measurements for each bone are taken can be found in Louchart (2002).

The list of modern osteological specimens examined for comparisons and measurements is given in an Appendix. The acronyms for the museums and other institutions are as follows: BMNH: Natural History Museum (formerly British Museum of Natural History) (Bird Group), Tring, UK; CAS: California Academy of Sciences, San Francisco, USA; FMNH: Field Museum of Natural History, Chicago, USA; IPH: Institut de Paléontologie Humaine, Muséum National d'Histoire Naturelle, Paris, France; IRSN: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; LAC: Laboratoire d'Anatomie Comparée, Muséum National d'Histoire Naturelle, Paris, France; MCZ: Museum of Comparative Zoology, Peabody Museum, Harvard University, USA; MVZ: Museum of Vertebrate Zoology, University of California Berkeley, USA; RMCA: Royal Museum for Central Africa, Tervuren, Belgium; SAM: Iziko South African Museum, Cape Town, South Africa; UCBL: Université Claude Bernard – Lyon 1, Villeurbanne, France; USNM: Smithsonian Institution, National Museum of Natural History, Washington, DC, USA. Many African species are unavailable as skeletal specimens in collections, either because they are rare, little studied, or their countries of distribution are little explored zoologically. In these cases, identifications are tentative and based on evidence from related, available species.

Indications on the external (ornithological) measurements, body weights, ecology and distribution of extant birds derive from Del Hoyo et al. (1992, 1994, 1996, 1997, 1999), Dunning (1993) and Sinclair and Ryan (2003) unless indicated otherwise. The fossil specimens are stored at the National Museums of Tanzania in Dar es Salaam, Tanzania.

Abbreviations: dist., distal; e, estimated; frag., fragment; l., left; Loc., Locality; MNI, minimal number of individuals; NR, number of remains; prox., proximal; r., right.

Ages of the localities are as follows (Harrison 2005; Deino 2011). The localities of Lower Laetolil Beds are 3.85–4.4 Ma. The localities of Upper Laetolil Beds situated in intervals that are between below Tuff 1 and Tuff 6 are 3.6–3.85 Ma. The localities of Upper Laetolil Beds that comprise the interval between Tuffs 6 and 8 are 3.6–3.7 Ma. The localities of Upper Laetolil Beds situated above Tuff 8 (or between Tuff 8 and Yellow Marker Tuff) are *ca.* 3.6 Ma. The localities of Upper Ndolanya Beds are 2.66 Ma.

Systematic Paleontology

Class Aves Linnaeus, 1758
Order Struthioniformes Latham, 1790
Family Struthionidae Vigors, 1825
For the sake of completeness, the records of eggshells belonging to ostriches from Laetoli are mentioned here (see Harrison and Msuya 2005 for descriptions).

Order Ardeiformes Wagler, 1831
Family Ardeidae Vigors, 1825
Genus cf. *Ardea* Linnaeus, 1758

cf. *Ardea* sp.

Material: incomplete prox. l. humerus, EP 467/05 (Fig. 18.1a).

Measurements: proximal width: ~22.0, depth of caput humeri: 6.7.

Locality: Laetoli Loc. 18, Upper Ndolanya Beds.

NR: 1, MNI: 1.

Remarks: There is increasing evidence, including from large genetic datasets (e.g., Hackett et al. 2008), that the herons (Ardeidae) are not related to the families of the traditional order 'Ciconiiformes' in which they have generally been placed. They do appear as the sister-family to the ibises (Threskiornithidae), which are also often placed in the polyphyletic 'Ciconiiformes'. The Ardeidae are placed here in their own order Ardeiformes.

This proximal humerus displays the distinctive features of the family Ardeidae, including a well-marked oblique incisura capitis, a dorsally protruding tuberculum dorsale, and a deep impressio coracobrachialis. Compared with the Threskiornithidae, the incisura capitis is shallower, and the plane formed by the bony wall around the foramen pneumaticum is less oblique relative to the global plane of the humerus. The fossil, although fragmentary, matches *Ardea* in morphology and size, whereas members of other genera found in Africa are all smaller, and differ slightly in details (e.g., Kellner 1986). Within the genus *Ardea* there are several species similar in size to the heron of Laetoli. In addition, the genus is very homogeneous morphologically. Thus, the fossil cannot be assigned specifically. The same measurements on two individuals of *A. melanocephala* (male and female) are respectively 23.85 and 7.55, and 23.6 and 7.7; in two *A. cinerea* (one female and one unsexed) respectively 25.8 and 7.7, and 22.35 and 5.6; while in one male of the larger *A. goliath* they are 36.1 and 12.5. So, taking into account intraspecific variability, the fossil corresponds in size to *A. alba*, *A. melanocephala* or *A. cinerea*, or large individuals of *A. purpurea* (Kellner 1986). All four species are common today in most of Africa, including Tanzania. The fossil is assigned here to cf. *Ardea* sp., given its fragmentary nature. Fossil herons belonging

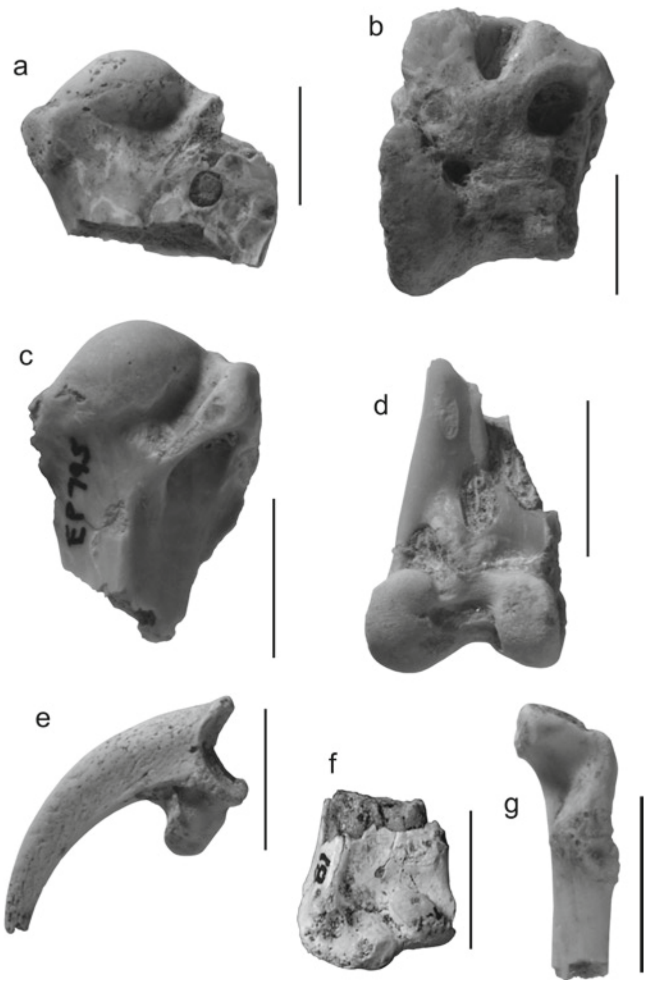

Fig. 18.1 (**a**) cf. *Ardea* sp., prox. l. humerus (EP 467/05), incomplete, in caudal view. (**b**) *Aegypius* sp., dist. r. tibiotarsus (EP 2767/00), lateral fragment, in cranial view. (**c**) cf. *Buteo* sp., prox. l. humerus (EP 795/05), lacking parts of crista bicipitalis and crista delt. pect., in caudal view. (**d**) Aquilini indet. sp. A, dist. l. tibiotarsus (EP 521/04), in cranial view, with small amounts of remaining matrix. (**e**) cf. Aquilini indet. sp. B, pedal phalanx cf. 2 of digit I (EP 066/04), in lateral view. (**f**) *Falco* cf. *eleonorae*, dist. l. humerus (LAET 76-18-601), incomplete, in cranial view. (**g**) *Francolinus* sp. A aff. *F. (Peliperdix) sephaena*, prox. r. coracoid (EP 1259/03), in dorsal view. Scale bars are equal to 1 cm

to *Ardea*, and of similar size, are known from the late Miocene of Chad and Ethiopia (Louchart et al. 2008). The heron from Laetoli indicates an aquatic setting – a water-body fringe, a marsh, or a swamp. Herons in this genus feed on small vertebrates and invertebrates.

Order Falconiformes Sharpe, 1874
Family Accipitridae Vieillot, 1816
Genus *Aegypius* Savigny, 1809, s.l.

Aegypius sp.

Material: dist. r. tibiotarsus, EP 2767/00 (Fig. 18.1b).

Measurements: depth of condylus lateralis: ~19.8.

Locality: Laetoli Loc. 3, Upper Laetolil Beds, between Tuffs 7 and 8.

NR: 1, MNI: 1.

Remarks: This distal tibiotarsus differs from eagles (Aquilinae) by, among other features, shallower sulcus extensorius and depth of condyles greater relative to distal width. Its morphology matches the genus *Aegypius* and differs from other Old World vultures (see Louchart 2002). The genus *Aegypius* (s.l.) comprises two extant species: *A. monachus* and *A. (Torgos) tracheliotus*. In modern *A. monachus* the homologous depth of condylus lateralis is 19.0–20.6 ($n=5$), and in *A. (Torgos) tracheliotus* 18.7–21.8 ($n=3$). The fossil could, therefore, correspond to both species, or alternatively it could represent a species ancestral to one of them or both. It is assigned here to *Aegypius* sp. Watson (1987) mentioned a ninth cervical vertebra he assigned to '*Torgos* sp.', also from Upper Laetolil Beds at Loc. 3, but the specimen has not been relocated in the collection. This vertebra would indeed be congruent with the tibiotarsus.

A. monachus is a Palearctic species, while *A. (T.) tracheliotus* lives today in the Afrotropical region, including Tanzania, where it inhabits savannas, especially in more arid areas. It nests and roosts on trees, and feeds on large vertebrate carcasses.

Genus cf. *Buteo* Lacépède, 1799

cf. *Buteo* sp.

Material: prox. l. humerus, EP 795/05 (Fig. 18.1c).

Measurements: depth of tuberculum ventrale: 6.5.

Locality: Laetoli Loc. 5, Upper Laetolil Beds, between Tuffs 3 and 5.

NR: 1, MNI: 1.

Remarks: This proximal humerus is diagnostic of the Accipitridae, and matches closely the tribe Buteonini, but it differs in morphological details from *Pernis*, *Elanus*, *Milvus* (Milvini), *Accipiter*, *Melierax* (Accipitrini), *Circus* (Circini) and other tribes more distant to the Buteonini (see Otto 1981; Schmidt-Burger 1982). Among the African Buteonini, it matches only the genus *Buteo* in all details, and differs slightly from *Butastur*. Within the diverse genus *Buteo*, eight species live in subsaharan Africa today (migrant or resident). The fossil is compatible in size with a small *Buteo* species. The depth of tuberculum ventrale is 7.7–11.0 ($n=20$) in *B. buteo*, and 10.3–11.6 ($n=7$) in *B. rufinus* (Louchart 2002). Hence, the fossil corresponds to a species the size of *B. auguralis*; all other African *Buteo* being larger. *Buteo auguralis* lives in west and central Africa today. The fossil could correspond to a closely related extinct species, or to its ancestor, with a different geographical distribution. The fossil is referred here to cf. *Buteo* sp., because its fragmentary nature does not allow to ascertain a more precise identification.

Buteo buzzards live in a range of habitats from forest to semi-desert, but need clearings to hunt small vertebrates and invertebrates.

Tribe Aquilini (*sensu* e.g., Helbig et al. 2005)

Aquilini indet. sp. A

Material: dist l. tibiotarsus, EP 521/04 (Fig. 18.1d).

Measurements: distal width: 12.6.

Locality: Laetoli Loc. 1, Upper Laetolil Beds, between Tuffs 7 and 8.

NR: 1, MNI: 1.

Remarks: This distal tibiotarsus of an Accipitridae, is distinctly flattened with a high width/depth ratio. The incisura intercondylaris makes a rather deep incision between the two condyles, in caudal or cranial view, as in *Aquila*, *Spizaetus*, *Stephanoaetus*, and to a lesser extent in *Lophaetus* for instance (Aquilini), and unlike in other Accipitridae. Thus, the fossil belongs to an eagle (Aquilini) of small stature. It is difficult to assign it to a genus, however. Among African eagles it is slightly larger than *A. pennata* (for which the distal width is 10.5–10.8 ($n=2$). It would match in size species such as *Spizaetus africanus* or *A. ayresii* (formerly placed with *A. pennata* and others in '*Hieraaetus*', but now placed in *Aquila* because '*Hieraaetus*' has proved to be polyphyletic; see Sangster et al. 2005). It is identified here as Aquilini indet.

These smaller eagles hunt diverse vertebrates, preferrably in open settings, but otherwise live in a range of habitats according to species.

cf. Aquilini indet. sp. B

Material: pedal phalanx cf. 2 of digit I, EP 066/04 (Fig. 18.1e).

Measurements: maximal height of proximal (articular) end including the processus flexorius: 12.1; without the proc. flexorius: ~8.0.

Locality: Laetoli Loc. 10E, Upper Laetolil Beds, between Tuffs 5 and 7.

NR: 1.

Remarks: This claw belongs to a member of the Accipitridae of medium/large size, slightly smaller than *Aquila nipalensis* (for one individual of which measurements are respectively 13.2 and 8.8; Louchart 2002). It would probably correspond in size to *A. rapax*, but this single claw does not allow a generic assignment. However, it comes from a bird larger than the Aquilini indet. sp. A above, and it constitutes an additional species. It is identified here as cf. Aquilini indet. sp. B.

Family Falconidae Leach, 1819
Genus *Falco* Linnaeus, 1758

Falco cf. *eleonorae* Gené, 1839

Material: dist. l. humerus, LAET 76-18-601 (Fig. 18.1f).

Measurements: distal width: ~12.2 e.

Localities: Laetoli Loc. 18, Upper Ndolanya Beds (area 2 above BT).

NR: 1, MNI: 1.

Remarks: This distal humerus matches the distinctive and homogeneous morphology of members of the genus *Falco* (Falconidae). Its dimensions are larger than in *F. subbuteo* – distal width 9.9–11.4 ($n=19$) (Solti 1996) – and in *F. concolor* – distal width 10.9 ($n=1$). It is smaller than in *F. biarmicus* – distal width 13.3–15.7 ($n=5$) (Solti 1981). It is in the range of the size of humeri of the slender-statured and long-tailed falcon *F. eleonorae* – distal width 12.4–13.1 ($n=2$). All the other species of the continent are smaller or larger. Because of the fragmentary nature of the fossil, it is identified here as *Falco* cf. *eleonorae*. This species is today a regular visitor to East Africa during its annual migrations from the Mediterranean Basin to Madagascar. It feeds mainly on birds during its breeding season, which coincides with the autumn migration of passerines in the Mediterranean region. It feeds on insects outside the breeding season. The fossil likely belongs either to this species or to its direct ancestor. Ecology and migration routes of this ancestor, however, might not have been exactly the same as in the extant species. This constitutes the earliest record of a falcon potentially referrable to this peculiar species, and the second record for the family in Africa (after the early Pliocene of Langebaanweg, South Africa; Rich 1980).

Falconiformes indet.

Material: pedal phalanx, EP 2534/00; pedal phalanx prox. frag., EP 263/05.

Measurements: EP 2534/00: minimal width: 4.5; EP 263/05: minimal width: 3.1.

Localities: EP 2534/00: Laetoli Loc. 9, Upper Laetolil Beds, between Tuffs 6 and 8; EP 263/05: Laetoli Loc. 17, Upper Laetolil Beds, between Tuff 8 and Yellow Marker Tuff.

NR: 2.

Remarks: Although recent progress in understanding birds phylogeny and relationships between families lends support to the absence of a close relationship between the Accipitridae and Falconidae (e.g., Hackett et al. 2008), a number of skeletal parts are similar in both families, in particular those for which shape is clearly associated with convergent predatory function. This is the case for these fragmentary pedal phalanges, which could belong to either of these families. This is why the traditional Order Falconiformes is a useful category in this instance. These pedal phalanges belong to such diurnal raptors. EP 2534/00 represents a medium-sized one, while EP 263/05 is a smaller one.

Order Galliformes Temminck, 1820

Fossils of Galliformes dominate the avian assemblages at Laetoli. Modern members of Galliformes occurring naturally in Africa and Eurasia all belong to the families Numididae (guineafowl) or Phasianidae (comprising francolins, partridges, pheasants, turkeys, grouse, quails etc., following e.g., Kriegs et al. 2007). This is also the case of all known Neogene fossils of Galliformes from these continents. Therefore, although specimens of other families were examined, detailed comparisons were restricted to modern members of these two families. The guineafowl are sometimes considered a subfamily of the Phasianidae, but analyses of recent molecular phylogenies using large genetic datasets place them more distant from the latter than the New World quails (family Odontophoridae) (e.g., Kriegs et al. 2007). Consequently, they fully deserve family status as Numididae. There is strong osteological similarity and homogeneity between francolins (*Francolinus* s.l.) and other African Phasianidae on the one hand, and Numididae (endemic in Africa) on the other hand. In addition, there is a significant overlap in size between most elements of the larger francolins and the smaller guineafowl. The identification of isolated and fragmentary postcranial elements, even to the family level, is often difficult. Some of the fossils remain identified in categories, such as "*Francolinus* sp. B/Numididae small". Some particular elements, such as the distal tibiotarsus or the tarsomatatarsal hypotarsus, are extremely variable in shape individually, and are of little use for separating taxa.

Nevertheless, some elements exhibit diagnostic characteristics, among which the following were used here. The proximal humerus is relatively wider, extended dorso-ventrally in francolins than in guineafowl, with the tuberculum ventrale more protruding ventrally. The hollow just distal to the caput humeri (emergent second fossa tricipitalis) is generally deeper in francolins than in guineafowl (except *Guttera*). On the distal humerus, the processus flexorius is much more extended ventro-distally in francolins than in guineafowl. On the proximal carpometacarpus, the processus extensorius is narrower in francolins (proximo-distally) and generally extended more proximally (this being variable). On the proximal femur, the femoral head is proportionately smaller in francolins (relative to the rest of the epiphysis). Generally in francolins the femoral head is extended less proximally than in guineafowl. On the proximal tarsometatarsus, often the general plane of the cotyles is slightly less sloping dorsally in francolins than in guineafowl, but this is very variable. The ratio of proximal or distal width of tarsometatarsus relative to total length, useful among genera of guineafowl, is not useful to separate them from large francolins (independently from spurs); but the ratio between width of shaft and width of proximal or distal epiphyses is useful. In large francolins the shaft is proportionately much wider relative to epiphyses than in otherwise similar-sized guineafowl. Finally, when different elements are likely to belong to the same species, it may be used to make more precise identifications, because some inter-segment proportions are diagnostic for certain genera (e.g., within guineafowl).

For consideration of *Afropavo*, see under Phasianidae, and for *Pavo*, see under *Acryllium* and Louchart (2003).

Family Phasianidae Horsfield, 1821

The following diagnostic characteristics were used to differentiate between genera among the Phasianidae. On the coracoid, the cotyla scapularis tends to be more concave in *Alectoris* than in francolins. On the proximal humerus, the proximal epiphysis is proportionately larger in *Alectoris* and *Perdix* than in francolins, and more extended in the direction disto-dorsal to proximo-ventral; in these genera the caput humeri is extended more proximo-ventrally. In addition, the second fossa tricipitalis is much deeper in *Alectoris*, as well as in *Ptilopachus*, than in *Francolinus*. In *Coturnix* this fossa is also deeper and the caput humeri is more protruding proximo-ventrally. On the distal humerus, the processus flexorius is slightly more prominent ventro-distally in francolins than in *Alectoris*. On the proximal carpometacarpus, the processus extensorius is more strongly developed proximo-cranially in *Alectoris* than in francolins, and the whole proximal epiphysis is larger relative to the metacarpals; in *Perdix* and *Coturnix* the processus extensorius is also more developed than in francolins. In *Afropavo* the depth/width ratio of the proximal femur and the depth/width ratio of the proximal carpometacarpu are both greater than in francolins and guineafowl. For additional characteristics of *Afropavo* see Louchart (2003). It should be noted that the absence of a spur on the tarsometatarsus shaft is not diagnostic at this level, because some francolins lack spurs in females or even in both sexes.

Genus *Francolinus* Stephens, 1819

This very diverse genus, essentially African, comprises four subgenera: *Francolinus*, *Peliperdix*, *Scleroptila* and *Pternistis* (see Crowe et al. 1992a, b; Crowe 1993). The latter three occur in Africa, where they are endemic. *Peliperdix* comprises five species, which are "quail-like" and the smallest of francolins. *Scleroptila* comprises seven species of quail-like "red-winged francolins", larger than *Peliperdix* species (except males *F. (Pel.) sephaena*), but smaller than most species of *Pternistis*. *Pternistis* comprises 24 species of partridge-like "spurfowl", which vary in size from the size of *Peliperdix* to much larger (six times heavier for *F. (Pt.) erckelii*, the largest francolin).

Osteologically the different subgenera may be diagnosable with reasonably complete postcranial skeletons of individuals, comprising complete elements, using osteometrics (see Crowe 1992). But with isolated proximal or distal ends of postcranial elements, as in the present case, it is not possible to use these criteria. For the parts available, there is a strong osteological uniformity between the numerous species and the four subgenera (in shape and size), as well as often important individual variability within species, and greatly overlapping sizes across species and subgenera, combined with sexual size dimorphism. Altogether, these generally allow only an imprecise identification of the fossils. It is even difficult to assign them consistently to species. However, today only two or three species of francolins live in real syntopy (in the same location), and in these cases they are generally of contrasting size. Therefore, it may be reasonable to give tentative assignments to unnamed species of differing sizes.

For the francolins at Laetoli, the distribution of the width of the distal humeri, the most common skeletal part, and the most diagnostic for separating francolins from guineafowl, shows that there are two size groups. This variation could correspond to two species or more, each showing sexual size dimorphism comparable to modern species. Here two species are recognized, one smaller, the size of *F. (Peliperdix) sephaena*, and one larger, the size of a larger *F. (Pternistis)* species. The various skeletal elements were assigned to one or the other of these species, when possible, using size, proportions, and a few discrete characters (see below).

In modern francolins sexual size dimorphism is often not important enough to make obvious bimodal distributions in measurements (there are extensive overlaps in many species). In addition, too few individuals could be examined, belonging to only a minority of the species, and sometimes specimens were unsexed. However, fossils at the extremes of the range of a size group are indicated as corresponding potentially to females or males of the species concerned. Otherwise, no potential sex is indicated.

Once again, some fossils are assigned to more inclusive groups, such as *Francolinus* sp. or *Francolinus* sp. A/B, if they are too fragmentry, insufficiently diagnostic, and/or are potentially in the domain of overlap between species A and B.

Fig. 18.2 (**a**) *Francolinus* sp. A aff. *F. (Peliperdix) sephaena*, complete r. carpometacarpus (EP 1903/03), in ventral view. (**b**) *Francolinus* sp. A aff. *F. (Peliperdix) sephaena*, prox. r. femur (EP 1646/00), in cranial view. (**d–e**) *Francolinus* sp. A aff. *F. (Peliperdix) sephaena*, dist. r. tarsometatarsus (EP 227/01), in dorsal view. (**d**) and medial view (**e**). (**c**) *Francolinus* sp. A aff. *F. (Peliperdix) sephaena*, prox. r. humerus (EP 1903/03), in caudal view. (**f**) *Francolinus* sp. A aff. *F. (Peliperdix) sephaena*, shaft of l. tarsometatarsus with base of spur (EP 709/01), in medio-dorsal view. Scale bars are equal to 1 cm

Francolinus sp. A aff. *F. (Peliperdix) sephaena* (A. Smith, 1836)

Material: prox. l. humerus, EP 102/03; prox. r. humerus, LAET 76-18-384; prox. l. carpometacarpus, EP 561/05; prox. r. carpometacarpus, LAET 76-18-663. Size possibly corresponding to females: prox. l. coracoids, EP 1156/01 and EP 1260/03; prox. r. coracoids, EP 1642/00, EP 219/01, EP 1259/03 (Fig. 18.1g) and EP 1596/04 (frag.); prox. r. humerus, EP 1559/01; possibly associated complete r. carpometacarpus (Fig. 18.2a) and subcomplete l. carpometacarpus, EP 1903/03; prox. l. carpometacarpus, EP 1103/05; dist. r. coracoid, EP 480/03b; prox. r. femur, EP 1646/00 (Fig. 18.2b); prox. r. tarsometatarsus, EP 364/04; dist. r. tarsometatarsus, EP 227/01 (Fig. 18.2d, e). Size possibly corresponding to males: possibly associated incomplete l. and r. coracoids, sternum cranial part frag., prox. r. humerus (Fig. 18.2c) and dist l. and r. ulnas, EP 1903/03; prox. l. coracoid, EP 4131/00; dist. l. humeri, EP 1457/03 and EP 684/05; dist. r. ulna, EP 2330/00; prox. r. femurs, EP 1272/01 and EP 147/04; dist. l. tibiotarsus, LAET 76-18-113; shaft of l. tarsometatarsus with base of spur, EP 709/01 (Fig. 18.2f); shaft of l. tarsometatarsus with part of spur, LAET 75-3300 (Fig. 18.3a, b).

Tentatively referred: prox. r. coracoid, EP 811/00; prox. l. tibiotarsus, EP 794/05b. Size possibly corresponding to females: prox. l. coracoid, EP 3079/00; prox. r. coracoid, EP 1461/04. Size possibly corresponding to males: dist. l. humerus, LAET 76-4212; dist. r. humerus, EP 271/01 (Fig. 18.3c); prox. r. femur, EP 191/03.

Measurements: see Tables 18.2–18.8.

Localities: see Tables 18.9 and 18.10.

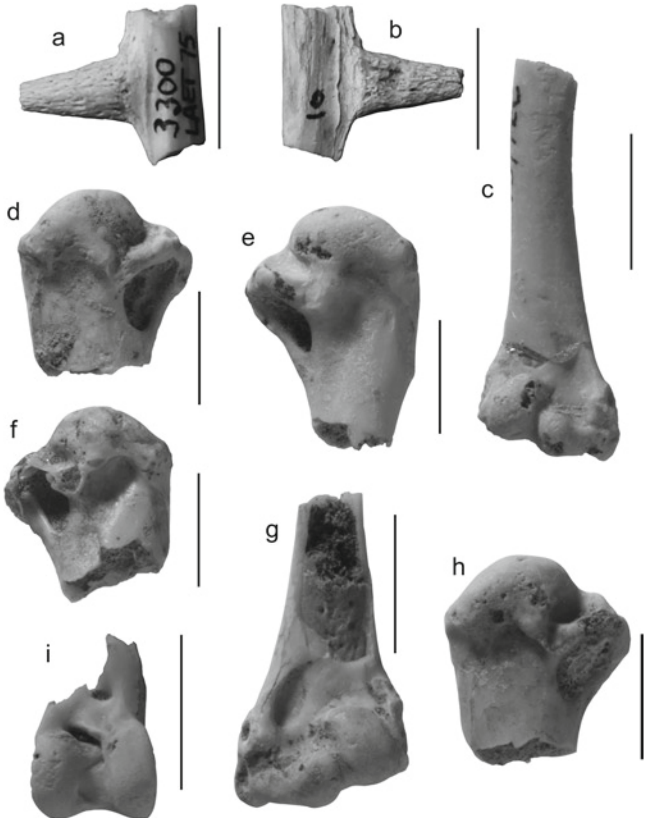

Fig. 18.3 (**a**–**b**) *Francolinus* sp. A aff. *F. (Peliperdix) sephaena*, shaft of l. tarsometatarsus with part of spur (LAET 75-3300), in medio-dorsal view (**a**) and latero-plantar view (**b**). (**c**) *Francolinus* cf. sp. A aff. *F. (Peliperdix) sephaena*, dist. r. humerus (EP 271/01), in cranial view. (**d**) *Francolinus (Pternistis)* sp. B, prox. l. humerus (EP 1175/00), in caudal view. (**e**) *Francolinus (Pternistis)* sp. B, prox. r. humerus (EP 1580/98), in caudal view. (**f**) *Francolinus (Pternistis)* sp. B, prox. r. humerus (EP 1102/03), in caudal view. (**g**) *Francolinus (Pternistis)* sp. B, dist. l. humerus (EP 3018/00), in cranial view. (**h**) *Francolinus (Pternistis)* sp. B, prox. l. humerus (EP 151/01), in caudal view. (**i**) *Francolinus (Pternistis)* sp. B, dist. l. tibiotarsus (EP 454/04), in cranial view. Scale bars are equal to 1 cm

Total NR: 41; total MNI (based on coracoids and localities): 19.

Remarks: All the elements are compatible in size, proportions and discrete characters with a species similar to *F. (Peliperdix) sephaena*. The humeri show a relatively deep second fossa tricipitalis, just distal to caput humeri, as in some species of *Peliperdix* (including *sephaena*), with individual variability. In some fossils it is as deep as in the smaller *Ptilopachus petrosus*. The Laetoli species also shares with *F. (Peliperdix) sephaena* its marked sexual size dimorphism, with females the weight of the small *F. (Pel.) coqui* and males 40% heavier on average, and little overlap. This dimorphism is less in the other species of the subgenus (as well as apparently in species of *Scleroptila* and the smallest species of *Pternistis*, based on existing ornithological measurement data). *Francolinus (Pel.) sephaena* would therefore appear to be the modern species closest to the fossils.

The two smaller tarsometatarsi lack spurs and are attributable to females (EP 227/01, Figs. 18.2c, d, and EP 364/04), while the two larger ones each have one spur, and correspond to males (LAET 75-3300, Figs. 18.3a, b, and EP 709/01, Fig. 18.2f). This is concordant with the present identification. In extant *Peliperdix* species, males have a tarsometatarsal spur, while females lack it.

However, some slight differences in proportions or discrete characters are observable on some elements, and possibly suggest a different species. The carpometacarpus EP 1103/05 has a processus extensorius more prominent cranially than in the modern *Peliperdix* specimens examined, but this may be individual variation. The tarsometatarsi are slightly larger relative to the other elements than in *F. (Pel.) sephaena*. Because not all modern species of francolins were examined, and because of the incomplete and fragmentary nature of the remains, as well as the uncertainty regarding the placement in the same species of unassociated remains, from several localities and units, it is best not to name a new species. To emphasize their close relation to *F. (Pel.) sephaena*, albeit with small differences, these fossils are referred here to *Francolinus* sp. A aff. *F. (Peliperdix) sephaena*. For an unknown reason taphonomically, coracoids are well-represented and tibiotarsi scarce for the species A, while it is the reverse for the species B (see below).

Today the five species of *Peliperdix* live in different habitats, ranging from equatorial forest to woodlands, forest edge (*sephaena*), miombo woodlands, brushland (*sephaena*), wooded grassland and savanna. The fossil species indicates the presence of at least a minimal cover of bushes and trees, even scattered, which *Peliperdix* francolins use for shelter and perching.

Francolinus (Pternistis) sp. B

Material: prox. l. humeri, LAET 75-1114 and EP 1175/00 (Fig. 18.3d); prox. r. humeri, EP 1580/98 (Fig. 18.3e), EP 270/01 and EP 1102/03 (Fig. 18.3f); dist. l. humeri, EP 3018/00 (Fig. 18.3g) and EP 1102/05; dist. r. humeri, EP 647/98 and EP 1652/00; possibly associated dist. r. humerus, prox. r. radius and dist. r. tibiotarsus frag., EP 661/04a; prox. l. carpometacarpus, EP 1745/04; prox. r. carpometacarpus, EP 1331/03; dist. l. ulna, EP 480/03b; prox. l. femur, EP 3910/00; dist. l. femur, EP 1169/00; dist. r. tibiotarsi, LAET 75-1113, LAET 78-4919 and EP 1101/04. Size possibly corresponding to females: incomplete l. humerus, EP 1160/05; prox. l. humerus, EP 151/01 (Fig. 18.3h); prox. r. humerus, LAET 76-7E-30; dist. r. humerus, EP 3189/00; prox. r. carpometacarpus, EP 4173/00; prox. l. femur, EP 4332/00; prox. r. femur, EP 943/01; dist. l. femur, EP 1158/04; prox. r. tibiotarsus, EP 2766/00; dist. l. tibiotarsi, EP 2827/00, EP 4333/00, EP 429/03 and EP 454/04 (Fig. 18.3i); dist. r. tibiotarsi, EP 1650/00, EP 2459/03 and EP 783/04; complete l. tarsometatarsus, LAET 75-1440/1441 (Fig. 18.4a–c); incomplete l.

tarsometatarsus (lacking part of shaft), EP 1345/01; prox. l. tarsometatarsus, EP 1355/04; dist. r. tarsometatarsus, LAET 75-1058. Size possibly corresponding to males: prox. r. humerus, EP 3911/00; dist. l. humerus, EP 3852/00; dist. r. humerus, LAET 79-5474; prox. r. femur frag., EP 1459/04; dist. l. femur, LAET 78-4757; prox. r. femur, EP 1164/01 (Fig. 18.4d); prox. l. tibiotarsi, EP 038/00 and EP 272/01; shaft of r. tibiotarsus, LAET 75-2133; shaft of r. tarsometatarsus with base of spur, EP 1284/04 (Fig. 18.4e, f).

Tentatively referred: possibly associated prox. l. scapula and prox. l. coracoid, EP 265/05; prox. l. coracoid, EP 264/05 (Fig. 18.4g); dist. r. femur, EP 3019/00; prox. r. tibiotarsus, EP 1880/00; dist. r. tibiotarsus, EP 298/05; prox. l. tarsometatarsi, EP 1433/00 and EP 150/01; dist. r. tarsometatarsus frag., EP 1104/03; pedal phalanx, EP 1985/00. Size possibly corresponding to females: prox. l. humerus, EP 1526/03; dist. l. tibiotarsus, EP 273/01; prox. r. tarsometatarsus, EP 1374/00; dist. l. tarsometatarsus slightly juvenile, EP 264/98. Size possibly corresponding to males: prox. l. carpometacarpi, EP 648/98 (Fig. 18.4h) and EP 431/03; prox. r. carpometacarpus, EP 794/05a; dist. r. carpometacarpus, EP 1881/00; prox. l. femur, EP 683/05; dist. l. tarsometatarsus, EP 1651/00.

Measurements: see Tables 18.1–18.8.

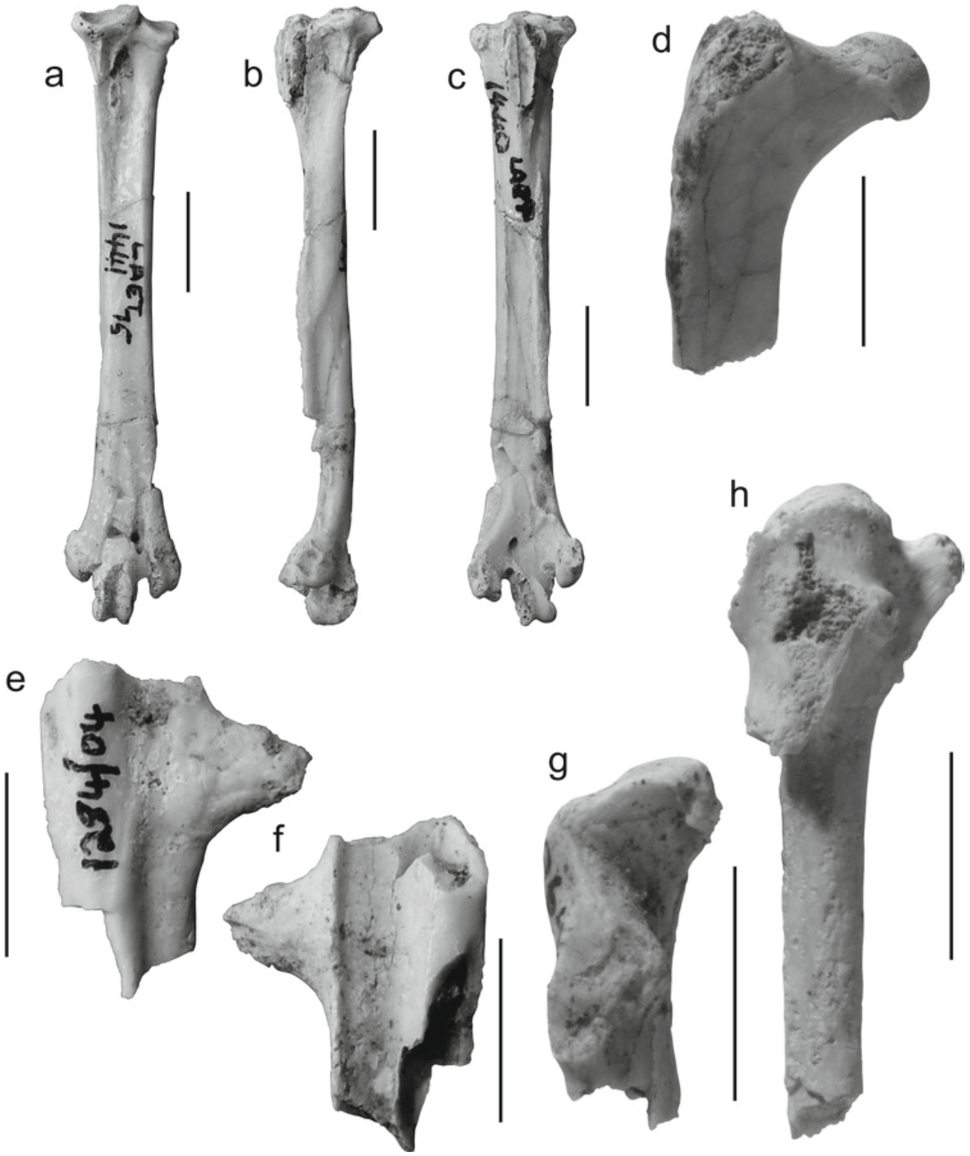

Fig. 18.4 (**a**–**c**) *Francolinus (Pternistis)* sp. B, complete l. tarsometatarsus (LAET 75-1440/1441), in dorsal view (**a**), medial view (**b**) and plantar view (**c**). (**d**) *Francolinus (Pternistis)* sp. B, prox. r. femur (EP 1164/01), in cranial view. (**e**–**f**) *Francolinus (Pternistis)* sp. B, shaft of r. tarsometatarsus with base of spur (EP 1284/04), in medio-dorsal view (**e**) and latero-plantar view (**f**). (**g**) *Francolinus (Pternistis)* cf. sp. B, prox. l. coracoid (EP 264/05), in dorsal view. (**h**) *Francolinus (Pternistis)* cf. sp. B, prox. l. carpometacarpus (EP 648/98), in ventral aspect. Scale bars are equal to 1 cm

Localities: see Tables 18.11 and 18.12.

Total NR: 70; total MNI (based on humeri and localities): 24.

Remarks: This species is by far the best represented bird at Laetoli. The humeri have a second fossa tricipitalis (just distal to caput humeri) on average moderately deep, as is usual in *Pternistis* specimens (and shallower than in species A), but of noticeably variable depth individually, from shallow to rather deep (more variable than in species A). Four of the seven fossil carpometacarpi are slightly larger than in the modern male *F. (Pt.) erckelii* examined, the largest extant francolin. In contrast, the other elements attributable to male individuals of species B are mostly slightly smaller than this specimen. This reflects a special characteristic of the fossil species, apparently having allometrically larger carpometacarpi than modern francolins of similar size.

Table 18.1 Measurements (mm) of the scapulae of Laetoli Galliformes and of modern species for comparison

Taxon		Width of cranial end (oblique)
Fossil	*Francolinus (Pternistis)* sp. B	10.5 (1)
	Francolinus sp. ? A/B	9.8 (1)
	Numididae indet. small	12.0+ e (1)
Modern	*Francolinus (Peliperdix) coqui*	8.1 (1)
	F. (Peliperdix) sephaena M	9.6 (1)
	F. (Pternistis) squamatus M	10.0 (1)
	F. (Pternistis) leucoscepus F	9.8 (1)
	F. (Pternistis) erckelii M	12.0 (1)
	Ptilopachus petrosus F	6.95 (1)
	Afropavo congensis F	13.55 (1)
	Agelastes niger	12.0 (1)
	Numida meleagris	12.9–14.75 (3)
	Guttera plumifera	11.9–12.5 (2)
	Guttera pucherani	12.3–13.5 (2)
	Acryllium vulturinum	15.3–15.4 (3)

Ranges are provided, followed by number of specimens in parentheses

e estimated, + minimum, *F* female, *M* male

The largest tarsometatarsus (EP 1284/04, Fig. 18.4e, f) bears the base of a large spur, protruding from a prominent hypotarsal longitudinal crest, and corresponds to a male. Two smaller tarsometatarsi (LAET 75-1440/1441, Fig. 18.4a–c, and EP 1345/01) show a prominent hypotarsal longitudinal crest and apparently bear no spur (or, alternatively, a spur might have been present, and be lacking now if the thinnest part of the crest at its base broke, which is now difficult to assess); thus they probably correspond to female individuals. One tarsometatarsus (EP 264/98) lacks spur and crest, but this may be attributed to its slightly juvenile state. Hence, in this species males have at least one spur (and prominent hypotarsal crest), and females a prominent hypotarsal crest, but apparently no spur. This pattern is found in several modern species of *Pternistis*. Extant members of *Pternistis* display all combinations of presence and number of tarsometatarsal spurs, according to species: both male and

Table 18.2 Measurements (mm) of the coracoids of Laetoli Galliformes and of modern species for comparison

Taxon		Proximal (scapular) width	Proximal (scapular) depth	Distal (sternal) width [a]	Minimal width of corpus
Fossil	*Francolinus* sp. A aff. *F. (Peliperdix) sephaena*	5.6–7.5 (10)	3.6–4.6 (9)	8.3 (1)	3.1–3.5 (3)
	Francolinus (Pternistis) sp. B	8.9 (1)			3.6 (1)
	Francolinus sp. ? A/B	7.7 (1)	~4.7 (2)		3.7–3.9 (2)
	cf. *Agelastes* sp.	8.1 (1)	5.3 (1)		
	Numida/Guttera sp.	9.7 (1)			4.3 (1)
	Francolinus (*Pternistis*) sp. B/*Agelastes* sp.	8.4 (1)	5.4 (1)		
	F. (*Pternistis*) sp. B/*Guttera* sp.			9.9 (1)	3.9– ~4 (2)
	F. (*Pternistis*) sp. B/Numididae small	~9.0 (1)	6.9 (1)		
Modern	*Francolinus (Francolinus) pintadeanus* F	7.0 (1)	4.0 (1)	7.1 (1)	3.25 (1)
	F. (Peliperdix) coqui	6.75 (1)	4.1 (1)	7.2 (1)	3.2 (1)
	F. (Peliperdix) sephaena M	7.8 (1)	4.75 (1)	8.5 (1)	3.5 (1)
	F. (Pternistis) squamatus M	8.6 (1)	4.7 (1)	9.5 (1)	4.05 (1)
	F. (Pternistis) leucoscepus F	8.2 (1)	4.65 (1)	8.65 (1)	3.5 (1)
	F. (Pternistis) erckelii M	9.9 (1)	5.4 (1)	10.7 (1)	4.35 (1)
	Ptilopachus petrosus F				2.5 (1)
	Afropavo congensis F			12.2 (1)	4.9 (1)
	Agelastes niger	8.35 (1)		10.9 (1)	4.5 (1)
	Numida meleagris	9.0–10.75 (3)	5.9–7.0 (3)	9.8–12.2 (3)	5.1–5.75 (3)
	Guttera plumifera F	9.9 (1)	5.3 (1)	10.75 (1)	4.75 (1)
	Guttera pucherani	9.2–12.2 (3)	~6.9–7.75 (2)	8.85–11.7 (3)	4.1–4.8 (3)
	Acryllium vulturinum	10.3–11.2 (3)	7.5–7.6 (3)	12.0–12.7 (3)	5.2–5.55 (3)

Ranges are provided, followed by number of specimens in parentheses

F female, *M* male

[a] From lateral end of facies articularis sternalis to medial tip of angulus medialis

Table 18.3 Measurements (mm) of the humeri of Laetoli Galliformes and of modern species for comparison

Taxon		Total length	Proximal width	Depth of caput humeri	Distal width	Distal depth	Minimal width of shaft
Fossil	*Francolinus* sp. A aff. *F. (Peliperdix) sephaena*		12.5–13.4 (4)	5.5–5.6 (2)	10.0–10.8 (4)	5.1–5.8 (4)	4.7 (1)
	Francolinus (Pternistis) sp. B	57.0 (1)	14.5–16.3 (9)	6.2–7.0 (10)	11.6–13.2 (8)	6.2–7.1 (7)	4.9 (1)
	Francolinus sp. ? A/B				11.1 (1)	6.2 (1)	
	Numida/Guttera sp.	74.0 (1)	19.5–20.5 e (3)	8.1–~9.0 (3)	15.0–16.7 (5)	8.1–8.9 (6)	6.9–7.5 (2)
	Numididae indet. small		19.7 (1)				
Modern	*Francolinus (Francolinus) pintadeanus* F	50.75 (1)	12.7 (1)	5.2 (1)	9.6 (1)	5.3 (1)	5.2 (1)
	F. (Peliperdix) coqui	50.3 (1)	12.25 (1)	4.75 (1)	9.3 (1)	5.5 (1)	4.2 (1)
	F. (Peliperdix) sephaena M	52.4 (1)	13.3 (1)	5.7 (1)	10.5 (1)	5.75 (1)	4.5 (1)
	F. (Pternistis) squamatus M	58.9 (1)	14.85 (1)	6.3 (1)	11.4 (1)	6.35 (1)	5.55 (1)
	F. (Pternistis) leucoscepus F	57.6 (1)	14.0 (1)	5.8 (1)	11.55 (1)	6.0 (1)	4.9 (1)
	F. (Pternistis) erckelii M	66.8 (1)	18.3 (1)	7.05 (1)	14.2 (1)	7.5 (1)	6.05 (1)
	Ptilopachus petrosus	34.0–36.75 (2)	9.05–9.6 (2)	3.75–4.0 (2)	7.2–7.6 (2)	4.15–4.2 (2)	3.2–3.35 (2)
	Afropavo congensis	83.2–89.5 (4)	20.6–23.0 (4)	8.4–9.1 (4)	17.0–18.4 (4)	9.0–9.4 (4)	7.35–8.2 (4)
	Agelastes meleagrides		19.7 (1)		15.5 (1)		7.6 (1)
	Agelastes niger	64.9–67.35 (2)	18.05–18.7 (2)	7.6–7.7 (2)	14.5–14.6 (2)	7.6–7.8 (2)	6.55–7.2 (2)
	Numida meleagris	76.0–76.4 (2)	19.2–22.0 (8)	8.3–8.9 (2)	15.3–17.9 (8)	8.7–9.1 (2)	7.0–7.9 (8)
	Guttera plumifera	69.3–71.8 (2)	17.9–18.7 (2)	7.8 (1)	14.8–14.9 (2)	8.15 (1)	6.7–8.25 (2)
	Guttera pucherani	69.8–80.0 (4)	18.25–21.4 (5)	7.5–8.8 (4)	14.7–17.9 (5)	8.35–9.3 (3)	7.1–8.2 (5)
	Acryllium vulturinum	87.9–92.4 (3)	21.4–24.0 (4)	8.9–9.35 (3)	17.6–18.85 (4)	9.7–10.75 (3)	8.2–9.25 (4)

Ranges are provided, followed by number of specimens in parentheses

e estimated, *F* female, *M* male

Table 18.4 Measurements (in mm) of the ulnae of Laetoli Galliformes and of modern species for comparison

Taxon		Proximal width	Distal width (orthogonal)	Distal depth (orthogonal)	Greatest diagonal distal depth	Minimal width of shaft
Fossil	*Francolinus* sp. A aff. *F. (Peliperdix) sephaena*		5.4–5.8 (2)	6.0–6.2 (2)	6.7–6.9 (2)	3.3 (1)
	Francolinus (Pternistis) sp. B			~7.2 (1)		
	cf. *Agelastes* sp.		7.9 e (1)	~8.1 (1)	9.5 e (1)	4.2 e (1)
	Numididae indet. medium/large	11.8 (1)				
Modern	*Francolinus (Francolinus) pintadeanus* F	7.0 (1)				
	F. (Peliperdix) coqui	6.1 (1)	5.0 (1)	5.15 (1)	6.0 (1)	2.6 (1)
	F. (Peliperdix) sephaena M	7.0 (1)	5.6 (1)	6.2 (1)	7.0 (1)	2.75 (1)
	F. (Pternistis) squamatus M	7.3 (1)	6.1 (1)	6.5 (1)	7.3 (1)	3.35 (1)
	F. (Pternistis) leucoscepus F	6.9 (1)	5.8 (1)	6.7 (1)	7.2 (1)	3.05 (1)
	F. (Pternistis) erckelii M	9.1 (1)	7.4 (1)	8.8 (1)	9.55 (1)	3.9 (1)
	Ptilopachus petrosus F					2.05 (1)
	Afropavo congensis F	11.6 (1)	9.5 (1)	9.25 (1)	10.55 (1)	4.8 (1)
	Agelastes niger	8.9–9.7 (2)	7.4– ~7.6 (2)	7.6–7.9 (2)	8.8–9.1 (2)	4.05–4.2 (2)
	Numida meleagris	10.0– ~10.3 (2)	8.3–~8.6 (2)	8.15–8.7 (2)	9.4–10.2 (2)	4.0–4.6 (2)
	Guttera plumifera	9.45 (1)				
	Guttera pucherani	10.7–11.7 (3)	8.3 (1)	8.7 (1)	9.6–10.25 (3)	4.05–4.75 (3)
	Acryllium vulturinum	11.3–12.6 (2)	9.3–9.9 (3)	10.1–10.9 (3)	11.5–12.0 (2)	4.75–5.25 (3)

Ranges are provided, followed by number of specimens in parentheses

e estimated, *F* female, *M* male

Table 18.5 Measurements (mm) of the carpometacarpi of Laetoli Galliformes and of modern species for comparison

Taxon		Total length	Proximal width	Proximal depth of trochlea	Distal width	Distal depth (minimal)	Minimal width of corpus of major metacarpal
Fossil	*Francolinus* sp. A aff. *F. (Peliperdix) sephaena*	26.2 (1)	7.8–8.1 (3)	3.4–3.9 (3)	5.5 (1)	2.9 (1)	2.5 (1)
	Francolinus (Pternistis) sp. B		8.9 e; 9.2–~12.7 (6)	4.5–6.2 (5)	6.8 (1)	3.8 (1)	3.4 (1)
Modern	*Francolinus (Peliperdix) coqui*	26.1 (1)	7.6 (1)	3.4 (1)	4.85 (1)	2.8 (1)	2.3 (1)
	F. (Peliperdix) sephaena M	28.4 (1)	8.0 (1)	4.3 (1)	5.4 (1)	2.75 (1)	2.2 (1)
	F. (Pternistis) squamatus M	31.0 (1)	8.8 (1)	4.35 (1)	6.4 (1)	3.2 (1)	2.75 (1)
	F. (Pternistis) leucoscepus F	29.9 (1)	8.8 (1)	4.35 (1)	5.2 (1)	3.0 (1)	2.5 (1)
	F. (Pternistis) erckelii M	34.6 (1)	10.5 (1)	5.4 (1)	7.25 (1)	4.1 (1)	3.25 (1)
	Ptilopachus petrosus F	19.8 (1)					
	Afropavo congensis F	42.4 (1)	11.9 (1)	6.75 (1)	7.7 (1)	4.1 (1)	3.3 (1)
	Agelastes niger	34.8–36.9 (2)	11.2–11.3 (2)	5.15–5.2 (2)	6.7–7.0 (2)	3.5–3.7 (2)	3.0–3.1 (2)
	Numida meleagris	39.3–40.8 (2)	12.1–12.5 (2)	6.0 (2)	7.1–8.0 (2)	4.2–4.6 (2)	2.9–3.05 (2)
	Guttera plumifera	39.0 (1)	11.8 (1)				3.0 (1)
	Guttera pucherani	37.0–40.6 (3)	10.7–12.7 (3)	5.55–5.8 (2)	7.0 (1)	3.9 (1)	3.1–3.5 (3)
	Acryllium vulturinum	46.1–48.6 (2)	13.35–14.5 (3)	6.5–6.9 (3)	7.9–8.3 (2)	4.4–4.6 (2)	3.5–3.6 (2)

Ranges are provided, followed by number of specimens in parentheses

e estimated, *F* female, *M* male

Table 18.6 Measurements (mm) of the femora of Laetoli Galliformes and of modern species for comparison

Taxon		Proximal width	Proximal depth without crista trochanteris	Distal width	Minimal width of shaft
Fossil	*Francolinus* sp. A aff. *F. (Peliperdix) sephaena*	~9.8–10.5 (4)	10.2 (1)		4.2–4.3 e (2)
	Francolinus (Pternistis) sp. B	11.6–14.2 (5)	12.0 (1)	11.4–14.0 (4)	4.8–5.6 (3)
	Francolinus sp. ? A/B	11.5 e (1)	9.0 e (1)		
	F. (*Pternistis*) sp. B/*Guttera* sp.			12.3 e (1)	
	F. (*Pternistis*) sp. B/Numididae small			~14.7 (1)	
Modern	*Francolinus (Francolinus) pintadeanus* F	10.3 (1)	4.4 (1)	9.5 (1)	4.1 (1)
	F. (Peliperdix) coqui	9.8 (1)	5.7 (1)	8.9 (1)	3.75 (1)
	F. (Peliperdix) sephaena M	~10.3 (1)	~6.3 (1)	~10.6 (1)	4.15 (1)
	F. (Pternistis) squamatus M	12.1 (1)	7.8 (1)	11.25 (1)	4.8 (1)
	F. (Pternistis) leucoscepus F	~12.2 (1)	~7.3 (1)	11.2 (1)	4.7 (1)
	F. (Pternistis) erckelii M	~15.0 (1)	~10.0 (1)	14.8 (1)	6.1 (1)
	Ptilopachus petrosus F				2.95 (1)
	Afropavo congensis F	14.6 (1)	14.5 (1)	14.6 (1)	6.8 (1)
	Agelastes niger			14.35–14.7 (2)	6.1–6.2 (2)
	Numida meleagris	~17.0–18.6 (3)	12.0–14.5 (2)	15.2–16.65 (3)	6.9–7.7 (3)
	Guttera plumifera	15.6 (1)	8.65 (1)	13.9–14.4 (2)	5.7–7.1 (2)
	Guttera pucherani	15.2–17.3 (3)	~9.8–11.7 (2)	14.3–16.3 (4)	6.25–7.0 (4)
	Acryllium vulturinum	18.2–19.4 (3)	15.25–16.3 (2)	16.3–18.8 (3)	7.0–7.9 (3)

Ranges are provided, followed by number of specimens in parentheses

e estimated, *F* female, *M* male

Table 18.7 Measurements (mm) of the tibiotarsi of Laetoli Galliformes and of modern species for comparison

Taxon		Total length[a]	Proximal width[b]	Proximal depth[c]	Distal width	Minimal width of shaft
Fossil	*Francolinus* sp. A aff. *F. (Peliperdix) sephaena*				7.6 (1)	
	Francolinus (Pternistis) sp. B		9.5– ~11.0 (3)	~12.5– ~14.4 (3)	8.3–9.3 (8)	4.5–5.2 (3)
	Francolinus sp. ? A/B					~4.2- (1)
	Acryllium vulturinum	132.5 (1)			12.2 (1)	6.4 (1)
	Numida/Guttera sp.				11.4 e – 11.5 (2)	
	Francolinus (*Pternistis*) sp. B/*Agelastes* sp.				11.0 e (1)	5.4 (1)
	F. (*Pternistis*) sp. B/*Guttera* sp.				~9.8–10.8 (2)	
	F. (*Pternistis*) sp. B/Numididae small				~9.7–11.4 (5)	
Modern	*Francolinus (Francolinus) pintadeanus* F	66.0 (1)	8.0 (1)	~10.2 (1)	7.1 (1)	3.75 (1)
	F. (Peliperdix) coqui	62.5 (1)	7.5 (1)	~10.0 (1)	6.75 (1)	3.75 (1)
	F. (Peliperdix) sephaena M	75.6 (1)	9.3 (1)	~11.0 (1)	7.5 (1)	3.65 (1)
	F. (Pternistis) squamatus M	83.3 (1)	9.85 (1)	~12.0 (1)	9.2 (1)	4.75 (1)
	F. (Pternistis) leucoscepus F	79.7 (1)	9.7 (1)	~11.2 (1)	8.2 (1)	4.7 (1)
	F. (Pternistis) erckelii M	101.5 (1)	~12.0 (1)	~16.5 (1)	11.6 (1)	5.4 (1)
	Ptilopachus petrosus F				~5.7 (1)	2.8 (1)
	Afropavo congensis F	117.4 (1)	12.6 (1)	15.8 (1)	11.2 (1)	5.65 (1)
	Agelastes niger	107.4–111.5 (2)	12.0–12.5 (2)	16.5 (1)	10.55–10.7 (2)	5.65–6.1 (2)
	Numida meleagris	105.8–109.2 (2)	13.1–13.2 (2)	16.5– ~16.6 (2)	11.4–11.85 (2)	6.0–6.35 (2)
	Guttera plumifera	108.2–108.8 (2)	12.4–12.6 (2)	~14.75 (1)	10.2–10.25 (2)	5.4–6.65 (2)
	Guttera pucherani	113.0–119.3 (4)	12.6–13.9 (3)	16.7– ~16.9 (2)	9.8–11.5 (4)	5.5–6.85 (4)
	Acryllium vulturinum	128.6–146.0 (3)	13.6–15.75 (3)	17.1–19.3 (3)	12.2–13.75 (3)	6.0–6.6 (3)

Ranges are provided, followed by number of specimens in parentheses

e estimated, *F* female, *M* male

[a] Without cristae patellaris, cnemialis cranialis and cnemialis lateralis

[b] Without crista cnemialis lateralis

[c] Without crista cnemialis cranialis

female having two spurs, male two and female one, male two and female none, male and female one, male one and female none, or both sexes none. The insertion of the spur on the shaft differs between the species A and B. In both species, the spur emerges from the hypotarsal longitudinal crest situated along the plantar-medial border of the shaft, in the plantar-medial direction orthogonal to the long axis of the shaft. In the larger species, species B, the crest is more prominent and flatter, especially basal to the spur. The spur itself appears slightly flattened in the same plane as the crest, but it is incomplete and eroded.

It is difficult to place the fossil species B close to a particular extant species. Elements including the leg elements (the widths and depths of which are closely related to weight), show the presumed males on average slightly smaller than male *F. (Pt.) erckelii*, while females are on average similar in size to, or slightly larger than female *F. (Pt.) leucoscepus*. Thus, the fossil species would correspond approximately to the size and sexual size dimorphism of *F. (Pt.) jacksoni* or *F. (Pt.) castaneicollis* (based on ornithological data; not seen), for example. The former is a species that favors diverse montane habitats in Kenya, the latter an East African species of diverse habitats and altitudes. However, the fossil species apparently differs from them by the probable absence of a spur in females (spurs are present in females of these two modern species, although they are much reduced compared with males), as well as presumably by allometrically larger carpometacarpi.

Although not all extant species of *Pternistis* were seen, published ornithological data on size, presence of spurs and sexual dimorphism, suggest that the fossils do not match any modern species of francolin. It may be an extinct species of rather large size, but for the same reasons as for species A, it is better not to name a new species. Since no modern species of large *Pternistis* appears particularly closer to the fossils, they are assigned here only to *Francolinus (Pternistis)* sp. B.

In contrast to species A, the coracoids of species B are far more scarce than the tibiotarsi, which may be related to the activity of different predators. The proximal tibiotarsus EP 038/00 (Loc. 4; cf. male), and the distal tarsometatarsus EP

Table 18.8 Measurements (in mm) of the tarsometatarsi of Laetoli Galliformes and of modern species for comparison

Taxon		Total length	Proximal width	Proximal depth (without hypotarsus)	Proximal depth with hypotarsus	Distal width	Distal depth	Minimal width of shaft	Height of spur at base
Fossil	*Francolinus* sp. A aff. *F. (Peliperdix) sephaena*		~8.9 (1)			9.5 (1)	6.4 (1)	3.7–4.5 (4)	6.1; ca 6.0–6.5 (2 males)
	Francolinus (Pternistis) sp. B	61.2 (1)	9.4–11.0; 12.0 e (5)	5.8–5.9 (2)	~9.0–10.5 (3)	~9.5–11.7 (5)	6.9– ~7.2 (2)	4.9–5.4 (4)	~8.0 e (1 male)
	Francolinus sp. ? A/B		~9.8 (1)					4.6 (1)	
	cf. *Agelastes/Guttera* sp.		~12.5		~12.2 (1)	12.3 (1)			
	F. (*Pternistis*) sp. B/*Guttera* sp.		10.8–11.1; 12.0 e (4)	6.4 (1)					
	F. (*Pternistis*) sp. B/ Numididae small								
Modern	*Francolinus (Francolinus) pintadeanus* F	43.0 (1)	7.4 (1)		7.55 (1)	7.75 (1)	5.7 (1)	3.6 (1)	no spur
	F. (Peliperdix) coqui	37.85 (1)	7.3 (1)		6.8 (1)	7.15 (1)	4.8 (1)	3.95 (1)	4.5 (1)
	F. (Peliperdix) sephaena M	48.8 (1)	8.4 (1)	~5.2 (1)	8.35 (1)	8.65 (1)	6.2 (1)	4.0 (1)	5.3 (1)
	F. (Pternistis) squamatus M	54.9 (1)	9.65 (1)		~9.5 (1)	10.05 (1)	7.65 (1)	4.6 (1)	~4.5 (1)
	F. (Pternistis) leucoscepus F	56.3 (1)	9.2 (1)	~5.5 (1)	8.75 (1)	8.7 (1)	~6.0 (1)	4.1 (1)	no spur
	F. (Pternistis) erckelii M	63.5 (1)	12.7 (1)	6.4 (1)		12.1 (1)	8.8 (1)	6.25 (1)	2 spurs: prox. spur: ~6.0; dist. spur: ~6.5 (1)
	Ptilopachus petrosus F	31.3 (1)						3.0 (1)	no spur
	Afropavo congensis	79.0–96.0 (3)	12.0–13.0 (3)		12.5–15.3 (3)	11.35–13.2 (3)	9.0–9.3 (3)	4.35– ~5.3 (3)	4.6–9.3 (3)
	Agelastes niger	76.3–77.5 (2)	12.0–12.3 (2)		11.0 (1)	12.0–12.5 (2)	8.7 (1)	5.0–5.25 (2)	6.2 (1)
	Numida meleagris	66.0–70.7 (2)	13.0–13.9 (2)		12.1–12.3 (2)	13.2–14.3 (2)	9.4–10.2 (2)	5.9–6.1 (2)	no spur
	Guttera plumifera	75.2–76.3 (2)	11.6 (1)		10.9 (1)	12.4 (1)	8.6 (1)	4.3–5.3 (2)	no spur
	Guttera pucherani	77.6–79.6 (3)	10.8–12.65 (4)		11.8– ~12.5 (2)	12.5–14.5 (4)	8.7– ~10.7 (2)	4.65–6.0 (4)	no spur
	Acryllium vulturinum	89.9–101.7 (3)	13.3–15.25 (3)		13.4–14.7 (2)	14.0–17.75 (3)	10.75–11.4 (3)	5.3–6.95 (3)	no spur

Ranges are provided, followed by number of specimens in parentheses

e estimated, *F* female, *M* male

Table 18.9 Localities comprising fossils assigned to *Francolinus* sp. A aff. *F. (Peliperdix) sephaena*

Specimen(s)	Locality	Unit	Horizon
EP 1156/01, EP 1903/03 and EP 1103/05	Laetoli Loc. 1	Upper Laetolil Beds	Between Tuff 6 and Yellow Marker Tuff
EP 1642/00, EP 1646/00, EP 219/01, EP 227/01 and EP 480/03b	Laetoli Loc. 3	Upper Laetolil Beds	Between Tuffs 6 and 8
EP 684/05	Laetoli Loc. 6	Upper Laetolil Beds	Between Tuffs 5 and 7
EP 4131/00, EP 1457/03 and EP 364/04	Laetoli Loc. 8	Upper Laetolil Beds	Between Tuffs 5 and 7
EP 1272/01	Laetoli Loc. 9 S	Upper Laetolil Beds	Below Tuff 2
LAET 75-3300	Laetoli Loc. 10	Upper Laetolil Beds	Between Tuff 3 and below tuff 1
EP 709/01	Laetoli Loc. 10W	Upper Laetolil Beds	Below Tuff 2
EP 1596/04 and EP 561/05	Laetoli Loc. 12	Upper Laetolil Beds	Between Tuffs 5 and 8
EP 2330/00	Laetoli Loc. 17	Upper Laetolil Beds	Between Tuff 7 and Yellow Marker Tuff
EP 147/04	Laetoli Loc. 22	Upper Laetolil Beds	Between Tuffs 5 and 7
EP 1259/03 and EP 1260/03	Laetoli Loc. 7E	Upper Ndolanya Beds	
LAET 76-18-113, LAET 76-18-384, LAET 76-18-663 and EP 102/03	Laetoli Loc. 18	Upper Ndolanya Beds	
EP 1559/01	Silal Artum	Upper Ndolanya Beds	

Table 18.10 Localities comprising fossils tentatively assigned to Francolinus sp. A aff. F. (Peliperdix) sephaena

Specimen(s)	Locality	Unit	Horizon
EP 191/03	Laetoli Loc. 4	Upper Laetolil Beds	Between Tuffs 7 and 8
EP 3079/00, EP 271/01 and EP 794/05b	Laetoli Loc. 5	Upper Laetolil Beds	Between Tuffs 3 and 5
EP 1461/04	Laetoli Loc. 6	Upper Laetolil Beds	Between Tuffs 5 and 7
EP 811/00	Laetoli Loc. 10E	Upper Laetolil Beds	Between Tuffs 5 and 7
LAET 76-4212	Laetoli Loc. 11	Upper Laetolil Beds	Between Tuffs 7 and 8

Table 18.11 Localities comprising fossils assigned to *Francolinus (Pternistis)* sp. B

Specimen(s)	Locality	Unit	Horizon
EP 3018/00, EP 1164/01 and EP 1102/05	Laetoli Loc. 1	Upper Laetolil Beds	Between Tuff 6 and Yellow Marker Tuff
LAET 75-2133, EP 454/04 and EP 1745/04	Laetoli Loc. 2	Upper Laetolil Beds	Between Tuffs 5 and 7
EP 1650/00, EP 1652/00, EP 2766/00, EP 480/03b and EP 661/04a	Laetoli Loc. 3	Upper Laetolil Beds	Between Tuffs 6 and 8
EP 038/00	Laetoli Loc. 4	Upper Laetolil Beds	Between Tuffs 6 and 8
LAET 78-4919, EP 2827/00, EP 270/01, EP 272/01, EP 429/03 and EP 1355/04	Laetoli Loc. 5	Upper Laetolil Beds	Between Tuffs 3 and 5
LAET 75-1113, LAET 75-1114, EP 3852/00, EP 151/01 and EP 1459/04	Laetoli Loc. 6	Upper Laetolil Beds	Between Tuffs 5 and 7
EP 3910/00, EP 3911/00, EP 943/01 and EP 783/04	Laetoli Loc. 7	Upper Laetolil Beds	Between Tuffs 5 and 8
EP 1169/00, EP 1175/00 and EP 4173/00	Laetoli Loc. 8	Upper Laetolil Beds	Between Tuffs 5 and 7
LAET 75-1440/1441 and EP 2459/03	Laetoli Loc. 9S	Upper Laetolil Beds	Below Tuff 2
EP 1284/04	Laetoli Loc. 10E	Upper Laetolil Beds	Between Tuffs 5 and 8
EP 647/98, EP 1580/98, EP 3189/00 and EP 1102/03	Laetoli Loc. 10W	Upper Laetolil Beds	Below Tuff 2
LAET 78-4757, EP 4332/00, EP 4333/00, EP 1331/03 and EP 1101/04	Laetoli Loc. 11	Upper Laetolil Beds	Between Tuffs 7 and 8
EP 1158/04	Laetoli Loc. 13	Upper Laetolil Beds	Between Tuffs 6 and 8
EP 1160/05	Laetoli Loc. 13	Upper Laetolil Beds	Between Tuffs 5 and 8
EP 1345/01	Laetoli Loc. 22E	Upper Laetolil Beds	Between Tuffs 3 and 8
LAET 75-1058, LAET 76-7E-30 and LAET 79-5474	Laetoli Loc. 7E	Upper Ndolanya Beds	

Table 18.12 Localities comprising fossils tentatively assigned to *Francolinus (Pternistis)* sp. B

Specimen(s)	Locality	Unit	Horizon
EP 1433/00 and EP 3019/00	Laetoli Loc. 1	Upper Laetolil Beds	Between Tuff 6 and Yellow Marker Tuff
EP 1880/00 and EP 1881/00	Laetoli Loc. 2	Upper Laetolil Beds	Between Tuffs 5 and 7
EP 1651/00	Laetoli Loc. 3	Upper Laetolil Beds	Between Tuffs 7 and 8
EP 1985/00, EP 273/01, EP 431/03 and EP 794/05a	Laetoli Loc. 5	Upper Laetolil Beds	Between Tuffs 3 and 5
EP 1374/00, EP 150/01 and EP 683/05	Laetoli Loc. 6	Upper Laetolil Beds	Between Tuffs 5 and 7
EP 298/05	Laetoli Loc. 10	Upper Laetolil Beds	Between Tuff 3 and below Tuff 1
EP 264/98	Laetoli Loc. 10E	Upper Laetolil Beds	Between Tuffs 5 and 7
EP 648/98 and EP 1104/03	Laetoli Loc. 10W	Upper Laetolil Beds	Below Tuff 3
EP 1526/03	Laetoli Loc. 12E	Upper Laetolil Beds	Between Tuffs 5 and 7
EP 264/05 and EP 265/05	Laetoli Loc. 17	Upper Laetolil Beds	Between Tuff 8 and Yellow Marker Tuff

264/98 (Loc. 10E; cf. female) are subadult. The distal tibiotarsus LAET 75-1113 bears an exostosis (Loc. 6).

The diverse species of *Pternistis* live today in a variety of different habitats, from primary forest to open grassland or montane heathlands. This fossil francolin is not a useful indicator, except that it indicates the presence of at least a minimal cover of bushes and trees, even scattered, which francolins use for shelter.

Francolinus sp. ? A/B

Material: prox. l. and r. scapulas, EP 1903/03; prox. l. coracoids, EP 479/03, EP 685/03 (frag.), EP 686/03 (frag.) and LAET 75-3507; dist. r. humerus, EP 3125/00; prox. l. femur frag., EP 818/04; dist. l. tibiotarsus, EP 1256/00; prox. r. tarsometatarsus, EP 1460/03.

Measurements: see Tables 18.1–18.3, 18.6–18.8.

Localities: EP 1903/03: Laetoli Loc. 1, Upper Laetolil Beds, between Tuffs 7 and 8; EP 685/03 and EP 686/03: Laetoli Loc. 2, Upper Laetolil Beds, between Tuffs 5 and 7; EP 479/03: Laetoli Loc. 3, Upper Laetolil Beds, between Tuffs 7 and 8; EP 818/04: Laetoli Loc. 7E, Upper Laetolil Beds, above Tuff 8; EP 1460/03: Laetoli Loc. 8, Upper Laetolil Beds, between Tuffs 5 and 7; EP 3125/00: Laetoli Loc. 10, Upper Laetolil Beds, below Tuff 3; LAET 75-3507: Laetoli Loc. 10E, Upper Laetolil Beds, between Tuffs 5 and 8; EP 1256/00: Laetoli Loc. 22S (Nenguruk Hill), Upper Ndolanya Beds.

NR: 10.

Remarks: These remains are too fragmentary or undiagnostic for a more precise assignment. They belong to francolin(s) within the size overlap between large *Peliperdix* and smaller *Pternistis* spp., and thus are tentatively assigned to species A/B.

cf. *Francolinus* sp. indet.

Material: pedal phalanx, EP 2768/00; two l. pedal phalanges, EP 228/01.

Locality: Laetoli Loc. 3, Upper Laetolil Beds, between Tuffs 6 and 8.

NR: 3.

Remarks: These fragmentary fossils belong to Galliformes and correspond in size to francolins.

Family Numididae de Sélys Longchamps, 1842

Among the four genera of Numididae (i.e., *Agelastes*, *Numida*, *Guttera*, *Acryllium*), there are differences in skeletal proportions, especially for leg elements, which are useful for separating taxa if complete bones are available (see e.g., *Acryllium* below). In addition, in the humeri of *Guttera* the second fossa tricipitalis, just distal to the caput humeri, tends to be deeper than in the other three genera (but variable individually). In the distal coracoid of *Numida* the distal width/minimal shaft width ratio is lower than in the other Numididae and in large francolins. In addition, some fragmentary bones can be tentatively assigned on the basis of intra-element proportions and size (see below). Other osteological diagnostic characteristics are not useful here because the skeletal parts concerned (e.g., crania, cervical vertebrae, furcula, spurs or bumps on tarsometatarsus) are lacking.

Genus cf. *Agelastes* Bonaparte, 1850

cf. *Agelastes* sp.

Material: dist. l. ulna, LAET 75-2312 (Fig. 18.5a).

Tentatively attributed: prox. l. coracoid, EP 812/00.

Measurements: see Tables 18.2 and 18.4.

Locality: Laetoli Loc. 10E, Upper Laetolil Beds, between Tuffs 5 and 8.

NR: 2; MNI: 1.

Remarks: This identification is tentative and based in part on the occurrence in the same locality of the ulna matching *Agelastes* sp. or a small *Guttera* sp. or a small *Numida meleagris*, and the coracoid, matching either *Agelastes* or a large francolin *Pternistis*. For the ulna, *Pternistis* is excluded because it differs in proportions. In *Pternistis* species, such as *P. erckelii*, the distal depth and diagonal distal depth of the ulna are greater relative to the width of the shaft than in the Numididae. The fossil also seems too large for modern

Fig. 18.5 (**a**) cf. *Agelastes* sp., dist. l. ulna (LAET 75-2312), in ventral view. (**b**) cf. *Agelastes/Guttera* sp., dist. l. tarsometatarsus (EP 1002/01), in dorsal view. (**c–d**) *Numida/Guttera* sp., probably associated prox. (**c**, caudal view) and dist. (**d**, cranial view) l. humerus (EP 480/03a). (**e**) *Numida/Guttera* sp., complete r. humerus (LAET 76-3867), in caudal view. (**f**) *Numida/Guttera* sp., prox. r. humerus (EP 1373/00), in caudal view. Scale bars are equal to 1 cm

francolins (subgenus *Pternistis*) or for *F. (Pternistis)* sp. B above. If both elements belong to the same species, then the best match is *Agelastes* sp.

If confirmed, this assignment would be informative from a paleoecological perspective, because it would indicate the presence of primary forest, the habitat of both modern species, *A. meleagrides* and *A. niger*. They are restricted to equatorial West and Central Africa. More material is needed to confirm the identification. A few fossils from the middle Miocene (ca. 15 Ma) of Namibia have been referred to aff. *Agelastes* (Crowe 1992).

cf. *Agelastes/Guttera* sp.

Material: prox. and dist. l. radius, EP 480/03a; prox. r. tarsometatarsus, EP 106/00; dist. l. tarsometatarsus, EP 1002/01 (Fig. 18.5b).

Measurements: radius: proximal width: 4.9, proximal depth: 5.9, minimal width of shaft: 2.7; tarsometatarsi: see Table 18.8.

Localities: EP 480/03a: Laetoli Loc. 3, Upper Laetolil Beds, between Tuffs 7 and 8; EP 106/00 and EP 1002/01: Laetoli Loc. 11, Upper Laetolil Beds, between Tuffs 7 and 8.

NR: 3.

Remarks: The distal tarsometatarsus could belong to *Guttera*, *Agelastes* or *Afropavo*. *Pternistis* can be excluded on the basis of the larger size of the fossil. The proximal tarsometatarsus could belong to *Agelastes* or *Guttera*, while *Afropavo* is excluded because it has a maximal proximal depth (including hypotarsus) greater than proximal width (the reverse for Numididae). Most of the shaft (for both remains) is lacking so that the presence/absence of a spur is unknown (the former would indicate *Agelastes*, the latter *Guttera*). The radius is the size of *Agelastes* or *Guttera*. Therefore, the fossils match best with corresponding elements of small guineafowl, but it is not possible to make a more definitive identification. They are referred to cf. *Agelastes/Guttera* sp.

Agelastes spp. live in primary forests, whereas *Guttera plumifera* lives in primary or mature secondary forests, and *G. pucherani* lives in secondary or gallery forest to woodlands and forest-savanna mosaic.

Numida/Guttera sp.

Material: prox. l. coracoid, LAET 75-452b; possibly associated prox. and dist. l. humeri, EP 480/03a (Fig. 18.5c, d); complete r. humerus, LAET 76-3867 (Fig. 18.5e); prox. r. humerus, EP 1373/00 (Fig. 18.5f); dist. l. humerus, EP 3124/00; dist. r. humeri, LAET 79-5473, EP 037/98 and EP 1174/00; dist. l. tibiotarsus, EP 942/01; dist. r. tibiotarsus, LAET 75-1180.

Measurements: see Tables 18.2, 18.3, 18.7.

Localities: see Table 18.13.

NR: 11.

Table 18.13 Localities comprising fossils assigned to *Guttera/Numida* sp.

Specimen(s)	Locality	Unit	Horizon
EP 037/98	Kakesio 3	Lower Laetolil Beds	
LAET 76-3867 and EP 480/03a	Laetoli Loc. 3	Upper Laetolil Beds	Between Tuffs 4 and 8
LAET 75-452b	Laetoli Loc. 5	Upper Laetolil Beds	Between Tuffs 3 and 5
LAET 75-1180 and EP 1373/00	Laetoli Loc. 6	Upper Laetolil Beds	Between Tuffs 5 and 7
EP 942/01	Laetoli Loc. 7	Upper Laetolil Beds	Between Tuffs 7 and 8
EP 1174/00	Laetoli Loc. 8	Upper Laetolil Beds	Between Tuffs 5 and 7
EP 3124/00	Laetoli Loc. 10	Upper Laetolil Beds	Below Tuff 3
LAET 79-5473	Laetoli Loc. 7E	Upper Ndolanya Beds	Below greenstones

Remarks: The distal and proximal humeri differ from *Afropavo* and match the Numididae (see Louchart 2003). All but LAET 76-3867 conform to the size of either *Numida meleagris* or *Guttera pucherani*. The complete right humerus LAET 76-3867 corresponds to either a small *N. meleagris* or *Guttera* sp. (*G. plumifera* or small *G. pucherani*), and its distal depth tends to point toward *Guttera* (it is slightly smaller than in *N. meleagris*). The coracoid is the size of *N. meleagris* or *G. pucherani*, or *Afropavo congensis*. The proximal coracoid bears an exostosis. The distal tibiotarsi are the size of *N. meleagris* or *G. pucherani*. The best match for these fossils is *Numida/Guttera* sp., to which they are referred here.

Taken together, species in *Numida* and *Guttera* live today in a range of habitats encompassing primary, secondary, gallery forest, woodland, savannah with trees or bushes, to steppe and subdesert for *N. meleagris*, but at least with some trees or bushes and water holes.

Genus *Acryllium* G. R. Gray, 1840
Acryllium vulturinum Hardwicke, 1834

Material: complete r. tibiotarsus, EP 1649/00 (Fig. 18.6a).

Tentatively attributed: prox. frag. of l. pedal phalanx 1 of digit III, EP 711/00 (Fig. 18.6b).

Measurements: tibiotarsus EP 1649/00: see Table 18.7; pedal phalanx 1 III EP 711/00: proximal width: ~8.2, minimal width of corpus: 4.5.

Localities: EP 1649/00: Laetoli Loc. 3, Upper Laetolil Beds, between Tuffs 7 and 8.

Tentative assignment: EP 711/00: Laetoli Loc. 2, Upper Laetolil Beds, between Tuffs 5 and 7.

Total NR: 2; total MNI: 2.

Remarks: The complete tibiotarsus shows the distinctive large size and slender proportions of *Acryllium vulturinum*, and matches only this genus and species. Size indicates it may belong to a female individual.

The pedal phalanx 1 of digit III also corresponds to *A. vulturinum*, although a female peafowl *Pavo* sp. must be taken into account. *Pavo* is a genus of Phasianidae, now absent from Africa, but present in East Africa during the early Pliocene (Louchart 2003; Pickford et al. 2004). Proximal width in two modern *A. vulturinum* is ~7.2 and ~8.0 (estimated), minimal width of corpus ~4.0 and ~4.3 (estimated). The homologous measurements for modern *Pavo cristatus* are respectively 8.9–11.5 and 5.5–6.2 ($n=4$, the smallest being subadult), and for one *P. muticus* proximal width is 8.6. The fossil phalanx, although eroded and perhaps subadult too, appears smaller than in *Pavo* spp., and can be tentatively attributed to *A. vulturinum*.

The tibiotarsus is the first record for the genus *Acryllium*. *Acryllium vulturinum* is restricted to East Africa and lives today in drier and more open habitats than other guineafowl, especially semi-arid acacia thorn-scrub and grassland with trees and bushes. With its long legs and neck, it appears especially well-adapted to tall grasslands.

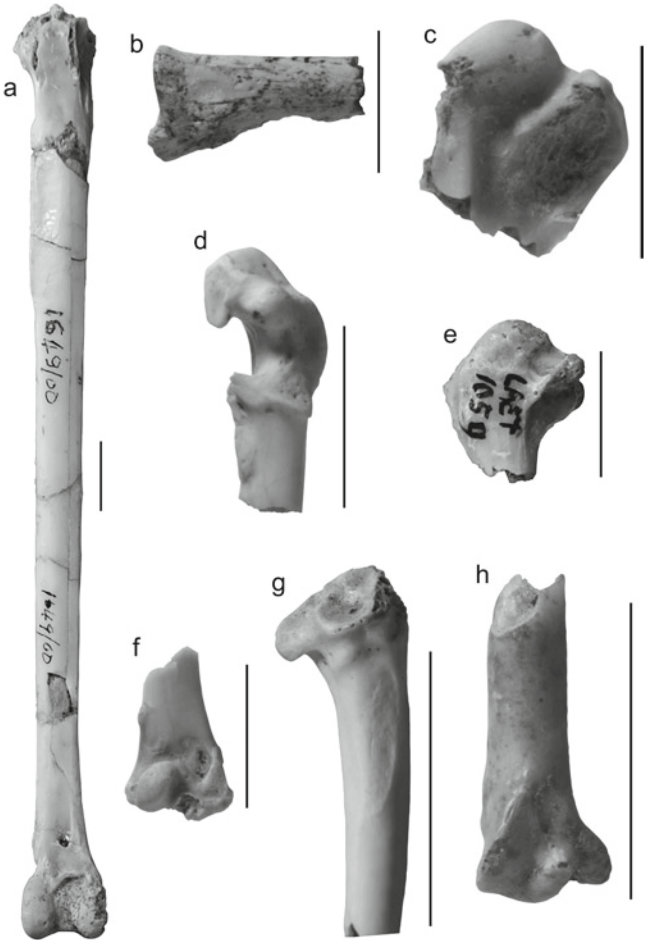

Fig. 18.6 (**a**) *Acryllium vulturinum*, complete r. tibiotarsus (EP 1649/00), in cranial view. (**b**) cf. *Acryllium vulturinum*, prox. frag. of l. pedal phalanx 1 of digit III (EP 711/00), in medial view. (**c**) Calidrinae indet., prox. l. humerus, incomplete (EP 298/01), in caudal view. (**d**) *Columba* sp., prox. r. coracoid, incomplete (EP 1103/03), in dorsal view. (**e**) *Streptopelia* sp., prox. l. humerus (LAET 75-1059), in caudal view. (**f**) *Streptopelia* sp., dist. r. humerus, incomplete (EP 2699/00), in cranial view. (**g**) *Streptopelia* sp., prox. r. ulna, incomplete (EP 728/05), in ventral view. (**h**) *Streptopelia* sp., dist. l. ulna (EP 1654/00), in ventral view. Scale bars are equal to 1 cm

Numididae indet. small

Material: prox. l. scapula, EP 480/03a; prox. l. humerus, LAET 74-183.

Measurements: see Tables 18.1 and 18.3.

Localities: EP 480/03a: Laetoli Loc. 3, Upper Laetolil Beds, between Tuffs 7 and 8; LAET 74-183: Laetoli Loc. 4, Upper Laetolil Beds, between Tuffs 6 and 8.

NR: 2.

Remarks: These two fossils correspond to one of the smaller guineafowl species in the genera *Numida*, *Guttera* or *Agelastes*.

cf. Numididae indet.

Material: dist. l. tarsometatarsus, EP 335/00.

Locality: Laetoli Loc. 8, Upper Laetolil Beds, between Tuffs 5 and 6.

NR: 1.

Remarks: As attested by its imperfectly fused metatarsi, and very fibrous surface, this distal tarsometatarsus belongs to a pullus (chick), and its morphology shows it is a Galliformes. It seems to be compatible with a pullus of a guineafowl. Although the taxon cannot be identified precisely, it is indicative that it was breeding at or near the locality.

Francolinus (Pternistis) sp. B/*Agelastes* sp.

Material: prox. l. coracoid, EP 192/05; dist. r. tibiotarsus, EP 301/03.

Measurements: see Tables 18.2 and 18.7.

Locality: Laetoli Loc. 16, Upper Laetolil Beds, between Tuff 7 and just above Tuff 8.

NR: 2.

Remarks: The coracoid could belong to a large *Pternistis* or *Agelastes*, while the tibiotarsus may belong to either a large *Pternistis*, *Guttera*, *Agelastes* or female *Afropavo*. They are from the same locality, and are assigned altogether here to *Francolinus (Pternistis)* sp. B/*Agelastes* sp.

Francolinus (Pternistis) sp. B/*Guttera* sp.

Material: dist. r. coracoid, LAET 75-2536; r. coracoid frag., EP 070/05; dist. r. femur, EP 944/01; dist. l. tibiotarsi, LAET 75-2134 and EP 1794/00; prox. l. tarsometatarsi, LAET 74-239, LAET 75-2304 and EP 510/01; prox. r. tarsometatarsus, LAET 75-1939.

Measurements: see Tables 18.2, 18.6–18.8.

Localities: LAET 75-1939, LAET 75-2134, LAET 75-2304 and LAET 75-2536: Laetoli Loc. 2, Upper Laetolil Beds, between Tuffs 5 and 7; EP 1794/00: Laetoli Loc. 2, Upper Laetolil Beds, between Tuffs 6 and 7; EP 510/01: Laetoli Loc. 2, Upper Laetolil Beds, between Tuffs 3 and 5; EP 944/01: Laetoli Loc. 7, Upper Laetolil Beds, above Tuff 7; LAET 74-239: Laetoli Loc. 8, Upper Laetolil Beds, between Tuff 5 and above Tuff 8; EP 070/05: Laetoli Loc. 11, Upper Laetolil Beds, between Tuff 7 and just above Tuff 8.

NR: 9.

Remarks: These remains correspond in size and proportions to a large *Pternistis* sp. or a small *Guttera* sp., such as *G. plumifera*, to the exclusion of other taxa. In addition, one distal tibiotarsus could also belong to *Agelastes* and one proximal tarsometatarsus to *Agelastes* or *Afropavo*. Given their occurrences in localities with more precisely identified remains, the most probable assignment for all these fossils is *Francolinus (Pternistis)* sp. B/*Guttera* sp.

Francolinus (Pternistis) sp. B/Numididae small

Material: prox. r. coracoid frags., EP 1987/03 and EP 1462/04; prox. and dist. l. coracoid, EP 480/03a; dist. r. coracoid, LAET 75-3548; wing phalanges 1 of major digit, EP 2241/00 and EP 370/04; synsacrum frags., EP 1671/00 and EP 2525/03; prox. l. femur, LAET 76-4141; dist. l. femurs, EP 485/01, EP 803/03 and EP 2039/03; possibly associated dist. l. tibiotarsus, tarsometatarsus frag. and pedal phalanx, LAET 76-3862a; dist. l. tibiotarsi, EP 1055/98, EP 1003/01, EP 1459/03, EP 1157/04 (frag.) and EP 069/05; dist. r. tibiotarsi, EP 614/03 and EP 804/03; prox. r. tarsometatarsus, EP 2765/00; dist. l. tarsometatarsi, LAET 75-2273 (lacking medial trochlea) and EP 3366/00 (lacking lateral trochlea); trochlea of dist. tarsometatarsus, EP 190/03; pedal phalanges, EP 1061/98 (prox. frag.), EP 574/01, EP 480/03a, EP 2461/03 (frags.), EP 2462/03, EP 366/04 (prox. frag.) and EP 728/04.

Measurements: see Tables 18.2, 18.6–18.8.

Localities: EP 2525/03: Laetoli Loc. 1NW, Upper Laetolil Beds, between Tuffs 6 and 8; EP 614/03: Laetoli Loc. 2, Upper Laetolil Beds, between Tuffs 3 and 5; LAET 76-3862a, EP 1671/00, EP 2765/00 and EP 480/03a: Laetoli Loc. 3, Upper Laetolil Beds, between Tuffs 4 and 8; EP 190/03: Laetoli Loc. 4, Upper Laetolil Beds, between Tuffs 7 and 8; EP 2039/03 and EP 1462/04: Laetoli Loc. 6, Upper Laetolil Beds, between Tuffs 5 and 7; EP 2241/00 and EP 1987/03: Laetoli Loc. 7, Upper Laetolil Beds, between Tuffs 5 and 7; LAET 75-3548, EP 1459/03, EP 366/04 and EP 370/04: Laetoli Loc. 8, Upper Laetolil Beds, between Tuff 5 and above Tuff 8; EP 485/01, EP 803/03 and EP 804/03: Laetoli Loc. 9, Upper Laetolil Beds, between Tuffs 5 and 8; EP 1055/98, EP 1061/98, EP 2461/03 and 2462/03: Laetoli Loc. 9S, Upper Laetolil Beds, below Tuff 2; EP 728/04: Laetoli Loc. 10, Upper Laetolil Beds, below Tuff 3; LAET 75-2273 and EP 574/01: Laetoli Loc. 10E, Upper Laetolil Beds, between Tuffs 5 and 8; LAET 76-4141, EP 1003/01 and EP 069/05: Laetoli Loc. 11, Upper Laetolil Beds, between Tuff 7 and above Tuff 8; EP 1157/04: Laetoli Loc. 13, Upper Laetolil Beds, between Tuffs 6 and 8; EP 3366/00: Laetoli Loc. 15, Upper Laetolil Beds, between Tuffs 6 and 7.

NR: 33.

Remarks: Seven of these fossils correspond in proportions and size to either larger *Francolinus (Pternistis)* like *F. (Pt.)* sp. B, or species of guineafowl in *Guttera* or *Agelastes* (five remains), or *Guttera*/*Numida* (two remains). In addition, EP 3366/00 (Loc. 15) and the tibiotarsus and tarsometatarsus LAET 76-3862a (Loc. 3) are only assignable to *Francolinus* or Numididae, and are juvenile.

Phasianidae indet./Numididae indet. medium/large

Material: prox. l. ulna, EP 480/03a.

Measurements: see Table 18.4.

Locality: Laetoli Loc. 3, Upper Laetolil Beds, between Tuffs 7 and 8.

NR: 1.

Remarks: This fossil corresponds to either *Acryllium*, *Afropavo*, a large *Numida meleagris* or a large *Guttera pucherani*.

Order Charadriiformes Huxley, 1867
Family Scolopacidae Vigors, 1825
Subfamily Calidrinae Reichenbach, 1849

Calidrinae indet.

Material: prox. l. humerus, EP 298/01 (Fig. 18.6c).

Measurements: depth of tuberculum ventrale: 5.5; depth of caput humeri: 3.2.

Locality: Laetoli Loc. 5, Upper Laetolil Beds, between Tuffs 6 and 8.

NR: 1; MNI: 1.

Remarks: On this proximal humerus of a Charadriiformes, the ventral border of the crista bicipitalis is very longitudinal, and the second (more proximo-dorsal) fossa tricipitalis is not very deep nor wide, a combination which, with general shape and other details, agrees with the family Scolopacidae and differs from other families (see also Strauch 1978). Among the genera of Scolopacidae, the depth of the second fossa tricipitalis in the fossil agrees with *Calidris* or *Philomachus*, whereas in *Gallinago*, *Tringa* and other related genera it is deeper. The fossil matches *Calidris* and *Philomachus* in every other morphological detail, and is tentatively attributable to either of these calidrine genera (subfamily Calidrinae). Among the genera of Scolopacidae occurring in Africa, only *Limicola* (*L. falcinellus*) was not seen, but it is closely related to *Calidris*. For instance, the fossil is compatible in size with *C. canutus* or *P. pugnax*. Being a single partial element, it is only referrable tentatively to Calidrinae indet.

This shorebird is indicative of the presence of either a river or lake shoreline with low or no vegetation or a marshy or humid grassland setting. Today, all of the species in the calidrine genera *Calidris*, *Philomachus* and *Limicola* occurring in subsaharan Africa, are long distance migrants in the non-breeding season, and they breed in the Palearctic. If it is confirmed, this record constitutes evidence of long distance bird migrations between the Palearctic and subsaharan Africa fully developed at 3.5–3.8 Ma. Such direct evidence exists from Olduvai Bed I in the latest Pliocene (ca. 1.8 Ma; Matthiesen 1990; Louchart 2008), and other, more indirect lines of evidence show that many long distance migrations were probably fully developed by the end of the Miocene (Louchart 2008).

Order Columbiformes Latham, 1790
Family Columbidae Illiger, 1811
Genus *Columba* Linnaeus, 1758

Columba sp.

Material: prox. r. coracoid, EP 1103/03 (Fig. 18.6d).

Measurements: proximal width: 7.1, proximal depth: 5.

Locality: Laetoli Loc. 10W, Upper Laetolil Beds, below Tuff 3.

NR: 1; MNI: 1.

Remarks: The proximal coracoid of *Columba* differs from that of *Streptopelia* and the other African dove genera in being generally stouter, in all views. In medial view, the facies articularis clavicularis is wider in *Columba*, and a more prominent extension is formed dorsally by the facies articularis scapularis. The flat extension of the processus procoracoideus is also wider dorso-ventrally in medial view. In lateral view, the facies articularis humeralis and the impressio ligamenti acrocoracohumeralis are again thicker dorso-ventrally in *Columba*. All these features allow this fossil to be identified as a member of the genus *Columba*. The element is fragmentary, but its size would agree approximately with some African species, such as *C. guinea*, *C. livia* or *C. albinucha*. It is assigned here to *Columba* sp. The different species in this genus live in Africa in a wide range of habitats, from primary forest, thickets, woodlands and savanna, to cliffs and rocky landscapes, or semi-arid open country environments.

Genus *Streptopelia* Bonaparte, 1855

Streptopelia sp.

Material: prox. l. humeri, LAET 75-554, LAET 75-1059 (Fig. 18.6e); prox. r. humerus, EP 927/03; dist. r. humerus, EP 2699/00 (Fig. 18.6f); prox. r. ulna, EP 728/05 (Fig. 18.6g); l. ulna lacking most of prox. end, EP 1654/00 (Fig. 18.6h); dist. r. ulna, EP 903/05; wing phalanx 1 of major digit, EP 661/04b; dist. l. femur, EP 344/03 (Fig. 18.7b); dist. r. femur, EP 1273/01; prox. l. tibiotarsus, EP 3092/00.

Measurements: humeri: see Table 18.14; ulnae: see Table 18.15; wing phalanx 1 of major digit EP 661/04b: length of pila cranialis part: 11.7, total length including the small flattened distal extension: 10.4, maximal width: 4.9; femur EP 344/03: distal width: 5.1, distal depth: 4.2, minimal width of shaft: 2.4; femur EP 1273/01: distal width: 4.6, distal depth: 3.7; tibiotarsus EP 3092/00: proximal width: 4.45, proximal depth without crista cnemialis cranialis: 5.1.

Localities: see Table 18.16.

NR: 11; MNI: 7.

Remarks: The genera *Streptopelia* and *Treron* have several species in Africa of similar size. Some differences in skeletal morphology can be used here to distinguish between these genera. On the proximal humerus, the base (distal) of the crista bicipitalis, where it attaches to the shaft, forms a much more convex curve (with a shorter radius of curvature) in *Streptopelia* and other doves than in *Treron* (in caudal or cranial view). On the proximal ulna, the processus cotylaris dorsalis is more protruding, much more dorsally i.e., straight and orthogonal to the shaft (rather than recurving distally), and is narrower in *Treron* than in *Streptopelia* and other doves. With these main differences it is possible to assign the fossils to *Streptopelia*. The species in *Oena* and *Turtur* all have much smaller and generally more slender skeletal elements than *Streptopelia*. Among the species in *Streptopelia*, the fossils appear slightly smaller than *S. roseogrisea* (*n* = 2) and *S. decipiens* (*n* = 1), but larger than *S. senegalensis* (*n* = 1) and *S. capicola* (*n* = 1). They are also much smaller than *S. semitorquata* (*n* = 1). Given the intraspecific variability in size in these species, as seen from body weights for instance (Dunning 1993), the fossils could correspond to species the size of *S. capicola* or *S. turtur*. They are assigned here to *Streptopelia* sp.

Habitats vary considerably within and between species in *Streptopelia*, covering almost all kinds of landscapes. However, they all require a minimum of trees or bushes, that are at least scattered.

Columbidae indet. (sp. C)

Material: dist. r. humerus, LAET 76-18-651.
Measurements: see Table 18.14.
Locality: Laetoli Loc. 18 (trench 1), Upper Ndolanya Beds.
NR: 1; MNI: 1.

Remarks: This distal humerus is difficult to assign to a genus, but its size suggests an additional species, larger than *Streptopelia* sp. and much smaller than *Columba* sp. described above; it would approach the size of *S. roseogrisea*.

cf. Columbidae indet.

Material: prox. l. coracoid frag., EP 138B/01.
Measurements: minimal width of corpus: 2.3.
Locality: Laetoli Loc. 6, Upper Laetolil Beds, between Tuffs 5 and 6.
NR: 1.

Remarks: This fragmentary fossil is only tentatively assignable to Columbidae indet., although it matches the size of *Streptopelia* sp. above, for instance.

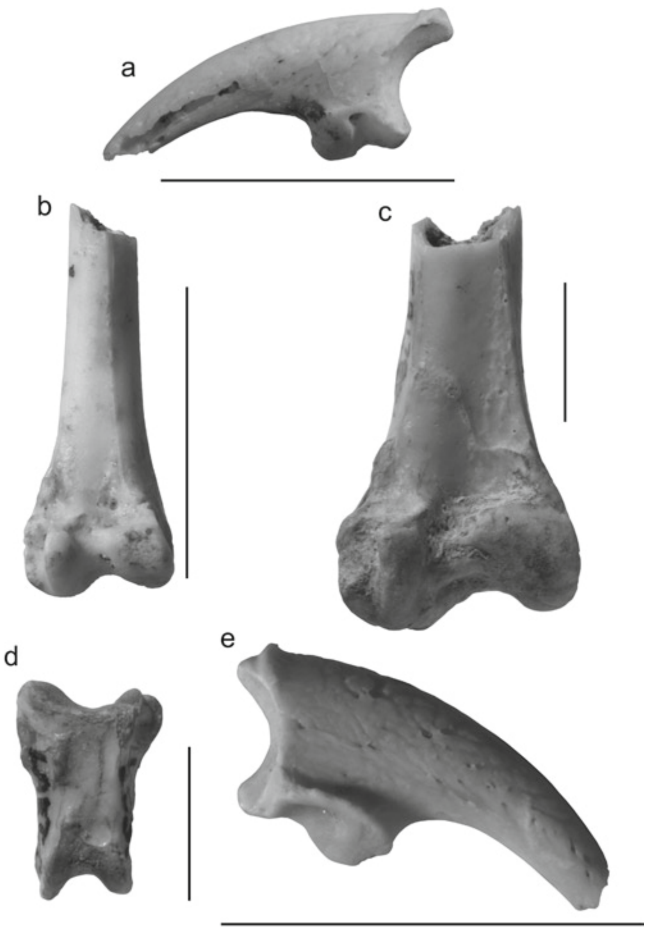

Fig. 18.7 (**a**) *Tyto* sp., r. pedal phalanx 2 of digit I (EP 2230/03), in medial view. (**b**) *Streptopelia* sp., dist. l. femur (EP 344/03), in caudal view. (**c**) *Bubo* cf. *lacteus*, dist. l. femur (EP 1788/03), in caudal view. (**d**) *Bubo* cf. *lacteus*, l. pedal phalanx 1 of digit II (LAET 75-2534), in dorsal view. (**e**) *Asio* sp., pedal phalanx 3 of digit II (EP 520/04), in lateral view. Scale bars are equal to 1 cm

Table 18.14 Measurements (mm) of the humeri of Laetoli Columbidae and of modern species for comparison

Taxon		Total length	Proximal width	Distal width	Distal depth	Minimal width of shaft
Fossil	*Streptopelia* sp.		9.8–10.4 (2)	7.9 (1)		~3.2 (1)
	Columbidae indet. (sp. C)			8.9 (1)	5.2 (1)	
Modern	*Columba guinea* M	48.1 (1)	14.9 (1)	11.2 (1)	7.8 (1)	5.2 (1)
	Streptopelia senegalensis M	26.9 (1)	8.3 (1)	6.65 (1)		3.1 (1)
	S. decipiens M	36.9 (1)	11.6 (1)	8.85 (1)	5.55 (1)	5.35 (1)
	Streptopelia capicola	27.2 (1)	8.25 (1)	6.4 (1)		2.8 (1)
	Streptopelia semitorquata	43.0 (1)	13.6 (1)	10.15 (1)	6.3 (1)	4.7 (1)
	S. roseogrisea	34.0 (1)	11.3 (1)	8.35–8.8 (2)	5.2–5.5 (2)	4.3 (2)
	Turtur abyssinicus	25.2 (1)	7.55 (1)	6.2 (1)	3.9 (1)	2.8 (1)
	Turtur afer	24.4–24.7 (2)	7.65–7.9 (2)	5.8–6.05 (2)	3.55–3.75 (2)	2.75–2.9 (2)
	T. tympanistria	25.3–26.5 (2)	7.85–8.5 (2)	6.4–6.7 (2)	3.8–3.95 (2)	2.75–3.4 (2)
	Oena capensis	21.9 (1)				2.35 (1)
	Treron waalia	40.0 (1)	12.2 (1)	9.9 (1)	6.3 (1)	4.4 (1)
	Treron australis M	37.2 (1)	11.4 (1)	8.5 (1)	5.7 (1)	3.85 (1)

Ranges are provided, followed by number of specimens in parentheses
M male

Table 18.15 Measurements (mm) of the ulnae of Laetoli Columbidae and of modern species for comparison

Taxon		Total length	Proximal width	Distal width	Orthogonal distal depth	Greatest diagonal distal depth	Minimal width of shaft
Fossil	*Streptopelia* sp.		4.7 (1)	~4.2–4.4 (2)	4.35–4.4 (2)	~4.7–5.0 (2)	
Modern	*Columba guinea* M	55.7 (1)		6.6 (1)	6.9 (1)	7.7 (1)	3.65 (1)
	Streptopelia senegalensis M	32.25 (1)					2.2 (1)
	Streptopelia decipiens M	43.0 (1)	6.1 (1)	4.85 (1)	5.15 (1)	5.45 (1)	2.8 (1)
	Streptopelia semitorquata	49.8 (1)					3.25 (1)
	Streptopelia roseogrisea	42.2 (1)	5.6 (1)			5.55 (1)	2.85 (1)
	Turtur abyssinicus			3.6 (1)	3.4 (1)	3.8 (1)	2.0 (1)
	Treron waalia	47.5 (1)					2.9 (1)
	Treron australis M	43.35 (1)	5.8 (1)	4.7 (1)	4.7 (1)	5.3 (1)	2.75 (1)

Ranges are provided, followed by number of specimens in parentheses

M male

Table 18.16 Localities comprising fossils assigned to *Streptopelia* sp.

Specimen(s)	Locality	Unit	Horizon
EP 2699/00	Laetoli Loc. 2	Upper Laetolil Beds	Between Tuffs 5 and 7
EP 1654/00, EP 344/03, EP 661/04b, EP 728/05	Laetoli Loc. 3	Upper Laetolil Beds	Between Tuffs 7 and 8
EP 3092/00	Laetoli Loc. 5	Upper Laetolil Beds	Between Tuffs 3 and 5
EP 1273/01	Laetoli Loc. 9S	Upper Laetolil Beds	Below Tuff 3
LAET 75-554	Laetoli Loc. 10	Upper Laetolil Beds	Between Tuff 3 and below Tuff 1
EP 927/03, EP 903/05	Laetoli Loc. 10E	Upper Laetolil Beds	Between Tuffs 5 and 7
LAET 75-1059	Laetoli Loc. 7E	Upper Ndolanya Beds	

Order Strigiformes Wagler, 1830
Family Tytonidae Ridgway, 1914
Genus *Tyto* Billberg, 1828

Tyto sp.

Material: r. pedal phalanx 2 of digit I, EP 2230/03 (Fig. 18.7a).

Measurements: maximal height of proximal (articular) end including the processus flexorius: 6.6; height of prox. (articular) end without the processus flexorius: 5.1; width of articular part of proximal end (without the lateral and medial bony extensions): 3.15.

Locality: Laetoli Loc. 7, Upper Laetolil Beds, between Tuffs 7 and 8.

NR: 1; MNI: 1.

Remarks: This claw of pedal digit I is diagnostic of the family Tytonidae and genus *Tyto* among Strigiformes (see Louchart 2002), including being very compressed mediolaterally at the articular extremity with a processus flexorius with relatively little prominence. Among the two (or three if *'Phodilus' prigoginei* belongs to *Tyto* as suggested by König and Weick 2008) barn-owls s.l. living in Africa today, pedal phalanges of *T. alba affinis* (the subsaharan subspecies) and *T. capensis* differ only by size, while *'P.' prigoginei* is a much smaller species. Compared to the fossils, the measurements for *T. alba affinis* ($n=3$ including male and female) are 6.6–7.1; 4.6–5.0; 2.65–2.75, respectively. Other subspecies of *T. alba* from Europe and North Africa are smaller than *affinis*, including the pedal phalanges (see Louchart 2002). For *T. capensis* one unsexed individual measured 7.2; 5.0; 3.1. The fossil is intermediate between these two modern species in dimensions. The first of these three measurements is more variable individually than the others, and it depends on the prominence of the processus flexorius, which is, perhaps, related in part to the sex of the individuals. The other measurements would suggest that the fossil is closer to *T. capensis*, especially the proximal width. However, because it is only a single claw, it is better to identify it as *Tyto* sp.

Today, the natural habitats of the Barn-owl (*T. alba*) in Africa range from woodlands to deserts, and they nest and roost in cliffs, caves of hollow trees. The Grass-owl, *T. capensis*, lives in marshes and tall grasslands, both open habitats.

Family Strigidae Vigors, 1825
Genus *Bubo* Duméril, 1806

Table 18.17 Measurements (mm) of the pedal phalanx 1 of digit II of Laetoli *Bubo* cf. *lacteus* and of modern species for comparison

Taxon		Total length	Proximal width	Proximal depth	Distal width	Distal depth	Minimal width of corpus
Fossil	*Bubo* cf. *lacteus* (probable M)	14.6 (1)	9.9	7.8	~6.7	~6.3	6.6
Modern	*Bubo capensis* (1 M, 1 unsexed)	12.5–14.1 (2)	8.6–9.85 (2)	7.7–8.9 (2)	5.8–7.0 (2)	6.0–6.4 (2)	5.45–6.6 (2)
	B. africanus (2 F, 2 M)	9.9–11.8 (4)	7.0–7.7 (4)	5.7–6.7 (4)	4.5–5.0 (4)	4.6–5.2 (4)	4.2–5.0 (4)
	B. lacteus (probable F)	19.1 (1)	11.3 (1)	9.6 (1)	8.0 (1)	7.55 (1)	6.5 (1)

Ranges are provided, followed by number of specimens in parentheses

F female, *M* male

Bubo cf. *lacteus* (Temminck, 1820)

Material: dist. l. femur, EP 1788/03 (Fig. 18.7c); l. pedal phalanx 1 of digit II, LAET 75-2534 (Fig. 18.7d).

Measurements: femur EP 1788/03: distal width: 17.8, distal depth: 13.6; pedal phalanx 1 of digit II LAET 75-2534: see Table 18.17.

Localities: LAET 75-2534: Laetoli Loc. 2, Upper Laetolil Beds, between Tuffs 3 and 7; EP 1788/03: Laetoli Loc. 22, Upper Laetolil Beds, between Tuffs 2 and 7.

NR: 2; MNI: 2.

Remarks: The distal femur belongs to the Strigidae and differs from the Tytonidae because, for instance, the condylus lateralis on the cranial side of the bone forms a marked indentation at the proximal insertion on the shaft (in lateral view); and because in caudal view the edges of the shaft form an indentation on each side due to an abrupt enlargement at the insertion of the distal epiphysis (in Tytonidae the transition is more progressive) (see Louchart 2002). Within the Strigidae, the fossil matches *Bubo*, and differs slightly from the close (sub)genus *Ketupa* – König and Weick (2008) consider all species of *Ketupa* as members of *Bubo*. In *K. zeylonensis*, compared with *B. bubo*, the condylus lateralis appears less extended laterally and the space between it and the condylus medialis relatively reduced, in distal view the sulcus between the two condyli on the caudal side is shallower, and in medial view the proximal insertion of the condylus medialis on the cranial side of the shaft forms a better marked indentation. The femur can, therefore, be assigned to *Bubo* (subgenus *Bubo*). Among the species in *Bubo*, the femur is apparently larger than in *B. capensis*. In three modern *B. capensis*: the distal width is 14.9–16.8 ($n=3$; the smallest, a male; the largest unsexed, but probably a female – in *Bubo* as in most Strigiformes females are larger than males); and the distal depth is 11.0–12.8 ($n=3$; the smallest the male, the largest the other unsexed individual). The fossil distal femur matches, for instance, *B. ascalaphus* or males of populations of small *B. bubo* (Louchart 2002). In *B. africanus* it is much smaller (e.g., Brodkorb and Mourer-Chauviré 1984). The extinct species *B. leakeyae* (latest Pliocene of Olduvai Bed I) is also much smaller, being similar in size to *B. africanus* but with a larger coracoid (Brodkorb and Mourer-Chauviré 1984). For *B. lacteus*, the largest African eagle-owl, only one specimen could be examined, and it is presumably a female (as compared with measurements of a female in Brodkorb and Mourer-Chauviré 1984, and considering that there is apparently no overlap in this species between the females and the much smaller males; see König and Weick 2008). Its femur distal width is 20.2, and distal depth is 16.4. Since these dimensions of the femur, within the single genus *Bubo*, are closely linked to body weight (see Campbell and Marcus 1992), the match with *B. ascalaphus* or small *B. bubo* indicates a body weight around 2.0–2.2 kg for the fossil species. This could correspond to a male *B. lacteus*, and be larger than *B. capensis*.

The pedal phalanx (distinctive among Strigidae by its size and robustness) is also larger than in *B. capensis* in length and proximal width (Table 18.17). In *B. africanus* all measurements are much smaller. In the probably female individual of *B. lacteus* they are larger, but again, the fossil would presumably be compatible with a male *B. lacteus*. In addition, the fossil phalanx is larger and more robust than in *B. ascalaphus* and small individuals of *B. bubo* (Louchart 2002).

Together, the femur and the phalanx therefore correspond most probably with *B. lacteus* (male size). *Bubo vosseleri*, endemic in East Tanzania, is smaller than *B. capensis*, as are the other African *Bubo* species, except *B. shelleyi*. The latter species, living today in equatorial forests of West and Central Africa, cannot be excluded because it is intermediate in size between *B. capensis* and *B. lacteus* (König and Weick 2008). However, because it is less likely on biogeographical grounds, the fossils are identified here, tentatively, as *B.* cf. *lacteus*.

The fossil owl might represent the direct ancestor of *B. lacteus*. It is tentatively the earliest fossil record for this lineage, and also the earliest record for the genus *Bubo* in Africa. *Bubo* cf. *lacteus* was also identified from the latest Pliocene of Olduvai Bed I, Tanzania (Brodkorb and Mourer-Chauviré 1984).

Today *B. lacteus*, the Giant Eagle-owl, is widespread, although locally rare and endangered, in most of subsaharan Africa, including Tanzania. It lives in habitats from dry savanna with scattered trees and thorny shrubs, and semi-desert, to semi-open woodland and riverine forest with adjacent savanna. It is very eclectic as a predator, but feeds mainly on medium-sized mammals and other vertebrates.

Genus *Asio* Brisson, 1760
Asio sp.

Material: Pedal phalanx 3 of digit II, EP 520/04 (Fig. 18.7e).

Measurements: maximal height of proximal (articular) end including the processus flexorius: 5.6; height of prox. (articular) end without the processus flexorius: 4.0; width of articular part of proximal end (without the lateral and medial bony extensions): 3.0.

Locality: Laetoli Loc. 1, Upper Laetolil Beds, between Tuffs 7 and 8.

NR: 1; MNI: 1.

Remarks: This claw of digit II belongs to the Strigidae, and differs from the Tytonidae by, among others, wider articular surface relative to height. It is identical in all proportions to the homologous phalanx of *Asio*, and matches the size of *A. capensis* (homologous measurements in one male: 5.45, 4.0, 2.8). *Asio capensis* is common and widespread today in most of subsaharan Africa, including Tanzania. The similar-sized *A. flammeus* occurs only further north, while the also similar-sized *A. abyssinicus* is endemic to the area of the East African rift (in Ethiopia, Kenya, Uganda and Democratic Republic of the Congo). The phalanx could belong to either of these species, an ancestor or a closely related extinct lineage of *Asio*. It is identified here as *Asio* sp.

Depending on the species, *Asio* owls live in habitats ranging from forest to open grassland or marshes, among others, and this fossil provides little information regarding the environment.

cf. Strigidae (sp. C)

Material: prox. l. tibiotarsus, EP 3091/00.

Measurements: proximal width without crista cnemialis lateralis: 6.3 e, proximal depth without crista cnemialis cranialis: 6.3 e.

Locality: Laetoli Loc. 5, Upper Laetolil Beds, between Tuffs 3 and 5.

NR: 1; MNI: 1.

Remarks: This fragmentary proximal tibiotarsus with broken edges is difficult to identify, but the best match seems to be among the small Strigidae. It resembles, although with very slight differences in details and proportions, either *Athene*, *Glaucidium* or *Taenioglaux* (sensu König and Weick 2008). It corresponds in size to species of *Athene* or *Taenioglaux*, and is a different species from the other owls of Laetoli. It is assigned here to cf. Strigidae (sp. C).

cf. Strigiformes indet.

Material: prox. l. humerus frag., LAET 76-7E-28; distal l. humerus frag., EP 1458/03.

Localities: EP 1458/03: Laetoli Loc. 8, Upper Laetolil Beds, between Tuffs 5 and 7; LAET 76-7E-28: Laetoli Loc. 7E, Upper Ndolanya Beds (trench 1, step D).

NR: 2.

Remarks: These fragmentary humeri could only possibly belong to the Strigiformes. The proximal fragment belongs to a medium sized species, the distal fragment belongs to a smaller one.

Order Coliiformes Murie, 1872
Family Coliidae Swainson, 1837
Genus *Colius* Brisson, 1760

Colius sp.

Material: dist. l. ulna, EP 687/03 (Fig. 18.8a); dist. r. ulna, EP 1356/04.

Measurements: ulna EP 687/03: distal width: 2.4, orthogonal distal depth: 2.7, greatest diagonal distal depth: 2.9, minimal width of shaft: 1.3; ulna EP 1356/04: distal width: 2.3, greatest diagonal distal depth: 2.8 e.

Localities: EP 687/03: Laetoli Loc. 2, Upper Laetolil Beds, between Tuffs 5 and 7; EP 1356/04: Laetoli Loc. 5, Upper Laetolil Beds, between Tuffs 3 and 5.

NR: 2; MNI: 2.

Remarks: These distal ulnae conform to the morphological characteristics of the distinctive family Coliidae (see Rich and Haarhoff 1985; Haarhoff 1993). Several characters, among those listed by the latter authors, can be used here to assign these fossils to one or the other of the two modern genera

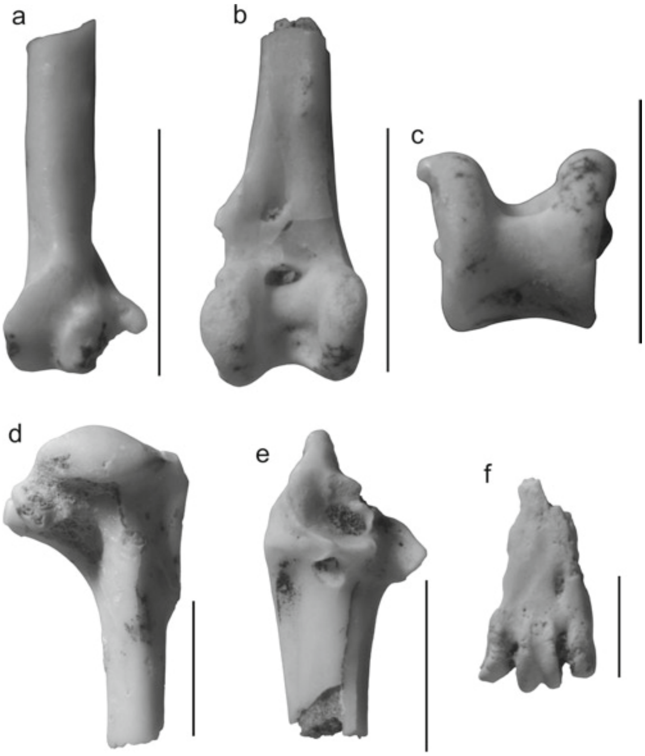

Fig. 18.8 (**a**) *Colius* sp., dist. l. ulna (EP 687/03), in ventral view. (**b**–**c**) Coliidae indet., dist. r. tibiotarsus (EP 1004/05), in cranial view (**b**) and distal view (**c**). (**d**) cf. Passerida indet., prox. r. humerus (EP 1283/04), in caudal view. (**e**) Oscines indet., prox. l. ulna (EP 1102/04), in ventral view. (**f**) Passeriformes indet., dist. l. tarsometatarsus (EP 158/03), in dorsal view. Scale bars are equal to 0.5 cm

Colius and *Urocolius*. The carpal tuberosity is more rounded in *Colius* than in *Urocolius* (in dorsal aspect), the condylus ventralis ulnaris is generally smaller relative to condylus dorsalis ulnaris in *Colius* than in *Urocolius*, and the condylus dorsalis ulnaris is rounded at base of shaft in *Colius* in dorsal or ventral view (whereas it tapers to a point at the base of shaft in *Urocolius*) (Haarhoff 1993). These features in the two fossil ulnae are of the *Colius* type. They can be assigned, therefore, to the genus *Colius*, and their size points to a single species. In *C. colius* the following measurements on the distal ulna (homologous to those taken on the fossils) are: greatest diagonal distal depth: 2.5–2.9 ($n=21$), minimal width of shaft: 1.0–1.3 ($n=18$); in *C. striatus* respectively: 2.6–3.2 ($n=53$), 1.1–1.7 ($n=51$); in *C. leucocephalus* respectively: 2.9 ($n=1$), 1.3 ($n=1$) (Haarhoff 1993); and in the extinct *C. hendeyi* (early Pliocene of Langebaanweg, South Africa) the greatest distal depth is 2.4–3.0 ($n=11$) (Rich and Haarhoff 1985). It appears that the two fossil distal ulnae dimensions fall within the range of either of these species. Hence, they cannot be assigned to species, but only to *Colius* sp.

Extant Coliiformes are today endemic in Africa. Mousebirds in the genus *Colius* (four extant species) live in diverse habitats, from forest edges and woodland to more open environments with bushes or scrubs, or even semi-desert, but always with at least scattered trees or bushes. Coliidae are essentially frugivorous.

Coliidae indet.

Material: dist. r. tibiotarsus, EP 1004/05 (Fig. 18.8b, c).

Measurements: distal width: 3.4, distal depth: 3.0.

Locality: Laetoli Loc. 2S, Upper Laetolil Beds, between Tuffs 5 and 7.

NR: 1; MNI: 1.

Remarks: This distal tibiotarsus shows the diagnostic features of the Coliidae (see Rich and Haarhoff 1985; Haarhoff 1993), but it bears no distinctive features to distinguish between the genera *Colius* and *Urocolius*. Since its dimensions are compatible with modern species in both genera (Rich and Haarhoff 1985; Haarhoff 1993), it can be assigned to Coliidae indet. only. However, it is larger than the largest specimen of the extinct *C. hendeyi* (see above). It is possible that it represents the same species as *Colius* sp. from Laetoli described above, since it is compatible in size, and therefore does not constitute evidence for an additional mousebird.

Order Passeriformes Linnaeus, 1758
Suborder Oscines (sensu Ericson et al. 2002)
Parvorder Passerida Sibley et al., 1988

cf. Passerida indet.

Material: prox. r. humerus, EP 1283/04 (Fig. 18.8d).

Measurements: proximal width: 7.0, minimal width of shaft: 2.2.

Locality: Laetoli Loc. 10E, Upper Laetolil Beds, between Tuffs 5 and 8.

NR: 1; MNI: 1.

Remarks: This small proximal humerus of a passerine displays a deep double fossa tricipitalis, which is characteristic for the Passerida. Within this extremely diverse group, characters are lacking here for precise identification. This species is about the size of a sparrow, for instance.

Passeriformes Oscines indet.

Material: prox. l. ulna, EP 1102/04 (Fig. 18.8e).

Measurements: proximal width: 4.6.

Locality: Laetoli Loc. 11, Upper Laetolil Beds, between Tuffs 7 and 8.

NR: 1.

Remarks: This proximal ulna belongs to an Oscines because the tuberculum ligamenti collateralis ventralis is not protruding ventrally as in the Suboscines. It corresponds to a bird the size of a sparrow, like the humerus above, and there are no indications whether it corresponds or not to the same species.

Passeriformes indet.

Material: dist. l. humerus, EP 1106/03; dist. l. tarsometatarsus, EP 158/03 (Fig. 18.8f).

Measurements: humerus EP 1106/03: distal width: 5, minimal width of shaft: 1.8; tarsometatarsus EP 158/03: distal width: 5.8, distal depth: 3.9.

Localities: EP 158/03: Laetoli Loc. 17, Upper Laetolil Beds, between Tuff 7 and Yellow Marker Tuff; EP 1106/03: Laetoli Loc. 10W, Upper Laetolil Beds, below Tuff 3.

NR: 2.

Remarks: These two remains are not sufficiently diagnostic for more precise assignment within the Passeriformes. They correspond to one or two species roughly the size of a sparrow.

Aves indet.

Twenty fossil parts remain unidentified, being too fragmentary. They come from almost all the localities of the Upper Laetolil Beds. Almost all represent medium sized birds, often the size of the abundant francolins or guineafowl. A few of these bones are juvenile (from Locs. 2, 8 and 16). Two others (pedal phalanges) bear exostoses (Locs. 10W and 10E).

Discussion

With at least 21 different taxa in 11 families (Table 18.18), the fossil bird assemblages from Laetoli provide important new information. Most of them are similar to and closely related to extant species, and probably represent these same species or their direct ancestors. The two francolin species show differences with the species examined in the different subgenera, but the fossils are too fragmentary or isolated to

Table 18.18 Occurrences of the fossil bird taxa in the main stratigraphic units at Laetoli

Family	Taxon	Lower Laetolil Beds	Upper Laetolil Beds	Upper Ndolanya Beds
Ardeidae (herons)	**cf. *Ardea* sp.**			1 (1)
Accipitridae (Old World vultures, eagles, hawks etc.)	***Aegypius* sp.**		1 (1)	
	cf. *Buteo* sp.		1 (1)	
	Aquilini indet. sp. A		1 (1)	
	cf. Aquilini indet. sp. B		1	
Falconidae (falcons)	***Falco* cf. *eleonorae***			1 (1)
	Falconiformes indet.		2	
Phasianidae (gamefowl)	***Francolinus* sp. A aff. *F. (Peliperdix) sephaena***		34 (16)	7 (3)
	***Francolinus (Pternistis)* sp. B**		67 (23)	3 (1)
	Francolinus sp. ? A/B		9	1
	cf. *Francolinus* sp. indet.		3	
Numididae (guineafowl)	**cf. *Agelastes* sp.**		2 (1)	
	cf. *Agelastes/Guttera* sp.		3	
	***Numida/Guttera* sp.**	1	9	1
	Acryllium vulturinum		2 (2)	
	Numididae indet. small		2	
	cf. Numididae indet.		1	
	Francolinus (*Pternistis*) sp. B/*Agelastes* sp.		2	
	Francolinus (*Pternistis*) sp. B/*Guttera* sp.		9	
	Francolinus (*Pternistis*) sp. B/Numididae small		33	
	Phasianidae indet./Numididae indet. medium/large		1	
Scolopacidae (snipes, sandpipers, stints etc.)	**Calidrinae indet.**		1 (1)	
Columbidae (pigeons and doves)	***Columba* sp.**		1 (1)	
	***Streptopelia* sp.**		10 (6)	1 (1)
	Columbidae indet. (sp. C)			1 (1)
	cf. Columbidae indet.		1	
Tytonidae (barn-owls)	***Tyto* sp.**		1 (1)	
Strigidae (owls)	***Bubo* cf. *lacteus***		2 (2)	
	***Asio* sp.**		1 (1)	
	cf. Strigidae (sp. C)		1 (1)	
	cf. Strigiformes indet.		1	1
Coliidae (mousebirds)	***Colius* sp.**		2 (2)	
	Coliidae indet.		1 (1)	
Passeriformes (songbirds)	**cf. Passerida indet.**		1 (1)	
	Oscines indet.		1	
	Passeriformes indet.		2	

Taxa in bold characters are the different taxa; other taxa or groups may correspond to one of the taxa in bold; the number of different taxa is therefore the number of taxa in bold. For a taxon, the numbers provided are the number of remains (NR) followed by the minimum number of individuals (MNI) in parentheses

allow assignment to extinct species. In addition, more of the modern species of francolins would need to be examined, but even then it will be difficult to reach more precise identifications because of great overlap in skeletal morphology and size between modern species of francolins. Some of the taxa from Laetoli represent the earliest record known for several genera or species worldwide (i.e., *Falco* cf. *eleonorae*, *Acryllium vulturinum*, *Streptopelia* sp., *Bubo* cf. *lacteus*), or at least in Africa (i.e., *Columba* sp., *Bubo*, *Asio* sp.).

Compared with the earlier study by Watson (1987), the present analysis provides more precise identifications and evidence for more bird taxa, benefiting from both larger fossil collection and comparison with enlarged modern samples. In addition, some attributions differ from those of Watson. These include the assignment of some francolin fossils to the smaller or the larger species. Also, the identification of guineafowl fossils as *Numida* by Watson (1987) is revised here with caution, because he apparently did not take into account all genera and species of guineafowl, and it appears that these fossils could belong to *Numida* or alternatively to *Guttera* (*G. pucherani* for instance).

In terms of biogeography and distributions, all the genera and species recognized here (with the exception of cf. *Agelastes*), occur today in East Africa, including Tanzania. This is in contrast to some of the earlier Mio-Pliocene localities in East or Central Africa, in which the bird faunas include extinct taxa, as well as modern taxa that occur today in South Asia for instance, but no longer in Africa (Louchart et al. 2008).

Considering the three main stratigraphic units, some differences in composition deserve highlighting. The single avian bone from the Lower Laetolil Beds belongs to a guineafowl, either *Numida* or *Guttera* sp. Then, 93% of the fossils derive from the Upper Laetolil Beds. Yet the remaining fossils, from the Upper Ndolanya Beds, contain two interesting species not represented in the Upper Laetolil Beds – the heron and the falcon – as well as the Columbidae sp. C. In addition, the relative proportion of fossils and individuals of the smaller species of francolin vs. the larger one differ between the Upper Laetolil Beds and the Upper Ndolanya Beds. The smaller francolin species is relatively better represented in the more recent Upper Ndolanya Beds. It is unclear, however, whether this can be attributed to a taphonomic bias or a paleoenvironmental difference, and the ecological requirements of these francolins are insufficiently known.

In terms of composition of the assemblages, the dominant birds are francolins (50% of the bird remains), followed by guineafowl (9%; NB: in addition 18% are less precisely identifiable and are either francolin or guineafowl), and then followed by doves (4.5%), and all the other taxa.

These relative abundances are similar when considering only the Upper Laetolil Beds localities. Some of the identifications remain tentative (such as for guineafowl), so that the different Galliformes represented yield little paleoenvironmentally relevant information. All guineafowl and francolins need at least a few trees or bushes, as do the doves and the mousebirds. In addition, *Acryllium vulturinum* indicates the presence of semi-open thornscrub or grassland with trees and bushes. The different birds of prey (diurnal and nocturnal) are indicative of the presence of open or semi-open habitats on the landscape where they tend to hunt, while they roost either in trees or on cliffs or rocky outcrops with crevices. The absence of confirmed taxa restricted to woodland or forest can be explained by the likely taphonomic origins of the bird fossils. They belong to small and medium-sized birds, which were the potential prey of owls, eagles or hawks, including those represented in the assemblage. The bird remains are likely to derive from predation by birds of prey, and possibly also mammalian carnivores, and the skeletal parts are probably the remains left behind after the prey has been eaten, or through owl regurgitation pellets. A taphonomic analysis would help testing this hypothesis. Since such birds of prey tend to hunt in rather open landscapes, birds that prefer these habitats may be over-represented, and forest birds may be absent, considering the limited number of fossils collected. The calidrine wader reveals the presence of an aqueous setting (i.e., marsh, humid grassland), or a lake or river shore, open or forested. Similar observations also apply to the birds represented in the Upper Ndolanya Beds (except that *Acryllium*, among others, is not represented). The heron indicates the presence of standing water or a stream.

The dominance of terrestrial birds (vs. water birds or shore birds) is in contrast to the bird faunas at many Miocene and Pliocene African localities, but similar for instance – considering rich bird assemblages – to Langebaanweg (early Pliocene, ca. 5 Ma, South Africa; Rich 1980), Aramis (early Pliocene, 4.4 Ma, Ethiopia; Louchart et al. 2009) and Ahl Al Oughlam (late Pliocene, ca. 2.5 Ma, Morocco; Mourer-Chauviré and Geraads 2008).

Prints and trails of birds were recorded at Laetoli, and assigned to ostriches, guineafowl, francolins, a bustard and other birds (Leakey 1987; Harrison 2005). Prints of guineafowl appeared more numerous than those of francolins (the opposite of skeletal remains), but the overlap in size between small and medium sized guineafowl and large francolins means that some of the tracks assigned to guineafowl might be those of large francolins. In addition, the processes involved in the fossilization of tracks and bones depend on a number of different factors, many of which could influence their preservation in contrasting ways. These records should be interpreted with caution in any attempt to determine the relative abundance of species in the past communities.

The skeletal remains may have implications regarding the identification of some fossil eggs. Harrison (2005) studied the eggs other than ostrich eggshells, identified as belonging to at least five different species. Among them, are at least two species of francolins, which likely correspond to the two species identified from fossil bones, a guineafowl and a larger bird the size of a bustard. The guineafowl eggs are assigned to *Numida*, which, if confirmed, may allow to consider that the fossil bones assigned here to *Guttera/Numida* sp. would also be more likely to represent the latter genus. The skeletal remains alone do not permit the generic assignment. Last, the large egg, as suggested by Harrison (2005) as a possibility, might correspond to *Acryllium vulturinum*, now it is recorded as fossil, and further comparisons may yield a firmer identification for this egg. Among the localities with eggs of Galliformes, Loc. 10E is interesting because it yielded eggs of guineafowl, and fossil bones of most of the galliform taxa represented, yet among confirmed guineafowl it comprises the two bones assigned to cf. *Agelastes* sp. It would be interesting to check whether some of the eggs might prove similar to those of the species in this genus, which would be a critical taxon in terms of paleoenvironment.

A few of the fossil bones belong to juvenile individuals (i.e., with fibrous cortical surface, imperfectly fused epiphyses). In addition to a few Aves indet. being juvenile, the pedal phalanx tentatively assigned to *A. vulturinum* may be immature, two bones of *Francolinus* sp. B (larger sp.) are immature, three bones identified as either large francolin or guineafowl are juvenile, and one bone identified as cf. Numididae indet. belongs to a pullus (chick). The bones of juveniles and immatures derive from diverse localities of the Upper Laetolil Beds. They are indicative of breeding activity of the species near the locality, especially for the probable guineafowl pullus.

Most of the birds were likely resident species (e.g., francolins, guineafowl), but two were probably passage or wintering migrants from the Palearctic region (the falcon *F.* cf. *eleonorae* and the calidrine wader).

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Appendix: List of the Modern Comparative Osteological Specimens Examined

Ardeidae: *Botaurus stellaris* LAC 2005.1629, UCBL 32.1, UCBL 32.2; *Ixobrychus minutus* UCBL 31.1 to UCBL 31.7; *Nycticorax nycticorax* LAC 1997.210, UCBL 30.1 to UCBL 30.3; *Butorides striatus* LAC (1indiv.); *Ardeola ralloides* UCBL 28.1 to UCBL 28.5; *Bubulcus ibis* UCBL 29.1 to UCBL 29.4; *Egretta garzetta* LAC 1997.226, UCBL 26.1 to UCBL 26.6; *Ardea alba* LAC (1 indiv.), IPH (1 indiv.); *A. cinerea* SAM.ZO-56105, SAM.ZO-58208, UCBL 24.1 to UCBL 24.6, UCBL 24.8 to UCBL 24.15; *A. melanocephala* SAM.ZO-56879, SAM.ZO-58742; *A. goliath* SAM.ZO-58694; *A. purpurea* LAC 1995.159, UCBL 25.1 to UCBL 25.7, UCBL 25.9, UCBL 25.10. Threskiornithidae: *Geronticus eremita* LAC 1997.750. Accipitridae: *Pernis apivorus* UCBL 103.1; *Elanus caeruleus* LAC 1884.152; *Milvus migrans* UCBL 100.1; *Gypaetus barbatus* BMNH 1845.1.12.1, BMNH 1876.8.7.7; *Gyps africanus* USNM 430826; *G. rueppellii* USNM 346395; *G. fulvus* BMNH 1861.3.24.6, BMNH 1954.30.55; *Aegypius monachus* BMNH Vel Cat 4 A, BMNH 1872.10.25.5, BMNH 1848.3.8.2, IPH 797, LAC 1876.217, LAC 1995.4, UCBL 84.1; *A. (Torgos) tracheliotus* IRSN 3875, LAC 1895.11, RMCA 91012A01; *Circaetus gallicus* UCBL 108.1; *Circus cyaneus* IPH 586, UCBL 105.1; *C. macrourus* IPH 503; *Accipiter gentilis* BMNH 1860.7.22.15, BMNH 1864.3.8.12; *A. nisus* UCBL 96.1; *Butastur indicus* LAC 1866.182; *Buteo buteo* LAC 1997.278; *B. rufinus* BMNH 1183 A; *Aquila pomarina* LAC 1997.271; *A. clanga* BMNH 424 A; *A. rapax* LAC 1864.26; *A. nipalensis* BMNH S/1980.11.4; *A. heliaca* BMNH 1954 30.48; *A. chrysaetos* LAC 1995.4, BMNH S/1973.66.57; *A. verreauxii* BMNH 1860.4.23.7; *Aquila wahlbergi* BMNH 1904.10.29.21; *A. (Hieraaetus) fasciatus* LAC 1997.946; *A. (H.) pennatus* IPH 1117, LAC (Guizeh); *Polemaetus bellicosus* BMNH S/1957.9.1; *Lophaetus occipitalis* BMNH 1850.8.15.61, BMNH S/1955.4.6; *Spizaetus cirrhatus* BMNH S/2002.45.1; *S. ornatus* LAC 1889.150; *Stephanoaetus coronatus* BMNH S/1954.30.42. Pandionidae: *Pandion haliaetus* UCBL 109.1 to UCBL 109.4. Falconidae: *Falco eleonorae* IPH, IPH 87; *F. concolor* LAC 1883.505; *F. subbuteo* BMNH S/1999.36.1; *F. biarmicus* BMNH S/1996.45.1, BMNH S/1956 14.6; *F. cherrug* BMNH S/1981.5.2; *F. peregrinus* BMNH S/1976.60.6, BMNH S/1976.14.1, BMNH S/1998.48.19. Phasianidae: *Alectoris graeca* UCBL 126.1; *A. rufa* LAC 1997.1125; *Ammoperdix heyi* FMNH 348117; *Francolinus (Francolinus) francolinus* LAC 1884.326; *F. (Francolinus) pintadeanus* CAS 61093; *F. (Peliperdix) coqui* USNM; *F. (Peliperdix) sephaena* USNM 558463; *F. (Pternistis) squamatus* FMNH 93388; *F. (Pternistis) leucoscepus* USNM 430614; *F. (Pternistis) erckelii* USNM 556785; *Perdix perdix* LAC 1998.57, UCBL 129.2; *Coturnix delegorguei* IRSN 37319, IRSN 37320; *C. adansonii* IRSN 37605, IRSN 37606; *Ptilopachus petrosus* IRSN 37318, IRSN 48162; *Pavo cristatus* BMNH S/1952.2.131, BMNH S/1973.66.68, BMNH S/1952.2.132, BMNH S/1987.14.1, BMNH 1859.9.6.421, CAS 42736, LAC 1923.2257, LAC 1910.399, LAC 1914.228, LAC A4427, RMCA 93137A05, UCBL 455.2; *P. muticus* BMNH S/1966.52.37, BMNH S/1998.41.1, BMNH S/1952.2.34, BMNH 1847.12.11.13, BMNH 1869.10.19.26, LAC 1887.1147; *Afropavo congensis* BMNH S/1989.19.16, BMNH S/1977.20.1, BMNH S/1975.16.1, UCBL 1988.1. Numididae: *Agelastes meleagrides* LAC 1882.137; *A. niger* BMNH S/1961.3.1, IRSN 41605; *Numida meleagris* BMNH S/1999.43.66, LAC A 4374, LAC 1835.103, LAC 1880.213, LAC 1885.332, LAC 1909.7, LAC 1921.60, RMCA A2 014 A01, UCBL 453.1 to UCBL 453.3; *Guttera plumifera* FMNH 313049, RMCA (QA01)-86337; *G. pucherani* BMNH S/1971.4.5, CAS 86157, LAC 1888.187, MCZ 342098, RMCA 83364; *Acryllium vulturinum* LAC 1880.1985, LAC 1893.612, RMCA 98025 A12, RMCA 98025 A07, RMCA 89049 A08. Turnicidae: *Turnix suscitator* MVZ 133111, MVZ 133103; *T. varia* MVZ 154111. Jacanidae: *Jacana spinosa* MVZ 85598, MVZ 85599. Rostratulidae: *Rostratula benghalensis* MVZ 120048, USNM 613012. Haematopodidae: *Haematopus ostralegus* UCBL 147.1, UCBL 147.2. Ibidorhynchidae: *Ibidorhyncha struthersii* USNM 292766. Recurvirostridae: *Himantopus himantopus* UCBL 190.1 to UCBL 190.3; *Recurvirostra avosetta* UCBL 191.1 to UCBL 191.3. Burhinidae: *Burhinus oedicnemus* UCBL 194.1 to UCBL 194.6. Glareolidae: *Cursorius cursor* UCBL 197.1; *Glareola pratincola* UCBL 195.1. Charadriidae: *Vanellus vanellus* UCBL 149.1 to UCBL 149.8; *Charadrius hiaticula* UCBL 150.1 to UCBL 150.3; *Pluvialis squatarola* UCBL 153.1 to UCBL 153.4. Scolopacidae: *Arenaria interpres* UCBL 157.1 to UCBL 157.5; *Gallinago gallinago* UCBL 158.1 to UCBL 158.7; *Lymnocryptes minimus* UCBL 160.1;

Scolopax rusticola UCBL 161.1 to UCBL 161.4; *Numenius arquata* UCBL 163.1 to UCBL 163.4; *Limosa limosa* UCBL 166.1 to UCBL 166.7; *Tringa totanus* UCBL 171.1 to UCBL 171.3; *Actitis hypoleucos* LAC 1997.694; *Calidris canutus* LAC 2004.637, UCBL 178.1; *C. alba* UCBL 186.1, 186.2; *C. alpina* UCBL 184.1 to UCBL 184.6; *Philomachus pugnax* UCBL 189.1 to UCBL 189.4. Phalaropodidae: *Phalaropus fulicarius* UCBL 192.1, 192.2. Thinocoridae: *Thinocorus orbignyanus* USNM 290109. Chionidae: *Chionis alba* USNM 489489. Stercorariidae: *Catharacta skua* UCBL 198.1; *Stercorarius parasiticus* UCBL 200.1. Laridae: *Larus ridibundus* UCBL 212.1 to UCBL 212.13. Sternidae: *Sterna sandvicensis* UCBL 226.1, 226.2. Alcidae: *Alca torda* UCBL 227.1. Columbidae: *Columba guinea* FMNH 330207; *C. oenas* LAC 1993.115; *C. (Aplopelia) larvata* SAM. ZO-58091; *Streptopelia senegalensis* IRSN 37866; *S. decipiens* USNM 430797; *S. capicola* IRSN 52449, LAC 1870.592; *S. semitorquata* IRSN 23402; *S. roseogrisea* IRSN 24693, LAC 1884.333; *Turtur abyssinicus* FMNH 319944; *T. afer* CAS 84511, CAS 84273; *T. tympanistria* CAS 84471, CAS 71597; *Oena capensis* IRSN 38120, LAC 2000.69; *Treron waalia* IRSN 37790; *T. australis* FMNH 313707, LAC 1871.412. Tytonidae: *Tyto alba affinis* SAM.ZO-58526, SAM.ZO-57012, SAM.ZO-56755; *T. capensis* SAM.ZOT-2075. Strigidae: *Otus scops* UCBL 246.1, UCBL 246.2; *Bubo bubo* LAC A.4065; *B. capensis* SAM.ZO-56325, SAM. ZO-58175, SAM.ZO-58272; *B. africanus* SAM.ZO-58868, SAM.ZO-58181, SAM.ZO-58702, SAM.ZO-56863; *B. lacteus* SAM.ZO-58019; *B. (Ketupa) zeylonensis* LAC 1986.05; *Glaucidium (Taenioglaux) capense* LAC 1997.746; *Athene noctua* UCBL 251.2 to UCBL 251.4; *Aegolius funereus* UCBL 257.1; *Asio flammeus* SAM.ZO-58156; *A. capensis* SAM.ZOT-1279. Coliidae: *Colius striatus* LAC 1997.520. Capitonidae: *Lybius dubius* LAC 1997.879.

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Chapter 19
Beetles (Insecta: Coleoptera)

Frank-T. Krell and Wolfgang Schawaller

Abstract Nine fossil beetles and seven fossil brood balls made by dung beetles are described from Laetoli (Pliocene). Seven beetles are Tenebrionidae, tribes Tentyriini and Molurini, one is a June beetle of the tribe Schizonychini (Scarabaeidae: Melolonthinae) and one a rhinoceros beetle (Scarabaeidae: Dynastinae) described as *Calcitoryctes magnificus* sp.n. Seven fossil dung beetle brood balls are described as *Coprinisphaera laetoliensis* ichnosp. n. and *C. ndolanyanus* ichnosp. n., the first formally described scarab ichnofossils from Africa. Two specimens of *C. laetoliensis* show the largest known traces of kleptoparasites described as *Lazaichnus amplus* ichnosp. n. The fossil beetles and brood balls of Laetoli weakly indicate a grassland, rather than a dense woodland habitat.

Keywords Tenebrionidae • Scarabaeidae • Ichnofossils • *Coprinisphaera*

Introduction

With more than 350,000 described species, the beetles (Coleoptera) form the largest order of organisms with the oldest stem-group representatives recorded from the Early Permian (Ponomarenko 2002; Grimaldi and Engel 2005). As hard-shelled insects they are well-represented in the fossil record, often, however, as single elytra or flattened sandwiches of several layers of dark cuticle, lacking or hiding crucial characters (Krell 2000). Apart from amber inclusions, three-dimensional, undistorted beetle fossils are rare and known from only a few lagerstätten (Krell 2006), mainly Oligocene-Miocene Riversleigh in Queensland (Duncan et al. 1998), Miocene Barstow Formation in California (Park and Downing 2001), Eocene London Clay of Bognor Regis (Britton 1960), and particularly the Miocene of Rusinga and Mfangano Island in Lake Victoria, Kenya (Leakey 1952; Paulian 1976). These fossils give unique insights in the actual shape of Tertiary insects. The beetle fossils from Laetoli belong to only two families, Tenebrionidae (darkling beetles) and Scarabaeidae (scarab beetles). They are mineralized, filled replicas of the exoskeleton without preservation of the original cuticle. Despite the fairly detailed preservation, they lack crucial specific and generic characters, particularly legs, preventing us from formally describing most of them as new species, but classification at tribal level is possible. Additionally, mineralized dung beetle brood balls are present, the spherical dung portions covered by a soil layer that coprophagous scarab beetles form in their underground nests as food provision for their larvae. All specimens are deposited in the National Museum of Tanzania, Dar es Salaam.

Tenebrionidae (W. Schawaller)

The beetle family Tenebrionidae (Darkling Beetles) is one of the largest families of Coleoptera worldwide with about 20,000 recent species. The family displays high morphological and ecological plasticity with species inhabiting the seashore, sandy and rocky deserts, and woodland habitats up to the alpine zone above the timberline. In spite of this recent diversity, fossil records of tenebrionids are poor. The serrate antenna of one fossil from the Mesozoic Crato Formation in Brazil might point to the family Tenebrionidae, although definite tenebrionid family characters cannot be seen. This would be the only fossil record of a tenebrionid beetle from the Mesozoic (Wolf-Schwenninger and Schawaller 2007). Younger fossil tenebrionids are known from Tertiary deposits, for example from the Florissant Fossil Beds in Colorado (Wickham 1914) and from the Messel deposits in Germany (Hörnschemeyer 1994). Tenebrionids from Baltic Amber are listed by Spahr (1981), and tenebrionids from Dominican

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Amber have been described by Kaszab and Schawaller (1984) and Doyen and Poinar (1994).

From Laetoli, seven remnants of beetles have been found that probably belong to the family Tenebrionidae. They can be assigned to four species and are described and figured, but not named. Although the fossils are well preserved, they can be classified only by the general external morphology, but not by distinct generic and/or specific characters. Thus, they are not formally described as new taxa.

Tentyriini Species a (? Genus *Tentyria*)

EP 734/05 (Fig. 19.1)

Laetoli Locality 3 [localities described by Harrison and Kweka 2011]: Upper Laetolil Beds, 60–70 cm above Tuff 7.

Description. Joint elytra, pronotum, dorsal part of head, and venter of anterior thorax preserved. Combined elytra of oval shape, widest before the middle, length of elytra 13.5 mm, maximal width of combined elytra 9.0 mm. Elytral surface without recognizable punctural rows or striae and without recognizable surface structure. Pronotum as wide as long, widest just before the middle, surface convex, with dense but not confluent punctation. Dorsal side of head with similar punctation as on pronotum, clypeus without tooth or other modification, eyes somewhat prominent, kidney-like and only slightly excavated by the genae. Without prominent prosternal process. Anterior and middle coxal cavities widely separated, posterior coxal cavities not preserved. Last abdominal ventrites not distinguishable.

EP 1598/04 (Fig. 19.2)

Laetoli Locality 12: Upper Laetolil Beds, between Tuffs 5 and 8.

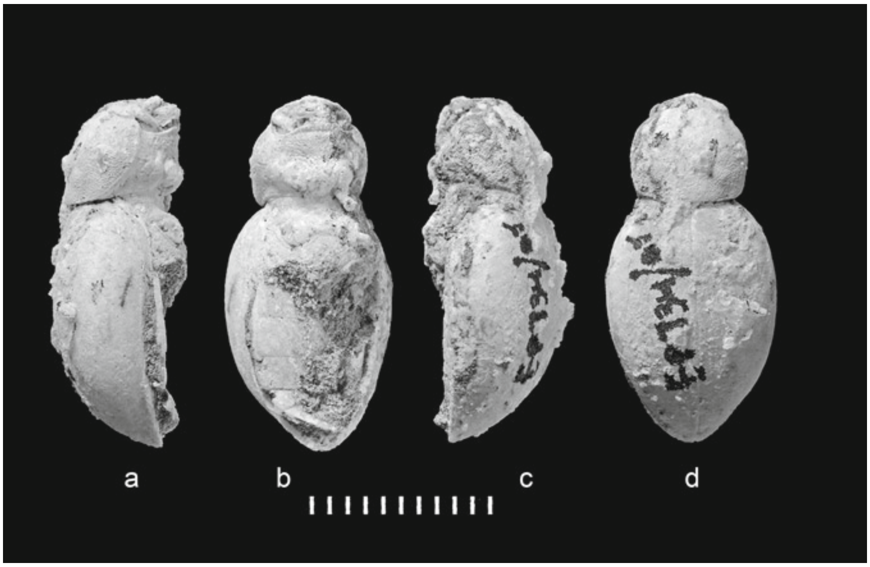

Fig. 19.1 Tentyriini species A (?genus *Tentyria,* Tenebrionidae), Laetoli. EP 734/05; (**a**) right side; (**b**) ventral; (**c**) left; (**d**) dorsal. Scale in mm

Fig. 19.2 Tentyriini species A (?genus *Tentyria,* Tenebrionidae), Laetoli. EP 1598/04; (**a**) right side; (**b**) ventral; (**c**) frontal; (**d**) left; (**e**) dorsal. Scale in mm

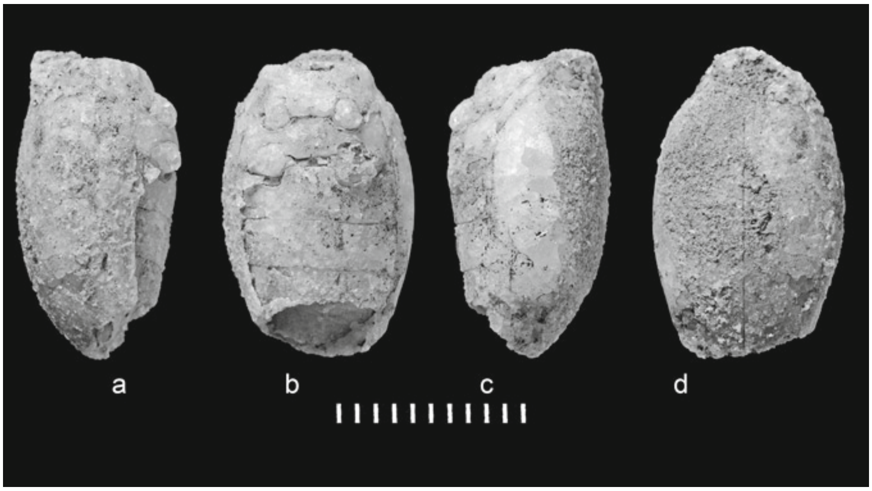

Fig. 19.3 Tentyriini species A (?genus *Tentyria,* Tenebrionidae), Laetoli. EP 1670/00; (**a**) right side; (**b**) ventral; (**c**) left; (**d**) dorsal. Scale in mm

Description. Joint elytra without tip, pronotum, head, venter of thorax and abdominal ventrites preserved. Combined elytra of oval shape, widest before the middle, length of elytra 13.0 mm, maximal width of combined elytra 8.0 mm. Elytral surface without recognizable punctural rows or striae or other recognizable surface structure. Pronotum as wide as long, widest just before the middle, surface convex, surface with dense but not confluent punctation. Dorsal side of head with similar punctation as on pronotum. Clypeus without tooth or other modification, eyes somewhat prominent and kidney-shaped, only slightly excavated by the genae. Without prominent prosternal process. Anterior, middle and posterior coxal cavities widely separated. Five visible abdominal ventrites, ventrites 3 and 4 not distinctly shorter than ventrite 2, last visible ventrite 5 shorter than ventrites 3 and 4 combined.

EP 1670/00 (Fig. 19.3)

Laetoli Locality 3: Upper Laetolil Beds, 60–70 cm above Tuff 7.

Description. Joint elytra without tip, venter of posterior thorax and basal abdominal ventrites 1–3 preserved. Combined elytra of oval shape, widest before the middle, length of elytra 15.0 mm, maximal width of combined elytra 9.8 mm. Elytral surface without recognizable punctural rows or striae and without recognizable surface structure. Anterior coxal cavities not preserved, middle and posterior coxal cavities widely separated. Only three basal abdominal ventrites preserved.

EP 669/04 (Fig. 19.4)

Laetoli Locality 3: Upper Laetolil Beds, 60–70 cm above Tuff 7.

Description. Joint elytra, venter of posterior thorax and all abdominal ventrites preserved. Combined elytra of oval shape, widest before the middle, length of elytra 14.0 mm, maximal width of combined elytra 8.5 mm. Elytral surface without recognizable punctural rows or striae or other recognizable surface structure. Anterior coxal cavities not preserved, middle and posterior coxal cavities widely separated. Five visible abdominal ventrites, ventrites 3 and 4 of similar length and slightly shorter than ventrite 2, last visible ventrite 5 longer than ventrites 3 and 4 combined.

Fig. 19.4 Tentyriini species A (?genus *Tentyria,* Tenebrionidae), Laetoli. EP 669/04; (**a**) from right; (**b**) ventral; (**c**) left; (**d**) dorsal. Scale in mm

Taxonomy. These four fossils represent the same species because of similar characters. The large body size and the general shape of pronotum and elytra, the elytra without punctural rows or striae, the structure of the head with slightly prominent eyes and the shape of the eyes, the wide distance of all coxal cavities, and the shape of the abdominal ventrites coincide with recent species of the genus *Tentyria* Latreille, 1802 (tribe Tentyriini Eschscholtz, 1831, subfamily Pimeliinae Latreille, 1802). Quite similar is the closely related genus *Rhytinota* Eschscholtz, 1831. However, the recent congeners possess a narrower pronotum, narrower and longer elytra and non-prominent eyes.

Zoogeography. The numerous extant species of the genus *Tentyria* are distributed mainly in the Mediterranean region, Arabia, and Central Asia. Species of the genus *Rhytinota* occur today in eastern Africa and the Indian subcontinent (Gebien 1937).

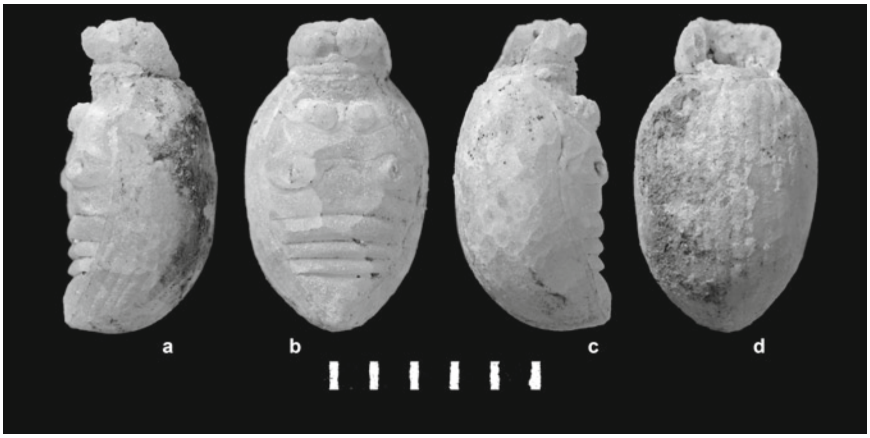

Fig. 19.5 ?Tentyriini species B (Tenebrionidae), Laetoli, EP 351/03; (**a**) from left; (**b**) ventral; (**c**) right; (**d**) dorsal. Scale in mm

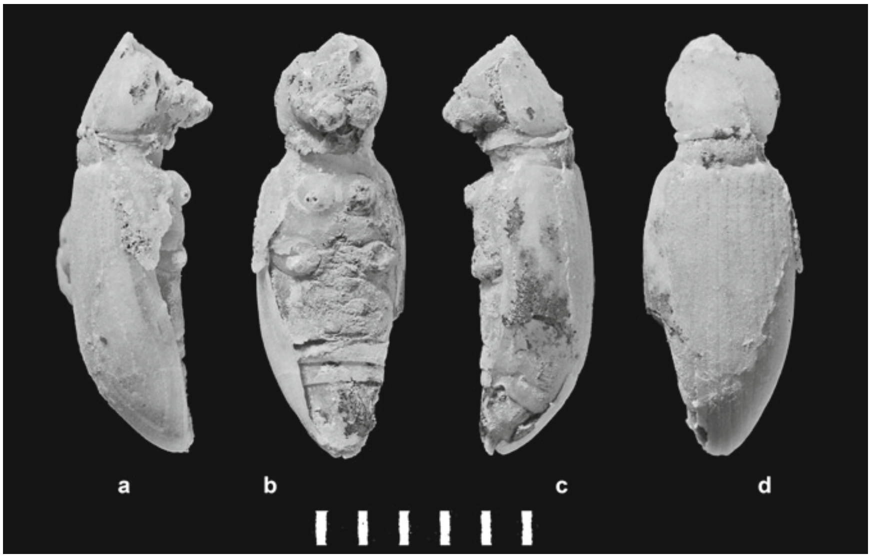

Fig. 19.6 ?Tentyriini species C (Tenebrionidae), Laetoli, EP 2777/00; (**a**) from right; (**b**) ventral; (**c**) left; (**d**) dorsal. Scale in mm

? Tentyriini Species B (? Genus)

EP 351/03 (Fig. 19.5)

Laetoli Locality 3: Upper Laetolil Beds, 60–70 cm above Tuffs 7.

Description. Joint elytra, venter of complete thorax and all abdominal ventrites preserved. Combined elytra of oval shape, widest at anterior third, length of elytra 6.5 mm, maximal width of combined elytra 4.0 mm. Elytral surface with an uncertain number of rows of fine punctures or striae, elytral intervals slightly convex without recognizable surface structure. Without prominent prosternal process. Anterior coxal cavities touching each other, middle coxal cavities slightly separated, posterior coxal cavities widely separated. 5 visible abdominal ventrites, ventrites 3 and 4 of similar length and distinctly shorter than ventrite 2, last visible ventrite 5 longer than ventrites 3 and 4 combined.

Taxonomy. From the general shape of the joint elytra, this fossil might also belong to the tribe Tentyriini. However, because of the nearly confluent anterior coxal cavities and the structure of the elytra with rows of fine punctures or striae and with slightly convex elytral intervals, I feel unable to assign this and the following fossil specimen to any tenebrionid genus, but they differ on the species level because of distinctly different shape of the elytra.

? Tentyriini Species C (? Genus)

EP 2777/00 (Fig. 19.6)

Laetoli Locality 3: Upper Laetoli Beds, 60–70 cm above Tuff 7.

Description. Joint elytra without tip, pronotum, venter of complete thorax and all abdominal ventrites preserved.

Combined elytra of longitudinal shape, widest at anterior third, length of elytra 11.5 mm, maximal width of combined elytra 3.5 mm. Elytral surface with at least 6 rows of distinct punctures without striae, elytral intervals nearly flat without recognizable surface structure. Pronotum as wide as long, widest shortly before the middle, surface convex, with dense but not confluent punctation; without prominent prosternal process. Anterior coxal cavities touching each other, middle coxal cavities slightly separated, posterior coxal cavities widely separated. Five visible abdominal ventrites, basal ventrite 1 long, nearly as long as ventrites 2, 3 and 4 combined.

Taxonomy. The general shape of the joint elytra might point to the tribe Tentyriini. However, as in the previous fossil, the nearly confluent anterior coxal cavities and the structure of the elytra with rows of distinct punctures prevent a definitive assignment to any genus.

Molurini Species a (? Genus *Arturium*)

EP 668/04 (Fig. 19.7)

Laetoli Locality 3: Upper Laetolil Beds, 60–70 cm above Tuff 7.

Description. Joint elytra, venter of posterior thorax preserved. Combined elytra oval shaped, widest at anterior third, length of elytra 13.0 mm, maximal width of combined elytra 9.0 mm. Elytral disc with two high undulated keels and with a somewhat lower humeral keel, medial part of elytral between the humeral keels flat, lateral parts of elytra besides the humeral keels vertical and not to be seen in dorsal view, surface between the keels slightly uneven und densely punctured. Middle and posterior coxal cavities widely separated. Abdominal ventrites not preserved.

Taxonomy. From the larger body size and the dorsal structure of the elytra the fossil might be assigned to the genus *Arturium* Koch, 1951 (tribe Molurini Latreille, 1829, subfamily Pimeliinae Latreille, 1802), although further characters cannot be compared.

Zoogeography. The genus *Arturium,* with few recent species, is restricted to eastern Africa.

Biology

Recent tenebrionids belong roughly to two ecological groups. One group includes characteristic dwellers of dry and even arid habitats. The second, probably larger, group populates decayed wood and fungi and could be considered as an indicator of mature forests. A compact body with short legs are characters of the tenebrionid forest dwellers, whereas slender bodies with longer legs are connected with running behavior in open habitats, including deserts. Unfortunately, body appendages are not preserved in the Laetoli tenebrionids, so no conclusions can be deduced about their former habitat based on morphology alone.

The taxonomic assignment of some fossil tenebrionids to the tribes Tentyriini and Molurini clearly points to an open habitat during the Pliocene. Nearly all recent species of these tribes are soil dwellers in steppes, savannahs and deserts, and today eastern Africa is populated with abundant elements of these tenebrionid tribes. The fossil tenebrionids from Laetoli give no hint of woodland or forested habitats.

Scarabaeidae (F.-T. Krell)

With about 31,000 described extant species (Jameson and Ratcliffe 2002) the Scarabaeoidea are one of the largest superfamilies in the Coleoptera. They are distributed world-wide and comprise such varied groups as dung beetles, stag beetles, and chafers, ranging from just over 1 mm to 170 mm body length. In the fossil record they are fairly well represented with about 230 species described from the Upper Jurassic to the Pleistocene (Krell 2007). However, apart from fossil brood balls made by dung beetles, Pliocene scarab fossils are

Fig. 19.7 Molurini species A (?genus *Arturium*, Tenebrionidae), Laetoli, EP 668/04; (**a**) from right; (**b**) ventral; (**c**) left; (**d**) dorsal. Scale in mm

rare (Krell 2007) with some extant species recorded, but only two extinct species described: the dung beetle *Copris kartlinus* Kabakov, 1988, from the Kisatibi Formation in Georgia, and the dubious *Melolonthites laterosinuatus* Piton and Théobald 1935, from the Mio/Pliocene cinerites of Varennes, France, represented by only one elytron.

Scarabaeoidea is a monophyletic group diagnosed by two autapomorphies: antenna with a lamellate club and anterior border of hind wings with sclerotized field proximal to a pinch, as part of a spring folding mechanism (Krell 2006). Both characters are rarely preserved in fossils and are missing in the Laetoli scarabs. Most fossil scarab beetles, including the two specimens described below, were identified on the basis of other characters typical for Scarabaeoidea, such as enlarged prothorax adapted for digging with short and powerful legs with tibiae toothed along outer edge, large and narrowly separated to contiguous pro- and mesocoxae, and transverse and narrowly separated to contiguous metacoxae. The body fossils from Laetoli are well-preserved three-dimensionally, but are lacking finer surface structures like punctation. In the melolonthine, even all sutures are blurred. Moreover, the legs apart from some femora are missing, hardly leaving any genus- or species-diagnostic characters. Both specimens are described, but only the exceptionally preserved rhinoceros beetle is named.

Apart from the two body fossils, seven fossil dung beetle brood balls were found at Laetoli. Fossil brood balls were recorded from Laetoli previously (Sands 1987) and also from other Pliocene sites in Africa, such as paleo-lake Chad (Duringer et al. 2000) and Makapansgat Limeworks in South Africa (Kitching 1980), as well as from the Pleistocene of Rutana in Burundi (Basilewsky 1951). However, none of the African specimens has been formally described and named as ichnospecies.

Dynastinae: Oryctini/Pentodontini

Calcitoryctes Krell, gen.n.

Derivatio nominis. From calcite (calcium carbonate) of which the specimen consists, and *Oryctes*, the type genus of Oryctini Mulsant, 1842, to which it might belong. Gender masculine.

Type species. Calcitoryctes magnificus sp.n.

Diagnosis. Outer side of mandibles entire or slightly denticulate. Clypeus truncated with rounded angles. Head with tubercle. Pronotum without sculpture. Ventrites 1–4 much shorter than 5 and 6. Pygidium ca. three times as broad as long, transversally bulged with strong apical impressions on both sides. Some extant *Oryctes* Illiger, 1798, and *Cyphonistes* Burmeister, 1847, species have a similar pygidium, but *Oryctes* is much larger and has a deeply emarginated clypeus and *Cyphonistes* has never one tubercle on the head (Endrődi 1985). Within Pentodontini Mulsant, 1842, it resembles the South/East African genus *Pentodontoschema* Péringuey, 1901 (Péringuey 1901; Ferreira 1966) from which it differs by the margined base of the pronotum, the concave apical part of the pygidium and the probably less denticulated mandibles. It differs from *Heteroligus* Kolbe, 1900, by the missing pronotal tubercles and the concave apical part of the pygidium and from *Phyllognathus* Eschscholtz, 1830, by the more slender mandibles (Endrődi 1985).

Calcitoryctes magnificus Krell, sp.n.

Derivatio nominis. Magnificus (adj.) (post-classical Latin) = magnificent.

Holotype. EP 2704/00 (Fig. 19.8), Laetoli Locality 2: Laetolil Beds, upper unit between Tuffs 5 and 7, deposited in the National Museum of Tanzania, Dar es Salaam.

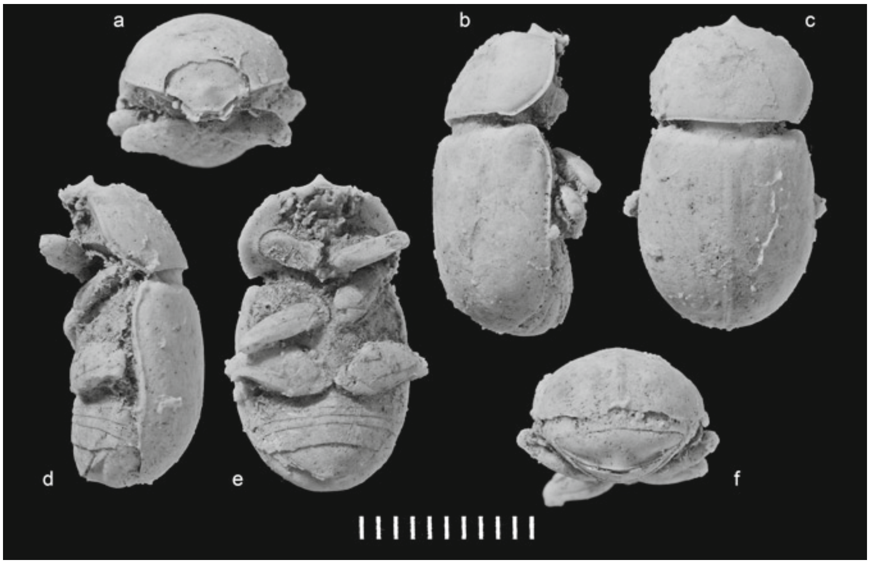

Fig. 19.8 *Calcitoryctes magnificus* sp.n. (Scarabaeidae, Dynastinae), holotype, Laetoli, EP 2709/00; (**a**) from frontal; (**b**) right; (**c**) dorsal; (**d**) left; (**e**) ventral; (**f**) caudal. Scale in mm

Description. Complete body with all femora apart from the right profemur; length: 18.4 mm; maximum width of pronotum: 9.5 mm; maximum width of elytra: 10.5 mm. Body with left profemur and all other femora present. Mandibles protruding beyond clypeus laterally and anteriorly; outer side of mandibles entire or slightly denticulate, basally broad, slightly emarginated to a relatively sharp tip, possibly with a denticle in the middle. Labium basally broadly rectangular, apically with a deep emargination before the double-convex anterior border, incised in the middle (Fig. 19.9). Only scape and pedicel of the left antenna present, both short as typical for Dynastinae. Clypeus truncated with rounded angles, anterior margin bluntly triangular, lateral margins slightly emarginated. Head with median conical tubercle, steeper declined posteriorly than anteriorly; from the tubercle, a slight bulge extends to the sides. Short ocular canthus present. Pronotum regularly convex without any sculpture; lateral margins regularly convex, broadest in the middle; laterally and basally margined, lateral margin broader and sharp. Anterior angles protruding and posterior angles obtuse. Anterior margin without tubercle. Basal margin convex. Scutellum rounded. Elytra broadest just behind the middle. Sutural interval basally broad, apically tapered and slightly elevated. Shallow traces of probably three discal stripes visible. Humeral callus and anteapical callus present. Epipleura narrow (maximum 0.65 mm), with sharp border, extending to pygidium. Ventrites 1–4 short, ventrite 5 longer than 3+4 together, ventrite 6 as long as 3–5 together. All coxae touching. Hind femora much thicker than middle and slightly thicker than fore femora (ratio length/width f: 2.1; m: 2.6; h: 1.9). Propydidium not fully covered by elytra, not produced posteriorly; no stridulatory area visible due to preservation. Pygidium short (3.1 × as broad as long) as in most Oryctini. Basal half of pygidium forms a strongly convex transversal bulge (visible from ventral), apical half impressed and convex, with strong impressions on both sides, margin of the tip of the pygidium slightly protruding.

Classification. The only character separating the tribes Pentodontini and Oryctini in the current typological classification is the tibial apex. Tibiae are not preserved in this specimen. However, since the tibial apex is variable within tribes and the tribes themselves are only typologically defined (Ratcliffe 2003:249), both groups might not survive a phylogenetic analysis as equally ranked taxa as one might become a subgroup of the other. Therefore, it is not a serious shortcoming that *Calcitoryctes* cannot be unequivocally assigned to one of these groups.

Melolonthinae: Schizonychini, Species a

EP 2156/03 (Fig. 19.9)

Laetoli Locality 7: Laetolil Beds, upper unit between Tuffs 5 and 7 [body, one femur]

Description. Length: 12.4 mm; maximum width of pronotum: 5.0 mm; maximum width of elytra: 6.1 mm; height of specimen: 5.1 mm. No microsculpture or punctation visible due to preservation. Labrum medianly incised, Prementum bilobate, with a median furrow extending to mentum. Clypeus seems to be separated from the frons by a slight transversal bulge. Pronotum: Sides slightly diverging in basal third, then straight strongly converging to head. Elytra: Lateral border behind the humeral callus slightly emarginate, then elytra broadened, widest just behind the middle. All coxae adjacent.

Classification. The elevated frontoclypeal suture and the strongly incised labrum are characters of Schizonychini Burmeister, 1855, and, together with the shape of the elytra, might even indicate that the specimen belongs to *Schizonycha* (Pope 1960; Lacroix 1989), which is a speciose genus containing abundant African species. However, two crucial characters for Schizonychini, the enlarged ventrite 6 and the metepimeron (Lacroix 1989), are not sufficiently preserved

Fig. 19.9 Melolonthinae, Schizonychini species A (Scarabaeidae), Laetoli, EP 2156/03; (**a**) from right; (**b**) ventral; (**c**) frontal; (**d**) left; (**e**) dorsal. Scale in mm

to allow a reliable tribal classification. Preservation of antennae, claws, mouthparts and setation would be necessary for generic classification.

Ichnofossils

A small and a large type of fossil dung beetle brood balls were found at Laetoli, similar to the abundant brood balls described as *Coprinisphaera* Sauer, 1955, from South America. Genise et al. (2000) have already assigned the "structure resembling a dung ball of *Heliocopris*" mentioned by Sands (1987: 423) to this ichnogenus and counted Laetoli in the localities with *Coprinisphaera* ichnofacies. All formally described scarab ichnofossils are from the Americas (Krell 2007). The fossil dung beetle brood balls were recently revised by Genise (2004) and Laza (2006) and classified into nine ichnospecies. To facilitate the integration of the Laetoli ichnofossils into the current ichnological classification, they will be named although ichnospecies-specific characters are often not clearly visible due to the replacement of original material and infilling with calcium carbonate.

These balls represent the prepared portions of resources that dung beetles form from available feces as food provision for their larvae. The brood balls of large tunnelling dung beetles are generally covered by a layer of soil to prevent desiccation (Halffter and Edmonds 1982), whereas the surface of brood balls of large rollers such as *Scarabaeus* L., 1758 or *Kheper* Janssens, 1940 is either only smoothened (Lengerken 1954) or covered by the mother beetle's feces (Sato and Imamori 1987).

Whereas the American fossil brood balls are mostly hollow spheres with the original soil cover preserved, the Laetoli fossils are steinkerns of calcium carbonate rendering it impossible to identify whether the outer layer was originally formed by soil or dung. I interpret the faint line between the outer layer and the infilling (Figs. 19.10–19.12) as the border between the original dung portion and larval chamber. The thickness of the outer layer is not only an indication of the thickness of a possible soil cover, but also of the amount of dung still in existence at the time when the dung consumption by the larva ended. The longer the larva feeds, the thinner the walls become (Lengerken 1954). Successful development of the larva and hatching of the beetle results in thin walls of the brood ball. Thick walls might indicate that the development was disturbed or unsuccessful.

Coprinisphaera laetoliensis Krell, ichnosp. n.

Derivatio nominis. Adjective meaning 'from Laetoli', the type locality.

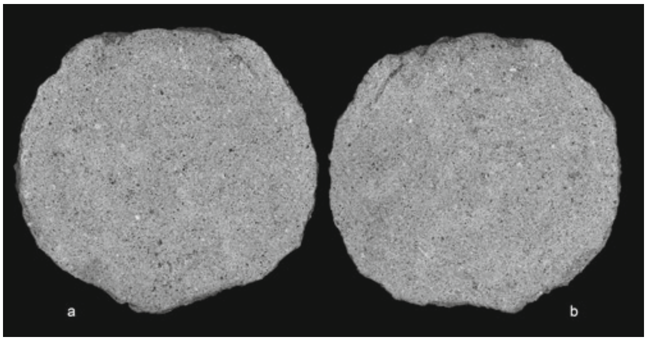

Fig. 19.10 *Coprinisphaera laetoliensis* isp.n., fossil dung beetle brood ball, Laetoli, holotype, EP 224/04. Cut; (**a**) cut half; (**b**) counterpart

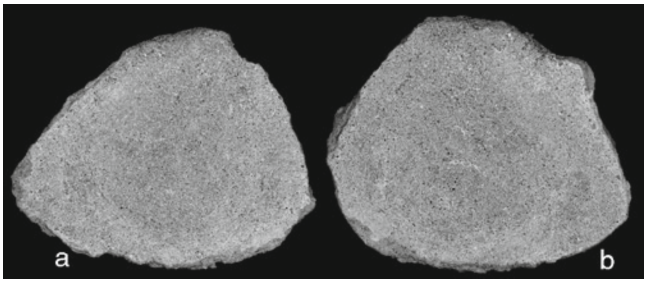

Fig. 19.11 *Coprinisphaera laetoliensis* isp.n., fossil dung beetle brood ball, Laetoli, EP 1719/03. Cut; (**a**) half cut; (**b**) counterpart

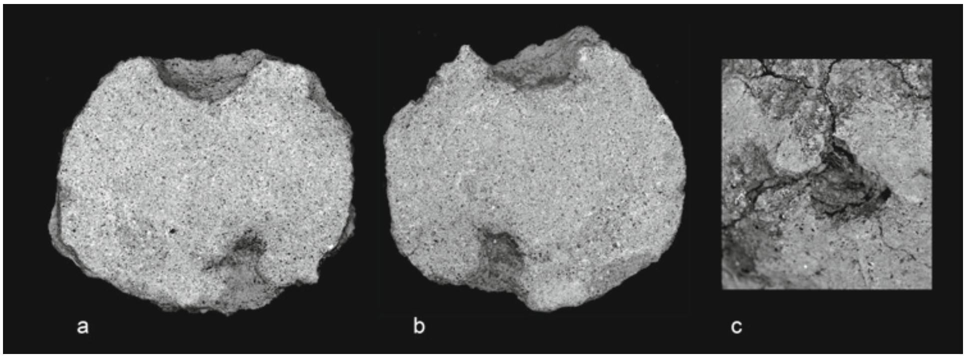

Fig. 19.12 *Lazaichnus amplus* isp.n., traces of kleptoparasites in fossil dung beetle brood ball, Laetoli. Holotype of *L. amplus* in paratype of *Coprinisphaera laetoliensis*, EP 1719/03; (**a**) half cut; (**b**) counterpart; (**c**) outer opening of *L. amplus*

Fig. 19.13 *Coprinisphaera laetoliensis* isp.n., fossil dung beetle brood ball, Laetoli, holotype, EP 224/04. Before cut; (**a**) from top; (**b**) lateral. Scale in mm

Holotype. EP 224/04 (Figs. 19.10, 19.13), Laetoli Locality 15: Upper Ndolanya Beds; deposited in the National Museum of Tanzania, Dar es Salaam.

The specimen is the fossilized empty, abandoned brood ball, replaced and filled by calcium carbonate. Cut medianly in half. Maximum height: 53.4 mm; equatorial diameter: 55.5 mm; diameter of upper opening: 22.5 mm. Regular sphere with wide upper opening surrounded by collar in form of a flat bulge (11–12 mm wide). Bottom with a small, oval depression of about 13 mm diameter. upper lateral thickness of the wall: ca. 4.5 mm, about 10 mm at the bottom.

Biology. Thin wall, broad opening and undamaged outer surface indicate that the beetle hatched successfully; no signs of kleptoparasitic or secondary intrusion.

Paratype. EP 1719/03, Specimen B (see Fig. 19.12) (of 3 specimens), Laetoli Locality 15: Upper Ndolanya Beds; deposited in the National Museum of Tanzania, Dar es Salaam. Cut medianly in half, some outer cracks fixed by glue; spherical with upper opening; height: 47.5 mm, equatorial diameter: 54 mm; opening: 22 mm; thickness of the wall: 10.5–15.8 mm, bottom with two deep holes of 9–10 mm diameter (ventral hole: Fig. 19.12a, b; ventrolateral hole: Fig. 19.12c).

Biology. The size of the holes in the outer wall indicate infestation by larger kleptoparasites of genera such as *Onthophagus* Latreille, *Hyalonthophagus* Palestrini or *Pedaria* Laporte, being the holotype of *Lazaichnus amplus* ichnosp.n. (described below). Kleptoparasitic species invade and lay their eggs in a dung portion collected by another species, generally reducing the reproductive success of the host significantly (Rougon and Rougon 1980; Gonzáles-Megías and Sánchez-Piñero 2003). The thick walls show that the dung material had not been exhausted, probably due to unsuccessful or abbreviated development of the host larva. The upper opening might indicate that the host larva might have hatched.

Additional material. EP 1077/01 (see Fig. 19.14), Laetoli Locality 15: Upper Ndolanya Beds. Flat sphere with large opening (55.5 mm × 38.8 mm) on one side and a deep small hole (10 mm diameter) on the other. Height: 48 mm; equatorial diameter: 60 mm. Filled with a lighter (replaced dung) and a darker substance in the area of the small hole and probably indicating the development space of a kleptoparasite (paratype of *Lazaichnus amplus* ichnosp. n., described below). Due to the large, irregular opening the ichnospecies-specific collar is missing. Thus, this specimen is not designated as a paratype of *C. laetoliensis*.

Biology. The large upper opening (see Fig. 19.14) might have been caused by a vertebrate predator. Modern examples of brood balls opened by bat-eared foxes (*Otocyon megalotis* (Desmarest, 1822)) show similarly shaped holes (see Fig. 19.15). These foxes excavate dung beetle brood balls on a regular basis to prey on the larvae (Nel and Maas 2004).

EP 1719/03, Specimen A (Figs. 19.11, 19.16), Laetoli Locality 15: Upper Ndolanya Beds, cut medianly in half; flat pear-shaped; height: 48.5 mm, equatorial diameter: 58.6 mm, maximum width of neck: 27 mm; bottom flat with central round area of ca. 14 mm diameter (contact zone of brood ball to ground); lateral thickness of the wall 6–8.5 mm, 4–10 mm at the bottom; no signs of kleptoparasitic or secondary intrusion. Surface with six dorsoventral ribs which were possibly caused by filled cracks of the surrounding soil. Because of the different shape (rather pear-shaped than spherical), which is similar of the shape of *Vondrichnus planoglobus* Duringer et al., 2007 (Fig. 19.10a, d; termite nest), it is not designated as a paratype. Because a thick outer wall can be distinguished from the inner chamber, and because it forms part of a series of three fossil brood balls likely found together (the other two being typical *Coprinisphaera*), it is identified as *Coprinisphaera*. Since the three balls were not found in close proximity, I do not classify them as *Quirogaichnus* Laza, 2006 which was introduced for clusters of brood balls in a distinct chamber or cavity.

Biology. The thin walls and undamaged outer surface indicate a regular development of the larva. However, an upper opening is not clearly defined. The irregular internal part of the neck could be the opening (diameter 13 mm).

EP 1719/03 Specimen C, Laetoli Locality 15: Upper Ndolanya Beds: flat pear-shaped with flat bottom; height: 47.9 mm; equatorial diameter: 60.6 mm; surface with large, deep cracks; no indication of kleptoparasitic or secondary intrusion. Because of this suboptimal infilling or incipient disintegration this specimen was not cut. Due to poor preservation, I do not designate it as a paratype.

Description. Spherical, solid structures with sometimes flattened underside resulting in a slight pear-like shape; height: 47.5–53.4 mm; equatorial diameter: 54.0–55.5 mm (all specimens: 53.4–60.6 mm). Dorsal opening on top with

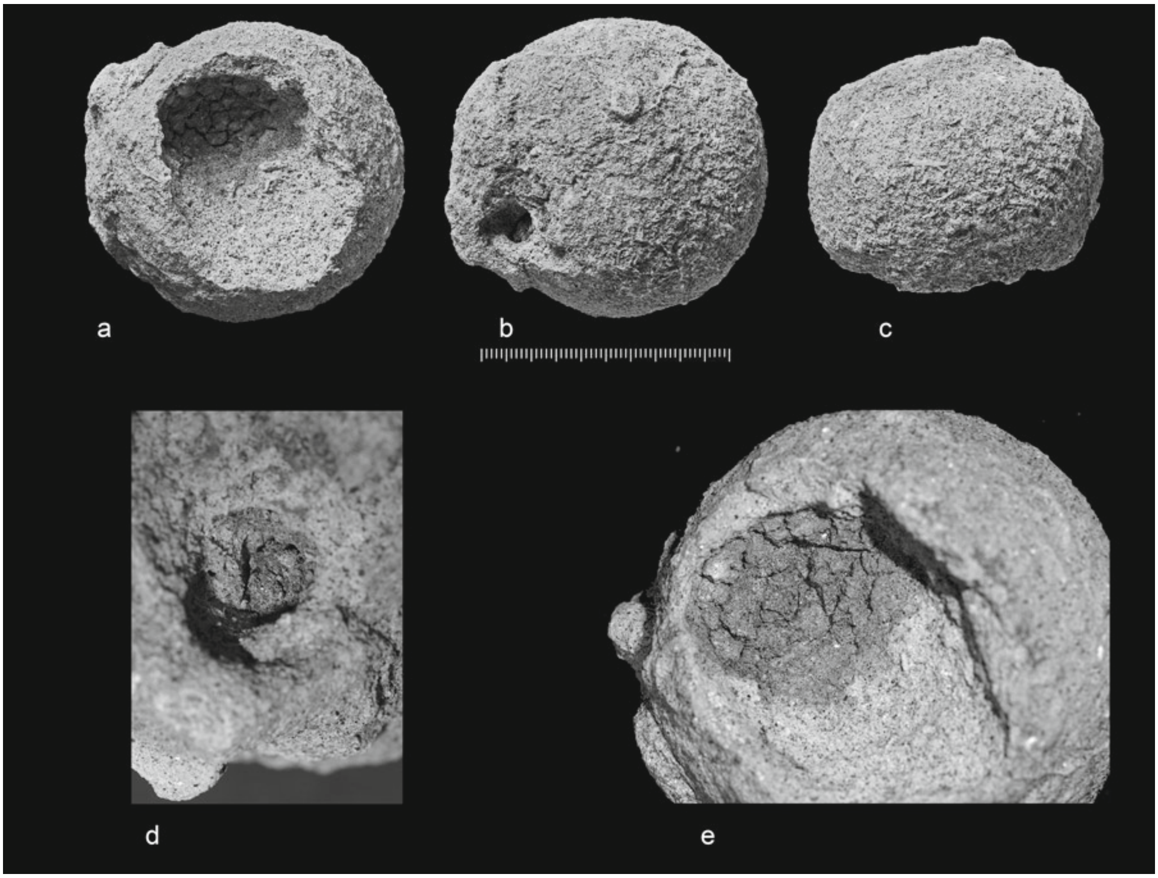

Fig. 19.14 *Lazaichnus amplus* isp.n., traces of kleptoparasites in fossil dung beetle brood ball, Laetoli. Paratype of *L. amplus* in *C. laetoliensis*, EP 1077/01; (**a**) from top; (**b**) bottom; (**c**) lateral; (**d**) outer opening; (**e**) view in large opening showing the dark internal trace of *L. amplus*. Scale (for Fig. 19.14a–c) in mm

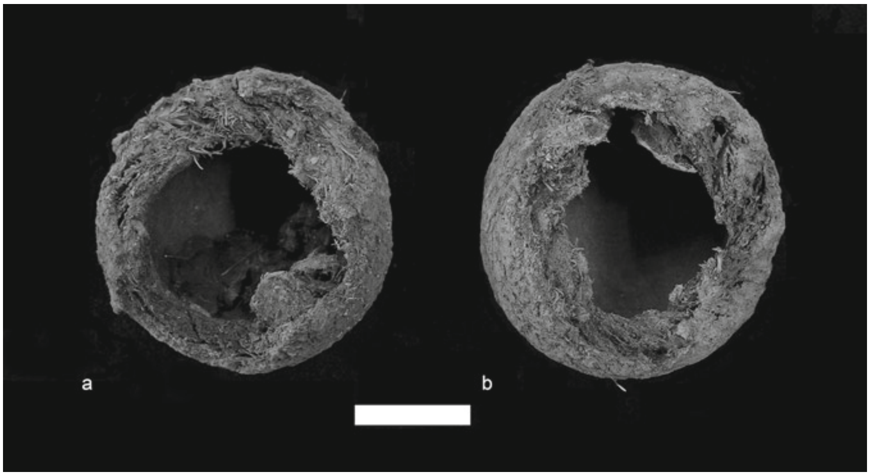

Fig. 19.15 Recent dung beetle brood balls excavated and preyed on by bat-eared foxes (*Otocyon megalotis*) in the Laetoli area, showing an irregular large opening. Scale: 30 mm. Specimens deposited in National Museum of Tanzania, Dar es Salaam. Photo: T. Harrison

surrounding bulge-like collar. Outer wall of sphere between 4.5 and more than 15 mm thick. Internal (filled) chamber opens directly to the upper aperture.

Diagnosis. Spherical to slightly pear-shaped structure with single chamber and upper opening with neck; differs from *Coprinisphaera kraglievichi* (Roselli, 1939) from

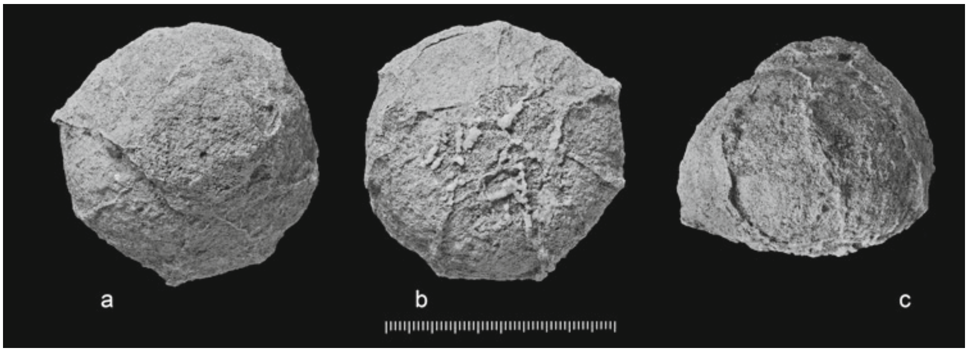

Fig. 19.16 *Coprinisphaera laetoliensis* isp.n., fossil dung beetle brood ball, Laetoli, EP 1719/03. Before cut; (**a**) from top; (**b**) bottom; (**c**) lateral. Scale in mm

Uruguay and Argentina by the larger size (more than 53 mm equatorial diameter versus 32–42.4 mm).

Discussion. The size of dung beetle brood balls varies intraspecifically, but generally stays within 20–30% (Lengerken 1954; Klemperer and Boulton 1976; Klemperer 1983; Sato and Imamori 1987). A brood ball of 60.6 mm diameter is unlikely to belong to the same species as one of 32 mm diameter. Although, according to a recently published convention (Bertling et al. 2006), the possible tracemaker should not be considered as defining character for ichnospecies, I consider it inappropriate to typologically combine specimens under one ichnospecific name that are most likely produced by different tracemaker species.

Trace maker. Sands's (1987) interpretation of a *Coprinisphaera* from Laetoli as resembling a brood ball of *Heliocopris* Hope might be right. The large size and the shape (spherical to slightly pear shaped) of the brood balls are typical for extant *Heliocopris* (cf. Klemperer and Boulton 1976), but could also be produced by large *Catharsius* Hope species or even by large rollers such as *Kheper* Janssens (Sato and Imamori 1987) in which the mother beetle scrapes the brood balls into a spherical shape during the development of the larva.

Nomenclatural note. Coprinisphaera Sauer, 1955 is a junior subjective synonym of *Fontanai* Roselli, 1939 (Laza 2006), but is in prevailing usage (Krell 2007). Genise et al. (2006) and Krell (2008) proposed conservation of *Coprinisphaera* with the International Commission on Zoological Nomenclature. The ICZN (International Commission on Zoological Nomenclature 2008) has ruled that *Coprinisphaera* is to be maintained as the valid name.

Coprinisphaera ndolanyanus Krell, ichnosp. n.

Derivatio nominis. Adjective meaning "belonging to Ndolanya", the stratigraphic unit where it was found.

Holotype. EP 824/01 (Fig. 19.17), Laetoli Locality 18: Upper Ndolanya Beds; deposited in the National Museum of Tanzania, Dar es Salaam; maximum height: 33.7 mm; equatorial diameter: 27.1–27.6 mm, width neck: 10.5–12 mm; cut medianly in half. Pear-shaped (sphere with neck on top), tip of neck slightly impressed. Homogenous steinkern; no internal structures visible.

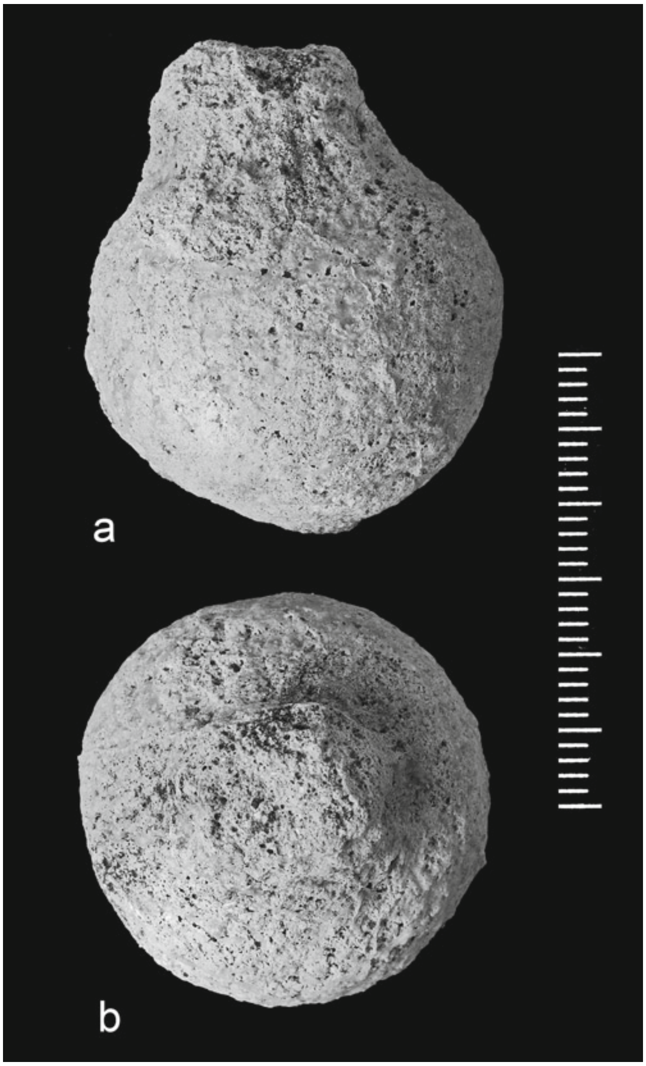

Fig. 19.17 *Coprinisphaera ndolanyanus* isp. n., fossil dung beetle brood ball, Laetoli. Holotype, EP 824/01. Before cut; (**a**) lateral; (**b**) from top. Scale in mm

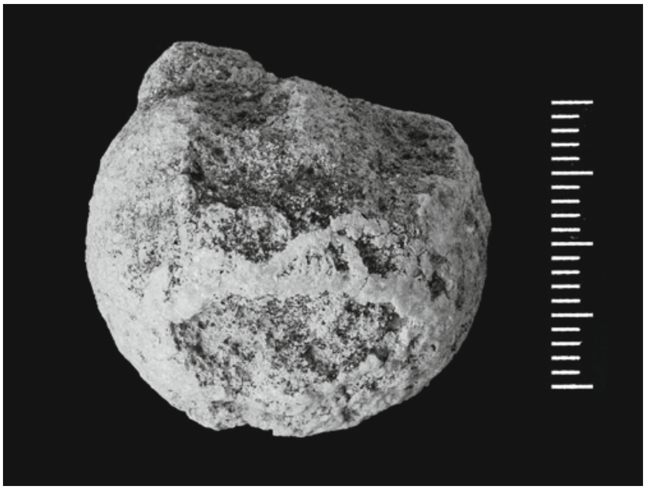

Fig. 19.18 *Coprinisphaera ndolanyanus* isp. n., fossil dung beetle brood ball, Laetoli. EP 3335/00. Scale in mm

Additional Material. EP 3335/00 (Fig. 19.18), Laetoli Locality 18: Upper Ndolanya Beds; maximum height: 30.0 mm; equatorial diameter: 27.5–28.4 mm; cut medianly in half. Sphere, one half with smooth surface, damaged on the other side (possible neck missing), next to damage with oval depression; no internal structures visible.

Description. Pear-shaped solid structure with upper impression in long neck, probably indicating a former opening; height: 30.0–33.7 mm; equatorial diameter: 27.1–28.4 mm; neck diameter: 10.5–12.0 mm. No internal structure visible.

Diagnosis. Pear shaped solid structure; differs from *Coprinisphaera kheprii* Laza, 2006 (height of holotype 56.1 mm) from Argentina by the smaller size and the longer, more slender upper protuberance. The upper protuberance of *C. tonnii* Laza, 2006 is thicker and more bulge-like than in *C. ndolanyanus,* containing an egg chamber. *Coprinisphaera ndolanyanus* differs from the globular *C. laetoliensis* from the same locality by the smaller size and the shape.

Discussion. A distinct outer wall of the brood balls is the diagnostic character that distinguishes *Coprinisphaera* Sauer (dung beetle brood balls) from *Pallichnus* Retallack, 1984 (supposedly pupal chambers). Neither specimen of *C. ndolanyanus* shows this character due to the type of preservation (original substance replaced by calcium carbonate). However, the pear-shaped form of the holotype is an unequivocal indication of scarabaeine brood balls (Halffter and Edmonds 1982) which originally might not have had a different outer wall structure than *C. laetoliensis*. *Coprinisphaera ndolanyanus* is much smaller than the holotype of the pear-shaped *C. kheprii*, but other known specimens assigned to *C. kheprii* have an equatorial diameter from 28.5 to 60.5 mm. This size range is much larger than the 20–30% size range of brood balls of a single dung beetle species (see above). Thus, I compared the size of *C. ndolanyanus* with the size of the holotype of *C. kheprii* only. The equatorial diameter of the smallest *C. kheprii* would fall into the specific size range of *C. ndolanyanus*, but the minimum height of *C. kheprii* is 50 mm, much larger than in the latter.

Trace maker. Pear-shaped brood balls are typical for dung rollers (Scarabaeini, Gymnopleurini) (Lengerken 1954) that are abundant in recent Afrotropical coprocenoses.

Lazaichnus amplus Krell, ichnosp. n.

Derivatio nominis. Amplus (Latin) = vast, spacious; adjective.

Holotype. EP 1719/03, Specimen B (Fig. 19.12) (paratype of *Coprinisphaera laetoliensis* ichnosp.n.), Laetoli Locality 15: Upper Ndolanya Beds; deposited in the National Museum of Tanzania, Dar es Salaam. *Coprinisphaera* is cut medianly in half, hitting one hole of *Lazaichnus amplus* (11.4 mm diameter). The other hole has an outer diameter of 8–11 mm.

Paratype. EP 1077/01 (Fig. 19.14) (*Coprinisphaera laetoliensis*), Laetoli Locality 15: Upper Ndolanya Beds; deposited in the National Museum of Tanzania, Dar es Salaam. The chamber behind the opening of *Lazaichnus* is visible in the large upper opening in *Coprinisphaera*. Hole diameter: 14–15.3 mm with lateral lighter infilling, diameter of proper hole: 8.5 mm.

Description. Holes in fossil dung beetle brood balls of 8–15.3 mm diameter, with a simple gallery or an expanding chamber extending into the inner core of the brood ball.

Diagnosis. Holes leading to a gallery in fossil dung beetle brood balls (*Coprinisphaera*), differ from the only other species of the ichnogenus, *Lazaichnus fistulosus* Mikulaš and Genise, 2003, by the larger diameter of the opening and the simple structure of the gallery, which forms a simple tube or a chamber in *L. amplus*, but often a more complex system of tubes in *L. fistulosus*.

Trace maker. The large diameter of the holes indicates kleptoparasites much larger than *Cleptocaccobius* Cambefort or kleptoparasitic *Aphodius* Illiger (the most abundant representatives of this guild in Africa). Current Afrotropical kleptoparasites of a matching size belong to *Onthophagus*, *Hyalonthophagus* and *Pedaria* (Scarabaeinae).

Biology

Schizonychini, Dynastinae, dung beetles and their kleptoparasites are distributed in all vegetation zones, from tropical rain forest to arid regions. The same is true for the paleoenviroments of the *Coprinisphaera* ichnofacies, but most are associated with open grasslands (Genise et al. 2000). Schizonychini feed on leaves as adults and on roots as larvae.

Dynastinae feed on various living and rotting plant material. Thus, the scarab fossils and ichnofossils do not contradict the current hypothesis of a savanna-forest ecotone paleoenvironment at Laetoli (Kingston and Harrison 2007; Su and Harrison 2007).

Conclusions

Laetoli is one of the few lagerstätten where insect fossils are preserved three-dimensionally. Whereas reconstructions are the only way to visualize the body shape of common fossil imprints, the Laetoli fossils are almost undistorted replicas of the original bodies which made formal description and naming of an exceptionally character-rich rhinoceros beetle fossil possible. External morphology of beetles is often a reliable indicator of habits, habitats or soil types (e.g., Medvedev 1965). Adaptive traits are most clearly expressed in the legs, the body parts interacting most extensively with the physical environment. However, with legs missing or only partly preserved the beetle fossils of Laetoli do not indicate a particular habitat.

Extant dung beetles producing brood balls of the size found at Laetoli are distributed in subtropical and tropical regions. In the Afrotropics, the highest abundance of dung beetles is in savannas (Cambefort and Walter 1991), where we also find the highest density of kleptoparasitic dung beetles (Krell et al. 2003). The existence of large fossil dung beetle brood balls in Laetoli, some with traces of kleptoparasites, indicates a higher probability for grassland rather than an arboreal area.

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Chapter 20
Lepidoptera, Insecta

Ian J. Kitching and S. Sadler

Abstract A fossil Lepidoptera from Laetoli is described and illustrated. EP 352/03 is a pupa of an Emperor Silkmoth (Saturniidae) belonging to the tribe Bunaeini of the subfamily Saturniinae. Comparisons are made with pupae of several extant species of Bunaeini, the closest match being with *Cirina forda*, allowing aspects of the biology of EP 352/03 to be predicted.

Keywords Fossil • *Cirina* • Pupa • Saturniidae

Introduction

This paper describes and illustrates a well-preserved fossil of a lepidopteran pupa from Laetoli. It is somewhat dorsoventrally compressed, but most of the important morphological features are visible and show that it is a species of Emperor Silkmoth (Saturniidae) in the subfamily Saturniinae, tribe Bunaeini.

Lepidoptera Phylogeny and Classification, with Special Reference to Saturniidae

The Lepidoptera, butterflies and moths, include some of the most attractive and conspicuous of all insects, as well as some of the world's most destructive agricultural pests. There are presently some 150,000 described species, arranged into 46 superfamilies, although the total number of extant species may be double, or even triple that figure (Kristensen and Skalski 1998). The phylogenetic interrelationships of the lower lepidopteran lineages (i.e., those as far as the Ditrysia) are generally agreed, and form a classical "Hennigian comb". Among the lowest three superfamilies, there is still some disagreement as to whether Micropterygoidea or Agathiphagoidea is the closest sister-group of the remaining Lepidoptera, although the weight of evidence is in favor of the former. These two superfamilies, together with the Heterobathmioidea, are the Lepidoptera that lack the characteristic proboscis that is generally associated with butterflies and moths. This structure, among others, is a synapomorphy of the Glossata, within which there are six clades: Eriocranioidea, Acanthopteroctetoidea, Lophocoronoidea, Neopseustoidea, Exoporia and Heteroneura. The first five taxa are relatively species poor, with most Lepidoptera belonging to the Heteroneura, characterized by different forewing and hindwing venations. The relationships among the five heteroneuran groups, Incurvarioidea, Nepticuloidea, Tischerioidea, Palaephatoidea and Ditrysia, remain problematical, particularly with regard to the relationships of Palaephatoidea (Davis 1986).

The Ditrysia, which comprises almost 99% of extant lepidopteran species, is characterized by a specialized female genital structure in which copulation and oviposition take place through two separate openings, connected by an internal tube through which spermatozoa are transferred from one system to the other. The group is relatively homogeneous in structure, which has made resolving its internal phylogenetic structure difficult. Consequently, the interrelationships of its 33 constituent superfamilies remain unclear (Minet 1991; Kristensen and Skalski 1998). Minet (1983) tentatively united all ditrysian superfamilies, except Tineoidea, Gracillarioidea, Yponomeutoidea and Gelechioidea, as the taxon Apoditrysia, on the basis of the structure of abdominal sternum II. Minet (1986) proposed Obtectomera for a large subset of Apoditrysia characterized by immobility of pupal segments I-IV. However, this feature is subject to considerable homoplasy, but Minet (1996) found additional support for the group in the structure of the pretarsus.

Historically, the Lepidoptera were divided into Microlepidoptera (small moths) and Macrolepidoptera (large moths and butterflies), both of which are rendered polyphyletic in the current classification. However, on the basis of a modification of the first axillary sclerite of the forewing base,

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Minet (1991) restricted and redefined the Macrolepidoptera to include the superfamilies: Mimallonoidea, Lasiocampoidea, Bombycoidea, Drepanoidea, Geometroidea, Noctuoidea, Axioidea, Calliduloidea, Hedyloidea, Hesperioidea and Papilionoidea.

Of these, the only superfamily relevant to the fossil material discussed below is Bombycoidea, comprising families: Eupterotidae, Bombycidae, Endromidae, Mirinidae, Saturniidae, Carthaeidae, Lemoniidae, Brahmaeidae and Sphingidae. The relationships among these groups were analyzed by Minet (1994) and summarized by Lemaire and Minet (1998). Again, the only family pertinent to the specimens discussed below is Saturniidae. The family was redefined by Minet (1994) and now includes eight subfamilies. Oxyteninae, Cercophaninae, Arsenurinae, Ceratocampinae and Hemileucinae are exclusively New World in distribution; Agliinae, Salassinae and Saturniinae are found mostly in the Old World, with only a few Saturniinae genera (i.e., *Actias*, *Antheraea*, *Callosamia*, *Copaxa*, *Eupackardia*, *Hyalophora*, *Rothschildia*, *Saturnia*) in the New World. Minet (1994) and Lemaire and Minet (1998) recognized a further subfamily, Ludiinae, but this is now placed as a tribe (as Micragonini) within Saturniinae, which also contains the tribes Attacini, Bunaeini, Saturniini and Urotini (Nässig and Oberprieler 1994; Oberprieler 1997). Attacini and Saturniini are found throughout the World, but Bunaeini, Micragonini and Urotini are exclusively African, the sole exception being the Urotini genus, *Sinobirma*, which is found in NE Burma and SW China (Rougerie 2003).

Fossil History of Lepidoptera

The most recent comprehensive review of fossil Lepidoptera is that of Kristensen and Skalski (1998), from which the following summary is largely derived. They noted that compared to other insect groups, the fossil records of Lepidoptera is poor, which they attributed, in part at least, to the relative fragility of lepidopteran wings and bodies. Overall, only some 600–700 fossil Lepidoptera were known at that time, of which 70–80% were preserved in amber or other resins. The majority of lepidopteran fossils are of adults, but fossil caterpillars, larval mines and cases, pupae (Kristensen and Skalski 1998, and references therein), and even an egg (Gall and Tiffney 1983), have been recorded, together with dissociated scales and remains in the stomachs of fossil bats (Richter and Storch 1980). The lepidopteran fossil record is also relatively short, with fossils that can be unambiguously assigned to the order only occurring in the last 60 million years or so.

The richest source of Lepidoptera fossils is Baltic amber from the early Eocene (~55–54 Ma), with relatively few, though no less important, samples coming from the rather younger Dominican amber (late Eocene to middle Miocene, ~40–15 Ma). Lepidoptera from sedimentary rocks are most frequent in the late Eocene Florissant shales of Colorado. Other sites in the Northern Hemisphere that have yielded fossil Lepidoptera occur in Croatia, France, Germany, Great Britain, Italy and southern Russia. Southern Hemisphere sites are much less frequent, with Pre-Quaternary fossil Lepidoptera reported only from Brazil (Martins-Neto and Vulcano 1989) and Australia (Rozefelds 1988).

Lepidopteran fossils from Africa are extremely rare. A geometrid moth preserved in fossil Zanzibar copal was described and illustrated, but not formally named, by Evers (1907), who considered it to be close to the genus *Hyperythra*, and particularly *H. lutea* (Stoll) from SE Asia. Leakey (1952) illustrated an apparently large lepidopteran larva from the early Miocene deposits on Rusinga and Mfangano Islands in Lake Victoria, Kenya. The general smooth shape and secondary annulations of the body suggest this fossil may belong to the family Sphingidae (hawkmoths), although it lacks the anal horn typical of larvae of that family. Hill (1987) reported damage to fossil bones from Laetoli consistent with that caused by larvae of ceratophagous tineid moths. He also reported similar examples of damage to fossil bovid bones from the Shungura Formation, Omo Valley, Ethiopia.

Kristensen and Skalski (1998) provided a group-by-group summary of known lepidopteran fossils. The majority are amber-preserved Microlepidoptera, which, due to their small size, are perhaps more readily entrapped in resin than larger moths and butterflies. It is also possible that the readily detached scales that cover the bodies of Lepidoptera prevent larger and stronger individuals from becoming so easily ensnared in sticky resin, such individuals merely sacrificing some of their scales in order to make good their escape. Most macrolepidopteran fossils are compression fossils, consisting of single wings to entire specimens, and can be extremely well preserved, even providing details of wing patterns (e.g., the butterfly, *Prodryas persephone*, see Kristensen and Skalski 1998: Fig. 20.2.7).

Of the superfamily Bombycoidea, which includes the hawkmoths (Sphingidae), emperor silkmoths (Saturniidae) and true silkmoths (Bombycidae), only two formally named fossils are known, both currently placed in the Sphingidae. A fossil from Pliocene deposits at Willershausen, Germany, that purportedly shows several segments of a prepupal caterpillar with an anal horn, was named by Kernbach (1967) as *Sphingidites weidneri*. However, Kozlov (1988) considered the family assignment of *Sphingidites* to be unsubstantiated. Certainly, an anal horn is typical of most sphingid larvae, but it also occurs on larvae of several other families, both within and outside Bombycoidea, and thus the assignment of *Sphingidites* to family Sphingidae must be treated as tenuous at best. Moreover, Brauckmann et al. (2001) considered that both the genus and species names were *nomina nuda* because the original description did not include a differential diagnosis. A more convincing sphingid fossil is that of *Mioclanis shanwangiana*, described by Zhang et al. (1994) from middle Miocene (~15–17 Ma) deposits at Shanwang, Shandong, China. This fossil is a large, fat-bodied moth seen in dorsal view. The wing venation, general shape, and especially the shape and relative sizes of the two pairs of wings, are consistent with it being a hawkmoth. A third candidate for a sphingid fossil is the larva mentioned above that was illustrated by Leakey (1952), but further study is required to confirm its placement in this family. A fourth fossil, *Sphinx snelleni*, described as a sphingid from the upper Jurassic Solenhofen limestone deposits in Bavaria, Germany, by Weyenbergh (1869) has since proved to be a wood wasp of the hymenopteran family Siricidae. Skalski (1990) recorded Sphingidae from Baltic amber, but Ross (1996) considered this claim also to be unsubstantiated. There are no known fossils of any other bombycoids.

Description

Field Number: EP 352/03
Locality: Laetoli Loc. 3
Horizon: Laetoli Beds, upper unit, 60–70 cm above Tuff 7. From a soft pale brown clay horizon, 11 cm thick, rich in fossil plant material, insects, and ruminant coprolites (see Harrison 2011, Harrison and Kweka 2011).

EP 352/03 (Fig. 20.1a, b) is the pupa of a large species of Macrolepidoptera. Length: 37 mm; width: 15 mm; depth: 11 mm; width slightly greater and depth rather less than they would have been in life due to dorso-ventral compression. Head: genae and labrum lacking protuberances; eyes rugose; antennae broad (indicating a pectinate antenna in the adult moth); proboscis short (and thus probably non-functional in the adult), reaching only as far as the ends of the antennae, with several shallow transverse grooves basally. Thorax: a low median ridge running from near the anterior edge of the prothorax to the posterior edge of the metathorax; anterior edge of prothorax with a transverse rugose ridge, highest towards the midline but there notched; prothoracic spiracle slit-like, without strongly raised anterior and posterior raised flanges but with short, low, even rims; foreleg visible ventrally between proboscis and antennae; mesothorax with a pair of subdorsal raised circular calli; metathorax with a pair of transversely elongate calli, anterior margins indented, posterior margins raised and slightly overhanging (Fig. 20.1c); forewings broad, meeting on the midline posterior to the ends of the antennae and proboscis; hindwings with posterior edges only visible along posterior edges of forewings. Abdomen: surface of anterior segments apparently smooth, without conspicuous roughness or rugosity, but posterior segments covered in numerous minute bumps, especially ventrally; spiracles with raised elliptical rims; posterior margins of segments strongly overhanging, those of segments 2, 3 and 7 with internal radial supporting struts (Fig. 20.1g); segment 8 ventrally complete and unmarked, only a single gonopore visible ventro-medially on segment 9, indicating the pupa is a male; dorsum of segment 10 with a pair of shallow median pits and a similar pair more laterally on the anterior margin, separated by a low, rounded ridge (Fig. 20.1h); cremaster broken but apparently trifurcate.

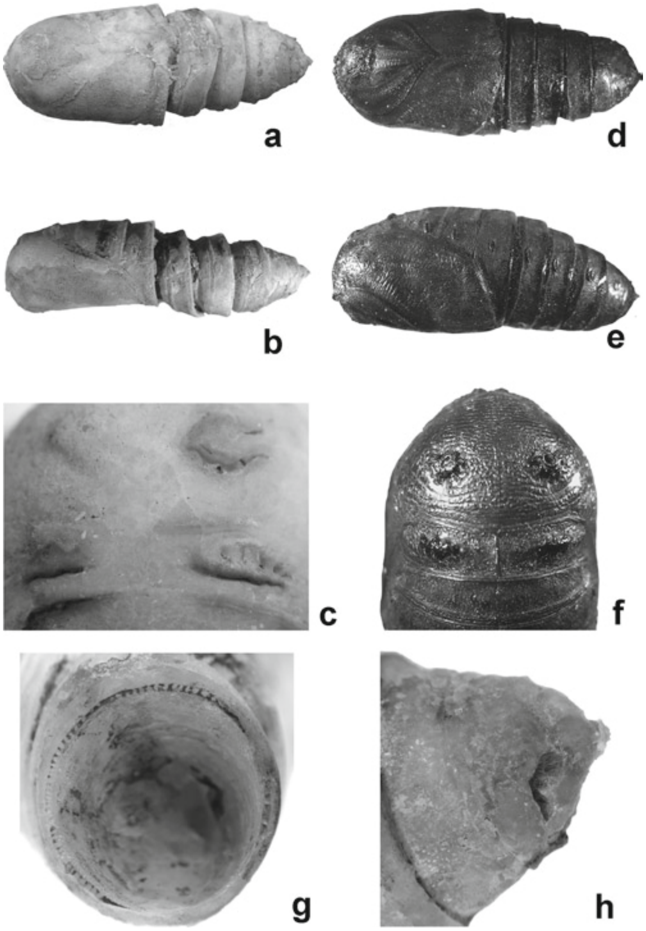

Fig. 20.1 (**a**) EP 352/03, oblique ventral view; (**b**) EP 352/03, lateral view; (**c**) EP 352/03, close-up of mesothoracic and metathoracic calli; (**d**) *Cirina forda* pupa, South Africa [BMNH], oblique ventral view; (**e**) *Cirina forda* pupa, South Africa [BMNH], lateral view; (**f**) *Cirina forda* pupa, South Africa [BMNH], close-up of mesothoracic and metathoracic calli; (**g**) EP 352/03, posterior view showing radial supporting struts around the posterior margin of abdominal segment 7; (**h**) EP 352/03, oblique dorsal view of abdominal segment 10 showing the shallow L-shaped groove

Taxonomy

Based on a survey of the immature stages collection of the Natural History Museum, London (BMNH), EP 352/03 undoubtedly belongs to tribe Bunaeini, subfamily Saturniinae, of the emperor silkmoth family Saturniidae. This tribe currently contains about 190 species classified into between 15 and 23 genera depending upon the classification adopted, and is exclusively Afrotropical in distribution. However, the immature stages of only a relatively small number of these species have been described and specimens of even fewer are represented in the BMNH collections. Thus, the following comparison, encompassing only twelve species from nine genera, is far from comprehensive. The nomenclature follows Bouyer (1999).

Athletes ethra (Westwood) differs from EP 352/03 in having interrupted longitudinal subdorsal ridges along the first three abdominal segments, much higher metathoracic calli, low ridges along the inner edges of the eyes and a pair of low protuberances on the genae lateral to the labrum at the base of the proboscis. The latter two of these features are also found in *Pseudobunaea epithyrena* (Maassen and Weyding), in which the prothoracic ridge is almost absent. *Bunaea alcinoe* (Stoll) likewise has extremely reduced prothoracic ridges and also has conspicuous raised flanges either side of the prothoracic spiracle that are lacking in EP 352/03. *Imbrasia ertli* Rebel lacks both a prothoracic ridge and mesothoracic calli, and *Pseudimbrasia deyrollei* (Thomson) is another species with conspicuous protuberances at the base of the proboscis. Other species of *Imbrasia* are closer matches for EP 352/03. *Gonimbrasia* (*Gonimbrasia*) *zambesina* (Walker) has a prothoracic ridge that is slightly too high and rather larger thoracic calli. Also, in ventral view, the head and thorax of that species, as well as that of *G.* (*G.*) *tyrrhea* (Cramer), is parallel-sided, whereas EP 352/03 converges somewhat anteriorly. This latter shape is found in both *Gonimbrasia* (*Nudaurelia*) *macrothyris* (Rothschild) and *G.* (*G.*) *belina* (Westwood), but in these two species, the prothoracic ridge is higher and the general body surface apparently rougher than in EP 352/03. *Imbrasia obscura* (Butler) differs in having a pair of deep pits dorsally on abdominal segment 10, unlike the shallow grooves of EP 352/03. The closest match for EP 352/03 is *Cirina forda* (Westwood) (Fig. 20.1d–f), which agrees in most essential characters, particularly in having radial supporting struts around the posterior margins of abdominal segments 2 and 3 dorsally and around the entire circumference of segment 7, and a pair of shallow L-shaped grooves on the dorsum of abdominal segment 10. The seven available pupae of *C. forda* differ in being somewhat smaller (26–29 mm in length) and having a pair of minute lateral protuberances on the labrum that are not apparent on EP 352/03 (but which could have been compressed or worn away).

We can confidently conclude, therefore, that EP 352/03 is a member of the saturniid tribe Bunaeini, probably very near *C. forda* (Fig. 20.2). However, we cannot identify it for certain with that (or any other) particular species due to the large number of as-yet unexamined species in the tribe. For the same reason, we refrain from formally describing and naming the specimen. Nevertheless, it is the first fossil Saturniidae, and apparently also the first fossil lepidopteran pupa, to be discovered in mainland Africa.

Paleobiology

Although we cannot identify EP 352/03 with any particular extant species, knowing that it is a member of the tribe Bunaeini allows us to predict certain aspects of its paleobiology. Bunaeini conform to the caricature of saturniid moths described by Janzen (1984). Thus, the adult of the species to which EP 352/03 belonged would be broad-winged with eyespots on the hindwing used in a flash-defence (the eyespots of *C. forda* [Fig. 20.2] are reduced and not typical of the group). It has a reduced, non-functional proboscis and so would not feed. Females would probably emerge from the pupa in the evening and once the wings had expanded and dried, would call the nocturnally active males using pheromones produced from glands at the tip of the abdomen. Being

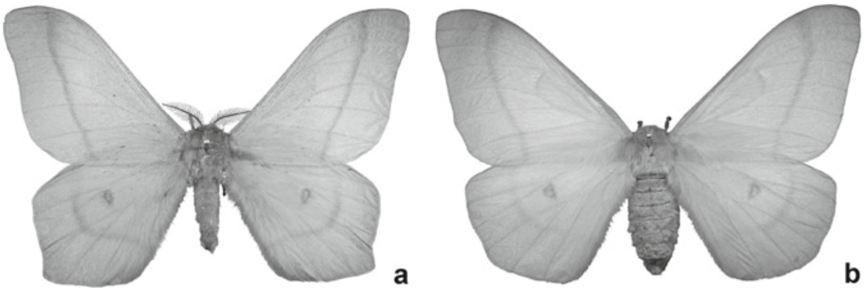

Fig. 20.2 (**a**) *Cirina forda* adult male: N.W. Rhodesia [Zambia]: Solwezi, 27.ix.1917, H.C. Dollman leg. [BMNH]. (**b**) *Cirina forda* adult female: N.W. Rhodesia [Zambia]: Solwezi, 11.x.1917, H.C. Dollman leg. [BMNH]

a male, EP 352/03 has strongly bipectinate antennae that it would have used to locate a female as quickly as possible. Mating would typically last a few hours and the pair would separate before dawn. The mated female would then search out the larval host plant on which to lay her batch of several hundred eggs. Following mating, and being unable to feed, the adult of the species to which EP 352/03 belonged would have died within a matter of days.

Extant bunaeines feed on trees belonging to many genera in a wide variety of families, but with a preponderance of records from Euphorbiaceae, Myrtaceae and especially Fabaceae (Robinson et al. 2001). Such plants can be nutritionally poor and larval development protracted, exposing them to predation for an extended period, and so saturniid larvae have developed a variety of defensive mechanisms, including camouflage and poisonous spines (Janzen 1984). Full grown *Imbrasia* and *Cirina* larvae are large (60–100 mm in length), black with numerous white and yellow speckles, and have either spinose protuberances ("scoli") or dense hairs (e.g., illustrations in Oberprieler 1995). Such a colour pattern is suggestive of aposematism, advertising unpleasant or poisonous qualities, but bunaeine larvae are apparently palatable. They are also often highly gregarious, those of *C. forda* forming compact, writhing masses of several hundred individuals. When full grown, the larvae descend from the trees, find a patch of soft, damp soil, then dig down around 10 cm (sometimes more) to pupate in an earthen cell (Oberprieler 1995). Bunaeine emperor silkmoths are found in a wide variety of habitats, from rainforest to semi-deserts. Where there is a pronounced dry season, this is generally passed in the pupal stage and there is only a single generation per year, with adult emergence synchronized with the arrival of the rainy season to ensure availability of fresh leaf growth for the caterpillars. Where there is a lesser or no marked seasonality, it is the rate of larval development that constrains the number of generations per year, generally to no more than two (Oberprieler 1995). *Cirina forda* inhabits a variety of woodland habitats, including bushveld and thornveld, mainly below 1,500 m (Cooper and Cooper 2002), and it is likely that the species to which EP 352/03 belonged inhabited similar habitats.

As a result of their large size and great numbers, bunaeine larvae can be important as defoliators of plantation trees. For example, *Gonimbrasia* (*Nudaurelia*) *cytherea* (Westwood) can be a serious pest of pine plantations in South Africa (Tooke and Hubbard 1941; Van den Berg 1973, 1975). But bunaeines are perhaps even more important as a food resource. The most famous is undoubtedly the Mopane Worm, *Gonimbrasia* (*G.*) *belina*, enormous quantities of which are collected each year for both local consumption and for export (Oberprieler 1995; Latham 1999, 2001; Mbata et al. 2002; Mbata and Chidumayo 2003). However, larvae of many other bunaeine (and other saturniid) species are collected as food by humans. Those of *C. forda* are collected in many parts of southern Africa (Oberprieler 1995), and so it is entirely possible that the species to which EP 352/03 belongs was collected and eaten by the hominins living contemporaneously at Laetoli.

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Chapter 21
Trace Fossils Interpreted in Relation to the Extant Termite Fauna at Laetoli, Tanzania

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Abstract The Laetolil Beds of Pliocene volcanic ashes contain numerous trace fossils. Many of them resemble the hives and foraging passages of extant termites, having been preserved and more or less altered by deposition of calcite and other minerals from ground water. The most abundant nest-like structures at Locs. 9 and 10 resemble hives of the termite *Macrotermes herus* that still occurs at the site. At Loc. 10W the commonest nest-like structures are flattened ovoids, which seem to have been small discrete hives filled with thin carton shelves. No exact modern counterpart is known. Several rarer types of hives may have been built by other *Macrotermes* species, and some by Apicotermitinae. At Kakesio a series of small, distinctive fossil hives with thick carton shelves and walls seem to have been built by another termite, of which again no modern counterpart is known. The extant termite fauna at Laetoli is briefly described. The general lack of information about the structures built by modern termites is discussed.

Keywords Hive • Endocast • Ventilation shaft • Foraging gallery • *Macrotermes* • *Hodotermes* • *Odontotermes* • Apicotermitinae

Introduction

Laetoli is notable for the many Pliocene fossils preserved in beds of volcanic ash. The ash possibly erupted from the volcano Satiman, 15 km to the East, and fell as primary air-fall ash in the Laetoli area (Hay 1987). Some of it was reworked by wind forming aeolian deposits, and some was probably transported as sheetwash and by rivers. It appears that heavy ash falls were succeeded by long quiescent periods during which vegetation grew, and soils developed on and into the ash beds. Animal remains on the surface, such as bones, gastropod shells and birds' eggs, and some plant material, were preserved by later ash falls (Leakey and Harris 1987; Verdcourt 1987; Harrison 2005). Shallow roots and burrows, such as those of solitary bees and wasps, were fossilized as traces near the surface (Ritchie 1987). The soil was also disturbed to a considerable depth by the roots of plants and the burrows, galleries and nests of soil-dwelling animals. The most conspicuous of these appear to have been termites, whose hives and passages have been preserved and altered (Sands 1987; Darlington 2005a). Later the ash beds became consolidated into rock. The fossiliferous sediments at Laetoli are exposed by erosion along streams that are branches of the Garusi and Olaitole Rivers. Elsewhere there is vegetation, predominantly grassland, on top of dark grey deep-cracking clay soil, called black cotton soil or mbuga, derived from later tuffaceous deposits.

I visited Laetoli briefly in 1976, and for a longer period in 2005. I examined trace fossils exposed at Locs. 9, 10W and (in 2005 only) Kakesio 3 (see Harrison and Kweka 2011) and also looked at living termites at many sites. Between my two visits, William A. and Kathleen Sands made two long field trips to Laetoli. Their contribution (Sands 1987) remains the prime source for descriptions, illustrations and measurements of the trace fossils. Sands interpreted most of them as being derived from structures built by termites, a diagnosis with which I agree entirely.

Exposures at Locality 9

The exposures are in a wide valley bottom. The areas of interest consist of a broad flat upper shelf worn down to a hard yellowish layer of tuff. The edge of this layer forms an irregular step about 1 m high. Below it is another broad flat shelf worn down towards a hard pavement layer (Tuff 6) about 5 cm thick, cracked into a distinctive "crazy paving" pattern. A small part of the edge of this lower step is exposed at the southern end of the site as a near-vertical face about 150 cm high, but the area below that is thickly overgrown with scrub (see Harrison and Kweka 2011).

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Fossil Termite Hives

The whole exposure has many structures that appear to be the fossilized hives of termite nests. Many survive only as remnants whose original size cannot be determined. They are mostly about 50–150 cm in diameter, but a few are much larger.

The bottom 5 cm or so of each hive became fossilized into a distinctive dense structure pierced by round holes about 8 mm across, called a "base-plate" by Sands (1987) (Fig. 21.1). They are flat or slightly concave, and are more resistant to weathering than the surrounding rock, so that they may be left standing up from the eroded rock surface around them, or perched on a short pillar. The rest of the contents of the hive have been altered by deposition and solution until they do not much resemble the original termite structures, but they have a characteristic structure of their own. Vermiform calcrete lumps are set in a soft matrix, which erodes away leaving a scatter of these lumps lying loose on and around the base-plates (Fig. 21.2). This resembles in miniature a deposit of the broken debris of stagshorn coral on a seashore. Sands (1987: 415) called this "broken columnar material", but as the debris is considerably altered, I prefer to use a more distinctive name and have adopted the field name of "twiglets".

A few hives are very large, up to 500 cm across, the central hive extending laterally into lobes that may be on the same level, or may extend down for as much as 120 cm, where they expand into flat-floored subsidiary lobes at a lower level (Fig. 21.3). Where hives sit directly on top of the pavement layer (Tuff 6) it appears to sag beneath them, sometimes gently, but in other cases quite markedly, so that the pavement is upturned at the hive edge (Fig. 21.4). This might be a result of the weight of a large termite mound compressing the soil beneath it. Alternatively, the termites may have penetrated through cracks in the pavement and brought

Fig. 21.1 Laetoli, Loc. 9 (1976). Base-plate of a small fossil nest, eroded out and tilted sideways. The lens cap is 5 cm in diameter

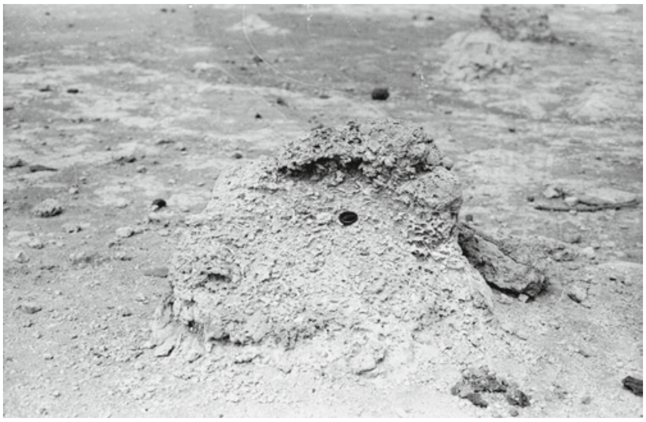

Fig. 21.2 Laetoli, Loc. 9 (1976). Remains of a small fossil termite hive eroded into a twiglet scatter on top of a base-plate, standing up from the erosion surface on Tuff 6. Probably built by *Macrotermes* sp. The lens cap is 5 cm in diameter

Fig. 21.3 Laetoli, Loc. 9 (2005). Remains of a large fossil termite hive (*upper left*) extending down into two long lobes at lower levels (*center and right*). Probably built by *Macrotermes* sp. The trowel is 24 cm long

Fig. 21.4 Laetoli, Loc. 9 (2005). Remains of the base-plate of a large fossil termite hive lying in a hollow in the pavement layer of Tuff 6, which is upturned at the edges. Probably built by *Macrotermes* sp. The trowel is 24 cm long

up soil from below to build their mound, causing the (then unconsolidated) soil beneath the pavement to subside.

A few relatively small hives are exposed in the step between upper and lower shelves, and these provide the only evidence of the structure of the hive roof. In most cases the hive contents are lost, leaving rounded hollows on the face of the step, all showing a domed roof with no ventilation passages. One hive seen in 1976 was 38 cm wide and 28 cm high, rounded in profile except for a flattened floor. It was particularly well preserved, showing endocasts of horizontal galleries 2–3 cm high. There was a gap between the top of the hive contents and the roof, crossed only by casts of small passages, with no sign of a ventilation system. A similar hive was found in 2005 in a chamber from which most of the roof had eroded away (Fig. 21.5). The chamber was 100 cm by 60 cm in width and at least 35 cm high. The upper part of the hive contents survived as five overlapping layers of calcrete 3–5 cm thick that appeared to be endocasts of horizontal galleries, preserving exactly the rounded ends where the galleries abutted the walls. These two hives were the only ones seen at this site in which the interior was preserved as endocasts, and not altered into twiglets. They may all have been nests of the same termite, but fossilized in different ways.

On the basis of these observations I can make a tentative interpretation. In the few very large hives, the flattened floors and extension of the hive periphery into lobes at the same or at lower levels suggests a species that has a centralized nest with brood and fungus combs in the same hive chamber. The large size points to this being a species of *Macrotermes* (Termitidae, Macrotermitinae). I have seen all these features in extant nests of *M. michaelseni* (Sjöstedt) around Kajiado, and of *M. herus* (Sjöstedt) at Mogotio, both sites being in Kenya. The most obvious difference between these two species is that *M. michaelseni* has a well-developed ventilation system in the mound above the hive (Darlington 1985), while *M. herus* does not, having only some small access passages and large flat-floored foraging passages and forage storage areas within the mound structure (Darlington 1988). Unfortunately, no intact roofs of the large fossil hives were found.

Fig. 21.5 Laetoli, Loc. 9 (2005). Remains of a small hive preserved as endocasts of the internal galleries, with the roof eroded away. Probably built by *Macrotermes* sp. The trowel is 24 cm long

The much commoner small hives, 50–100 cm in diameter, were probably smaller nests of the same species (or at least genus). There was no sign of subdivision into smaller chambers, within or outside the main hive, as would be expected in nests of *Pseudacanthotermes* or *Odontotermes* (Macrotermitinae), the only other termite genera that build nests of comparable size in the region. The few nests that were preserved as endocasts show galleries 2–5 cm high, such as are found containing fungus combs in extant small nests of both *M. michaelseni* and *M. herus* (Darlington 1985, 1988). Where the roof is preserved there is no sign of a ventilation system, suggesting that the builder was most similar to *M. herus*. It seems probable that both large and small hives were built by that species, which still occurs today at Laetoli.

Other Fossilized Structures

The Upper Laetolil Beds at Loc. 9 contain many calcified linear or vermiform structures of small size (at most a few centimeters in diameter). They are likely to be of two kinds: root casts and animal burrows. In dry tropical ecosystems the dominant burrow-makers are termites, followed perhaps by ants. Roots of trees and shrubs typically branch downwards, being reduced in size each time they branch, and they also tend to taper downwards even in the absence of branches. In contrast, termite passages may branch in any direction including upwards, and may also rejoin to form anastomosing networks. Small passages may branch off larger ones, but in general the passages do not change in size when they branch. Small termite passages are round in cross-section. Larger termite passages approximating to the horizontal usually have flat floors and low roofs (Darlington, 1982 in extant *M. michaelseni* nests, matched as trace fossils in Sands, 1987, Plate 11.1: 9 and 10). In contrast, roots are nearly always round in cross-section. Clear examples of all these structures were found as trace fossils at Laetoli, but it is likely that they occur together at some places, in which case they might be hard to distinguish.

At the southern end of the site, below Tuff 6, the deep ash layers are uniformly netted with a three-dimensional mesh of anastomosing passages that fork and rejoin without change in size. These look like termite passages, partly or wholly infilled with calcite to form either hollow pipes or solid rods. The original passages were round in cross-section and probably less than 1 cm in diameter, although in some places secondary solution has left a gap around the endocast, and in

Fig. 21.6 Laetoli, Loc. 9 (1976). Vertical section through anastomosing galleries in the layer below Tuff 6. The lens cap is 5 cm in diameter

other places the gap has been infilled with more calcite, thus exaggerating the size. These calcite casts are more resistant to solution and erosion than the surrounding rock, and can result in debris that somewhat resembles small twiglets, but is not concentrated into hive clusters as are the twiglets.

The anastomosing passages occupy a large volume of rock at fairly uniform density. They do not seem to be concentrated below or near to individual fossil hives, but they probably were not contemporary with them. At the best-exposed site (Fig. 21.6) the anastomosing passages were at high density and seemed all to be connected, showing they were all fossilized at the same time, perhaps when Tuff 6 was deposited. Such small passages probably would not survive for long in an active soil. The building and rebuilding of these passage networks must have been a major agent of bioturbation in what were then unconsolidated ash soils.

The main foraging galleries of extant *Macrotermes michaelseni* are not arranged like this (Darlington 1982), but as a horizontal network of flat-floored passages of varying size, with characteristic elongated pits for the temporary storage of forage, but it was noted that there were some connections from the main foraging galleries to small deeper-lying passages, which may correspond to the anastomosing passages at Laetoli. It would be difficult to trace such small passages in a modern soil, but the deposition of calcite has made them visible at Laetoli. It may be that this is how termites explore the soil to find dead roots of trees and shrubs, which we presume to be an important food source for them, although we cannot easily measure it.

Exposures at Locality 10W

Locality 10W has by far the greatest variety of termite trace fossils of any locality visited. Erosion has cut a gorge up to about 5 m deep into the Upper Laetolil Beds leaving isolated remnants as cliffs and pillars up to 4 m high. The upstanding faces contain many excellent vertical sections of fossilized structures within what used to be soils (see Harrison and Kweka 2011).

About half way up the local sequence a thin but distinct horizon of soft clay marks the erosion surface of a fossil soil formed during a long interval without fresh deposition. It is 6–8 cm thick, and is cracked into a crazy-paving pattern. Both Sands (1987: 410 onwards and Plate 11.2) and Darlington (2005a) mistakenly called this clay horizon Tuff 1 (T. Harrison, personal communication). Below it is a bed of reworked ash about 150 cm deep containing many termite-like features and root casts, probably contemporary with that fossil soil. Below that again is the true Tuff 1, dated at 3.76 Ma (Drake and Curtis 1987).

Above the clay horizon is another bed of ash 170 cm deep showing weak bedding structures at intervals of 50–100 cm. On top of this bed is Tuff 2, a harder layer about 30 cm deep, which caps the well-preserved vertical profiles.

Fossil Termite Nests

Flattened Ovoids

By far the commonest type of fossil hive at Loc. 10W is the flattened ovoid (called "thick-layered ovoid" by Sands 1987: 410). It is circular or oval in plan; in vertical profile it is biconvex with the roof more deeply curved than the floor, and rounded at the edges. Sands measured a series of exposed ovoids and found mean values of 34.5 ± 16.4 cm diameter and 14.6 ± 6.3 cm height ($n = 46$), a ratio of width to height of 2.4:1. In the best-preserved examples the hive contents have been converted into thick, roughly horizontal layers of calcrete, incompletely separated by very narrow horizontal cracks. The whole structure is more resistant to erosion than the surrounding rock, resulting in ovoids perched on the top of pillars of rock, some of which are several meters tall.

One ovoid has been broken to disclose a vertical face (Fig. 21.7; Sands 1987, Plate 11.4:25) showing how the layers and the cracks are related to each other. It appears that the layers are endocasts of horizontal galleries, while the cracks represent the shelves and pillars that separated them, now eroded out. The galleries were about 1 cm high and the shelves were only 1–2 mm thick, and at their outer edges were joined to an equally thin smooth external wall. Another ovoid sectioned in the wall of the gorge also shows the pattern of endocasts and shelves very clearly (Fig. 21.8). A thin layer of tuff lies just above its roof, but this nest was younger than the tuff and was built down through it from a later soil.

Fig. 21.7 Laetoli, Loc. 10W (1976). Vertical face of a flattened ovoid, exposed by erosion and then broken. The lens cap is 5 cm in diameter

Fig. 21.8 Laetoli, Loc. 10W (2005). Vertical section through a flattened ovoid *in situ*. The hive was built down from a higher soil profile to just below a thin tuff, some fragments of which have slipped down. The lens cap is 5 cm in diameter

The ovoids do not appear to have been built by fungus-growing termites because the galleries were too narrow to accommodate fungus combs, and no traces were found of any external structures that could have been associated fungus comb chambers. The shelves and pillars were so thin that they were probably built out of pure organic carton.

The interpretation of these very distinctive structures is somewhat controversial. Sands (1987, Fig. 11.12: 69) proposed that the ovoids originated as the lower central part of nests of *Macrotermes herus* (as *M. subhyalinus*), the rest of the nest and mound having collapsed around them. I saw no sign of any collapsed structures around ovoids seen in vertical section, and Fig. 21.8 would seem to exclude this explanation. Sands interpreted the "thick layers" (my endocasts) as built shelves, and the cracks between (my shelves) as the passages occupied by the termites.

Of the extant termite fauna, the likeliest candidate as builder would be *Hodotermes mossambicus* (Hagen). At present they appear to live inside cracks in the rock, so their nests are inaccessible. In other areas they are known to build polycalic nests, in which a very large nest is split up into many discrete parts called calies or subsidiary hives, each housed in a separate chamber, and dispersed over an area of many tens of square meters. Modern *H. mossambicus* calies in South Africa are larger than the Laetoli ovoids, but are not so flattened. Supplementary calies are smaller and more flattened than those in which the brood is kept (Coaton 1958). The internal structure consists of thin horizontal shelves and pillars built of hard blackish carton.

I excavated seven extant *H. mossambicus* supplementary calies in 1980 at Kajiado, Kenya, 250 km from Laetoli as the crow flies. The chambers had a mean width of 43.64 ± 5.14 cm ($n = 7$) and mean height of 23.86 ± 6.20 cm ($n = 7$), the ratio of width to height being 1.8:1 (unpublished observation). This is rather closer to the size and shape of the Laetoli ovoids than the South African calies. The soil at Kajiado is a red clay-loam up to about 1 m deep over Precambrian metamorphic rocks, and so is very different from the ash beds at Laetoli.

Trace fossils in argillaceous sandstone of late Miocene and Pliocene age (3–7 Ma) in the Djourab desert of Chad were interpreted by Schuster et al. (2000) as being calies of *Hodotermes*. They are flattened spheres containing thin horizontal shelves supported by pillars and ramps, with the gaps between the shelves (about 1 cm) infilled by dark sediment. The calies averaged 40 cm in diameter and 27 cm high, the ratio of width to height being 1.48:1. They do somewhat resemble the Laetoli ovoids, although they are more rounded, and their internal structure is much better preserved. They differ in that each of the Chad calies has a wide, deep hollow in the middle of the top surface, possibly caused by erosion. In a later paper (Duringer et al. 2007) these structures were given the name *Coatoniscus globosus*, but their interpretation remained much the same. They were on average 40 cm in diameter and 20 cm high ($n = 73$) a ratio of width to height of 2:1. The same paper also described another type of trace fossil, given the name *Termitichnus schneideri*. It consisted of flattened hives containing horizontal galleries supported by shelves and separated by pillars and ramps, and surrounded by a wall. In some ways these resemble the Laetoli ovoids, although their shape is more flattened, with the ratio of width to height being 3.5:1 ($n = 21$) (calculated from Duringer et al. 2007, Fig. 6). They differ in that the Chad fossil hives are surrounded at the periphery by large funnel-shaped exit ramps (of which the Laetoli ovoids show no sign), which taper into long straight radial galleries connected at intervals to short perpendicular galleries ending in globular structures (none of which have been seen at Laetoli). The Chad fossil hives have an external wall that is moulded to the ends of the shelves giving an undulating outline, whereas in the Laetoli ovoids the wall is smoothly rounded. Duringer et al. (2007) see the presence of an external wall as distinctive of *Termitichnus* and its absence as characteristic of *Coatoniscus globosus* and thus, by inference, of *Hodotermes*. This needs to be tested in modern calies of *H. mossambicus*, as previous observers (including myself) were not looking for this feature.

Thus, the identification of the ovoid builders at Laetoli remains elusive, but they seem to have built their nests out of organic carton, and there is no evidence that they were fungus-growing termites.

Probable *Macrotermes* Nests

The remnants of base-plates upstream of the gorge (Loc. 10) look similar to those at Loc. 9. At Loc. 10W there are also a few structures resembling hives at Loc. 9, with twiglet scatters on and around base-plates, or lobes at the same or lower levels.

One very large hive has eroded out and fallen on its side (Fig. 21.9; Sands 1987, Plate 11.8:49). Its surviving dimensions are 190 × 150 cm wide, and about 90 cm high. From its size it must be the hive of a *Macrotermes*, but it is fossilized in a unique way. It consists of thin, (originally) horizontal shelves 2–4 cm apart supported on many vertical pillars. This seems to be much less altered than the twiglets, but still is not very similar to modern termite hive structures. The clay horizon runs right through this nest, closer to the bottom than the top. If this nest was *M. herus*, whose hive is high in the soil profile, it suggests that the nest was alive at a time when the clay horizon was covered by only a shallow layer of a later soil.

In 1976 a particularly interesting nest was exposed in the vertical face of an isolated block of cliff (Fig. 21.10; Darlington 2005a). A small hive of surviving dimensions 50–55 cm in diameter and 25 cm high, on a flat floor 125 cm below the clay horizon, was exposed and partly eroded into twiglets. In contact with it was a vertical shaft running up to, and (originally) apparently through, the clay horizon. The shaft appeared to be an endocast of a ventilation shaft. The bottom of the shaft branched laterally at the level of the top of the hive but did not enter the surviving hive structure. It was not directly above the center of the hive, but towards one edge. Above the clay horizon the shaft continued up for about 150 cm, but appeared lumpy and misshapen because of deposition of calcite on its outer surface. The same nest was found in 2005 but in a damaged and more eroded condition. The shaft, now broken above the hive, was oval, 12.5 cm by 9 cm in horizontal section.

Fig. 21.9 Laetoli, Loc. 10W (1976). Large fossil hive that has eroded out and fallen on its edge. Diameters of the fossil hive were 190 cm by 150 cm. Probably built by *Macrotermes* sp.

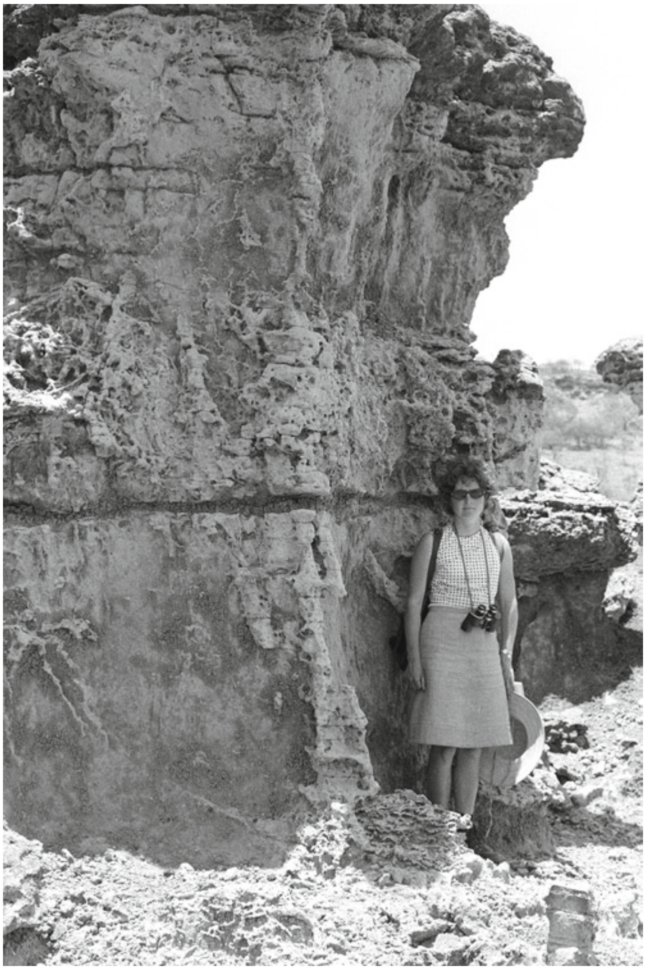

Fig. 21.10 Laetoli, Loc. 10W (1976). Vertical profile about 5 m high. The cap at the top of the profile is Tuff 2. The dark layer at head height is the clay horizon. The human scale is standing on the top of Tuff 1. Bottom center is a fossil hive reduced to a core and twiglet scatter, with the endocast of what appears to have been a ventilation shaft rising almost vertically above it. The shaft was broken by erosion at the clay horizon, but appeared to have continued above it. The clay horizon represents the surface of a buried paleosol that was probably contemporary with the hive. This fossil resembles extant nests of *Macrotermes jeanneli* on ash soils at Lake Baringo, Kenya (Reproduced from Darlington (2005a) by permission of the publishers, Birkhauser Verlag)

These structures resemble what is found in modern nests of *M. jeanneli* (Grassé) in northern Kenya (Darlington 1984; Darlington et al. 1997). Each nest has a single tall chimney, open at the top, through which metabolic gases are vented to the atmosphere. The Laetoli nest differs from a typical *M. jeanneli* nest in the great depth of the hive below the presumed soil level, as well as the absence of a distinct earth mound above it. However, some living nests near Lake Baringo in Kenya show exactly the same features, perhaps in response to the unconsolidated soil in which they are built. This, and a similar fossil nearby (now lost), may have been nests with single ventilation shafts, including the tall external chimneys, which were alive (or at least, still in good repair) when the clay horizon was buried under fresh ash falls.

Shafted Chambers

Sands (1987) described a "shafted chamber" with its center 80 cm below the clay horizon. It was a bell-shaped chamber 104 cm wide and 60 cm high, with a lobe on one side 60 cm long. Two vertical shafts 10 × 12 cm and 14 × 12 cm in cross-section arose from its roof up to a height of 65 cm where they opened onto the present erosion surface. The chambers and shafts were filled with soft unconsolidated material showing no internal structure. He also described a second shafted chamber with its centre 80 cm above the clay horizon. The hive was 80 cm wide and 48 cm high, with four shafts arising from its roof, which however were not straight or vertical. Neither of these chambers was found or recognized in 2005.

In 2005 I found and partly cleared a new smaller chamber fitting Sands' general description, with its floor 145 cm below the clay horizon. It was subspherical, 65 cm wide and about 50 cm high. The roof funnelled upward into a single vertical shaft about 10 cm in diameter. The chamber contents were soft and unconsolidated, with a faint pipe-like structure a few centimeters in diameter, its walls strengthened by ridges, crossing the middle at an angle. I do not know what termite built these hives, but possibly a *Macrotermes* species.

Inverted Pear-Shape Chambers

Fig. 21.11 Laetoli, Loc. 10W (2005). Inverted pear-shape structure *in situ*, with the contents removed by erosion. The structure was 41 cm high and a maximum of 32 cm wide

Two enigmatic structures were found in vertical sections. They were taller than broad, and wider at the top than at the bottom. The first was a cavity 70 cm high, 40 cm wide in the upper half and 30 cm in the lower half. The floor was 160 cm below the clay horizon. The interior of the chamber was fairly smooth, with no obvious access holes, and no external structures were visible. The interior was full of soft, crumbly clay, with no clear features in it. The second structure was smaller but otherwise similar, 41 cm high, 32 cm wide in the upper part and narrower below (Fig. 21.11). The floor was 50 cm above the clay horizon. This was in the riverbank upstream of the cliffs.

They look like termite-built structures, but not anything now known from the area. The best match in the literature might be one of the Apicotermitinae, such as *Apicotermes lamani* (Sjöstedt) (Grassé 1981, Fig. 28). If so, the preserved chamber was a space within which the hive was more or less free-standing. The mode of preservation of these fossils was similar to that of the shafted chambers.

Vertical Shafts

Larger ones (4–10 cm in diameter) have already been discussed above, but there were also smaller ones of about 3 cm in diameter. They all appeared to be endocasts of straight-sided, smooth, near-vertical shafts with some small shallow pits in the internal walls. The shafts were oval or circular in cross-section and did not branch. Some shafts are surrounded by knobbly calcite deposits that obscure their original shape and size. The shafts may be of several different origins, but the evidence is insufficient to make positive identifications.

Anastomosing Passages and Root Casts

The deep ash beds contain anastomosing passages cast in calcite, similar to those at Loc. 9. They are locally at very high density, and clumped, suggesting that they may not all have been contemporary. Sands (1987, Plate 11.2) estimated the density of passages in 20 cm deep layers, and found the highest densities in the section from 20 cm below the clay horizon to 130 cm above it.

Kakesio 3

This is an exposure of the Lower Laetolil Beds to the southwest of Laetoli, 30 km away by road. It is a sloping exposure along the north side of the Kakesio River valley.

Many small fossil hives are exposed as circular, near-horizontal sections (e.g., Fig. 21.12). They consist of white, layered calcite in horizontal shelves a few mm thick, separated by about 1 cm of grey tuffaceous sediment. A robust white calcite wall surrounds the whole structure. The mean diameter of the hives was 39.4 ± 5.1 cm ($n = 25$) at Kakesio, and 42.1 ± 5.8 cm ($n = 14$) at Emboremony (T. Harrison, personal communication). A few empty hives seen in vertical section had flat floors and domed roofs, the roof height being less than the basal diameter. These hives were described and illustrated by Sands (1987: 421 onward and Plate 11.9, 52–58) who called them "thin-layered ovoids".

The hives appear to have had flat shelves of organic carton supporting galleries that became filled in as endocasts. At their edges the shelves were joined to a continuous wall of carton surrounding the hive, which had the shape of an upright cylinder near its base. The shelves and walls, being organic matter, then wasted away by bacterial decay, and were replaced by pure calcite. The shelves are often distorted, as these beds have been vertically compressed (T. Harrison, personal communication).

These look very different from the flattened ovoids at Loc. 10W. The Kakesio hives had shelves, originally of carton, that were thicker and more robust than those of the ovoids, and were joined to an external wall of similar thickness surrounding the whole nest. Sands (1987) did not know what these nests were, and nor do I.

Fig. 21.12 Kakesio, 3 (2005). Looking down onto the basal part of an eroded hive. The lens cap is 5 cm in diameter

Discussion of Preservation

Trace fossils in the Laetolil beds are difficult to interpret, partly because they have been changed since they were formed. Cycles of solution and deposition within the beds appear to have altered the structures to a greater or lesser extent. The least altered hives are those where endocasts have preserved the original shape of the internal spaces. Greater alteration produces a hard base-plate in the bottom part of the hive, the rest of it becoming twiglets in a soft matrix, bearing little resemblance to the original hive structure, but surprisingly consistent between many hives. The most altered, where the hive contents have become a uniform soft clay infill, are seen in the shafted chambers and the inverted pear-shaped chambers, which probably were built by different termites. Fortunately, the external walls and roofs of the hives are usually well preserved in vertical sections.

Modern Termites at Laetoli

The extant termite fauna at Laetoli is scant because of the relatively high altitude and the dryness. Sands (1987) listed 13 species (Table 21.1) of which only three build large structures in the soil, as follows.

Hodotermes mossambicus

The structure of the nests has already been discussed. There is no surface mound, but characteristic small conical piles of soil pellets, sometimes with fragments of forage, thrown out onto the surface indicate the presence of a nest. They eat grass, including green grass. At Laetoli *H. mossambicus* is common on the exposures, and at Kakesio on valley-bottom sediments, but it was not seen at all on the black cotton soil.

Macrotermes herus

This large fungus-growing termite occurs at fairly high altitudes in East Africa (Pomeroy et al. 1991) and mainly feeds on dead grass. It builds blunt-conical mounds of soil with no external openings (except the flight holes built once a year to permit the nuptial flight of the alates). The mounds are 100–150 cm high and are usually kept clear of vegetation if the nest is active. The hive is high in the mound (in all the extant nests examined at Laetoli) with the roof well above the surrounding soil level, and the floor well below. The soil mound

Table 21.1 Classified list of the extant termite species found at Laetoli, from Sands (1987), with some of the names amended

Family	Subfamily	Genus – species (authority)
Kalotermitidae		*Bifiditermes jeannelanus* (Sjöstedt)
Hodotermitidae		*Hodotermes mossambicus* (Hagen)
Rhinotermitidae		*Coptotermes amanii* (Sjöstedt)
Termitidae	Termitinae	*Amitermes messinae* Fuller
		Microcerotermes parvus (Haviland)
		Microcerotermes masaiaticus Harris
		Cubitermes zavataria Ghidini
		Promirotermes pygmaeus Harris
		Angulitermes nilensis Harris
	Macrotermitinae	*Macrotermes subhyalinus* (Rambur) here called *M. herus* (Sjöstedt)[a]
		Odontotermes patruus (Sjöstedt) here called *O. montanus* Harris[b]
		Microtermes sp.
	Nasutitermitinae	*Trinervitermes bettonianus* (Sjöstedt)

[a] Sands (1987) identified this taxon as "the high-altitude form of *M. subhyalinus*". The implied synonymy of *herus* with *subhyalinus* was never formalized, and later work supports the interpretation that *M. herus* is a distinct species (Bagine et al.1994; Brandl et al. 2007)

[b] Using samples from the smaller nests on the exposures, Sands (1987) identified this termite as *O. patruus*, originally described by Sjöstedt from what is now the Democratic Republic of the Congo. We initially identified young nests at Embakasi, Kenya, as *O. patruus*, but they were later shown to be *O. montanus* on the basis of mtDNA sequence data (Davison et al. 2001)

overlying the hive is almost solid, with small or flat-floored passages in it, but no ventilation system (Darlington 1988).

Mounds occur among the exposures at Loc. 15 and in a regular array on the valley slopes above them. At the upper edge of the mound distribution the *M. herus* mound pattern overlaps with the equally regular but lower density pattern of lenticular mounds built by *Odontotermes montanus* Harris, some of the *M. herus* mounds being built on top of lenticular mounds. *Macrotermes herus* mounds are not found on black cotton soil, unless there is a slope or the soil is very thin, suggesting that they cannot tolerate seasonal waterlogging of the clay soil.

Odontotermes montanus

This is another fungus-growing termite, and probably it also mainly eats dead grass. In Kenya it occurs at altitudes of 1,540 m and above (Harris 1960), especially on black cotton soils. At Laetoli it occupies the grassland on black cotton soil that overlies the Laetolil beds and so surrounds the exposures. *Odontotermes montanus* builds lenticular mounds, which are wide, low mounds 10–20 m in diameter, but usually less than 1 m high and completely covered in vegetation. This may be grass turf similar to the surrounding grassland, but many mounds are marked out by the growth of unpalatable woody herbs, as on the slope above Loc. 16. The mounds often have a small number of near-vertical air shafts opening at the surface, 3–10 cm in internal diameter. Within the mound the top 80–100 cm of soil contains no termite structures other than the air shafts. Below that, the nest is dispersed in many small domed chambers that house the sponge-like, layered fungus combs. The air shafts do not communicate directly with the chambers. All the structures in the lenticular mounds we dug at Laetoli fit the dimensions of the nests of *O. montanus* excavated at Embakasi (Darlington 2005b) and other sites in Kenya.

On other soil types at Laetoli, especially on shallow soils, what appears to be the same termite builds smaller and more centralized nests with ventilation shafts grouped close together and often with raised rims. At Embakasi, young nests of *O. montanus* were built like this (Darlington 2005b). Although this species is now more widely distributed and abundant at Laetoli than *M. herus*, there are no fossils that look remotely like *Odontotermes* nests, of this or any other species. The smaller vertical shafts at Loc. 10W could, from their size, have been *Odontotermes*, but it seems most improbable that the shafts would be so well preserved while all trace of the chambers disappeared.

Discussion

My aim was to interpret the Laetoli trace fossils in comparison to the modern living termites. The time interval (minimum of 4.4 Ma) is fairly short in evolutionary terms, and the climate and vegetation do not appear to have changed much. However, the ash was more or less unconsolidated when the trace fossils formed, whereas later it was transformed into rock. Thus, the best fauna for comparison might be sought in superficial sediments on valley bottoms and slopes. The black cotton soil formed on later volcanic deposits is entirely different, and so it is not surprising that there are no comparable trace fossils in the Laetolil beds.

I am reasonably confident in interpreting all the fossil hives at Loc. 9 as being built by a *Macrotermes* species resembling *M. herus*, and also the relatively few matching structures at Locs. 10 and 10W. A very few hives at Loc. 10W seem to have belonged to other species of *Macrotermes*, some resembling *M. jeanneli*. The shafted chambers might also have been built by *Macrotermes*, but of an unknown kind. The inverted pear-shaped structures may have been made by Apicotermitinae. The biggest puzzle is the flattened ovoid, of which all we can deduce with confidence is that the termite built small hives or calies out of carton. The hives at Kakesio 3 are distinctive, and different from the other fossil hives.

Interpretation is hindered by the alteration that has occurred in the process of fossilization. However, the biggest difficulty is that so little is known about the structure of even the most abundant extant termite nests. Taxonomists work with the animals themselves, and rarely even mention the nests. A few enthusiasts have published drawings and photographs of nest structures, but rarely in a systematic manner. Grassé (1984) reviewed all the available information. Only for a handful of the most conspicuous mound-building species do we really know what the internal structure of their nests is like, and even more rarely do we know how their foraging passages and other external structures are laid out. It remains a badly neglected aspect of termite behaviour and ecology. With the discovery of trace fossils at several interesting paleontological sites in Africa, it is increasingly apparent that we simply do not know enough to interpret them properly.

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Chapter 22
Gastropoda

Peter Tattersfield

Abstract This paper reports on a study of 892 fossil gastropod specimens from the Laetolil and Upper Ndolanya Beds at Laetoli and other sites on the Eyasi Plateau, Tanzania, collected between 1998 and 2005. The material examined represents a sample of a larger collection of over 5,000 specimens, including a large number of urocyclid slug shells. Sixteen gastropod species have been identified in the material and all can be assigned, with varying degrees of confidence, to recent genera of East African Mollusca. Ten species previously described from the site by B. Verdcourt in 1987 have been identified in the material, and a further six species have been newly recognized. The latter includes two new species that are described formally as *Euonyma harrisoni* sp. nov. and *Halolimnohelix rowsoni* sp. nov., and a further four species that can be assigned to generic level only – *Cerastus* sp., *Subuliniscus* sp., *Streptostele* sp. and *Gulella* sp. Overall the material is dominated by medium to very large shelled species, and, unlike many recent East African land-snail faunas, it contains very few micromollusks. It is considered unlikely that this reflects a methodological bias against small specimens during sampling, so it is probable that small species were absent from the Pliocene fauna or that they have not been preserved. The gastropod data and knowledge about the ecological affinities of the taxa concerned have been used to make inferences about the environmental conditions that prevailed during the Pliocene. Within the Upper Laetolil Beds, specimens have been assigned to one of a series of four stratigraphic subunits, thus enabling finer examination of the variation in environmental conditions over this period. The gastropod fauna from the Lower Laetolil Beds is highly distinctive, being dominated by large, robust achatinids and lacking urocyclid slugs. This suggests that conditions were relatively dry at that time, although not to the extent that they could be classified as semi-arid. Savanna habitats may have been prevalent over this period and large trees were probably absent or scarce. Several taxa vary in frequency across the subunits of the Upper Laetolil Beds, thus suggesting changes in environmental conditions over this period. The three lower subunits (up to Tuff 7) are characterized by high frequencies of *Euonyma* and *Subulona*, which would indicate the presence of woodland. Based on the gastropod data, woodland in the Upper Laetolil may have peaked between Tuffs 3–5. Above Tuff 7 the gastropod fauna changes to one dominated by *Edouardia* and *Trochonanina*, suggesting the return of more xeric conditions, perhaps comprising a savanna or bushland ecosystem associated with scattered trees or patches of woodland. The gastropod fauna of the Upper Ndolanya Beds is characterized by *Euonyma* and *Subuliniscus* and a high frequency of urocyclid slugs. This suggests the occurrence of woodland or possibly forest conditions, which appear to have been relatively widespread in the area since the same fauna appears to be present at all of the Upper Ndolanya Bed localities sampled. This conclusion differs from other reconstructions of the Upper Ndolanya environment using alternative lines of evidence, which suggests that the area was dominated by open woodland-bushland and grassland.

Keywords Mollusca • Gastropoda • Land snails • Taxonomy • Environmental reconstruction • Paleoecology • *Halolimnohelix rowsoni* sp. nov. • *Euonyma harrisoni* sp. nov.

Introduction

The fossil Mollusca of the Pliocene deposits at Laetoli and neighboring sites have been previously described in detail by Verdcourt (1987), and Pickford (1995) provided a short list collected at Kakesio. This paper reports on analysis of a total of 206 lots and 892 individual specimens that were loaned to me for study from the National Museums of Tanzania. The material was collected during 1998–2005 from more than 30 localities at Laetoli and other sites on the Eyasi Plateau (see Harrison and Kweka 2011). It represents a subset of a larger collection of mollusks (over 5,000 specimens collected since 1998) that I have not seen. The material that I have examined is largely in good condition and

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many of the specimens retain evidence of external shell microsculpture, which is helpful for identification. However, some specimens are internal molds that are difficult to identify, and there is a single specimen of a streptaxid that has apertural dentition, but whose aperture is unfortunately obstructed with calcite.

The objectives of the project were to review and where appropriate supplement the taxonomy of the material, and then to utilize the faunal list for environmental reconstruction. The material examined spans a time period of about 1.7 myrs, including specimens from the Lower Laetolil Beds (3.85–4.4 Ma), the Upper Laetolil Beds (3.6–3.85 Ma) and the Upper Ndolanya Beds (2.66 Ma) (see Deino 2011). The Upper Laetolil Beds can be further subdivided into four stratigraphic subunits that allow the faunas to be arranged in a temporal sequence, from oldest to youngest: (1) below Tuff 3, (2) between Tuffs 3 and 5, (3) between Tuffs 5 and 7, and (4) above Tuff 7. Terry Harrison has also contributed to the analysis of the Mollusca using these divisions.

Taxonomy and Ecology

In total, 16 taxa have been identified in the material examined (Figs. 22.1–22.4). These comprise 10 species that were recognized and discussed by Verdcourt (1987), plus six taxa that have been recognized from Laetoli for the first time. All of the identified taxa are terrestrial gastropod species and they all clearly have close relatives in the current East African mollusk fauna. Of the species recognized by Verdcourt (1987), only one taxon, *Trochonanina* sp. B, has not been confidently identified in the present material. Of the six newly recognized taxa, two, *Halolimnohelix rowsoni* and *Euonyma harrisoni*, have been introduced as new species. The other four taxa are not formally described because the available material is considered to be inadequate.

The following text provides an account of each taxon, and, where possible, considers possible affinities with recent species. For each taxon it also reviews the known geographical distribution and habitat associations, upon which the subsequent interpretation of the molluscan assemblage has been based. It should be noted that the material collected at Laetoli also includes numerous slug shells (over 3,000 specimens recovered since 1998). Data on slug shells and their stratigraphic provenience have been provided by T. Harrison, but I have not personally examined the material. These are briefly discussed in the overall review of the site's fauna by Harrison (2011). The higher level classification of pulmonate families adopted in this chapter follows Bouchet and Rocroi (2005) The following abbreviations for shell metrics are used. H = Shell height; D = Maximum shell diameter; h = aperture height; d = aperture diameter.

Systematics

Family: Succineidae
Genus: 'Succinea'
Species: sp. A

Material Examined. One incomplete shell (EP 1364/01) with apex missing from the Lower Laetolil Beds at Emboremony 1. Figs. 22.1a, b.

Identification and Taxonomy. Shell succineiform. The incomplete specimen (H = 6.5 mm, D = 4.1 mm) has 2 very rapidly expanding whorls. When alive the animal would probably have had 3 whorls. The height of the penultimate whorl (2 mm) is approximately one half that of the body whorl when measured at the aperture. Whorls strongly convex and separated by a deep suture. Aperture oval with rounded base, about h = 4 mm tall and d = 2.8 mm. The body whorl has rather coarse and irregular transverse growth lines or striae; the other whorl is almost smooth or with only faint traces of radial sculpture.

There is no doubt that this specimen belongs in the Succineidae but its assignment to *Succinea* is made with qualification. It is unlikely that any of the African members of the family belong in Draparnaud's genus (Verdcourt 1972) and the whole group is in need of revision based on characters other than shell morphology.

Ecology. Unlike their Palaearctic relatives, which are almost always associated with wetland habitats, the East African succineids may often be found in well-drained situations that are rarely inundated. Fieldwork by the author and colleagues indicates that they are very rarely found in forest habitats in East Africa at the present time, and Herbert and Kilburn (2004) note that in eastern South Africa succineids may occur in savanna, aloe-covered hillsides, seasonally dry river courses and even open grassland. In East Africa, Pickford (1995) comments that *Succinea* is 'characteristic of seasonally waterlogged ground, even in semi-arid to arid country'. Within the present day Endulen-Laetoli area, Andrews et al. (2011) report the occurrence of areas of impeded drainage and seasonal waterlogging supporting *Acacia* woodland that would appear to be potentially suitable for succineids.

Verdcourt (1987) did not identify any succineids from Laetoli. However, Pickford (1995) has reported the genus from the East Africa fossil record, from the early Miocene and Pleistocene to Recent deposits in Kenya.

Family: Cerastidae
Genus: Edouardia Gude, 1914
Species: laetoliensis Verdcourt, 1987

Material Examined. 144 specimens in 52 lots. Figures. 22.1c–e. EP 042/00, EP 1005/01, EP 1171/01, EP 1328/01, EP 170/00, EP 1908/03, EP 196/01, EP 2084/03, EP 2251/03, EP 230/01, EP 235/00, EP 240/99, EP 2466/03, EP 265/00, EP 268/98,

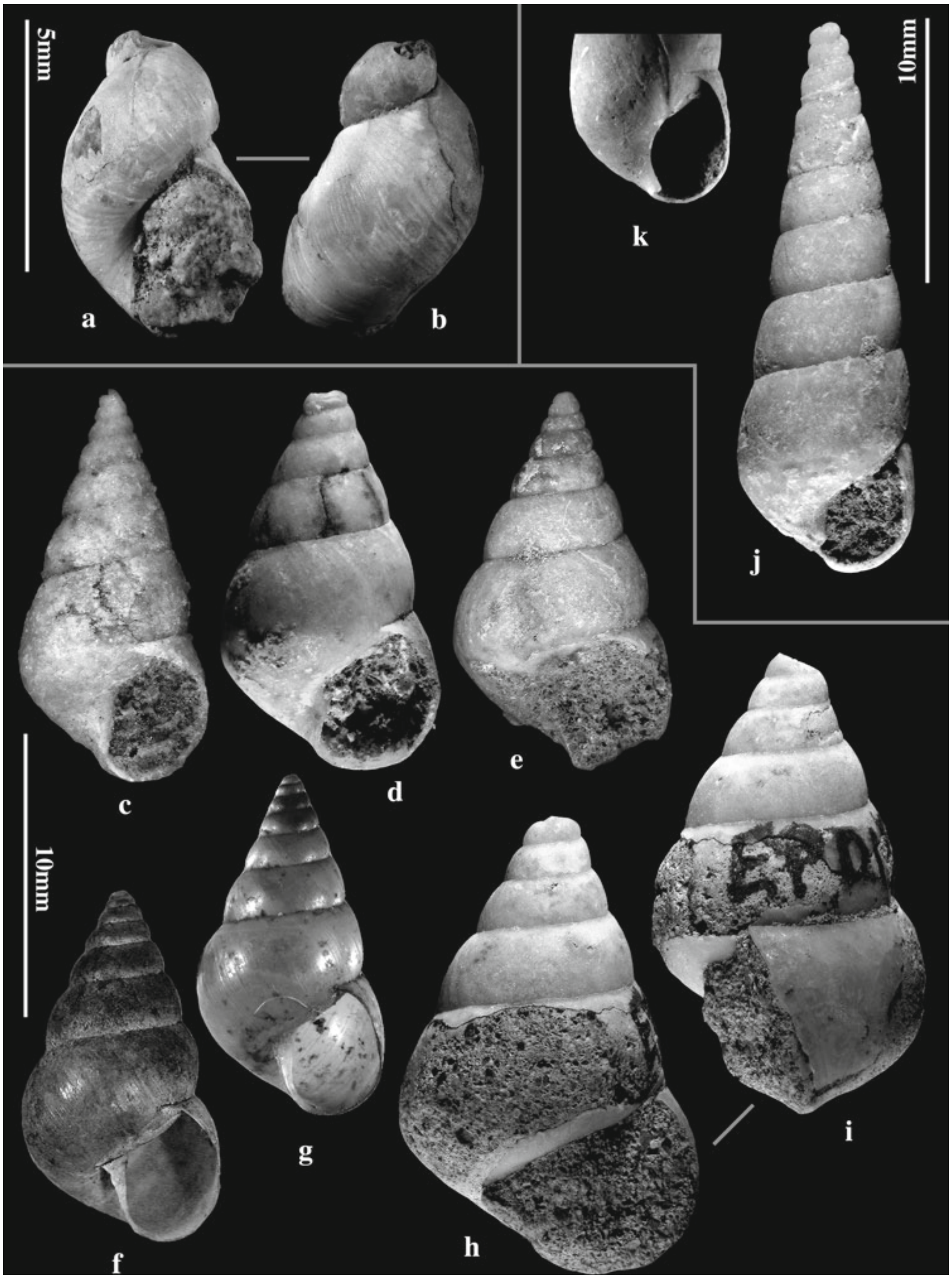

Fig. 22.1 (**a**, **b**) *Succinea* sp. A (EP 1364/01); (**c**) *Edouardia laetoliensis* Verdcourt (EP 170/00); (**d**) *E. laetoliensis* (EP 515/03); (**e**) *E. laetoliensis* (EP 938/03); (**f**) Syntype of *E. tumida* (Taylor, 1877) from Zanzibar, Tanzania (BMNH.1910.9.5.15), H = 12.6mm); (**g**) Specimen of *E. metula* (von Martens, 1895) from Kilifi, Kenya (NMW.1968.130.00031), H = 12mm); (**h**, **i**) *Cerastus* sp. A (EP 013/98); (**j**) *Subulona pseudinvoluta* Verdcourt (EP 690/03); (**k**) *S. pseudinvoluta* Verdcourt (EP 928/04)

EP 2773/00, EP 2834/00, EP 3026/00, EP 484/03, EP 515/03, EP 710/01, EP 938/03, EP 025/99, EP 1013/03, EP 1116/03, EP 1236/04, EP 1287/04, EP 1363/04, EP 1464/03, EP 1553/03, EP 1645/03, EP 1664/00, EP 1886/00, EP 2430/00, EP 284/01, EP 3132/00, EP 3195/00, EP 4266/00, EP 638/04, EP 657/01, EP 667/04, EP 701/04, EP 738/00, EP 788/04, EP 850/04, EP 875/04, EP 1464/04, EP 409/04, EP 527/04, EP 1103/04, EP 1281/01, EP 834/00.

Identification and Taxonomy. *Edouardia* is a widespread genus in East and southern Africa, comprising a large number of taxa with conical shells of small to moderate size. The body whorl of some species has a carinate keel (e.g., *natalensis* [Pfeiffer, 1846]), although Verdcourt (1963) notes that this character occurs ‘rarely in the East African fauna at the present time’. Connolly (1939) deals with the typification of the genus and lists 20 species from the South African fauna

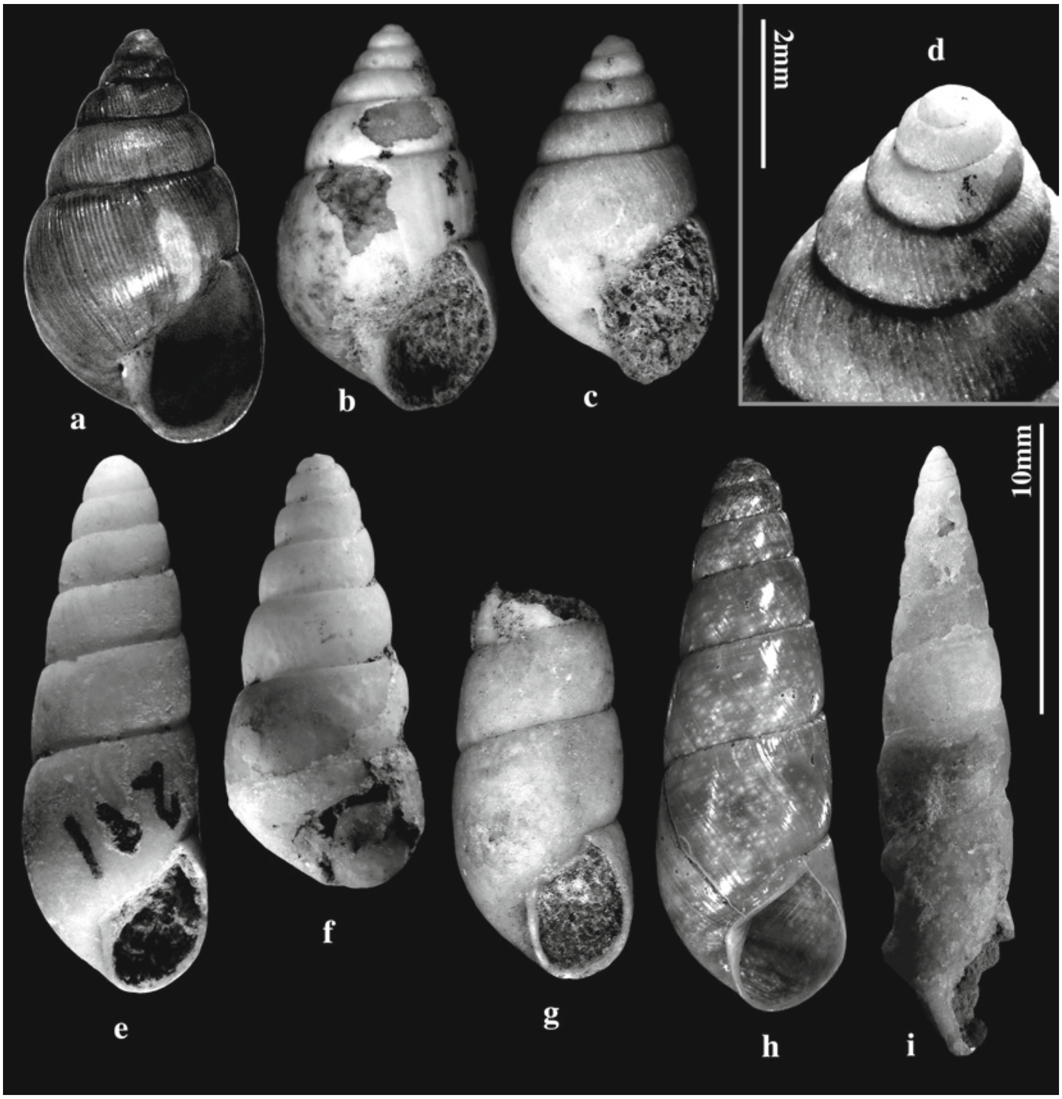

Fig. 22.2 (**a**) Syntype of *Pseudoglessula gibbonsi* (Taylor, 1877) from Mozambique (BMNH.1910.9.5.13), H = 15.7 mm); (**b**) *P.* aff. *gibbonsi* (EP 656/01); (**c**, **d**) *P.* aff. *gibbonsi* (EP 635/04); (**e**) *Euonyma leakeyi* Verdcourt (EP 281/01); (**f**) *E. harrisoni* sp. nov. (holotype, EP 3329/00); (**g**) *E. leakeyi* Verdcourt (EP 1663/00); (**h**) Holotype of *E. curtissima* Verdcourt, 1968 from Chania Gorge, thika, Kenya (SMF.186867), H = 18.3 mm; (**i**) *Subuliniscus* sp. A (EP 1330/98)

and Verdcourt (2006) lists a similar number from East Africa. It is recognized that a major taxonomic revision of the genus is required.

The material examined closely matches Verdcourt's description of *Edouardia laetoliensis*, in terms of shell shape, size and sculpture. Juvenile specimens have an angled or carinate shell profile, which becomes rounded in adult shells. One specimen (lot EP 1908/03) may retain signs of weak radial sculpture on the base, and specimens in lot EP 527/04 possibly exhibit some evidence of weak irregular ribbing across the lower whorls.

Variation in shell size and shape is exemplified by the narrower shell and low whorls of specimen EP 170/00 (Fig. 22.1c) and the more tumid whorls and broader shell of EP 515/03 and EP 938/03 (Figs. 22.1d, e). However, these differences are considered to represent intraspecific variation and all the material has been assigned to *E. laetoliensis*. Most of the shells examined fall within the size range described for *E. laetoliensis* by Verdcourt (1987) (maximum H = 13.6 mm and D = 7.7 mm) although a few are slightly taller.

Verdcourt's (1987) generic assignment of this species is retained here. Comparison with recent species could suggest an affinity with *tumida* (Taylor, 1877) (Fig. 22.1f) or *metula* (von Martens, 1895) (Fig. 22.1g), which currently occur in central and coastal Tanzania. However, as noted by Verdcourt (1987), confident generic placing is not easy because there are other sub-Saharan cerastid genera that have a very similar shell form, especially *Rachis* and *Rhachistia*.

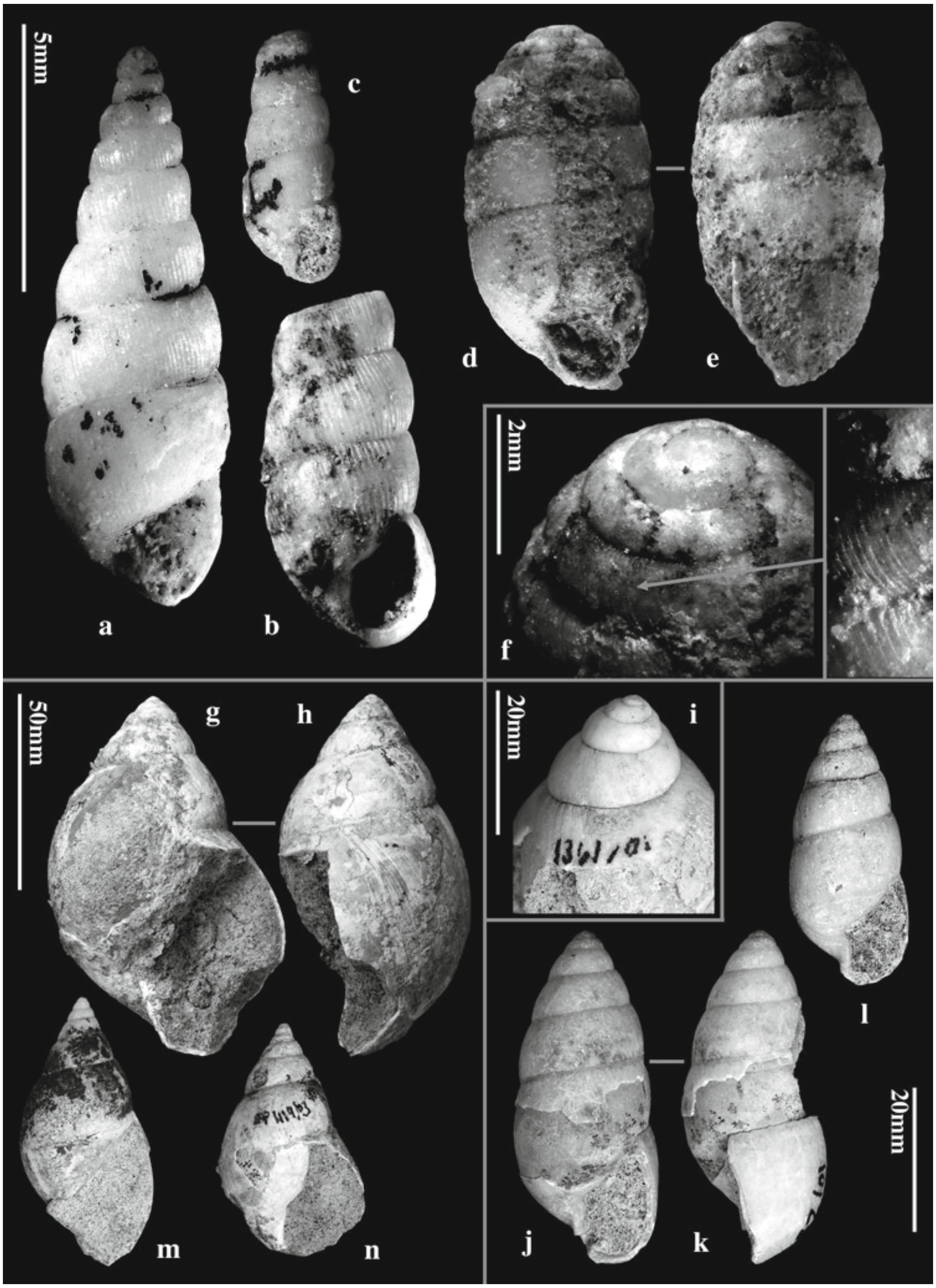

Fig. 22.3 (**a**) *Streptostele* aff. *horei (*EP 1905/03); (**b**) *S.* aff. *horei* (EP 528/04); (**c**) *Streptostele* sp. A (EP 2233/03); (**d–f**) *Gulella* sp. A (EP 1170/01), (**g**, **h**) *Burtoa nilotica* (Pfeiffer) (EP 539/98); (**i**) *B. nilotica* (EP 1361/01); (**j–l**) *Limicolaria martensiana* (EP 1182/01); (**m**) *Achatina (Lissachatina)* indet. (EP 1362/01); (**n**) A. (L.) indet. (EP 1119/03)

Ecology. At present, species of *Edouardia* are characteristically found in open woodland, savanna, bushland and Miombo type vegetation. Recent fieldwork in African forests by the author and colleagues has suggested that *Edouardia* is rarely present in closed canopy evergreen forest habitats in East Africa, and that it tends to occur at low or moderate altitudes where it is frequently associated with open and deciduous woodland. Verdcourt (2000) lists four species from East African coastal forests and Herbert and Kilburn (2004) report 10 species from eastern South Africa, some of which occur in forest habitats (personal observation). Pickford (1995) states that *Edouardia*'s altitudinal range in East Africa extends from the coast to 2,600 m and that it usually occurs where the annual rainfall is between 500 and 1,270 mm.

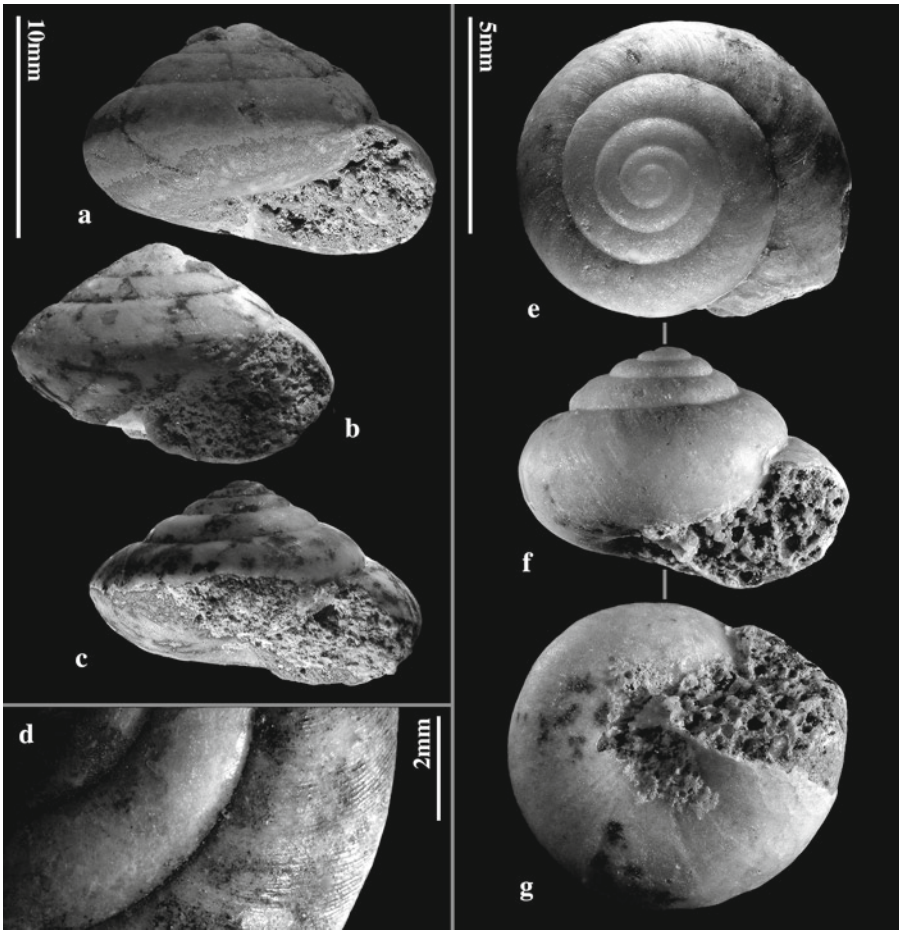

Fig. 22.4 (**a**) *Trochonanina* sp. B (EP 229/01); (**b**) *T.* sp. B (EP 1168/01); (**c**, **d**) *T.* sp. B (EP 754/98); (**e**–**g**) *Halolimnohelix rowsoni* sp. nov. (holotype, EP 1660/00)

Many *Edouardia* species are associated with rocky outcrops and/or tree trunks. Several of the extant species accumulate soil or other detritus on their shell, presumably to provide camouflage. Many species exhibit a climbing behavior and individuals can sometimes be found several meters from the ground, on trees or other vertical surfaces. It should be noted that members of the other East African cerastid genera *Rachis* and *Rhachistia,* to which the Laetoli material also resembles, are typically low altitude or coastal, bushland/woodland edge species.

Family: Cerastidae
Genus: Cerastus Martens, 1860
Species: sp. A

Material Examined. Figures. 22.1h, i. Two specimens have been examined from lots EP 013/98 and EP 850/04. Both specimens lack the apex and have damaged apertures, which are partly obscured by volcanic ash. The largest (EP 013/98) lacks part of the body whorl, but an ash mold is present, which provides an indication of the original profile of the shell; the specimen from lot EP 850/04 is corroded. These, and a further specimen that has not been examined, were all collected from the Lower Laetolil Beds at Kakesio. The material is too poor for formal description.

Identification and Taxonomy. Specimen EP 013/98: H = 17.2 mm, D = 11.2 mm. The shell probably originally had 5½–6 whorls and would have been slightly taller (perhaps 1 mm at most) than the damaged specimen. The aperture is 6.4 mm tall, and approximately 7 mm wide. The smaller specimen (EP 850/04) is 15.3 × 9.3 mm, with 5½ whorls.

The shell is conical with a straight outline and slightly convex whorls (Figs. 22.1h, i). The spire angle is about 45°, and the apex appears to be quite blunt, although part of it is missing. The aperture is rounded, but the outer edge is missing. However, the ash mold within the aperture shows some flaring at the position of the outer edge, which suggests that the shell may have originally had a lip or been thickened. The columella is missing from both specimens. The umbilicus is obscured by ash but it is probably closed, or at most very narrow. No evidence of shell sculpture is visible on either of the specimens.

The material is not adequate to make a confident generic assignment, but it has been placed in *Cerastus* based on the shape of the shell, its relatively tumid whorls and rounded aperture. Most recent *Cerastus* species have a lip or thickened aperture, so it is unfortunate that the aperture of the available specimens is not intact. The material can be separated from *Edouardia,* which is the other cerastid in the material studied, by its larger size, broader shell and the absence of any radial sculpture. However, it is also recognized that some extant species of *Edouardia* have a shell form similar to that of the species being considered here. The absence of radial ribbing and shell shape separates it from *Pseudoglessula* cf. *gibbonsi*, which is the other conical species of comparable size in the collection. The shell of this *Cerastus* is more elongated and less conical than most recent species currently assigned to the cerastid genus *Conulinus*.

Verdcourt (1963) described *Cerastus miocenicus* from Miocene deposits on Rusinga Island, Kenya, and he also proposed a variety of the species, which he named subspecies *majus*. The narrower apical angle and the absence of any sign of a keel, or of the strong shell sculpture present in *miocenicus*, separate this taxon from Verdcourt's (1963) two taxa.

Ecology. At present, *Cerastus* is a widespread genus in highland areas of East Africa, being represented by about seven species and several subspecies. However, Verdcourt (1963) notes that several different taxa currently assigned to *Cerastua* also occur in quite different semi-arid habitats in Somalia, and Verdcourt (1984) discusses the disjunct distribution of the genus in Africa. In view of the uncertain generic assignment of this species and the disparate ecologies of the extant species currently assigned to the genus, it is not considered appropriate to draw any strong inferences about environmental conditions from its occurrence.

Family: Subulinidae
Genus: Subulona Martens, 1889
Species: pseudinvoluta Verdcourt, 1987

Material Examined. 26 lots comprising in total 114 specimens. Figures. 22.1j, k. EP 072/04, EP 083/99, EP 1162/04, EP 1193/98, EP 1361/04, EP 1663/00, EP 1885/00, EP 1984/03, EP 2018/00, EP 2158/03, EP 2292/03, EP 2370/03, EP 2935/00, EP 3131/00, EP 338/00, EP 377/04, EP 4182/00, EP 512/01, EP 577/01, EP 578/00, EP 690/03, EP 808/03, EP 928/04, EP 935/03, EP 283/01, EP 753/98.

Identification and Taxonomy. Subulona is currently a widespread genus in sub-Saharan Africa with a largely equatorial distribution extending broadly from Mozambique and Malawi (van Bruggen 1993) and southeast Tanzania (Verdcourt 2006) across the Congo basin to the Guinea coast of West Africa (Pilsbry 1919). Verdcourt (2006) lists 27 species from East Africa. The genus is generally separable from other tall-spired subulinds by its swollen and often bulbous protoconch and truncate columella. The embryonic whorls are smooth or have short folds or grains below the suture (Pilsbry 1919). Some authors (Pilsbry 1905, 1919; Verdcourt 1963) have treated *Subulona* as a subgenus of *Homorus*.

The size and proportions of the largest shell in the current material (H = 31.2 mm, D = 7.5 mm, h = 6.1 mm, d = 4.2 mm, with 12½ whorls) are very close to those of the holotype specimen described by Verdcourt (1987). The truncate columella is clearly evident is some of the material (Fig. 22.1k). All material examined can be referred to *S. pseudinvoluta* Verdcourt. All the specimens studied closely match Verdcourt's description and photographs. It should be noted that photograph of the holotype shell (Plate 11.17 in Verdcourt [1987]) was reversed after preparation of the proofs (Verdcourt, personal communication), and it is shown as sinistral in error.

Ecology. The geographical distribution of *Subulona* immediately suggests an association with an equatorial rain forest habitat. Field experience in East Africa has also shown that the genus is generally associated with forest or well-treed habitats, where it is often found in abundance in the leaf litter, especially where there are quantities of decaying logs. The author has recorded various members of the genus from forest habitats in Tanzania (Eastern Arc ranges), Uganda (widespread) and western and central Kenya (Kakamega Forest, Cherangani Hills, Mount Kenya, Mount Elgon). Pickford (1995) comments that in Kenya the genus is 'seldom found below 1,500 m altitude' and that 'its distribution falls entirely within the 760 mm rainfall isohyet'. However, a small number of species currently assigned to *Subulona* occur at lower altitude and therefore contradict this pattern; for example, Verdcourt (2000) lists two species (*insularis* (Germain) and *kilwaensis* (Germain)) from the East African coastal forests.

Subulona is represented in the East African fossil record from the early Miocene (Verdcourt 1963; Pickford 1995, 2004).

Family: Subulinidae
Genus: Pseudoglessula O Boettger, 1892
Sub-genus: Kempioconcha Preston, 1913
Species: aff. *gibbonsi* (Taylor, 1877)

Material Examined. 14 lots containing 54 specimens. Figs. 22.2b–d. EP 1010/03, EP 1115/03, EP 1235/04, EP 155/04, EP 1662/04, EP 184/99, EP 2467/03, EP 2957/00, EP 542/98, EP 592/04, EP 635/04, EP 656/01, EP 735/04, EP 711/01

Identification and Taxonomy. The columella of specimens in the current material is smoothly rounded into the basal margin of the aperture with no sign of truncation (Fig. 22.2b, EP 656/01); this places the material in subgenus

Kempioconcha. The columella of *P. gibbonsi* is very similar (Fig. 22.2a) although the shell of the type in NHM is slightly larger (H = 15.7). The shell is ribbed on all whorls (Fig. 22.2d), with about 10 ribs/mm on whorl four and about 8 ribs/mm immediately behind the aperture. The material closely matches Verdcourt's (1987) description in other respects, and therefore the current material has all been assigned to *P. gibbonsi* (Taylor, 1877) (Fig. 22.2a). However, Taylor's material of *gibbonsi* was collected from Mozambique, and, as far as is known, there are no recent authenticated records of this species from Tanzania or elsewhere in East Africa. Verdcourt (1967) is doubtful about the only record from Tanzania, which was reported from Kondoa by Bourguignat (1889).

Numerous *Pseudoglessula* species have been described from Tanzania and other parts of East Africa and the genus is clearly in need of thorough revision. The shells of this species are shorter, broader and generally more obese than the specimens referable to the *P. boivini-subolivacea* complex that is both abundant and widely distributed in lowland and coastal Tanzania at the present time. Verdcourt (1967) provides extensive metrical data on shell size in this complex, which illustrates the larger size of the species from localities in Tanzania and Kenya. Furthermore, there is no trace in the current material of the peripheral angulation of the juvenile shell that is sometimes seen in *boivini*. Connolly (1939) notes that material referred by Smith (1899) to a variety of *boivini* from Malawi is identical to Mozambique material of *gibbonsi*. E. A. Smith's *lasti* and *emini*, both from Tanzania, are taller (H = 18 mm and 19 mm respectively) and wider (D = 11 mm) than both Taylor's *gibbonsi* and the material under study here.

Ecology. The habitat associations of *P. gibbonsi* in Mozambique (Mtisherra River Valley) are not known, but *Kempioconcha* is typically a group found in relatively dry woodland, coastal forest and Miombo in present-day Tanzania (personal observation). Pickford (personal communication) reports *Pseudoglessula* from *Acacia* woodland east of Lake Magadi, Kenya. Pickford (1995) comments that the large species of *Pseudoglessula* subgenus *Kempioconcha* are today restricted to altitudes below 1,400 m, and data collected by the author generally support this comment, although one species, *P. (K). transenna* Connolly, is present on Mount Kenya (Warui et al. 2001).

Family: Subulinidae
Genus: Euonyma Melvill and Ponsonby, 1896

A disparate range of subulinid taxa from East Africa have been assigned to *Euonyma* and many of these are probably not closely related. Verdcourt (1987) commented that there is a need for major revision of the described species, and this situation has scarcely changed since then. However, the extant East African species may be assigned either to a smooth-shelled and elongated '*magilensis* group', or to a group of typically smaller, costulate species. The *magilensis* group, at least, is almost certainly distinct from the southern African *Euonyma* species (Verdcourt 1968), which probably form a separate, third group. All of the material studied can be assigned to the *magilensis* group, which comprises three extant species – *E. magilensis* (Craven), *E. curtissima* Verdcourt and *E. achilles* Preston. These taxa have a wide, but highly disjunct distribution in central and north Kenya, and in northeast, coastal Tanzania (Verdcourt 1984).

In total, the material of *Euonyma* examined comprises 24 lots and 413 specimens. Two species have been recognized – *E. leakeyi* Verdcourt and *E. harrisoni* sp. nov., which is characterized by its broader shell. Within the material studied, and based on an analysis of larger shells because juvenile material is difficult or impossible to assign, it is apparent that *E. leakeyi* is confined to the Upper Laetolil Beds, whereas *E. harrisoni* is restricted to the Upper Ndolanya Beds.

Species: leakeyi Verdcourt, 1987

Material Examined. 370 specimens in 20 lots. Figs. 22.2e, g. EP 1234/04, EP 1238/98, EP 1282/01, EP 1327/01, EP 1348/01, EP 1463/03, EP 154/04, EP 1661/00, EP 1790/03, EP 281/01, EP 437/03, EP 637/04, EP 654/01, EP 736/04, EP 753/98, EP 2958/00, EP 1663/00, EP 4182/00, EP 2018/00, EP 928/04.

Identification and Taxonomy. Many of the *Euonyma* specimens in the material under study closely match Verdcourt's (1987) description of *E. leakeyi*, and can confidently be referred to this species. In terms of shell size and proportions they come closest to *E. curtissima* (Fig. 22.2h), which is currently only known living from Chania and Thika Gorges, near Thika in south central Kenya.

Species: harrisoni sp. nov.

Material Examined. 47 specimens in 8 lots have been examined, all from Upper Ndolanya Beds. EP 1015/00, EP 1300/01, EP 1333/03, EP 1510/04, EP 296/04, EP 3329/00, EP 822/01, EP 106/03. Fig. 22.2f. A further two specimens, also all from the Upper Ndolanya Beds, have been assigned to this taxon by T. Harrison, but have not been examined by the author.

Identification and Taxonomy. One of the specimens from EP 3329/00 is nominated as holotype. H = 14.7, D = 6.7. Whorls 6¼. The other 46 shells that have been examined by the author are nominated paratypes.

Verdcourt (1987) noted a wider specimen (LAET 7E 165) from the Upper Ndolanya Beds that had more convex whorls and a more shouldered suture, and he commented that it 'belongs either to this species (i.e., *leakeyi*) or a closely allied one'. The current material contains similar specimens, all from the Upper Ndolanya Beds, which are considered to be sufficiently distinct to describe as another species (Fig. 22.2f).

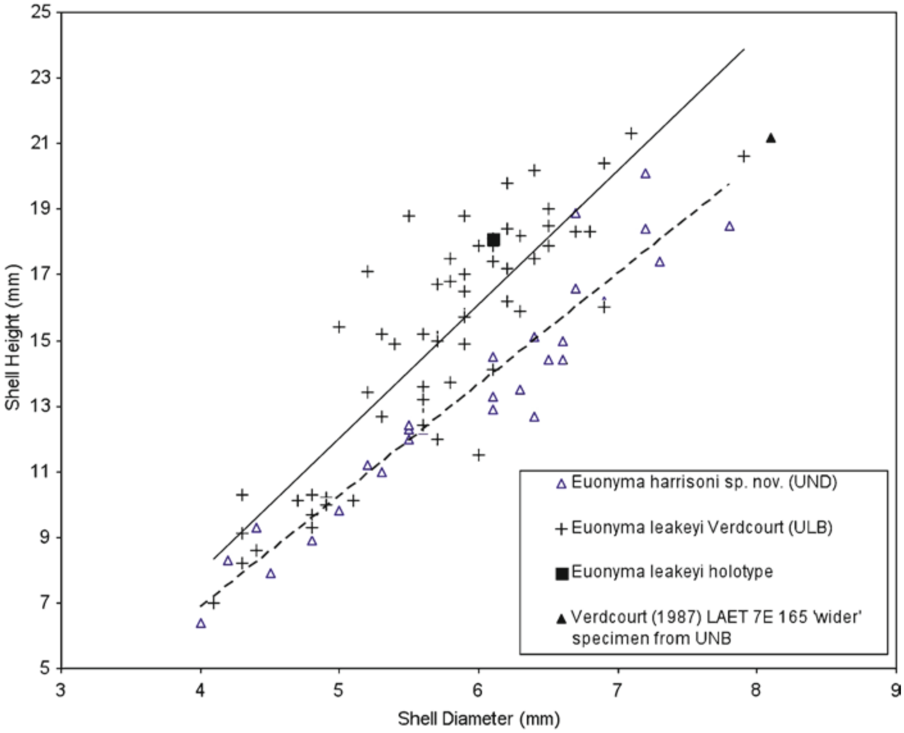

Fig. 22.5 Shell height versus diameter in *Euonyma harrisoni* sp. nov. (29 shells) (broken regression line) from the Upper Ndolanya Beds (*UNB*) and *E. leakeyi* Verdcourt (63 specimens) (solid regression line) from the Upper Laetolil Beds (*ULB*). Verdcourt's (1987) holotype and aberrant shell (LAET 7E 165) are also shown

Although there is some overlap, especially amongst smaller shells, a plot of shell height versus diameter demonstrates that specimens of *Euonyma* from the Upper Ndolanya Beds generally have more obese shells than typical *leakeyi* (Fig. 22.5). Furthermore, the single, 'wider' specimen (LAET 7E 165) described by Verdcourt (1987) and the *leakeyi* holotype, conform to this general pattern. This analysis lends support to Verdcourt's (1987) conjecture regarding the presence of a second species of *Euonyma*, which is hereby described as *Euonyma harrisoni*. On average, *harrisoni* shell diameter is 11–13.4% greater than that of *leakeyi,* over a shell height range of 13–20 mm. Similar analyses do not indicate any consistent differences in whorl number in these two taxa.

Euonyma harrisoni is named in appreciation of the assistance provided by Terry Harrison during the preparation of this paper. The columella of both *leakeyi* and *harrisoni* is rounded, with no evidence of truncation. Several individuals were noted to contain eggs or young snails within the shell aperture in both species, thus confirming the oviparous status of both of these species of *Euonyma*. Extant species of the *magilensis* group are also known to be oviparous (Verdcourt 1968), and this observation therefore perhaps lends further support to the identification of the material.

Ecology. At present, members of the *E. magilensis* group are found in various types of forest habitat including gallery forests along the River Thika in Kenya (*curtissima*), in dry, semi-deciduous forest types in northern Kenya (*achilles*) and in coastal and medium elevation Eastern Arc forests in northeast Tanzania (*magilensis*). The group appears to be characteristic of forests in areas with low to moderate rainfall levels, rather than true rainforest types, although Pickford (1995) and Verdcourt (1984) comment that the *magilensis* group is found in 'upland evergreen forest', and the author has collected abundant living material of *magilensis* from intermediate level evergreen rainforest in the East Usambara mountains in northeast Tanzania.

Family: Subulinidae
Genus: Subuliniscus Pilsbry, 1919
Species: sp. A

Material Examined. Fig. 22.2i. Two shells from lot EP 1330/98, from the Upper Ndolanya Beds at Loc. 22S. The smallest specimen and the lower part of the shell of the largest specimen are poorly preserved. However, the upper part of its shell appears to be relatively intact. The material is too poor for formal description. A further nine shells, also from the Upper Ndolanya Beds, that have not been examined by the author have been assigned to this species by T. Harrison.

Identification and Taxonomy. Shell size of the two shells examined: H = 21.2 mm, D = 5.5 mm and H = 15.7 mm, D = 5.9 mm. This is clearly a very elongated subulinid and its tentative assignment to *Subuliniscus* has been based on the pointed shell apex of the largest specimen, which is similar to the recent species of the genus. The smaller shell also appears to have a pointed apex. The related subulinid genus *Oreohomorus*, which also has a similar pointed apex, could represent an alternative genus for this species. A further possibility that may be considered is *Hypolysia*, which has a rounded columella (rather than a truncate one) but lacks the distinctly nipple-shaped apex present in the current material. *Hypolysia* is currently represented by only two species in East Africa, both from the Usambara mountains in northeast Tanzania.

No microsculpture is visible on the specimens, but it seems very unlikely that the fine, spiral microsculpture that is diagnostic of *Subuliniscus* (Pilsbry, 1919) could have been preserved during fossilization. The columella is truncate. No other information can be gleaned about the form of the shell aperture.

Ecology. Subuliniscus is currently a genus of highland areas in East Africa generally occurring in relatively high rainfall areas, although it also occurs in cloud forest on isolated mountains in north Kenya. In Nairobi forests it is often found in quantity on tree trunks about 1–2 m from the ground (Pickford, personal communication). The author has collected *Subuliniscus* from several sites in north and central Tanzania. Verdcourt (2006) lists 11 species from East Africa. The material is too poor to speculate about its affinities with the recent species.

Family: Streptaxidae
Genus: Streptostele L. Pfeiffer, 1856
Subgenus: Raffraya Bourguignat, 1883

Material Examined. In total, there are 12 lots containing 15 specimens of *Streptostele* in the material examined. EP 1434/00, EP 1169/01, EP 1463/04, EP 153/01, EP 163/03, EP 1662/00, EP 1905/03, EP 2774/00, EP 4060/00, EP 528/04, EP 3330/00, EP 2233/03.

Two species have been identified (Figs. 22.3a–c) although there is only one incomplete specimen of the smaller sp. A (EP 2233/03, Loc. 7, Upper Laetolil Beds, between Tuffs 7 and 8; Fig. 22.3c).

Species: aff. *horei* Smith, 1890

Identification and Taxonomy. The first two whorls are smooth but the rest of the shell is strongly ribbed, with about 9 ribs/mm on both whorl 7 and on the body whorl (whorl 9). The axis of the upper part of the shell is distorted, resulting in slightly curved profile, and the first three whorls are strongly contracted (Fig. 22.3a). The peristome is discontinuous (Fig. 22.3b) but there is evidence in some specimens (EP 258/04) of a slight thickening of the parietal area of the aperture, which may indicate the presence of a very weak denticle. The maximum size is about H = 11 mm, D = 3 mm and there are nine whorls, although these are estimated measurements because there are no intact shells in the collection studied. One specimen (EP 3330/00), from the Upper Ndolanya Beds at Loc. 18, is broader and has a more elongated aperture that the typical material; this may represent another species but it is thought more likely that the shell has been distorted during fossilization.

The material clearly belongs to the same species that Verdcourt (1987) considered to be closely related to *S. urguessensis* Connolly. This conclusion was largely based on the shape, presence of strong costae and the constricted upper whorls. However, examination of material of *S. urguessensis* from Nakuru in the Melvil-Tomlin Collection in the National Museum of Wales indicates that the apical whorls are not as severely constricted as the Laetoli material. Other recent species of *Raffraya* that have both the ribbed shells and the strongly constricted spire present on the Laetoli species include *S. nyiroensis* Connolly and *S. horei* Smith. Of these, the Laetoli material examined probably comes closest to *S. horei*.

Ecology. *Streptostele horei, S. urguessensis* and *S. nyiroensis* are all found in isolated mountainous areas that are set in the semi-arid lands of northern Kenya. However, *horei* is more widespread that the other two species, being recorded from the Democratic Republic of Congo and from near Lake Manyara (Rowson, personal communication) and near Lake Tanganyika (Verdcourt 2006) in Tanzania. Little is known about the habitats of these species, but they probably occur in woodland, cloud forest and/or scrub habitats.

Species: Species A

Figure. 22.3c. Represented by a single incomplete shell (EP 2233/03; Loc. 7, Upper Laetolil Beds between Tuffs 7 and 8), which lacks its apex. This species is smaller and more slender that the above *Streptostele.* The broken specimen is 4.4 mm long and 1.7 mm wide and it consists of 4¼ whorls. The shell is regularly ribbed, there being about 14 ribs/mm on the body whorl. This specimen is provisionally assigned to *Streptostele* although no further interpretation is possible because of the limited material available.

Ecology. Small, ribbed *Streptostele* currently occur in a range of habitats in East Africa. However, the affinity of this species with extant taxa cannot be established from the limited material that is available.

Family: Streptaxidae
Genus: Gulella Pfeiffer, 1856
Species: sp. A

Material Examined. Figs. 22.3d–f. One shell fragment (EP 1170/01) from Loc. 1 in the Upper Laetolil Beds, between Tuffs 7 and Yellow Marker Tuff. *Gulella* is a very diverse group that is now known to be polyphyletic. Current taxonomy is largely based on shell characters, and in particular the number and configuration of distinctive apertural processes.

Unfortunately, the aperture of the specimen is filled with calcite so any apertural processes that may be present are barely visible; X ray photography of the shell has not assisted in this respect.

A further specimen provisionally identified as *Gulella* (Harrison, personal communication) has also been recovered from the Upper Laetolil Beds (Locality 12E, EP 538/05) but has not been examined by the author.

Identification and Taxonomy. Pupiform. H=7.7 mm, D=3.9 mm, 7¼ whorls. Shell with slightly oblique regular radial ribbing on whorl 4, with about 16 ribs/mm. Aperture obscured by calcite. The presence of areas of harder, glassier material in the aperture indicates the presence of a parietal denticle and probably also a palatal denticle. The shell characters visible on the single shell that is available are shared with many recent *Gulella* species so further identification and speculation about its affinities with extant species are not possible.

Ecology. *Gulella* species currently occur in a wide range of habitats, spanning a very broad range of environmental conditions, in Africa. The richest *Gulella* faunas are generally found in forest habitats although some species also occur in relatively arid areas. No further assessment can be made regarding the possible habitat associations of the single specimen reported here.

Family: Achatinidae
Genus: Burtoa Bourguignat, 1889
Species: nilotica (Pfeiffer, 1861)

Material Examined. Seven specimens in two lots, EP 1361/01 (Emboremony 1, Lower Laetolil Beds) and EP 539/98 (Loc. 10, Upper Laetolil Beds, below Tuff 2). Figures. 22.3g–i.

Identification and Taxonomy. The seven specimens may confidently be referred to the extant genus *Burtoa.* The material examined appears to be homogenous and lies close to one of the current races of *nilotica* (Crowley and Pain 1959). Shell measurements are given in Table 22.1. The mean (apical) angle of the shell is about 75° (range 73–78°).

Verdcourt (1987) examined seven shells and tentatively assigned one specimen with a narrower apex to the fossil *B. nilotica verdcourti* Crowley and Pain, 1959. However, none of the shells from the current material appear to match this Miocene subspecies, which was collected on Rusinga Island, Kenya. As Verdcourt (1987) noted, a longer series of well-preserved material of *Burtoa* would be required to establish the status of this species in the Laetolil Beds.

Table 22.1 Shell dimensions of the six intact specimens of *Burtoa nilotica* (Pfeiffer) (EP 1361/01 and EP 539/98)

H (mm)	D (mm)	No. whorls
103	60	6½
109	66	6¼
90	59.5	6
95	58	5½
84	50	5¼

Ecology. *Burtoa* currently has a rather restricted distribution in East Africa being confined in Kenya to the area immediately around Lake Victoria, although according to Pickford (1995) and Crowley and Pain (1959) it extends further to the east in Tanzania and Pickford (personal communication) has found it to be abundant between Mounts Elgon and Kadam in eastern Uganda. It is generally associated with savanna and scrub habitats and is not found in forests. Crowley and Pain (1959) indicate that Laetoli would lie within the geographical range of subspecies *giraudi*, which is associated with savanna habitats. Pickford (1995) also comments on the current distribution of *Burtoa* in East Africa and states that it is an inland genus that is not often found below 500 m or above 1,700 mm elevation. He also notes that ‘at present, the genus *Burtoa* appears to be restricted to areas of tropical Africa where the rainfall is between 760 mm and 1,200 mm per year in two rainy seasons’. Fieldwork by the author and colleagues indicates that *Burtoa* is rare, very localized or completely absent from forest habitats at the present time because it has never been recorded in forest surveys in Kenya, Tanzania or Uganda over the past 18 years.

Family: Achatinidae
Genus: Limicolaria Schumacher, 1817
Species: martensiana (E.A. Smith, 1880)

Material Examined. Twenty shells examined, all from the Lower Laetolil Beds at Kakesio 1–6 (EP 1182/01). Figures. 22.3j–l.

Identification and Taxonomy. Verdcourt (1987) examined eight shells from the same site (Kakesio Road exposures). With the exception of two narrower specimens, all the shells examined from the current material closely match Verdcourt’s description, and, following Verdcourt (1987), these have been identified tentatively as *L. martensiana*. Verdcourt (1987) also suggested that the material might be assigned to race *catharia* Dall, 1910. Without a larger sample of material, it is not possible to decide whether the two narrow shells (H=374 mm, D=163 mm and H=432 mm, D=176 mm) represent a second species or whether they are extreme forms of the predominant one; however, the latter suggestion is considered most likely. Verdcourt (1987) reports the occurrence of smaller shells within one of the samples, and Pickford (1995) considers in some depth the reproductive strategies adopted by *Limicolaria*, concluding that at least some species of the genus have the ability to be both oviparous and viviparous. The Laetoli sample examined here includes specimens from Kakesio that contain eggs and embryos, thus providing confirmation of Pickford’s contention.

Ecology. *Limicolaria* is a widespread in much of East Africa. It occurs at low elevations, but is perhaps most frequent in upland areas, especially in association with human activity where it may be found in abundance in cultivated areas (typically small scale farms or 'shambas'). Its distribution is afrotropical, in both north and south hemispheres, extends to West Africa. It is absent or scarce in the drier parts of northern Kenya, and along the Indian Ocean coast zone, and it does not appear to be able to survive in arid and semi-arid areas.

Family: Achatinidae
Genus: Achatina Lamarck, 1799
Subgenus: Lissachatina Bequaert, 1950
Species: Unidentified

Material Examined. Thirteen shells and molds examined from Upper Laetolil Beds below Tuff 3 at Loc. 10W (EP 1119/03, 5 shells) and Loc. 22 (EP 153/04, 2 shells) and the Lower Laetolil Beds at Emboremony 1 (EP 1362/01; 6 shells). Figures. 22.3m, n.

Identification and Taxonomy. The taxonomy of *Achatina* is in need of revision, and, as noted by Verdcourt (1987), even fresh material can often not be named with confidence. The material examined has the same overall shape, size and relatively strong sculpture described by Verdcourt (1987) and it is clear that the specimens represent the same species. Although most of the larger shells examined fall within the general size range described by Verdcourt, one specimen, which is a mold, is considerably larger (H=94 mm long, D=48 mm).

Verdcourt (1987) suggested that the material might be a race of *A. fulica* Bowdich, but he also noted that the overall shape resembled *A. (Lissachatina) zanzibarica* Bourguignat and he named his material as that species whilst also noting that 'Absolutely no importance must be attached to this determination'. It is noted that the shell size of all the material under current study is generally smaller than recent specimens of *zanzibarica* that have been collected by the author from the Tanzanian coastal forests. The Laetolil material examined here does not yield any further information about specific identification, and, in view of these problems it is considered inappropriate to name the species.

Ecology. *Achatina* is a widespread genus in the lowland tropical Africa, with most species occurring below 1,200 m, and few above 1,500 m (personal observation; Pickford 1995; Pilsbry 1919). Some species such as the costal *A. zanzibarica* are forest species, whereas others are associated scrub and savanna vegetation.

Family: Urocyclidae
Genus: Trochonanina Mousson, 1869
Species: sp. B *sensu* Verdcourt, 1987

Material Examined. 62 lots comprising 96 specimens. Figures. 22.4a–d. EP 009/03, EP 009/98, EP 024/99, EP 041/00, EP 071/01, EP 073/04, EP 078/01, EP 1104/04, EP 1117/03, EP 1167/01, EP 1168/01, EP 1357/03, EP 1360/01, EP 1393/00, EP 1465/03, EP 1496/03, EP 1543/00, EP 1644/03, EP 1660/00, EP 1660/04, EP 169/00, EP 186/99, EP 1884/00, EP 1906/03, EP 1907/03, EP 1983/03, EP 2021/00, EP 2085/03, EP 2160/03, EP 2232/03, EP 2250/03, EP 226/03, EP 229/01, EP 2291/03, EP 2292/00, EP 236/00, EP 2428/00, EP 2594/00, EP 2772/00, EP 2778/00, EP 282/01, EP 282/99, EP 3025/00, EP 307/03, EP 3095/00, EP 3331/00, EP 348/03, EP 4335/00, EP 435/03, EP 526/04, EP 533/03, EP 602/04, EP 636/04, EP 655/01, EP 666/04, EP 754/98, EP 805/04, EP 814/00, EP 851/04, EP 946/01, EP 543/98, EP 267/98.

Identification and Taxonomy. As explained by Verdcourt (1987), this genus requires revision and much of the taxonomy of recent species is based on the soft anatomy. The size, shape and sculpture of the fossils under current study is very variable, but analysis of this variation does not appear to justify division of the material into more than one species.

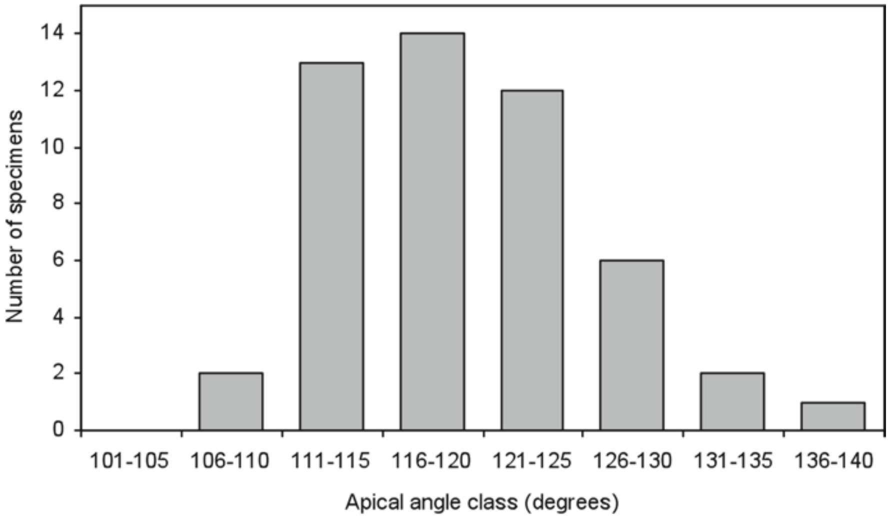

Fig. 22.6 *Trochonanina* species – frequency distribution of apical angle of shell ($n=50$)

Table 22.2 Shell diameter (D), number of whorls and the number of striae per mm on different whorls on seven shells of *Trochonanina* sp. B

					No. striae per mm on whorl:		
Specimen	Locality	Horizon	D (mm)	No. whorls	*4*	*5*	*6*
EP 1168/01	1	Upper Laetolil, Tuffs 7–8	13.1	5½	34	34	
EP 2021/00	5	Upper Laetolil, Tuffs 3–5	10.6	5	24	16	
EP 1906/03	1	Upper Laetolil, Tuffs 7–8	15.2	6¼	35		
EP 1360/01	Emboremony	Lower Laetolil	18.2	6¼	19	14	13
EP 754/98	10W	Upper Laetolil, below Tuff 2	12.1	5¾		18	
EP 169/00	16	Upper Laetolil, Tuffs 7–8	14.6	5½	28	28	
EP 267/98	10E	Upper Laetolil, Tuffs 6–7	14.7	5½	28		

Verdcourt (1987) tentatively allocated his material to two species based on the apical angle of the shell – sp. A and sp. B, with apical angles of about 132° and 118° respectively. However, he also commented that 'whether this is due to variation or the presence of two taxa is not absolutely clear but I think two distinct species are probably involved'.

In order to explore this further, the shell dimensions (H and D) and apical angles of 50 specimens chosen at random from the current material have been measured. In this sample, shell apical angle shows no sign of bimodality (Fig. 22.6). The modal angle class is 116–120°, which suggests that the specimens in the current material resemble most closely Verdcourt's sp. B, at least in terms of the apical angle of the shell. Verdcourt (1987) suggested that this taxon might be referred to *T. elatior* (von Martens), which, according to Verdcourt (2006), is currently widespread being reported from north Uganda, central Kenya and Tanzania generally.

The measurement of the apical angle of some shells may be prone to error or there may be a degree of size- or age-related variation. However, further analysis shows that apical angle is independent of both H and D. Well-preserved specimens show clear evidence of fine, regular transverse striae (Fig. 22.4d), which vary considerably in terms of density. On the seven specimens measured (Table 22.2) the estimated density of striae on whorl 4 ranges from about 19 to 35 per mm, and it appears to be reasonably constant across the range of whorls on some shells (e.g., specimens EP 1168/01 and EP 169/00). However, there is evidence of a slight decline in striae density with size on specimens EP 1360/01 and EP 2021/00. Some of the specimens have slightly keeled shells (e.g., EP 754/98 and EP 1168/01, Figs. 22.4b, c) whereas others of comparable size have a rounded periphery (e.g., EP 229/01, Fig. 22.4a).

Ecology. Most of the recent species of *Trochonanina* are associated with bushland, savanna, Miombo, woodland or grassland habitats. Verdcourt (2000) and Pickford (1995) both note that some species of *Trochonanina* may occur in forest, although in the author's experience this is relatively unusual. Pickford (1995) noted that *Trochonanina* is well represented in the East African fossil record, and considered that its presence 'provided evidence of relatively dry, perhaps grassy' conditions.

Family: Halolimnohelicidae
Genus: Halolimnohelix Germain, 1913
Species: rowsoni sp. nov.

Material Examined. Two shells from the Upper Laetolil Beds between Tuffs 6–8 - EP 313/01 (Loc. 3; paratype) and EP 1660/00 (Loc. 3; holotype) (Figs. 22.4e–g). Two further specimens (also from Loc. 3), which have not been examined, have also been provisionally assigned to this species (Harrison, personal communication).

Identification and Taxonomy. Refer to Table 22.3 for shell dimensions. Shell slightly depressed globular with weak irregular radial growth lines evident both on upper and lower surface. Whorls moderately tumid, with rounded periphery. Umbilicus partly obscured by sediment, but possibly open. There are fragments of an additional whorl near the umbilicus on shell EP 313/01, indicating that the specimen is incomplete and was formerly larger. No evidence of hair pits can be seen on either specimen.

These specimens are assigned to the Halolimnohelicidae based on their moderate size, globular shells, rather tumid whorls and very rounded peripheries. In some respects the specimens resemble juvenile streptaxid shells in genera such as *Gonaxis* or *Marconia*, although the whorls are perhaps too tumid and there is no evidence of the characteristic axial distortion of the shell of *Gonaxis*. Furthermore, the shell surface sculpture, or the impression of it, appears to be too fine and irregular for *Gonaxis/Marconia*. The base is convex, and the aperture seems crescentic rather than having the typically squarish shape found in young *Gonaxis* or *Gulella*.

It is recognized that such simple shell characters are not entirely diagnostic for the Halolimnohelicidae. However, it is also noted that most recent species of comparable size in other families/genera in the East African fauna tend to have other differentiating characters. These include keeled or carinate shells (e.g., *Trochonanina*, *Trochozonites*), strong spiral sculpture (e.g., *Tropidophora*) or generally more flattened apices and shell form (e.g., *Tayloria*, *Maizania*). Other globular species in the East African fauna (e.g., *Prositala*,

Table 22.3 Shell and aperture dimensions (mm) and whorl number for two specimens of *Halolimnohelix rowsoni* sp. nov

Specimen	H	D	h	d	No. whorls
EP 1660/00 (holotype)	6.2	8.0	3.7	4.5	5¼
EP 313/01 (paratype)	6.0	8.4	4.1	4.9	4¾

Kaliella, *Afroconulus*) tend to be much smaller (typically <5 mm).

The species has been placed in *Halolimnohelix* although this assignment cannot be made with confidence because classification of the Halolimnohelicidae is based largely on genital anatomy. It is noted that some species in other halolimnohelicid genera have broadly similar shell forms. For example, *Haplohelix* (e.g., *sjostedi* d'Ailly and *alticola* d'Ailly) and *Vicariihelix* (e.g., *keniensis alticola*).

The species is named after Ben Rowson (National Museum of Wales) in recognition of the assistance he provided during the preparation of this paper.

Ecology. At present, the Halolimnohelicidae is generally found in upland habitats with moderate to high rainfall, although it is also present in cloud forest on the summits of some of the isolated north Kenyan mountains, which have lower levels of rainfall. Its presence at Laetoli might therefore suggest a rather damper environment than indicated by the majority of the other taxa. Pickford (1995) comments that *Halolimnohelix* is especially common in the Kenyan uplands, in areas that receive more than 760 mm rain per annum, and that the genus has not been recorded in Kenya below 1,500 m altitude. Pickford (1995) also reports the first records for *Halolimnohelix* from the East African fossil record, from the early Miocene in western Kenya and late Pleistocene deposits on Mfangano Island on Lake Victoria.

Interpretation of the Paleoecology Using the Gastropod Assemblage

Sampling Issues

Land-snail fossils are ubiquitous and abundant at most of the Laetoli localities (see Table 22.4) and the majority of specimens examined are in reasonably good condition. Some species which have thin and/or poorly calcified shells, such as some semi-slug species in the Urocyclidae, may not have been preserved, but generally, the base rich substrates and rapid burial in reworked volcanic ashes appear to have led to well preserved assemblages. Most of the fossil mollusks were recovered as surface finds that had eroded out on to the exposed outcrops of the Laetolil and Upper Ndolanya Beds, but a few were recovered by excavation from *in situ* (Harrison, personal communication). In most cases the original stratigraphic provenience of the specimens could be inferred. The collection studied is dominated by medium to very large shelled species and the scarcity of micromollusks (maximum shell dimension <5 mm) is striking, in terms of both the number of species and individuals. Efforts were made during field sampling to ensure that representative samples of mollusks were collected at each locality (Harrison, personal communication), so these observations may reflect a true absence of small species in the original fauna, or possibly a loss of small species at the time of accumulation. However, no systematic screening of the sediments was undertaken, so it is possible that there may be a bias in the collections against the recovery of small gastropods (as there is for smaller rodents, see Denys 2011). Recent East African mollusk faunas, and especially those from more mesic habitats, may be rich in micromollusks, so any such bias could affect environmental reconstruction. Therefore, the approach adopted necessarily focuses on changes in the relative frequencies of the larger and more abundant taxa, rather than on shifts in the overall composition and diversity of the recorded assemblages. Although not studied directly by the author, the mollusk material collected at Laetoli also includes a large number of slug shells ('plates') from species in the Urocyclidae and data on these have been provided by T. Harrison for use in the interpretation (Table 22.4).

Interpretation of environmental conditions is also limited by identification and taxonomic problems, and by a lack of detailed knowledge about the specific ecological associations and geographical distributions of the taxa concerned. Of course, drawing inferences from the fossil gastropod fauna assumes that there have not been any major changes in the ecological associations of the genera and species concerned since the Pliocene. However, as noted for other East African fossil sites (Verdcourt 1963; Pickford 1995), such an assumption would appear to be reasonable given that the fossil taxa identified are clearly close to forms currently occurring in East African habitats.

Overall Character of the Pliocene Fauna

There are now published and unpublished data available on the distribution and composition of modern mollusk faunas from many sites throughout East Africa, and these may be used to assist in the interpretation of the Laetoli fossil assemblage, and thus contribute to the reconstruction of the paleoecology during the Pliocene. In particular, there has been much recent fieldwork by the author and colleagues, extending throughout Tanzania, Kenya and Uganda (see Seddon et al. 2005 for a summary), although most of this research has been restricted to forested sites that tend to support much richer faunas than those reported here. Pickford (1995) also provides mollusk lists for forest and upland woodland sites in Kenya, as well as from more xeric habitats including

Table 22.4 Number of specimens of gastropod taxa from Laetoli and other localities on the Eyasi Plateau (1998–2005 collections)

Locality	Stratigraphic unit	*"Succinea"* sp. A	*Edouardia laetoliensis*	*Cerastus* sp. A	*Subulona pseudinvoluta*	*Pseudoglessula* aff. *gibbonsi*	*Euonyma leakeyi*	*Euonyma harrisoni*	*Subuliniscus* sp. A	*Streptostele* aff. *horei*	*Streptostele* sp. A	*Gulella* sp. A	*Burtoa nilotica*	*Limicolaria martensiana*	*Achatina (Lissachatina) indet.*	*Trochonanina* sp. B	*Halolimnohelix rowsoni*	Indeterminate	Number of specimens	Urocyclid slugs
1	ULB 7–8		58							6		1				17		1	83	54
2	ULB 5–7		3		9										4	1			17	143
3	ULB 7–8		20		16		7			2						20	4		69	75
4	ULB 6–8		4													3			7	21
5	ULB 3–5		4		61		57								14	3			139	249
6	ULB 5–7		1		1					3						2			7	100
7	ULB 5–7		2		2								2			6			12	91
7	ULB 7–8										1					2			3	18
7E	UNB								2										2	12
8	ULB 5–7				59		7						3		3	3		2	77	320
8	ULB 7–8						3									1			4	9
9	ULB 5–7		1		4								1	1	8			1	16	140
9S	ULB 0–2		7			16	243						3		7			2	278	138
10	ULB 0–3		6		3	33	270						21		28	4		4	369	268
10E	ULB 5–7		3		37								8		29	3		1	81	769
10W	ULB 0–3		16		3	14	307						14		29	5		2	390	283
11	ULB 7–8		5				1									10			16	38
12	ULB 5–8																		0	23
12E	ULB 5–7											1							1	60
13	ULB 5–7				1										2				3	79
13	ULB 7–8				3											1			4	22
14	UNB																		0	1
15	ULB 6–7		2		1								1		5	2			11	227
15	UNB									1						1			2	142
16	ULB 7-YMT		4		1								1			6			12	32
17	ULB 7-YMT									1									1	13
18	UNB							44	3	2						1		3	49	146
19	ULB 5–8		1																1	11
20	ULB 6–8		3																3	31
21	ULB 5–7				2										1				3	45
22	ULB 0–3				19	1									2				22	1
22	ULB 5–7		1		4		2						1		8				16	39
22E	ULB 3–5				4		3								1				8	6
22E	ULB 5–7				2		5												7	23
22E	UNB							4											4	86
22S	UNB							1	6										7	83
Kakesio	LLB		3	3									14	166	54	10			250	0
Emboremony	LLB	1											8	1	18	3		2	33	0
Noiti 3	LLB														1				1	0
Esere	LLB												1		1				2	0
Olaltanaudo	LLB														2				2	0
Lobeleita	LLB													1	4	1			6	0
Silal Artum	UNB																		0	36
Total		1	144	3	232	64	905	49	11	15	1	2	78	169	221	105	4	18	2,018	3,834

upland savanna, *Acacia/Commiphora* steppe and from the north Kenyan desert (Suguta Valley). Other checklists of note include an account of the mollusks of the East African coastal forests (Verdcourt 2000), and of the Eastern Arc mountain ranges in southeast Kenya and Tanzania (Tattersfield et al. 1998).

Verdcourt (1987) reported 10 species of terrestrial mollusk from the Laetolil and Upper Ndolanya Beds and Pickford (1995) has added one further species, *Pupoides coenopictus*, from the Lower Laetolil Beds at Kakesio. This study has increased the total number of gastropod taxa known from Laetoli to 16 species (excluding urocyclid slugs). These totals are low compared with present day East African forest faunas. Seddon et al. (2005) provide estimates of species richness in forest habitats in various East African biogeographical zones, and shows that site diversity typically ranges between about 20 and 40 species, with the richest sites supporting up to 50–60 species. The poorest faunas are typically associated with deciduous or semi-deciduous forest, woodland or bushland vegetation types in areas of lower and/or highly seasonal rainfall. Amongst the forest sites studied recently, the coastal forests of Kenya and Tanzania and some of the north Kenyan mountain forests have returned the lowest numbers of species, but even in these sites the species totals typically lie between 20 and 30 species. In terms of similarities with existing faunas, the Pliocene fauna at Laetoli may resemble most closely those currently found at sites such as the riverine forest at Thika Gorge, Kenya, with possible affinities with damper and perhaps more elevated sites such as the northern Kenyan cloud forests on Marsabit, Kulal etc. However, assuming that there is not a major bias against micromollusks in the collection, these observations suggest that the Pliocene site did not support extensive areas of closed forest habitats and that it is likely that the predominant habitats ranged from grassland and savanna to woodland.

Paleoenvironmental Interpretation

The fossiliferous horizons and stratigraphy of the Pliocene deposits at Laetoli are summarized in Hay (1987), Su and Harrison (2007) and Ditchfield and Harrison (2011).

In addition to material recovered from localities from the Lower Laetolil Beds and the Upper Ndolanya Beds, marker tuffs can be used to designate four stratigraphic subunits within the Upper Laetolil Beds (see Su 2005; Su and Harrison 2007; Kovarovic and Andrews 2011). These subunits are: below Tuff 3, between Tuffs 3 and 5, between Tuffs 5 and 7, and above Tuff 7. Because of the small samples of mollusks recovered from many of the collecting localities it is not possible to examine geographical variation in the fossil fauna across the Laetoli area.

Table 22.4 shows the numbers of fossil gastropods recovered from the 32 collecting localities and details of their stratigraphic provenience. The table also illustrates the variation in the abundance of urocyclid slugs, relative to the total gastropod fauna, and Table 22.5 shows the frequency of each taxon within each of the grouped stratigraphic units as a percentage of the total number of gastropods (excluding urocyclid slugs) from the unit concerned. These data are also summarized on Fig. 22.7a, on which the three large shelled achatinids (*Limicolaria, Achatina* and *Burtoa*), the two *Euonyma* species (*E. leakeyi* and *E. harrisoni*) and all the species whose the overall frequency does not exceed 5% of the total collection have been grouped. Figure. 22.7b shows the contribution made by slugs to the total gastropod fauna.

Table 22.5 Frequency (%) of each gastropod taxon within each of the grouped stratigraphic units as a percentage of the total number of gastropods (excluding urocyclid slugs) from the unit concerned

	Stratigraphic unit					
	LLB	ULB 0–3	ULB 3–7	ULB 5–7	ULB 7-YMT	UNB
"*Succinea*" sp. A	0.3	0.0	0.0	0.0	0.0	0.0
Edouardia laetoliensis	1.0	2.7	2.7	4.6	45.3	0.0
Cerastus sp. A	1.0	0.0	0.0	0.0	0.0	0.0
Subulona pseudinvoluta	0.0	2.4	44.2	50.4	10.4	0.0
Pseudoglessula aff. *gibbonsi*	0.0	6.0	0.0	0.0	0.0	0.0
Euonyma leakeyi	0.0	77.4	40.8	5.8	5.7	0.0
Euonyma harrisoni	0.0	0.0	0.0	0.0	0.0	72.1
Subuliniscus sp. A	0.0	0.0	0.0	0.0	0.0	16.2
Streptostele aff. *horei*	0.0	0.0	0.0	1.3	4.7	4.4
Streptostele sp. A	0.0	0.0	0.0	0.0	0.5	0.0
Gulella sp. A	0.0	0.0	0.0	0.4	0.5	0.0
Burtoa nilotica	7.8	3.6	0.0	6.3	0.5	0.0
Limicolaria martensiana	57.1	0.0	0.0	0.4	0.0	0.0
Achatina (Lissachatina) indet.	27.2	6.2	10.2	22.9	0.0	0.0
Trochonanina sp. B	4.8	0.8	2.0	6.3	29.7	2.9
Halolimnohelix rowsoni	0.0	0.0	0.0	0.0	2.1	0.0
Indeterminate	0.7	0.8	0.0	1.7	0.5	4.4
No. gastropod specimens (excl. slugs)	294	1,059	147	240	192	68

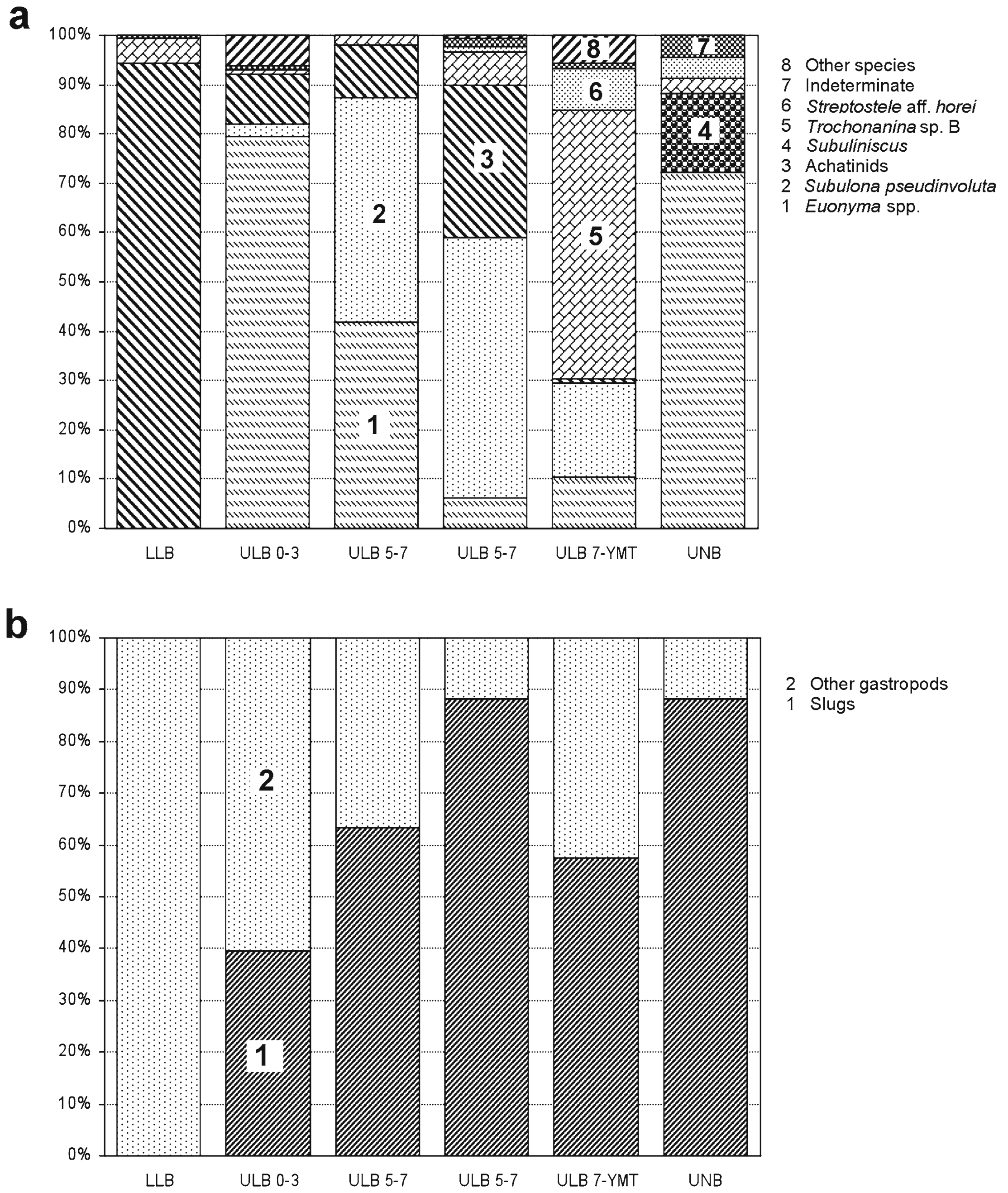

Fig. 22.7 (**a**) Percentage frequency of shelled gastropod species (i.e., snails) from samples in the Lower Laetolil Beds (*LLB*), four sub-units of the Upper Laetolil Beds (*ULB*) and the Upper Ndolanya Beds (UNB). (**b**) Percentage frequency of slugs and shelled gastropods (i.e., snails) from samples in the Lower Laetolil Beds (*LLB*), four sub-units of the Upper Laetolil Beds (*ULB*) and the Upper Ndolanya Beds (UNB)

Lower Laetolil Beds

According to Deino (2011), the Lower Unit of the Laetolil Beds spans at least 0.5 myrs. Clearly, there is ample opportunity for major shifts in environmental conditions, and hence also in faunal assemblages over a time span of this duration.

The mollusk fauna is highly distinctive, being dominated by large, robust, achatinids in the genera *Limicolaria*, *Achatina (Lissachatina)* and *Burtoa*, which collectively make up 92.2% of the 294 specimens recovered. The Lower Laetolil Beds are also characterized by the absence of urocyclid slugs, which are very common throughout the Upper Laetolil Beds and in the Upper Ndolanya Beds. The prevalence of the large achatinids probably suggests that climatic conditions at the time were relatively dry, although not to the extent that they could be classified as semi-arid. The presence of *Trochonanina* and *Edouardia*, which were recorded at lower frequencies, is consistent with this interpretation, as also is the reported occurrence (Pickford 1995) of *Pupoides coenopictus* from the Lower Laetolil Beds at Kakesio. However, the occurrence of *Cerastus* and '*Succinea'* may indicate damper conditions, at least locally or during some periods of time. A moist savanna environment, as defined by Hamilton (1982), with an annual rainfall of at least 500 mm is perhaps the most plausible reconstruction of the habitats present during this period, although such a conclusion is necessarily tentative because the achatinid genera concerned currently include species that occur in damper habitat types, including forest. Verdcourt (1987) discussed the problems associated with interpreting the achatinid fauna, and notes that species of all three genera currently occur across a wide range of climatic conditions, from low rainfall areas receiving 625 mm or less per year, to true rainforest conditions. According to Pickford (1995), the presence and dominance of *Limicolaria* suggests that annual rainfall was in the region of 760–1,020 mm, and that there were probably two rainy seasons. The complete absence of slugs from the fauna may indicate that refuges providing shelter from desiccation, such as fallen wood or deep layers of leaf litter, were absent or very scarce. This, therefore, may indicate that large trees were absent or very scarce within a savanna environment. Pickford (1995) also reported a *Pseudoglessula* species from Kakesio, which is a genus not found from the Lower Laetolil Beds during the current study. However, his specimens are not figured or described so it is not possible to comment whether they may be referred to *P.* aff. *gibbonsi*, which has been shown here to be abundant in the lower subunit (below Tuff 3) of the Upper Laetolil Beds or to another species.

Upper Laetolil Beds

The Upper Laetolil Beds spans a time period of ~0.25 myrs (Hay 1987; Deino 2011). Based an radiometric dates for Tuffs 2, 4 and 8 (Deino 2011) and average sedimentation rates, the ages of the four subunits can be estimated to be: below Tuff 3 (~3.80–3.85 Ma), between Tuffs 3 and 5 (~3.75–3.80 Ma), between Tuffs 5 and 7 (~3.65–3.75 Ma), and above Tuff 7 (~3.60–3.65 Ma).

Compared with the Lower Laetolil Beds, the mollusk fauna recorded in all horizons of the Upper Laetolil Beds is characterized by a large reduction in relative abundance of large achatinids and the occurrence of frequent urocyclid slugs. Overall, these observations indicate that the environmental conditions were generally damper compared with the Lower Laetolil period.

Each subunit within the Upper Laetolil is characterized by variation in the frequency of a small range of taxa, in particular, *Subulona pseudinvoluta*, *Euonyma leakeyi*, *Edouardia laetoliensis*, *Trochonanina* sp. B, and, to a lesser extent, *Pseudoglessula* aff. *gibbonsi*. The three lower subunits (from the bottom of the Laetolil Beds up to Tuff 7) are characterized by a high relative abundance of *E. leakeyi* and *S. pseudinvoluta,* which may indicate the presence of woodland, at least locally, within the area. Of these taxa, *Subulona* is likely to have the strongest affinity with damper conditions, so the observed increase in the relative frequency of this species over the three lower sub units may suggest a general increase in woodland cover and damper conditions over the course of this period. The increase in large achatinids (*Achatina (Lissachatina)* and *Burtoa*) would lend some support to this interpretation, but the higher frequencies of *Trochonanina* and *Edouardia* within the subunit between Tuffs 5–7 suggests that there may have been some areas or periods of time within this subunit that experienced less mesic conditions. However, the high abundance of urocyclid slugs within the subunit between Tuffs 3–5 and the accompanying high frequency of *Subulona* may indicate that woodland cover was at its peak over this period.

Compared with the three lower subunits that share several faunal characteristics, the mollusk fauna associated with the upper subunit, above Tuff 7, appears to be rather distinct. It is characterized by a relatively high frequency of *Edouardia laetoliensis* and *Trochonanina* sp. B, which would suggest the presence of substantially drier conditions compared with those present in the preceding periods (see Peters et al. 2008 for a similar conclusion based on a preliminary analysis of the Laetoli gastropods). The observed increase in the frequencies of these two species in the subunit immediately below Tuff 7 (i.e., between Tuffs 5–7) may indicate the onset of drier conditions prior to the deposition of Tuff 7. Notwithstanding this general conclusion, the occurrence of *Halolimnohelix rowsoni* and the continuing occurrence of *Subulona* indicate that forest or woodland conditions probably still persisted.

Recent studies of the fossil plants (Bamford 2011a, b), vegetation (Andrews and Bamford 2008; Andrews et al. 2011), birds (Harrison 2005; Louchart 2011), cercopithecids (Harrison 2011), mammal community structure (Su 2005; Kovarovic and Andrews 2007; Su and Harrison 2007, 2008; Bishop et al. 2011), ecomorphology (Kovarovic and Andrews 2007, 2011; Bishop et al. 2011), mesowear (Kaiser 2011; Hernesniemi et al. 2011), and stable isotopes (Kingston and Harrison 2007; Kingston 2011) all indicate that the environment at Laetoli was characterized by a higher density of woody vegetation cover than is presently found in the Laetoli area (see Andrews et al. 2011). The consensus view is that the ecology of the Upper Laetolil Beds was predominantly a woodland mosaic, with significant portions of bushland, shrubland and grassland, as well as riverine woodland and forests along ephemeral watercourses (see Su and Harrison 2008). The inferences derived from the Upper Laetolil mollusks are largely consistent with this interpretation, and indicate that the paleoecology was more mesic than at Laetoli today, with a greater predominance of woodlands and forest. In fact, the reconstructed ecological preferences of the mollusks indicate that the Upper Laetolil paleoecology was probably situated at the more heavily vegetated end of the spectrum of habitats that have been reconstructed from studies of the fossil vertebrate fauna.

The Upper Laetolil gastropod faunas differ throughout the sequence, and provide some of the best evidence to document changes in ecology through time. There appears to be a slight shift to somewhat drier conditions above Tuff 5, and this drying trend becomes more pronounced above Tuff 7. By comparison, the mammalian community remains relatively uniform throughout the Upper Laetolil Beds (Kingston and Harrison 2007; Su and Harrison 2008; Peters et al. 2008), with only weak indications of possible shifts in the ecology. Using ecomorphological evidence from ungulate postcranials, Kovarovic and Andrews (2011) have inferred that there is a shift to more open woodlands above Tuff 5, and that this increases above Tuff 7. This would be consistent with the evidence from the fossil gastropods. However, Bishop et al. (2011), in their study of bovid postcranial ecomorphology, suggest that forest-woodland cover is greatest in the Upper Laetolil Beds above Tuff 7. A similar conclusion can be drawn from the phytolith evidence, which indicates that conditions became more mesic in the Upper Laetolil Beds above Tuff 7 (Rossouw and Scott 2011).

Upper Ndolanya Beds

The Upper Ndolanya Beds represent a very brief time window dated to 2.66 Ma (Deino 2011). They are separated from the Upper Laetolil Beds by the Lower Ndolanya Beds (dated at 3.58 Ma), which are unfossiliferous, so there is a temporal hiatus of about 1 myrs between the deposition of the two main fossil-bearing horizons.

Examination of the mollusk fauna from the Upper Ndolanya Beds suggests the presence of woodland and/or patches of forest. This is indicated by the predominance within the fauna of *Euonyma* and *Subuliniscus*. Urocyclid slugs represent almost one half of the total gastropod specimens recovered from the Upper Ndolanya Beds (Fig. 22.7b), thus lending support to the conclusion that trees were frequent in the area at the time. However, this inference appears to be at odds with other lines of evidence relating to the paleoecology of the Upper Ndolanya Beds. Studies of ecomorphology, mesowear, stable isotopes and phytoliths (Kovarovic et al. 2002; Kingston and Harrison 2007; Su and Harrison 2007, 2008; Bishop et al. 2011; Hernesniemi et al. 2011; Kaiser 2011; Kovarovic and Andrews 2011; Rossouw and Scott 2011) all indicate that the Upper Ndolanya ecosystem was dominated by open woodland-bushland and grassland. One explanation for this discrepancy might be that the gastropods are restricted to more mesic microhabitats that are patchily distributed on a more local scale across the landscape. The main argument against such a presumption is that one would expect to see variation in gastropod communities between localities, reflecting different microhabitats, as well as the dominant vegetation type. However, the same gastropod community appears to be typical of all of the Upper Ndolanya Bed localities from which gastropods have been recovered (i.e., Locs. 7E, 18, 22E, 22 S), implying that woodland/forest habitats were relatively widespread, rather than localized.

These contradictions serve to highlight the importance of reconstructing past environments using a range of different paleoecological proxies. Study of the fossil gastropods from Laetoli offers the potential to provide a unique insight into the paleoecology of the site by virtue of the fact that gastropods are relatively common at most sites and occur throughout the sequence, that modern analogs commonly have relatively narrow environmental requirements and preferences (i.e., vegetation, humidity, precipitation, temperature and altitude), and that the fossils are autochthonous (i.e., have not moved or been transported far from the locations where they lived, died and were fossilized, compared with vertebrates that range more widely across the landscape). As a consequence, fossil gastropods are likely to provide a more accurate and more fine-grained reflection of local habitats at Laetoli than do fossil vertebrates.

Note

There have been two nomenclatural changes at the generic level since preparation of the manuscript. Pickford (2009) has introduced the genus *Kenyaella*, which incorporates all the species formerly assigned to *Euonyma* in the '*magilensis*' group, Verdcourt's (1987) *leakeyi* and the Miocene *K. koruensis* (Pickford, 2009); *Euonyma harrisoni*, which is described in this paper, may also be assigned to *Kenyaella*. Bank and Menkhorst (2008) have replaced the name *Edouardia* auctt. non Gude with the name *Gittenedouardia* and thus all African "*Edouardia*" are now assigned to the genus *Gittenedouardia*.

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