

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

# Vertebrate Paleobiology and Paleoanthropology Series

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

**Volume 1: Geology, Geochronology,  
Paleoecology and Paleoenvironment**

Edited by

**Terry Harrison**

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*Cover illustration:* Photograph of skull of *Serengetilagus praecapensis* (EP 3495/00) from Laetoli Locality 15 (© and courtesy of Alisa Winkler) superimposed on a view of the sunrise over Lemugurut from the base camp at Laetoli (© and courtesy Chris Harrison).

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*To Terri, Chris and Ben Harrison  
So that their contributions and sacrifices to the Laetoli project do not go  
unheralded*



## Preface

Laetoli in northern Tanzania is one of the most important paleontological and paleo-anthropological 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, presumably made by *A. afarensis*. In fact, the first Pliocene hominin from East Africa was found at Laetoli, only 10 years after the announcement of *Australopithecus africanus* from Taung in South Africa, although it was not recognized as such at the time.

Given the significance of Laetoli for understanding and interpreting the evolutionary history of early hominins the author recognized that renewed investigations at Laetoli and at other fossil localities on the Eyasi Plateau could produce worthwhile results that might contribute to resolving some long-standing issues in hominin evolution. With this in mind, a long-term program of geological and paleontological investigations, directed by the author, was initiated at Pliocene localities on the Eyasi Plateau, including the hominid-bearing localities in the Laetoli area. The overall objectives were simple; to recover additional fossil hominid specimens and to obtain more detailed contextual information on the paleontology, geology, dating, and paleoecology.

Between 1998 and 2005 the author directed eight expeditions to Laetoli to accomplish these goals. These campaigns produced a wealth of 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 new fossils and samples described and analyzed here, and the subsequent research by a team of international specialists in paleoanthropology, vertebrate paleontology, mammalogy, malacology, entomology, ecology, palynology, paleobotany, taphonomy, geology, geochronology, and stable isotopes.

The present volume provides a compendium of research papers dealing with the geology, geochronology, paleoecology, taphonomy and paleobotany, as well as presenting new information on the modern-day Serengeti ecosystem to help provide baseline data for modeling Laetoli during the Pliocene. The companion volume focuses on the morphology, systematics and paleobiology of the fossil hominins and the associated invertebrate and vertebrate fauna. Together, these two volumes aim is to provide 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, hardworking and resourceful team members who participated in the expeditions to Laetoli that contributed to the recovery of the material discussed and analyzed here. These volumes would not have been possible without them. I would especially like to single out the following individuals who were critical to the success of the field project: Peter Andrews, Remegius Chami, Amandus Kweka, Kaposhi Lasotumboyo, Moses Lilombero, Michael L. Mbago, Charles P. Msuya, Simon Mataro, Simon Odunga, Bill

Sanders and Denise Su. 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 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.

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New York

Terry Harrison



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## Chapter 1

# Laetoli Revisited: Renewed Paleontological and Geological Investigations at Localities on the Eyasi Plateau in Northern Tanzania

Terry Harrison

**Abstract** Laetoli, one of the key paleontological and paleoanthropological localities in Africa, is renowned for the recovery of fossil remains of early hominins belonging to *Australopithecus afarensis* and for the remarkable trails of hominin footprints. In addition, the faunas from the Upper Laetolil Beds (3.63–3.85 Ma) and Upper Ndolanya Beds (2.66 Ma) are from time periods that are generally poorly represented at other paleontological sites in East Africa. Fossils from these stratigraphic units provide important insights into the faunal and floral diversity during the Pliocene, and they serve as reliably dated reference faunas for comparison with other Plio-Pleistocene sites in Africa. The paleoecology of Laetoli is unusual for early hominin sites in East Africa in the absence of evidence for extensive or permanent bodies of water, and in having habitats that are reconstructed as being less densely wooded. Therefore, Laetoli provides key evidence for interpreting the possible diversity of hominin habitat preferences and for understanding ecological changes in East Africa during the Pliocene. The main goal of renewed fieldwork at Laetoli, starting in 1998, was to recover additional fossil hominid specimens and to obtain more detailed contextual information on the paleontology, geology, dating, and paleoecology. The substantially expanded fossil collections have added significantly to our understanding of the systematics and paleobiology of Pliocene East African faunas. The recovery of new *Australopithecus afarensis* specimens from the Upper Laetolil Beds has contributed information on the morphology, variation and evolutionary status of this taxon. Fossil hominins have been recovered for the first time from the Upper Ndolanya Beds. These include the first specimen of *Paranthropus aethiopicus* to be recovered from outside the Turkana Basin, and one of the oldest securely dated specimens definitively attributable to this taxon.

**Keywords** Pliocene • Fossil • Garusi • Laetolil Beds • Ndolanya Beds • *Australopithecus afarensis* • *Paranthropus aethiopicus*

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## Introduction

Laetoli in northern Tanzania is renowned as one of the most important paleontological and paleoanthropological localities in Africa. The site is significant for a number of reasons: (1) the sample of fossil hominins from the Upper Laetolil Beds (3.63–3.85 Ma) is relatively small (just over 30 specimens), but the site has produced the oldest and the second largest sample of *Australopithecus afarensis*, which includes the lectotype, L.H. 4 (Harrison 2011a); (2) the Upper Ndolanya Beds (2.66 Ma) have produced the only specimen of *Paranthropus aethiopicus* definitively known from outside of the Turkana Basin in northern Kenya and southern Ethiopia, and this find extends the distribution of the species 800 km to the south (Harrison 2002, 2011a); (3) the site is unique for the remarkable preservation of trails of footprints of hominins (see Hay and Leakey 1982; Leakey and Harris 1987); this evidence has been used to confirm earlier inferences based on anatomy that bipedalism was an important component of the terrestrial locomotor behavior of 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); (4) the Upper Laetolil Beds and Upper Ndolanya Beds sample time periods that are generally poorly represented at other paleontological sites in East Africa, and the abundance of fossils from these stratigraphic units provide important windows into the faunal and floral diversity during the Pliocene; (5) paleontological collections from the Lower Laetolil Beds (3.85–4.4 Ma), Naibadad Beds (~2.1–2.3 Ma), Olpiro Beds and Ngaloba Beds (late Pleistocene) contribute to a broader understanding of the evolutionary history of African hominins and their associated faunas, as well as to the archaeological record (Leakey and Harris 1987; Ndessokia 1990); (6) the mammalian fauna from Laetoli is remarkably diverse (Leakey and Harris 1987; Harrison 2011b), with 115 species currently identified from the Upper Laetolil Beds and Upper Ndolanya Beds (almost one-third of which are based on type material from Laetoli), along with the remains or traces of fossil amphibians, reptiles, birds,

insects, gastropods and plants; it thus serves as a key reference fauna, one that is reliably dated, for comparisons with other Plio-Pleistocene sites in Africa; (7) Laetoli is unusual for sites in East Africa in the absence of sedimentological or paleontological evidence for extensive bodies of water (i.e., rivers or lakes) and in having an inferred paleoecological setting with less extensive woodland than penecontemporaneous sites with fossil hominins; as a consequence, the ecological context at Laetoli has been extensively studied and debated (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 (8) the paleoecology at Laetoli provides important information on the possible range of hominin habitat preferences and on ecological changes in East Africa during the Pliocene that may have impacted on the mode and tempo of human evolution.

Given the importance of the site for understanding and interpreting the evolutionary history of early hominins and African faunas in general, the author recognized that renewed investigations at Laetoli and other fossil localities on the Eyasi Plateau could produce worthwhile results that might contribute to resolving some long-standing issues in hominin evolution. Following initial discussions about the feasibility and desirability of renewed fieldwork at Laetoli, Dr. Simon Waane, the Director of the Antiquities Unit in Dar es Salaam at the time, invited the author to direct a new long-term research effort at Pliocene localities on the Eyasi Plateau, including the hominid-bearing localities in the Laetoli area. Fieldwork began during the summer of 1998. Initial results confirmed that the localities were still remarkably productive, that new fossil localities could be discovered, that enlarged fossil collections would add significantly to our understanding of the paleobiology and taxonomic diversity of Pliocene East African faunas, that there was a high likelihood of finding new fossil hominins, and that overall the area had tremendous potential for paleontological and geological research. A long-term project was planned that involved an interdisciplinary team of more than 50 research scientists. The overall objective was to recover additional fossil hominin specimens, and to obtain more detailed contextual information on the paleontology, geology, dating, and paleoecology.

Building on the previous research effort directed by Mary Leakey (1974–1982), which laid an excellent foundation for future research (Leakey and Harris 1987), it was possible to design a more problem-oriented approach to renewed investigations, including a detailed study of the geochronology and stratigraphic context, a better appreciation of the preservation and taphonomy, and a broader multidisciplinary approach to understanding the paleoecology. The project focused on the critical role of understanding the paleoecology at Laetoli, not

simply as an adjunct to studies of the fossil hominid finds, but as an integral component of any investigation that aims to answer the much more important how and why questions pertaining to the evolutionary history of humans. The main objectives were: (1) to conduct surface collections of fossils at all of the currently known localities in the Laetoli area; (2) to actively prospect the region for new paleontological occurrences; (3) to conduct geological investigations at both the local and regional levels; (4) to obtain further radiometric age determinations to help constrain the estimated ages of the major stratigraphic units; (5) to attempt to reconstruct more comprehensively the paleoecology at Laetoli and neighboring localities; (6) to better document the taxonomy, phylogenetic relationships, paleobiology and zoogeographic relationships of the fauna; and (7) to recover additional fossil hominins.

Between 1998 and 2005 the author directed eight expeditions to Laetoli to accomplish these goals. The current compendium of chapters, and its companion volume on the Laetoli fauna (Harrison 2011b), represent the culmination of this research effort. The research presented here is the combined effort of a dedicated and experienced field crew who were responsible for collecting the new fossils and samples described and analyzed here, and subsequent research by a team of international scientists (50 researchers from 11 different countries) with expertise in paleoanthropology, vertebrate paleontology, mammalogy, malacology, entomology, ecology, palynology, paleobotany, taphonomy, geology, geochronology, and stable isotopes. A number of key findings from this research have already been published (Harrison 2002, 2005, 2010; Kovarovic et al. 2002; Scott et al. 2003; Darlington 2005; Bamford 2005; Andrews and Harrison 2005; Harrison and Msuya 2005; Andrews 2006; Armour-Chelu et al. 2006; Kovarovic and Andrews 2007; Kingston and Harrison 2007; Su and Harrison 2007, 2008; Andrews and Bamford 2008; Sanders 2008; Mollé et al. 2008; Peters et al. 2008), and four doctoral dissertations have appeared, which focused on clarifying the systematics, paleoecology, and environmental and geological context at Laetoli (Kovarovic 2004; Su 2005; Mollé 2007; Dehghani 2008).

## History of Paleontological Research at Laetoli

The paleontological significance of Laetoli was initially recognized during the 1930s. Louis and Mary Leakey first visited the area in 1935, and made a small collection of fossil vertebrates and terrestrial gastropods from localities at Laetoli, Naibadad, Ngai (probably Ngaloba) and Endolele (probably Esere), which were forwarded to the Natural History Museum in London. These included a hominin lower canine, which was the first hominin fossil to be recovered



from the Pliocene of East Africa, although the specimen was not identified as such until some decades later (White 1981). The Leakeys were accompanied by Peter Kent, who published a preliminary account of the geology of the area (Kent 1941). Ludwig and Margrethe Kohl-Larsen made collections in the Laetoli region in 1939 (at Garussi=Garusi, Deturi=Olaitole, Lemagrut Korongo, Gadjingero, Oldogom, and Marambu=Olduvai Side Gorge, Locality 1), as part of their multifaceted investigation of the ethnography, archaeology and paleontology of the Lake Eyasi region (Reck and Kohl-Larsen 1936; Kohl-Larsen 1943). This extensive faunal material housed at the Museum für Naturkunde, Berlin, and the Institut für Ur- und Frühgeschichte und Archäologie des Mittelalters and Institut und Museum für Geologie and Paläontologie at Eberhard Karls Universität Tübingen, was described by Dietrich (1941, 1942a, b, 1945, 1950, 1951) and Petter (1963). The 1939 collections included a hominin maxilla with P<sup>3</sup> and P<sup>4</sup> (Garusi I) and an isolated M<sup>3</sup> (Garusi II) (Hennig 1948; Weinert 1950; Remane 1950, 1954; Robinson 1953, 1955). An undescribed occipital fragment, apparently of a fossil hominin (Garusi III), has been lost (Kohl-Larsen 1943; Protsch 1981; Ullrich 2001).

Hennig (1948) described the original Garusi specimens as belonging to a new genus, *Praeanthropus*, but as he did not assign a species name, the *nomen nudum* was unavailable. Weinert (1950) later included the Garusi hominins in a new species, *Meganthropus africanus*. Subsequently, Senyürek (1955) transferred the species to *Praeanthropus*, thereby making Hennig's original generic name available. In the late 1970s, Delson identified a previously unrecognized hominin lower incisor in the collections in Berlin (White 1981; Ullrich 2001; Delson, personal communication).

Louis and Mary Leakey revisited the Laetoli region in 1959 (collecting at Laetoli, Esere, and sites along the Kakesio road), and in 1964 they made a one-day excursion from their base camp at Olduvai Gorge (Leakey 1987a). In addition, as part of his geological study of Olduvai Gorge, Hay (1976) reported the discovery of fossils from the Laetolil Beds at Silal Artum, and the Olduvai Side Gorge near Kelogi. These collections are housed in the National Museums of Kenya in Nairobi.

An intensive program of geological and paleontological investigation was initiated at Laetoli in 1974, under the direction of Mary Leakey, and the campaign continued until 1982. This phase of research laid the foundation for a sound appreciation of the geology, geochronology, and paleontology of the area (Hay 1976, 1978, 1981, 1986, 1987; Hay and Reeder 1978; Leakey 1981; Hay and Leakey 1982; Leakey and Harris 1987). During the course of these investigations Mary Leakey and her team recovered a large collection of fossils (over 10,000 mammal specimens) from the Laetolil Beds, including 25 hominins. In addition, they recovered a hominin cranium (L.H. 18) from the Upper Ngaloba Beds (Day et al. 1980; Magori and Day 1983), referable to *Homo*

cf. *H. sapiens*, and a mandible (L.H. 29) referred to *Homo* cf. *H. erectus* (now included in *A. afarensis*, see Harrison 2011a). A list of hominin specimens recovered prior to 1980 was published by Leakey (1987b: 116–117), and the individual specimens were figured and described in detail (Leakey et al. 1976; White 1977, 1980a, 1981, 1985; Day et al. 1980; Magori and Day 1983; Leakey 1987b). At the time, the collection of hominids from the Laetolil Beds comprised 15 isolated teeth, 9 jaw fragments or associated dentitions, and a partial skeleton of an immature individual. Johanson et al. (1978) combined the hominids from the Laetolil Beds with the more substantial sample from Hadar in Ethiopia, to create the hypodigm of a new species, *Australopithecus afarensis*. A partial mandible from Laetoli (L.H. 4) was designated as the type specimen.

In 1978, the remarkable discovery of fossilized footprints of hominids changed the emphasis of investigations at Laetoli. Renewed efforts focused mainly on the study of the trails and their significance for understanding early hominin locomotor behavior (Leakey and Hay 1979; Clarke 1979; White 1980b; Day and Wickens 1980; Charteris et al. 1981, 1982; Hay and Leakey 1982; Leakey 1978, 1979, 1981, 1987c; Robbins 1987; White and Suwa 1987; Tuttle 1985, 1987, 1990, 1994, 2008; Tuttle et al. 1990, 1991, 1992). In 1979, the hominin footprint trails were reburied to preserve them from weathering and erosion.

Several teams worked at Laetoli in the 1980s and early 1990s, but there was no systematic and sustained program of geological and paleontological investigation. The Institute of Human Origins (IHO), directed by D.C. Johanson, carried out paleoanthropological research at Olduvai Gorge and Laetoli from 1985 to 1988. Research was focused on Olduvai, but small collections of fossils were made at Laetoli, which included an isolated molar of a hominin discovered in 1987 (Kyauka and Ndessokia 1990). As part of this project, Ndessokia (1990) conducted detailed excavations in the Upper Ndolanya Beds and Olpiro Beds, and recovered a small sample of fossil mammals (which has not been relocated). In conjunction with geological research conducted by IHO, Manega (1993) carried out a study of the geochronology and geochemistry of the tuffaceous sediments associated with the Ngorongoro Volcanic Highlands, including those at Laetoli.

A joint Getty Conservation Institute-Government of Tanzania project was undertaken at Laetoli from 1994–1997 in an effort to preserve the hominin footprint trail at Loc. 8 from damage by erosion and root penetration (Anonymous 1995; Agnew et al. 1996; Feibel et al. 1996; Agnew and Demas 1998). The trails were re-excavated and then reburied following conservation and further documentation of the anatomical details of the prints (Feibel et al. 1996; Agnew and Demas 1998). The trails are currently still covered, but there has been recent discussion about whether they should be re-excavated to allow them to be exhibited to the general

public and be accessible for study by the scientific community (Mabulla 2000; Dalton 2008).

In 1993–1999 the Hominid Corridor Research Project (HCRP), under the direction of F. Schrenk and T.G. Bromage, surveyed localities at Laetoli and Kakesio (Kaiser et al. 1995; Kaiser 2000). During the mid-1990s, C. Musiba conducted his doctoral dissertation research on the ecomorphology, taphonomy and paleoecology of Laetoli (Musiba 1999). In 1998 he resumed investigations (Musiba et al. 2007, 2008), and since that time he has directed a paleontological and archaeological field school at the site.

It should be noted that there has been much confusion concerning the correct name to apply to Laetoli, as well the meaning of the name. During the mid-1930s, Louis Leakey referred to the area in an unpublished field report as Laetolil (or Litolio) (Leakey 1935). Kent (1941) referred to it as the Vogel River area (using an anglicized version of the early German name, Vogelfluss; Jaeger 1913; Obst 1915). His map identifies the area of exposed Pliocene sediments along the Vogel River as Laetolil, and he refers to the Laetolil Beds as part of the Vogel River Series. Later, Kohl-Larsen (1943) identified the main paleontological localities in the area, including the hominin-bearing localities, as Garussi (or Vogelfluss). This is the local name for the river valley (alternatively Garusi, Ngarusi or Eng'arusi) in which most of the fossil localities are situated. Kohl-Larsen also recovered fossils from several nearby valleys, including Gadjjengero, Oldogom, Marambu and Deturi. The last of these corresponds to the river valley known today as Olaitole (and evidently represents an incorrect transliteration of the same name), located just to the south of the Garusi River. The name Laetolil (or Laitole) was subsequently used by English-speaking geologists and paleontologists until Leakey (1987a) corrected the spelling to Laetoli to reflect a more accurate rendering of the name in Maa. However, as noted by Pickering (1969) the type locality of the Laetolil Beds (and most of the paleontological localities) is in the Garusi Valley, rather than the Olaitole Valley. Garusi would be a more appropriate name for the site, but the name Laetoli is retained here because of its historical association with the localities and fossil hominins. Leakey (1987a) attributes the name Laetoli to a Maa word for a local red lily, but I have not been able to confirm this. Instead, local informants tell me that it pertains to the river of that name. According to Ndessokia (1990), however, the word Laitoli means “salty plains” in Maa.

## Renewed Fieldwork (1998–2006)

In 1998 the author began work at Laetoli and at other sites on the Eyasi Plateau, and fieldwork continued until 2005. As part of the Laetoli project, the author revisited the

Manonga Valley in north-central Tanzania (Harrison 1997), about 170 km southwest of Laetoli, during the summer of 2006 to investigate the relationships between the lacustrine sediments in the Manonga Valley and the tuffaceous deposits at Laetoli.

Fossils were primarily recovered from the surface of the outcrops after they had eroded out of the sediments. All anatomically identifiable fossils were recovered. The same strategy was successfully adopted by the author in the Manonga Valley, starting in 1990, because such collections were considered essential for gathering the kinds of data critical for understanding the taphonomy, ecomorphology, paleobiology and community structure of the fauna. Although criticized at the time, it has since proved to be a very useful strategy, and one that has now become the vogue among teams working in eastern Africa. Excavations were carried out to recover specimens that were discovered *in situ*, but no full-scale program of excavations at targeted sites was implemented. Earlier excavations carried out by Mary Leakey and later by Prosper Ndessokia were not found to be sufficiently productive to merit such labor-intensive efforts. Systematic screening for microvertebrates and invertebrates was not undertaken, mainly because of the lack of fossil concentrations, but screening was used to recover associated remains and at localities where fossil hominins were found. Occurrences of fossil footprints and trails were recorded and photographed when exposed, but no effort was made to excavate and expose tuffs known to contain footprints, mainly because of concerns about how to conserve them properly. All material collected was catalogued in the field, and each specimen was marked with a field number, individually bagged with an accompanying field label that included information on locality, stratigraphic provenience and provisional taxonomic identification. The field catalogues are available on-line at <http://www.nyu.edu/gsas/dept/anthro/programs/csho/pmwiki.php/Home/Collections>. The collections are housed at the National Museum of Tanzania in Dar es Salaam. All holotypes are stored in a separate type cabinet, and the fossil hominins are housed in the Museum strong room.

As noted above, earlier collections by Louis Leakey and Mary Leakey and by Kohl Larsen are housed in museums and repositories outside of Tanzania (i.e., in England, Germany and Kenya). All of the material collected by Mary Leakey from 1974 onwards falls under the authority of the Department of Antiquities in Dar es Salaam, with the National Museum of Tanzania as the repository. Much of the material recovered by Mary Leakey was stored at Olduvai Gorge, but a part of the collection was sent on loan for study to Nairobi and to other international museums and researchers. A small but significant part of the collections, including the hominins and some of the type specimens from Laetoli, are still temporarily on loan at the Kenya National Museum. The Kenyan and Tanzanian authorities intend to repatriate

them in the near future. Unfortunately, other parts of the collection sent out on loan cannot be accounted for.

With the assistance of Denise Su, and in cooperation with the National Museums of Tanzania in Arusha and Dar es Salaam and the Department of Antiquities, a major effort was undertaken to reconstitute, rehabilitate and curate the Mary Leakey collections from Laetoli. All of the specimens at Olduvai Gorge, which were temporarily stored in wooden crates and cardboard boxes and wrapped in newspaper, were carefully rewrapped and transported back to the National Museum in Dar es Salaam, where they are now permanently curated. The specimens have now been individually bagged or boxed. Field labels, using information derived from a surviving partial copy of Mary Leakey's field catalogue in the archive of the Kenya National Museum were added to each bag. Data from the catalogue, which are essential to determine the stratigraphic provenance of the specimens, were entered into a database by Denise Su to create a permanent electronic catalogue. From the catalogue it can be determined that more than 80% of the Mary Leakey collections have been relocated and are now housed at the National Museum in Tanzania in Dar es Salaam. Without timely intervention it is very likely that the collections and the pertinent documentation would have been lost to the scientific community. The Leakey and Harrison collections, comprising more than 40,000 fossils, are fully accessible for study, subject to approval by the appropriate Tanzanian authorities. Only a small collection of fossils from the IHO project is retained in the National Museum in Dar es Salaam. The material collected by P. Ndessokia from the Upper Ndolanya Beds has not been relocated and is presumed lost. The location of collections made by other research teams after 1982 is unknown and they are currently not available for study.

## Field Seasons

### 1998 (July 31–August 25)

Field Personnel: E. Baker, C. Dawi, A. Kweka, T. Harrison, T.S. Harrison, M. Lilombero, T. Lubulila, A. Malyango, M. Mbago, C.P. Msuya, D. Munisi, F. Nsinge, C. Robinson, and W.J. Sanders (Fig. 1.1).

The expedition carried out geological and paleontological investigations at Laetoli and Kakesio. The area west of Kakesio was surveyed as far as Itinje in the Meatu District of Shinyanga Region. To the south of Laetoli, the Oldogom and Esere area were explored, largely on foot because of the dense vegetation and rugged terrain. New fossil occurrences were discovered at Oleisusu, Engesha, Olaltanaudo and Laetoli Loc. 22S (see Harrison and Kweka 2011). Locality 22S produced a hominin tibia from the Upper Ndolanya Beds. A total of 1,680 fossil mammal specimens were collected.

### 1999 (January 3–25)

Field Personnel: P. Abwalo, C. Dawi, T. Harrison, A. Kweka, M. Lilombero, M. Mbago, D. Munisi, and C.P. Msuya.

The field campaign was cut short by heavy rains that made the tracks impassable, and even access to the sites by foot proved extremely difficult. The expedition collected fossils at Laetoli, Kakesio and Esere, as well as several new localities. Mr. Simon Mataro (Department of Antiquities superintendent at Laetoli) directed us to previously unrecorded fossil localities south of Laetoli in the region of Noiti (located not

**Fig. 1.1** Laetoli field participants in the 1998 season. Back row (left to right): Freddie Nsinge, Amandus Kweka, Cosmas Dawi, Terri Harrison, Dominic Munisi, Tobias Lubulila, Eric Baker, Avelin Malyango, Chris Robinson. Front row (left to right): Moses Lilombero, Charles Msuya, Michael Mbago, William J. Sanders, Terry Harrison



far from Engesha, which we had surveyed in 1998). Noiti yielded abundant and well-preserved fossil wood, but no vertebrate remains. Members of the expedition explored the area south of Esere as far as Ngaiborgoso and the peak of Eseketeti, where the Precambrian basement underlying the Laetolil Beds is exposed, and west of Laetoli along the Emboremony River as far as Kakesio, which yielded fossils from the Lower Laetolil Beds. A new fossil occurrence was also discovered in a large valley south of the village of Sinoni, at a locality called Lobileita, which exposes the Lower Laetolil Beds overlying the Precambrian basement. Only 359 fossil mammals were collected.

### 2000 (January 16–February 7 and July 8–29)

Field Personnel: Winter – P. Andrews, R. Chami, C. Dawi, C. Feibel, T. Harrison, S. Hixson, A. Kweka, M. Lilombero, S. Mataro, C. Msuya, D. Munisi, and F. Nsinge. Summer – R. Chami, C. Dawi, T. Harrison, J. Kingston, A. Kweka, M. Lilombero, M. Mbago, K. McNulty, C. Msuya, D. Munisi, F. Nsinge, C. Robinson, L. Scott, and D. Su (Fig. 1.2).

During the course of the winter and summer field seasons, expedition team members made intensive paleontological collections and geological investigations at all of the Laetoli localities. Important new occurrences of fossils in the Upper Ndolanya Beds were discovered at Loc. 15. Craig Feibel discovered a clay horizon rich in fossil insects, seeds and ruminant dung at Loc. 3. The expedition also revisited Noiti, Emboremony, Lobeita, Oleisusu, and Kakesio. Exposures

of Laetolil Beds located to the southwest of Norsigidok were surveyed on foot, but the area yielded few fossils. Samples for the study of stable isotopes and palynomorphs/phytoliths were collected by John Kingston and Louis Scott. A systematic survey was made of modern bones and carcasses along the Gadjingero River, to provide baseline taxonomic and taphonomic data for interpreting the fossils at Laetoli. The collection of fossil mammals from the combined seasons totals 5183 specimens, including a mandibular fragment and an isolated canine of *A. afarensis* from Loc. 16.

### 2001 (July 5–28)

Field Personnel: P. Andrews, M. Bamford, Cosmas Dawi, A. Deino, M. Durru, T. Harrison, K. Kovarovic, M. Lilombero, M. Mbago, C.P. Msuya, D. Munisi, F. Nsinge, Shadrack (Fig. 1.3).

Fossils were collected at Laetoli, Emboremony and Kakesio. Samples of fossil wood were collected at Noiti by M. Bamford for thin section preparation at the University of Witwatersrand. Rock samples were obtained by A. Deino from Laetoli, Kakesio and Noiti for geochronology. Additional horizons were sampled for palynology. A new outcrop of Upper Ndolanya Beds was located at Silal Artum, and the fossil material recovered included a maxilla of *Paranthropus aethiopicus*. A total of 1,663 fossil mammals were recovered during the course of the field season. At the end of the season, Laetoli fossils stored at Olduvai Gorge and the Arusha Museum were transported to the National Museum of Tanzania in Dar es Salaam for permanent curation.

**Fig. 1.2** Laetoli field participants in the summer 2000 season. Back row (left to right): John Kingston, Cosmas Dawi, Louis Scott, Kieran McNulty (behind), Amandus Kweka (front), Michael Mbago, Freddie Nsinge, Chris Robinson. Front row seated (left to right): Denise Su, Dominic Munisi, Moses Lilombero, Remigius Chami. Front on ground: Terry Harrison. Missing from picture: Charles Msuya



**Fig. 1.3** Laetoli field participants in the 2001 season. Back row (*left to right*): Shadrack, Amandus Kweka, name unknown (lorry driver), Moses Lilombero, Peter Andrews, Charles Msuya, name unknown (lorry driver), Terry Harrison. Front row (*left to right*): Dominic Munisi, Freddie Nsingwe, Michael Mbago, Mohamedi Durru, Kris (Fire) Kovarovic, Denise Su. Missing from picture: Alan Deino and Cosmas Dawi



### 2003 (July 4–28)

Field Personnel: M. Bamford, C. Dawi, F. Kikwa, A. Kweka, T. Harrison, M. Lilombero, C. Msuya, E. Mwawembe, F. Nsingwe, S. Odunga, C. Robinson, and D. Su (Fig. 1.4).

The team made paleontological collections at Laetoli, Noiti, Emboremony, and Kakesio localities south of the Kakesio River. Additional fossil wood samples were collected at Noiti by M. Bamford. A total of 3,001 fossil mammals were recovered.

### 2004 (June 25–July 21)

Field Personnel: P. Andrews, M. Bamford, S. Cooke, C. Dawi, A. Deino, P. Ditchfield, B. Harrison, C. Harrison, T. Harrison, T.S. Harrison, S. Jones, J. Kingston, F. Kikwa, A. Kweka, G. Leliyo, L. McHenry, G. Mkude, G. Mollel, J. Msowaya, S. Mataro, E. Mwawembe, F. Mwawembe, E.A. Njau, F. Nsingwe, S. Odunga, L. Rossouw, W.J. Sanders, C. Swisher, M. Tallman, and S. Worthington (Fig. 1.5).

The team made extensive paleontological collections at all localities at Laetoli and Kakesio. Fossil vertebrates were also recovered from the Lower Laetolil Beds at Noiti 3. A total of 1,909 fossil mammals were collected. Stratigraphic, geomorphological and geochronological investigations were carried out by A. Deino, P. Ditchfield, L. McHenry, G. Mollel, and C. Swisher. An important focus of the field season was mapping and inventorying the modern vegetation in the Laetoli area by P. Andrews, M. Bamford, G. Leliyo and E. Njau. Triplicate samples were deposited in the following herbaria: National Herbarium of Tanzania, Arusha; Royal Botanic Gardens, Kew, London; University of Witwatersrand, Johannesburg. Additional samples were collected for analyses of stable isotopes and phytoliths by J. Kingston and L. Rossouw respectively.

### 2005 (May 27–June 15)

Field Personnel: J. Darlington, C. Dawi, P. Ditchfield, C. Fellmann, T. Harrison, F. Kikwa, A. Kweka, S. Mbegu, G. Mkude, S. Mataro, E. Mwawembe, F. Mwawembe, S. Nassoro, T. Rein, M. Seselj, and D. Su (Fig. 1.6).

The expedition revisited most of the localities at Laetoli and Kakesio, and collected 1,495 fossil mammals. Geological investigations were continued by P. Ditchfield and T. Harrison. A special focus of the field season was studying the fossil termitaries and termite traces, as well as documenting the distribution and taxonomy of the modern termite fauna at Laetoli.

## Results

### New Paleontological Collections

The Laetoli localities continue to be productive. During the course of renewed fieldwork, more than 25,000 fossils were collected (Table 1.1). These consisted mainly of fossil mammals (58.1%), but also included the remains of birds (4.9%), reptiles and amphibians (1.9%), invertebrates (33.3%) and plants (1.8%). Most of the fossil mammals (82.4%) were recovered from the Upper Laetolil Beds, but smaller samples came from the Lower Laetolil Beds (1.7%) and Upper Ndolanya Beds (15.8%). Representative fossil vertebrates were also recovered from the Olpiro and Ngaloba Beds, but no systematic collections were made. The fauna from the Lower Laetolil Beds is dominated by bovids and equids, which comprise more than half of the specimens collected, but this frequency is probably skewed by a strong taphonomic bias against smaller vertebrates (Table 1.2). The faunal collections from the Upper Laetolil Beds and Upper Ndolanya Beds are composed primarily of bovids and lagomorphs, which together represent 72.0% and 81.2% of all mammals

**Fig. 1.4** Laetoli field participants in the 2003 season. Back row (*left to right*): Amandus Kweka, Ephraim Mwawembe, Cosmas Dawi, Charles Msuya, Terry Harrison, Moses Lilombero, Chris Robinson. Front row (*left to right*): Simon Odunga, Freddie Nsinge, Denise Su, Marion Bamford, Francis Kikwa



**Fig. 1.5** Laetoli field participants in the 2004 season. Back row (*right to left*): Amandus Kweka, Simon Odunga, John Kingston, Steven Jones, Godson Leliyo, Carl Swisher, Steven Worthington, Terry Harrison, Moses Lilombero, Terri Harrison, Lloyd Rossouw, Efrem-Fred Njau, Peter Andrews. Middle row (*left to right*): Godwin Mollle,

Ben Harrison, Gregory Mkude, Chris Harrison, Freddie Nsinge, Joseph Msowaya, Siobhan Cooke, Melissa Tallman, Francis Kikwa, Felix Mwawembe, Marion Bamford. Front row (*left to right*) Lindsay McHenry, Ephraim Mwawembe, Cosmas Dawi, Peter Ditchfield. Missing from picture: Alan Deino and William J. Sanders

**Fig. 1.6** Laetoli field participants in the 2005 season. Back row (*left to right*) Maja Seselj, Gregory Mkude, Denise Su, Cosmas Dawi, Connie Fellmann, Seif Nassoro, Tom Rein, Francis Kikwa, Felix Mwawembe, Amandus Kweka. Front row (*left to right*): Terry Harrison, Peter Ditchfield, Samiyu Mbegu, Ephraim Mwawembe, Johanna Darlington



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

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

Specimen counts do not include fossils from the Olpiro or Ngaloba Beds

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

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

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

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

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

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

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

LLB Lower Laetolil Beds, ULB Upper Laetolil Beds, UNB Upper Ndolanya Beds

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

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

respectively. The mammalian fauna from the Upper Ndolanya Beds differs from that from the Upper Laetolil Beds in having a much higher percentage of bovids and a stronger bias against micromammals (Table 1.2). The 1998–2005 collection is now larger than that made by Mary Leakey in 1974–1979 (Table 1.3). It is interesting to note that the relative proportions of the most common mammalian taxa from the Upper Laetolil Beds (those taxa represented by more than 100 specimens) are remarkably similar between the two collections. This concordance suggests that these proportions are probably quite close to their representation in the fossil record. A key difference is that the 1998–2005 expeditions

recovered a smaller percentage of large mammals (i.e., Proboscidea, Rhinocerotidae, Equidae, Suidae and Giraffidae) and a higher percentage of micromammals (i.e. Rodentia and Leporidae) compared with the 1974–1979 collections (Table 1.3). This is almost certainly due to larger specimens having a higher recovery rate than smaller specimens, combined with the slower rate at which larger specimens erode out onto the surface. Although the material recovered by Kohl-Larsen was presumably more selectively sampled than either the Leakey or Harrison collections, his expedition did recover a high proportion of large mammal finds, which provides additional support for the scenario presented above.

**Table 1.3** Comparison of the relative proportions of common mammal taxa from the Upper Laetolil Beds collected by Leakey and Harrison

	Leakey collections (1974–1981) <sup>a</sup>		Harrison collections (1998–2005) <sup>b</sup>	
	N	%	N	%
Cercopithecidae	87	0.9	111	0.9
Rodentia	526	5.7	855	7.0
Leporidae	2,861	30.8	4,640	38.2
Carnivora	261	2.8	424	3.5
Proboscidea	228	2.5	158	1.3
Equidae	265	2.8	330	2.7
Rhinocerotidae	644	6.9	473	3.9
Suidae	324	3.5	244	2.0
Giraffidae	808	8.7	772	6.4
Bovidae	3,281	35.3	4,145	34.1
Total	9,285	99.9	12,152	100.0

Includes only those taxa represented by more than 100 specimens in each collection

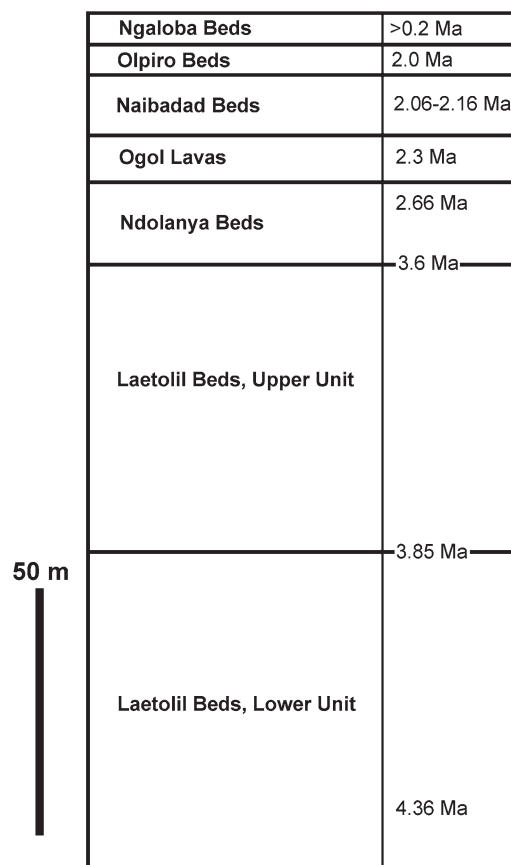
<sup>a</sup>Data from Leakey (1987a)

<sup>b</sup>Detailed information presented in Table 1.2

## Geological Investigations

Renewed geological research on the Eyasi Plateau focused on a better understanding of the local stratigraphic relationships, sedimentology and geochemistry of the tuffs and fossil-bearing horizons at Laetoli and Kakesio (Molle et al. 2011; McHenry 2011; Ditchfield and Harrison 2011; Adelsberger et al. 2011; Deino 2011). This has allowed a more refined appreciation of the stratigraphic provenance of fossil specimens, correlation of marker tuffs between localities, and a better understanding of the paleoenvironmental setting. Surveys of much of the Eyasi Plateau, between the villages of Endulen and Kakesio, have allowed a much better understanding of the regional geology, especially the contact between the Precambrian Basement and the Laetolil Beds, and the geographic distribution of the main sedimentary units. In addition, research in the Volcanic Highland Complex to the east of Laetoli has allowed a better understanding of the source of the volcanic materials that contributed to the regional sedimentary sequence. However, the general stratigraphic scheme for the sedimentary sequence follows that developed by Hay (1987) (see Fig. 1.7).

Further afield, the mineralogy of the Manonga Valley in north-central Tanzania, about 170 km to the southwest of Laetoli, has provided evidence of a direct relationship between the two sedimentary basins. Mutakyahwa (1997) showed that the Manonga Valley sediments were very likely derived from the same volcanic source as those at Laetoli. However, the fauna from the Manonga Valley is generally older (~4.0–5.5 Ma) than that at Laetoli, although it probably overlaps in age with the Lower Laetolil Beds (~3.8–4.4 Ma). This implies that Lake Manonga may have acted as a sedimentary basin for the accumulation of tuffs deposited distant from the volcanic centers during the late Miocene and early Pliocene,



**Fig. 1.7** Simplified stratigraphic scheme of Laetoli sediments showing the main stratigraphic units (*left*) and the chronology (*right*, Ma = megannum) (after Hay 1987; Ndessokia 1990; Manega 1993; Ditchfield and Harrison 2011; Deino 2011)

whereas sediments did not accumulate on the Precambrian basement in the Laetoli area proximal to the volcanic highlands until sometime later.



## Radiometric Age Determinations

Drake and Curtis (1987) published a series of K/Ar dates for Laetoli. These provided age estimates of 3.76 Ma to older than 4.3 Ma for the Lower Laetolil Beds and 3.49–3.76 Ma for the Upper Laetolil Beds. A K-Ar date of 2.41 Ma for the Ogol Lavas provided a maximum age for the underlying Ndolanya Beds. The Naibadad Beds were dated at 2.26 Ma. Ndessokia (1990) provided the first  $^{40}\text{Ar}/^{39}\text{Ar}$  dates, with estimated ages of 2.66 Ma for the Upper Ndolanya Beds, 2.15 Ma for the Naibadad Beds, and 2.0 Ma for the Olpiro Beds. Later, Manega (1993) reported  $^{40}\text{Ar}/^{39}\text{Ar}$  dates of 2.5 Ma for the Ndolanya Beds, 2.10–2.26 Ma for the Naibadad Beds, and 2.04 Ma for the Olpiro Beds. Amino acid racemization of ostrich eggshells provided ages of greater than 200 ka for the Upper Ngaloba Beds and greater than 290 ka for the Lower Ngaloba Beds (Manega 1993). Renewed research at Laetoli since 1998 has allowed a refinement of the geochronological framework at Laetoli (Deino 2011; Mollé et al. 2011; see Fig. 1.7). These new  $^{40}\text{Ar}/^{39}\text{Ar}$  dates confirm the earlier age estimates of the Upper Ndolanya (2.66 Ma) and Naibadad Beds (2.057–2.155 Ma), while the Ogol Lavas (2.3 Ma) are slightly younger. Most importantly, the new dates push back the age of the Upper Laetolil Beds (3.6–3.85 Ma), making *Australopithecus afarensis* and its associate fauna from Laetoli slightly older than previously estimated.

## Paleoecology

A major focus of renewed investigations at Laetoli has been on reconstructing the paleoecology. As noted earlier, study of the paleoecology provides critical evidence for understanding the context of early hominin evolution. It 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 taxa (ranging from plants and invertebrates to mammals) and modern-day ecosystems (ranging from soils and vegetation to micromammals), as well as a range of paleoecological proxies that can be applied to the fossil record (i.e., palynology, phytoliths, stable isotopes, mesowear, ecomorphology, and community structure).

## Systematics and Paleobiology of the Fauna

The contributions in Leakey and Harris (1987) provided the last detailed and 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, with many new localities and faunas reported. Renewed investigations at Laetoli have allowed a thorough revision of the systematics of the mammalian fauna from Laetoli, and 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 (which will be described elsewhere). Equally importantly, study of the non-mammalian fossils was considered 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. Research on the ostriches and birds' eggs has already been published (Harrison 2005; Harrison and Msuya 2005). The new accounts presented in the companion volume (Harrison 2011b) provide the basis for a significant systematic revision of the fauna. The current fauna comprises 115 species of mammals from the Laetolil and Ndolanya Beds (compared with 84 in 1987), and includes five new species of rodents, a new species of proboscidean, one new species of carnivoran, two new species of bovids, and a new genus of galagid. In addition, the non-mammalian fauna has been supplemented by one new species of ostrich (Harrison 2005), two new species of gastropods and four new species of insects. In addition to providing a more complete record of the faunal diversity associated with the early hominins at Laetoli, these studies provide a wealth of critical information that can be used in reconstructing the paleoecology and in better understanding the biogeography and biochronology of African Pliocene faunas.

## Additional Fossil Hominins

Renewed investigations at Laetoli have led to the recovery of additional fossil hominins. Two specimens, an isolated lower canine (EP 162/00) and a mandibular fragment with  $\text{P}_3\text{-M}_1$  (EP 2400/00), recovered from the Upper Laetolil Beds, are referable to *A. afarensis*. These have provided the basis, along with several other previously undescribed specimens, for a reassessment of the morphology and evolutionary status of the *A. afarensis* sample from the type locality of Laetoli. 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 these represent the first hominins from this stratigraphic unit. EP 1500/01 is important because it represents the only specimen of *P. aethiopicus* recovered from outside the Turkana basin, and is among the oldest securely dated specimens definitively attributable to

this taxon. A detailed account of the chronology, anatomy, paleobiology and systematics of the hominins from Laetoli is presented in Harrison (2011a).

## Conclusions

Laetoli, one of the key paleontological and paleoanthropological localities in Africa, is renowned for the fossil evidence of early hominins (i.e., *Australopithecus afarensis* and *Paranthropus aethiopicus*) and the remarkable trails of hominin footprints. In addition, the diverse faunas from the Upper Laetolil Beds and Upper Ndolanya Beds, dated to 3.63–3.85 and 2.66 Ma respectively, are from time periods that are generally poorly-represented at other paleontological sites in East Africa. Fossils from these stratigraphic units provide important windows into the faunal and floral diversity during the Pliocene, and they serve as reliably dated reference faunas for comparison with other Plio-Pleistocene sites in Africa. From a paleoecological perspective, Laetoli is also unusual for early hominin sites in East Africa in the absence of evidence for extensive bodies of water, and in having habitats that are reconstructed as being less densely wooded. This evidence provides key information on the possible diversity of hominin habitat preferences and on ecological changes in East Africa during the Pliocene that may have impacted on the mode and tempo of human evolution.

The main aim of renewed fieldwork at Laetoli, starting in 1998, was to recover additional fossil hominid specimens, and to obtain more detailed contextual information on the paleontology, geology, dating, and paleoecology. The results have confirmed that the existing localities are still remarkably productive and that new localities can be found. The substantially expanded fossil collections, numbering more than 25,000 specimens, have added significantly to our understanding of the systematics and paleobiology of Pliocene East African faunas. The recovery of new hominin specimens from the Upper Laetolil Beds has contributed information on the morphology, variation and evolutionary status of *Australopithecus afarensis*. Fossil hominins, recovered for the first time from the Upper Ndolanya Beds, included a partial maxilla of *Paranthropus aethiopicus*. This is the first specimen of *P. aethiopicus* to be recovered from outside the Turkana Basin, and is among the oldest securely dated specimens definitively attributable to this taxon.

The compendium of chapters in this volume, and its companion volume on the Laetoli hominins and their associated fauna (Harrison 2011b), present the results of this renewed research effort.

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## Chapter 2

# Paleontological Localities on the Eyasi Plateau, Including Laetoli

Terry Harrison and Amandus Kweka

**Abstract** Sixty paleontological localities are recorded at Laetoli and other areas on the Eyasi Plateau. These include several new localities at Laetoli, and many newly designated localities in the Kakesio and Esere-Noiti areas to the south and southwest of Laetoli. Descriptions of the locations, stratigraphic context and paleontological significance of each locality are presented. The Laetoli localities have produced a rich assemblage of fossils from the Pliocene-aged Upper Laetolil Beds and Upper Ndolanya Beds. The most productive localities are Localities 2, 10E and 18, which have each yielded more than 2,000 fossil mammals since 1974. In addition, smaller samples of fossil vertebrates and stone artifacts have been recovered from the Pleistocene Olpiro and Ngaloba Beds. Fossil hominins are presently known only from localities at Laetoli. The Upper Laetolil Beds have yielded the remains of *Australopithecus afarensis*, and tracks of fossilized footprints of hominins, presumably of *A. afarensis*, are known from Locality 8 (Footprint Site G). Three new specimens of *A. afarensis* have been recovered from Laetoli since 1998, and the provenance of these specimens is described here. In addition, fossil hominin specimens have been recovered from the Upper Ndolanya Beds for the first time. A cranium of an archaic form of *Homo sapiens* is known from the Upper Ngaloba Beds at Locality 2. Localities in the Kakesio area and the Esere-Noiti area have yielded relatively small, but important, collections of fossil vertebrates, invertebrates and plants from the Lower Laetolil Beds. No hominins have yet been recovered from this stratigraphic unit, although it is possible that they may be discovered in the future with more intensive collecting and surveying.

**Keywords** Garusi • Gadjjingero • Emboremony • Kakesio • Esere • Noiti • Laetolil Beds • Ndolanya Beds • Ngaloba Beds • Hominins • Fossil vertebrates

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## Introduction

The Laetolil Beds are widely distributed across the Eyasi Plateau on the northern side of Lake Eyasi, covering an area of more than 1,000 km<sup>2</sup> (Fig. 2.1). They extend as far south as Esere, Olpiro and Sinoni, west beyond the village of Kakesio, north as far as Lake Ndotu, and east just beyond Endulen (Fig. 2.2). The extinct volcanic centers of Lemagurut, Satiman, Oldeani, and Ngorongoro are located to the east, and these represent the potential sources of the tephra and lavas found in the region. The oldest of the volcanic centers, Satiman (previously Sadiman), has been inferred to be the most likely source of the Laetolil Beds (Hay 1987; Mollel et al. 2011).

During the Pliocene, volcanic ashes were blown southwest from the Satiman highlands in the direction of the prevailing winds today, and these settled on the relatively flat terrain of the southern Serengeti. Laetolil tuffs can be traced more than 50 km away in this direction (cognate sediments deposited in lake beds in the Manonga Valley, more than 150 km to the southwest, can be inferred to be derived from the same volcanic source; Mutakyahwa 1997; Mollel et al. 2011). As a consequence, the Laetolil Beds are thickest towards the east, closest to their source in the volcanic highlands, and they become thinner to the southwest. The richly fossiliferous Upper Laetolil Beds and Upper Ndolanya Beds are best exposed in the Laetoli area. West and south of Laetoli, the Laetolil Beds are extensively exposed, but the Upper Laetolil Beds have largely been lost through erosion, and outcrops of the underlying Lower Laetolil Beds predominate. West, beyond the village of Kakesio, and along the margin of the Eyasi Rift escarpment, the Laetolil Beds have been eroded away, presumably washed into the Eyasi basin, to expose the underlying Precambrian basement rocks.

Paleontological localities on the Eyasi Plateau occur in three main geographical areas: Laetoli, Kakesio, and Esere-Noiti (Fig. 2.2). The most productive localities are those associated with the Upper Laetolil Beds and Upper Ndolanya Beds at Laetoli, and this is where previous expeditions have