

Fauna of Selected Late Miocene to Early Pleistocene Fossil Sites and Implications for Hominid Evolution

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Abstract

An examination of the fossil fauna recovered from ten African sites, ranging in age from late Miocene to early Pleistocene, and including both hominid and non-hominid sites, has been undertaken in an attempt to shed light on the possible environments of a number of African hominid genera; namely *Sahelanthropus*, *Australopithecus*, *Paranthropus* and *Homo*. Faunal lists were compiled, compared, and discussed within an ecological framework. Three previously proposed models of hominid evolution, the terrestrial (or savanna), the semi-aquatic (or waterside) and the aquarboreal (or climbing and wading), were examined in light of the data. The results show that 1) arid habitats existed within the vicinity of all hominid sites; 2) water was present at all hominid sites; and 3) trees were present at all hominid sites. When combined with other data, including comparative data and the anatomy of hominid fossils, the savanna model, at least in its traditional form (with a focus on dry, arid landscapes), was considered to be a less effective model when compared with the waterside model. The waterside model, in turn, was found to be less effective at explaining certain aspects of hominid evolution, such as bipedalism, compared with the aquarboreal model.

Part 1

Chapter 1

Introduction and Methods

1.1 Introduction

Recently, a new human species, *Homo floresiensis*, was discovered on the Indonesian Island of Flores (Brown *et al.*, 2004). The discovery raises a number of questions about previously accepted models of hominid evolution. For example, the brain size of *Homo floresiensis* is similar or smaller to that observed in genera such as *Australopithecus* and *Pan*, yet in previous models increased brain size was a key criterion in defining *Homo* (Wood, 2000). In addition, the timing and mode of dispersal of the genus *Homo* now appears somewhat more complex than previous models might have predicted. While the parameters of this thesis do not allow for an in depth discussion of the implications of *Homo floresiensis*, it is nevertheless the intention that the conclusions will be able to accommodate this new species.

The aim of this thesis is to reveal possible environmental aspects of a number of African hominids by studying the associated faunal remains of ten African fossil sites, and to examine a number of models related to hominid evolution in light of the results. According to estimates based on molecular data, humans (*Homo*) and chimpanzees (*Pan*) branched into separate lineages between about 6 and 4 million years ago (Chen and Li, 2001). A number of models have been put forward to explain this separation, including two, the savanna (or terrestrial) and semi-aquatic (or waterside) models, which are often regarded as diametrically opposed (Roede *et al.*, 1991; Langdon, 1997; Morgan, 1997). Broadly, the savanna model proposes that human ancestors may have shifted from the forests to more arid, open habitats while the semi-aquatic model proposes that humans may have had a more aquatic past. Another model, the ‘aquarboreal’ (or climbing and wading) model, proposes that human and chimp ancestors may have lived in relatively wet forests such as swamp or mangrove forests, where they climbed and waded, and that humans became better adapted to more open waterside habitats, while chimpanzees remained in forests, both wet (*Pan paniscus*) and relatively dry (*Pan troglodytes*) (Verhaegen *et al.*, 2002).

The dominant model in human evolution ever since Darwin has been the terrestrial model, in which ape ancestors shift from an arboreal to a more terrestrial existence (Landau, 1982). Researchers often emphasise the open (Langdon, 1985) and arid (Coppens, 2000) nature of hominid habitats (Wheeler, 1991; Jablonski and Chapman, 1993). Though Darwin may have initiated the idea of terrestriality in human evolution (Landau, 1982), the idea of an open, arid habitat as the backdrop to the human evolutionary story can perhaps be traced back to Dart, who proposed that South Africa, by providing “vast *open* country with occasional wooded belts and a *relative scarcity of water*” (1925:199; emphasis added), “furnished a laboratory such as was essential to [the] penultimate phase of human evolution” (1925:199). Dart’s famous ‘Taung Child’ (*Australopithecus africanus*) was discovered in South Africa where, Dart noted, “climatic conditions appear to have fluctuated little since Cretaceous times” (1925: 199). Despite later studies showing that climatic conditions had fluctuated more than Dart may have been aware in South Africa since the time of *Australopithecus africanus* (Cadman and Rayner, 1989), his ideas of a dry, open savanna setting for human origins have continued to receive widespread support.

“Many hominid traits” for example, wrote Foley “may be adaptively linked to increased thermoregulatory stress and to movement in more open and terrestrial environments” (Foley, 1999: 332). Others have argued, however, that humans are not particularly well suited to dry, open conditions on account of their lack of sun protective fur and a relatively wasteful water cooling system (Verhaegen, 1987; Morgan, 1997). In fact, there have been many advocates for an alternative to the exclusively dry, open savanna model over the years (Hardy, 1960; Sauer, 1962; Morgan, 1972; Stewart, 1994, Broadhurst *et al.*, 1998, Verhaegen and Puech, 2000; Erlandson, 2001; Kuliukas, 2002; Tobias, 2003) yet orthodox science has remained unconvinced of the need for any change.

“The aquatic hypothesis is only one of several ideas rejected by orthodox science that has refused to go away” wrote Langdon (1997: 492), one of the few proponents of the terrestrial model who has publicly argued against the aquatic model. The aim of this thesis is to examine the fauna associated with a number of hominid and non-hominid sites and use the results to infer possible environmental contexts. A discussion of the savanna, aquatic and aquarboreal models of hominid evolution will then be undertaken in an attempt to determine which is the most effective in light of the data.

In Part II the faunal lists of individual selected sites are analysed and discussed within an ecological framework. The lifestyles and habitats of extant species are used in an attempt to infer possible lifestyles and habitats for fossil taxa that might share morphological characteristics or are considered to be closely related.

In Part III the sites are compared and contrasted. Tables are constructed to show the number of different taxa at each site and data is displayed in graph form in an attempt to compare sites. Taxa indicating dry habitats, wet habitats, and wooded or closed habitats are identified and graphs comparing the numbers at each site are constructed and the results analysed.

In Part IV the terrestrial (Langdon, 1997), semi-aquatic (Morgan, 1997) and aquarboreal (Verhaegen *et al.*, 2002), models of hominid evolution are discussed in light of the data. The anatomical characteristics of the fossil genera *Sahelanthropus*, *Australopithecus*, *Paranthropus* and *Homo* are discussed and other data is used in an attempt to test each model.

1.2 Methods

Unlike Vrba (1995), Spencer (1997) and Kappelman *et al.* (1997) who studied bovids, Denys (1999) who studied rodents, and Reed (1997) who studied a wider variety of mammalian species in an attempt to infer possible environmental data, this study examines every available animal taxa. In addition to hominid sites, three non-hominid bearing sites are examined for comparison.

Ten sites were chosen for the study (Table 1.1). An attempt was made to select fossil sites that included a range of hominid species, depositional situations, and ages. Sites with available faunal lists were preferred. Most of the mammalian faunal data comes from one source, (Turner *et al.*, 1999). The non-mammalian faunal data and mammalian faunal data for the sites of Manonga Valley (Tanzania), Toros-Menalla (Chad) and Humpata (Angola) come from other sources (see tables 2.1 to 11.1).

The order in which sites are examined is based on chronology (with the oldest sites examined first and the youngest examined last) and location (north to south). The sites, based on their

age, form three groups, late Miocene and early Pliocene (Toros-Menalla, Manonga Valley and Langebaanweg), mid-Pliocene (Hadar, Laetoli and Sterkfontein) and Plio-Pleistocene (East Turkana, West Turkana, Olduvai Gorge and Humpata).

The hominid sites are Toros-Menalla, Hadar, Laetoli, Sterkfontein, East Turkana, West Turkana and Olduvai Gorge. The non-hominid sites are Langebaanweg, Manonga Valley and Humpata.

Table 1.1, List of Sites Included in this study

Site	Formations	Age (estimate)	Hominids	References
Toros- Menalla (Chad)	TM 266	6-7mya	<i>Sahelanthropus tchadensis</i>	Vignaud <i>et al.</i> (2002)
Manonga Valley (Tanzania)	Tinde, Kiloleli	4-5mya	Nil	Harrison and Baker (1997)
Langebaanweg (South Africa)	Quartzose Sand, Pelletal Phosphorite	4.5mya	Nil	Gentry (1980)
Hadar (Ethiopia)	Hadar	3-4mya	<i>Australopithecus afarensis</i>	Johanson <i>et al.</i> (1982)
Laetoli (Tanzania)	Upper Laetoli Beds	3.5-3.8mya	<i>A. afarensis</i>	Leakey and Harris (1987)
Sterkfontein (South Africa)	Member 4	2.5-3mya	<i>A. africanus</i>	Tobias (1976)
East Turkana (Kenya)	Upper Burgi, KBS, Okote	1.4-1.9mya	<i>Paranthropus boisei</i> , <i>Homo ergaster</i> , <i>H. rudolfensis</i> , <i>H habilis</i> .	Schwartz and Tattersall (2003)
West Turkana (Kenya)	Nariokotome, Natoo	1.3-1.7mya	<i>P boisei</i> , <i>H. ergaster</i> , <i>H. erectus</i>	Schwartz and Tattersall (2003)
Olduvai Gorge (Tanzania)	Bed II	1.4-1.75mya	<i>P. boisei</i> , <i>H. habilis</i> , <i>H. erectus</i>	Schwartz and Tattersall (2003)
Humpata (Angola)	Cangalongue I-IV, Malola, Tchiua, Ufefua, Molo	1.3-1.8mya	Nil	Pickford <i>et al.</i> (1992)

Taxa were recorded as present if they appeared on a faunal list. No attempt has been made to determine whether the same taxa may have been recorded more than once on a list due to different identification and naming processes. Taxa were, wherever possible, compared to extant taxa, and on the basis of phylogeny and morphological similarity an attempt was made to infer possible habitat and behavioural variables. Ecological discussions were undertaken for each site based on the associated faunal remains.

Graphs and tables were constructed to allow comparison between sites. The number of dry and wet adapted taxa was calculated and a graph constructed for comparison. The number of wallowing and burrowing mammals, and the number of taxa indicating the presence of trees, were calculated and graphs constructed to allow comparisons.

1.3 Problems with the methodology

A number of problems arise as a result of comparing faunal lists from one site to another. For example, extensive surveying may have been carried out at certain sites, whereas others sites may have had less extensive surveying, meaning some sites may falsely appear to have a richer paleofauna than others. The period of time a deposit covers may also affect the number and diversity of species within a site. For example, if a formation contains sediments deposited over a few million years, it is likely to reveal a different picture than a formation with sediments deposited over a more limited time period, in the case of fossils formed in the aftermath of a volcanic eruption, for example. Certain environments are more likely to preserve fossils than others (Vrba, 1995). In addition, certain animals (large mammals, for example) are more likely to be preserved in the fossil record than animals such as birds, fish and insects, and certain fossils are likely to be of more interest to particular fossil hunters than others, potentially influencing the types of fossils discovered and collected. Soft body parts such as muscle tissue and organs are unlikely to be preserved, while the types of bones that are preserved are likely to be biased in favour of certain skeletal parts such as crania, jaws, teeth and long limb bones.

Identifying the taxonomic status of fossils is notoriously difficult and researchers often disagree as to which specimens should belong to which species or even which genus. For example, some researchers refer to the East Turkana early Pleistocene fossils ER 3733 and 3883, as *Homo erectus*, while others refer to them as *Homo ergaster* (Schwartz and Tattersall, 2000). Disagreements and mistaken classifications could influence the type of ecological inferences made about a site. The methodology is also limited in that there is no provision for determining between taxa that are well represented at a site and taxa that are rare. For these reasons the reader is urged to use caution when reading the results.

Part 2 Site Examinations

Chapter 2

Toros-Menalla

2.1 Introduction

The site at which *Sahelanthropus tchadensis* was discovered, Toros-Menalla 266 (TM 266), is a single locality from the Djurab desert, Northern Chad (Vignaud *et al.*, 2002). The hominid fossils come from a two meter thick unit informally known as the anthracotheriid unit (AU). The unit “corresponds to a shallow perilacustrine environment, subject to frequent inundation due to recurrent lateral variations of the shoreline” (Vignaud *et al.*, 2002: 153). The deposits include fluvial, lacustrine and wind blown sediments. The age of the deposits is estimated at between 6 and 7 million years based on faunal comparisons.

2.2 Methods

A list compiled by Vignaud *et al.* (2002) was used for this survey.

2.3 Results

The site has yielded an extensive fauna including fish, reptiles and mammals (Table 2.1). The fish include the catfish *Bagrus*, weakly electric fish *Gymnarchus*, tiger fish *Hydrocynus*, puffer fish *Tetraodon* and the birchir *Polypterus*.

Three species of crocodile have been recovered, *Crocodylus niloticus*, *Euthecodon* and an indeterminate species from the family Gavialidae. Other reptiles include two turtles, one each from the families Trionychidae and Testudinidae, a monitor lizard *Varanus* and two snakes, *Python cf. sebae* and an indeterminate species from the Colubridae family.

Apart from *Sahelanthropus*, the only primate discovered at TM 266 is from the sub-family Colobinae. The carnivorous mammalian fauna is represented by the otter Lutrinae sp. indet., a large cat *Machairodus*, and three hyaenids *Hyaenicitherium*, *Ictitherium* and an indeterminate member of the family Hyaenidae. Proboscids are represented by *Loxodonta*

and *Anancus kenyensis*. There is one equid *Hipparion*, one suid *Nyanzachoerus syrticus*, a giraffid *Sivatherium*, a hippo *Hexaprotodon* and an anthracotheriid *Libycosaurus petrocchii*.

Table 2.1 Faunal list from TM 266, Chad (Vignaud *et al.*, 2002)

MAMMILIA	Rodentia
Primates	<i>Xerus</i> sp.
<i>Sahelanthropus tchadensis</i>	Murinae indet.
Colobinae indet.	<i>Hystrix</i> sp.
Carnivora	REPTILIA
Lutrinae sp. indet.	Trionychidae indet.
<i>Machairodus</i> cf. <i>giganteus</i>	Testudinidae indet.
<i>Hyaenicitherium</i> cf. <i>hyaenoides</i>	<i>Python</i> cf. <i>sebae</i>
<i>Ictitherium</i> sp.	Colubridae indet.
Hyaenidae sp.	<i>Varanus</i> sp.
Proboscidea	<i>Crocodylus niloticus</i>
<i>Loxodonta</i> sp. indet.	<i>Euthecodon</i> cf. <i>nitriae</i>
<i>Anancus kenyensis</i>	Gavialidae gen. et sp.
Perrisodactyla	OSTEICHTHYES
<i>Hipparion</i> cf. <i>abudhabiense</i>	<i>Bagrus</i> group
Artiodactyla	Siluridae indet.
<i>Nyanzachoerus syrticus</i>	Perciformes indet.
<i>Libycosaurus petrocchii</i>	<i>Gymnarchus</i> sp.
<i>Hexaprotodon</i> sp.	<i>Labeo</i> sp.
<i>Sivatherium</i> cf. <i>hendeyi</i>	<i>Hydrocnus</i> sp.
<i>Kobus</i> sp.	<i>Sindacharax</i> sp.
Antilopini indet.	Alestini indet.
Ovibovini indet.	<i>Tetraodon</i> sp.
cf. Hippotragini gen. et sp.	BRACHYOPTERYGII
Bovini indet.	<i>Polypterus</i> sp.
Tubulidentata	INSECTA
<i>Orycteropus</i> cf. <i>gaudryi</i>	Scarabaeidae indet.
	Hodotermitidae indet.

Bovids are represented by three abundant species including a small kob with short horns *Kobus*, plus the tribes Ovibovini and cf. Hippotragini. Two less abundant species occur from the tribes Bovini and Antilopini (Vignaud *et al.*, 2002).

The Toros-Menalla deposits contain the aardvark *Orycteropus*, a ground squirrel *Xerus*, an indeterminate member of the sub-family Murinae and the porcupine *Hystrix*.

Arthropod nests have also been discovered suggesting the presence of Scarabaeidae and Hodotermitidae.

2.4 Discussion

The presence of the piscivorous tiger fish *Hydrocynus*, which grows up to six feet long (Le Danois, 1959), is an indication of a relatively large body of water, particularly as many of the specimens were fully grown (Vignaud *et al.*, 2002). The variety of crocodiles, including the fish-eating, aquatic-specialist Gavialidae (Hvass, 1964), is also an indication of a relatively large body of water. Well vegetated, swampy waters are indicated by the presence of fish that can tolerate poorly oxygenated waters such as the birchir *Polypterus* (Moyle and Cech, 1982) and *Gymnarchus*, which prefers muddy lakes and rivers (Moyle and Cech, 1982) and builds its nests in swampy reed beds (Le Danois, 1959). In all there are ten taxa of fresh water fish present including the puffer fish *Tetraodon*, which is mainly marine but also known to inhabit fresh water (Moyle and Cech, 1982).

Amphibious mammals include the large hippopotamid *Hexaprotodon*, the anthracotheriid *Libycosaurus petrocchii* (Young, 1981) and the otter Lutrinae sp. indet. So numerous are the semi-aquatic anthracotheriids that the fossil bearing unit has been informally named after them (Anthracotheriid Unit). The turtles and the large python *Python cf. sebae* are indicative of water (Hvass, 1964).

Wooded to forested regions are inferred by the presence of two proboscids, which tend to depend on shade and water (Kingdon, 1997). Giraffids rely on trees in relatively open woodlands (Kingdon, 1997). The remains of an indeterminate colobine monkey indicate that there was most probably forest present (Kingdon, 1997), while the remains of the liana-like papilionoid plant (Vignaud *et al.*, 2002) are indicative of at least gallery forest.

Bovids include the Antilopini, which are tolerant of hot, dry environments, and *Kobus*, which never lives far from permanent water (Kingdon, 1997). Hyaenids are the most numerous carnivores with three species present. Extant hyaenids tend to favour open arid environments (Macdonald, 2000). Their presence may therefore be an indicator of nearby open environments. The rodent *Xerus*, a ground squirrel, is indicative of more open, arid habitats (Kingdon, 1997), while the scarab beetle suggests the presence of herbivores.

TM 266 appears to have been within the vicinity of a large body of permanent water, possibly a lake, where swampy vegetation and at least gallery forests existed. More open, possibly arid regions, with possible grasslands and woodlands may have existed close by.

Chapter 3

Manonga Valley

3.1 Introduction

The Manonga Valley is a site from the Western Rift and has no hominid remains associated with it. The faunal assemblage for this survey comes from the Wembere-Manonga formation, specifically the Tinde and Kiloleli members which are estimated to be of early Pliocene age (about 4 to 5 mya). The deposits are mainly of lacustrine origin (Harrison and Baker, 1997).

3.2 Methods

Faunal lists were compiled using the work of Harrison and Baker (1997).

3.3 Results

Table 3 shows the list of species discovered in the Kiloleli formation. The only primate discovered belongs to the family Cercopithecidae. Three elephant species in three genera are represented; *Loxodonta*, *Elephas* and *Anancus*. The rhino *Ceratotherium* and the equid *Eurygnathohippus* are also present as is the giraffid *Sivatherium*.

There is one pig present in the Kiloleli formations, *Nyanzachoerus kanamensis*, and two species of the hippopotamus genus *Hexaprotodon*. Bovids are comparatively well represented, particularly the Alcelaphini tribe, which has one large and one small species of indeterminate genus, plus *Damalacra* and *Aepyceros*. The other bovids are the Hippotragini *Praedamalis*, the Reduncini *Kobus* and the Tragelaphini *Tragelaphus*.

The only carnivore discovered in the deposits is from the family Viverridae, and there is also a rodent from the family Muridae present.

The non-mammalian fauna includes reptiles, fish, gastropods, bivalves and insects.

The Reptilia include a crocodile *Crocodylus* and two Chelonia represented by the families Trionychidae and Pelomedusidae. Fish species include the lung-fish *Protopterus*, the cat fish *Clarias* and the freshwater perch *Lates*.

The Gastropoda are relatively well represented and include *Bellamya*, *Pila ovata*, *Lanistes ovum*, *Gabbiella* and *Cleopatra*. One bivalve species *Spothopsis wahlbergi* is also present.

There is evidence of a wasp Hymenoptera, indicated by the presence of vertical tunnels, at Kiloleli.

Table 3.1 Faunal list for Manonga Valley (Harrison and Baker, 1997)

MAMMALIA	Rodentia
Primates	Muridae gen. et sp. indet.
Cercopithecidae gen. et sp. indet.	REPTILIA
Carnivora	Trionychidae indet.
Viverridae gen. et sp. indet.	Pelomedusidae indet.
Proboscidea	<i>Crocodylus</i> sp.
<i>Deinotherium bozasi</i>	AVES
Elephantinae gen. et sp. indet.	indet.
<i>Loxodonta</i> cf. <i>exoptata</i>	OSTEICHTHYES
<i>Elephas ekorensis</i>	<i>Alestes</i> sp.
<i>Anancus</i> sp.	<i>Sindacharax</i> sp.
Perrisodactyla	Chiclidae indet.
<i>Eurygnathohippus</i> sp.	<i>Protopterus</i> sp.
<i>Eurygnathohippus</i> aff. <i>hasumense</i>	<i>Clarias</i> sp.
<i>Ceratotherium praecox</i>	<i>Lates</i> ?sp.
Artiodactyla	GASTROPODA
<i>Nyanzachoerus kanamensis</i>	<i>Melanoides</i> aff. <i>anomala</i>
<i>Hexaprotodon harvardi</i>	<i>Bellamya</i> aff. <i>capillata</i>
<i>Hexaprotodon</i> sp.	<i>Pila ovata</i>
<i>Giraffa</i> sp.	<i>Lanistes ovum</i>
? <i>Sivatherium</i> sp.	<i>Gabbiella</i> aff. <i>humerosa</i>
<i>Damalacra</i> sp.	<i>Cleopatra</i> aff. <i>ferruginea</i>
Acelaphini (larger sp.)	BIVALVIA
Acelaphini (smaller sp.)	<i>Spothopsis wahlbergi</i>
<i>Praedamalis</i> sp.	INSECTA
<i>Kobus</i> cf. <i>subdolus</i>	Hymenoptera indet
<i>Aepyceros</i> sp.	
<i>Tragelphus</i> sp.	

3.4 Discussion

The fact that so few carnivores and small mammals have been recorded for the Kiloleli formations is curious, particularly considering reptiles and fish have been discovered, suggesting that preservation problems are not responsible. The presence of hippos, crocodiles, fish and gastropods is indicative of water. The suid *Nyanzachoerus kanamensis* may have been a swamp specialist (Bishop, 1999). The large number of elephants (at least four genera) indicates that conditions were quite different from today, and since the bush elephant *Loxodonta* is today said to have a preference for shade and water (Kingdon, 1997) this is perhaps an indication of forested regions close to water. The tribe Alcelaphini is indicative of grasslands (Kingdon, 1997), while the presence of *Sivatherium* suggests open woodlands (Kingdon, 1997). The occurrence of *Kobus* indicates nearby water.

Taken together, the faunal remains at Manonga Valley suggest a large lake fringed by well wooded or forested regions, with nearby open woodlands and grasslands. Swampy conditions and reed beds close to the lake margin are probable.

The fact that no hominid species have been discovered at this location may be due to a number of reasons. Possibly they were present but have not yet been discovered. Alternatively, perhaps there was something about the location which made it undesirable for a hominid species. There may have been some geographical barrier limiting migration to the Manonga Valley. Perhaps its location in the Western Rift Valley has some significance, since most hominid sites in East Africa are located in the Eastern Rift Valley.

Chapter 4

Langebaanweg

4.1 Introduction to site

Langebaanweg is a fossil site from southwestern Africa, about 100kms north-north-west of Cape Town, about 15kms inland. It contains a rich vertebrate fossil assemblage dating from between about 7 and 4.5 million years ago. This sequence of sedimentary layers is called the Varswater formations, and is divided into three members. The lowest member, the Gravel

Member, is associated with marine deposits, while the higher deposits, the Quartzose Sand and the Pelletal Phosphorite Members have a rich vertebrate fauna and are surveyed here. No hominid remains have been found within these deposits. The sediments associated with the formation were laid down initially in a marine transgression, and later as part of a flood plain, a marsh and a tidal mudflat (Gentry, 1980).

4.2 Methods

The faunal lists were compiled using Turner *et al.*, (1999). Although non-mammalian fauna have been discovered at Langebaanweg, no lists were available for this study, and therefore only the mammalian fauna have been listed. This needs to be taken into account when a comparison of other sites is made.

4.3 Results

The mammalian faunal assemblage at Langebaanweg is extensive (Table 4.1). It includes a variety of carnivores, large herbivores, rodents, insectivores, as well as a primate, a hare and a hyrax.

The primate belongs to the genus *Cercopithecoides*, the hare to *Pronolagus* and the hyrax to *Procavia*. The carnivorous fauna is relatively varied with an otter *Enhydriodon*, mongoose *Herpestes*, genet *Genetta* and a civet *Viverra*. There is also a badger *Mellivora* and what may be an ancient wolverine *Plesiogulo* present. A number of large felids are recognized; *Machairodus*, *Homotherium*, *Dinofelis* and *Adelphailurus*, as well as the medium sized cats *Felis serval* and *F. caracal*. The hyaenids are also well represented with four genera; *Ikelohyaena*, *Hyaenicittherium*, *Hyaenictis* and *Chasmaporthetes*. There is a fox *Vulpes* present at Langebaanweg and, unusually for Africa, a bear *Agriotherium africanum*.

The large herbivores include two elephants, *Mammuthus* and *Anancus*, the ancient horse *Hipparion*, a rhinoceros *Ceratotherium*, an indeterminate member of the family Hippopotamidae, three giraffes; *Sivatherium*, *Giraffa* and *Palaeotragus*, and three pigs in two genera; *Nyanzachoerus* and *Pecarichoerus*. There are ten bovids from seven genera; *Damalacra*, *Kobus*, *Gazella*, *Raphicerus*, *Mesembriportax*, *Tragelaphus* and *Simatherium*, plus an indeterminate species from the tribe Ovibovini.

Table 4.1 Mammalian fauna from Langebaanweg (Turner *et al.*, 1999)

Primates	<i>Kobus subdolus</i>
<i>Cercopithecoides</i> indet.	<i>Kobus</i> sp.
Carnivora	<i>Gazella</i> cf. <i>vanhoepeni</i>
<i>Herpestes</i> sp.	<i>Gazella</i> sp.
<i>Genetta</i> sp.	<i>Raphicerus paralius</i>
<i>Viverra leakeyi</i>	<i>Mesembriportax acrae</i>
<i>Enhydriodon africanus</i>	<i>Tragelaphus</i> sp.
<i>Mellivora benfieldi</i>	<i>Simatherium demissum</i>
<i>Plesiogulo monspessulanus</i>	Ovibovini indet.
<i>Adelphailurus</i> sp.	Rodentia
<i>Machairodus</i> sp.	<i>Dendromus darti</i>
<i>Homotherium</i> sp.	<i>Dendromus averyi</i>
<i>Dinofelis barlowi</i>	<i>Desmodillus</i> sp.
<i>Felis caracal</i>	<i>Aethomys modernis</i>
<i>Felis serval</i>	<i>Aethomys adamanticola</i>
<i>Ikelohyaena abronia</i>	<i>Acomys mabele</i>
<i>Hyaenicititherium namaquensis</i>	<i>Euryotomys pelomyoides</i>
<i>Hyaenictis hendeyi</i>	<i>Rhabdomys</i> sp.
<i>Chasmaporthetes australia</i>	<i>Mystromys hausleitneri</i>
<i>Vulpes</i> sp.	<i>Mystromys pocockei</i>
<i>Agriotherium africanum</i>	<i>Stenodontomys saldanhae</i>
Proboscidea	<i>Graphiurus</i> sp.
<i>Mammuthus subplanifrons</i>	<i>Cryptomys broomi</i>
<i>Anancus</i> sp.	<i>Bathyergus hedeyi</i>
Perrisodactyla	<i>Hystrix</i> sp.
<i>Hipparion</i> cf. <i>baardi</i>	Insectivora
<i>Ceratotherium praecox</i>	<i>Elephantulus broomi</i>
Artiodactyla	<i>Elephantulus</i> sp.
<i>Pecarichoerus africanus</i>	<i>Macroscelides proboscideus</i>
<i>Nyanzachoerus kanamensis</i>	<i>Myosorex robinsi</i>
<i>Nyanzachoerus</i> cf. <i>jaegeri</i>	<i>Suncus varilla</i>
Hippopotamidae indet.	<i>Chrysochloris</i> sp.
<i>Sivatherium hendeyi</i>	Lagomorpha
<i>Palaeotragus</i> cf. <i>germaini</i>	<i>Pronolagus</i> sp.
<i>Giraffa</i> sp.	Hyracoidea
<i>Damalacra neanica</i>	<i>Procavia antiqua</i>
<i>Damalacra acalla</i>	

Fifteen rodent species have been recognised in the Langebaanweg formations from twelve genera (see Table 4.1). Insectivores are relatively diverse including three elephant shrews in two genera; *Elephantulus* and *Macroscelides*, and two shrews, *Suncus* and *Myosorex*. There is also a mole *Chrysochloris* present.

4.4 Discussion

Unfortunately, no non-mammalian faunal lists were available for this survey, though it is known that remains have been recovered from the Varswater formations including birds (including a penguin *Spheniscus*), gastropods and reptiles. The most frequent reptiles are Chelonia, and while small numbers of lizards and snakes have been discovered, there are no crocodiles known from the deposits (Hendey, 1974). Frogs are a common occurrence at Langebaanweg.

The mammalian fauna suggests a rich habitat with carnivores of all sizes represented; insectivores, small and large cats, a fox and various sized hyaenids. The otter suggests there was water and the serval usually inhabits savanna regions where grass grows, usually near water (Estes, 1991). The mouse shrew *Myosorex* is often associated with swampy conditions (Kingdon, 1997), while the elephant shrews prefer scrubby cover in relatively dry regions (Kingdon, 1997). At least one of the sabre toothed cats, *Dinofelis*, might have preferred closed conditions, while the larger bodied *Homotherium* may have been more suited to open habitats (Lewis, 1997). Extant hyaenids, although known to inhabit forest edges, are generally found in more open habitats (Kingdon, 1997). Bears can tolerate cooler regions and extreme seasonality. Some, such as the brown bear *Ursus arctos*, are known to inhabit a range of habitats from forest, to open alpine tundra, to desert (Macdonald, 2001). No bears inhabit Africa today.

The presence on the hippopotamus indicates water and grasslands (Kingdon, 1997). The diversity of large herbivores, with both grazing (*Damalacra*), and browsing (*Tragelaphus*) forms indicate that there was probably a great deal of lush growth available, both close to the water (*Kobus*, *Simatherium*) and further away (*Gazella*). There were probably open grasslands within the vicinity, since the rhinoceros *Ceratotherium* is a grazing form (Kingdon, 1997), open woodlands as evidenced by the giraffes, and more closed or intermediate habitats judging by the presence of *Nyanzachoerus* (Bishop, 1999). The tribe Ovivovini, presently unknown in Africa, contains species that are adapted to high alpine and arctic tundra conditions (Macdonald, 2001).

The variety of rodents suggests a variety of possible habitats, including dense woodland, thickets or forest (*Graphiurus*, *Dendromus*), sandy habitats (*Bathyergus*), arid habitats

(*Desmodillus*, *Cryptomys*, *Acomys*), savanna grasslands (*Mystromys*) and rocky habitats (*Aethomys*) (Kingdon, 1997). Open, possibly semi-arid grasslands or rocky ground with thick scrub is indicated by the presence of the rock hare *Pronolagus* (Kingdon, 1997) and rocky outcrops are also indicated by the rock hyrax *Procavia* (Estes, 1991).

The area of the Langebaanweg deposits was obviously close to the coast, at least during the early part of the deposition process as evidenced by the remains of penguins and other marine fauna in the lower Gravel Member. In the members surveyed here, there appears to have been water present and a variety of habitats in the vicinity including grasslands, woodlands and possibly scrubby vegetation. There appears to have been rocky outcrops nearby. The possibility that highland regions or seasonally cooler temperatures may have been a contributor to the ecology of the region is perhaps illustrated by the occurrence of the bear, a member of the tribe Ovivovini, and possibly also by the absence of crocodiles (Hendey, 1974).

Chapter 5

Hadar

5.1 Introduction

Hadar is an Ethiopian fossil site located next to the Awash River in the Afar depression of the Eastern Rift Valley. Surveying and excavations at Hadar have revealed the fossils of a number of hominid individuals, collectively placed in the species *Australopithecus afarensis*. There are some indications that the sediments at Hadar are associated with fluctuating lake levels, possibly related to ancient beaches (Johanson and Taieb, 1978). The formations containing hominid fossils are generally recognised as being of Pliocene age between 3 and 4 million years old (Johanson *et al.*, 1982).

5.2 Methods

The mammalian fauna at Hadar was compiled using the table of Turner *et al.* (1999) and the non-mammalian fauna was compiled using a paper by Johanson *et al.* (1982).

5.3 Results

The Hadar formations have revealed a rich faunal assemblage, including numerous mammals, birds, reptiles as well as fish, bivalves and crustaceans (Tables 5.1 and 5.2). Apart from *Australopithecus afarensis*, five primates have been identified including *Theropithecus*, *Parapapio* (two species), *Rhinocolobus* and a member of the sub-family Colobinae.

Carnivorous mammals are represented by an otter *Enhydriodon*, the sabre-toothed cats *Dinofelis* and *Megantereon*, two other felids *Panthera* and *Felis*, two hyaenids *Crocuta crocuta* and *Chasmaporthetes*, and the jackal *Canis*.

A relatively large number of elephant species have been recorded at Hadar including two species of the genus *Elephas*, plus *Loxodonta adaurora*, *Deinotherium bozasi* and the mammoth *Mammuthus*. Three rhinoceroses in two genera have also been identified; *Ceratotherium* (two species) and *Diceros bicornis*. Also well represented are suids, of which three species in three genera have been reported; *Nyanzachoerus kanamensis*, *Notochoerus euilus* and *Kolpochoerus afarensis*. The hippopotamus *Hexaprotodon* was also present at Hadar.

The extinct equid *Hipparion afarensis* has been discovered at Hadar, as have numerous giraffid species including *Sivatherium maurusium* and three species belonging to the *Giraffa* genus.

In terms of the number of taxa, the Bovidae are the best represented at Hadar with seventeen. Of these, five belong to the tribe Reduncini, with four from the genus *Kobus* as well as *Dorcadoxa porrecticornis*. The Alcelaphini have two representatives including an indeterminate species as well as *Damalops*, while *Aepyceros* is recognized by some authors as also belonging to the tribe Alcelaphini (Kingdon, 1997) and is placed in its own tribe, Aepycerotini, by others (Estes, 1991). The tribe Bovini have three representatives; two species of *Ugandax* plus *Pelorovis*. Two genera of Neotragini, *Raphiceros* and *Madoqua*, also occur at Hadar. The tribe Tragelaphini has two representatives, including *Tragelaphus*, while the Antilopini (*Gazella*) and Ovibovini (*Makapania*) are also present.

The small mammal fauna is made up entirely of rodents. These include the ground squirrel *Xerus* and two porcupines, *Xenohystrix crassidens* and *Hystrix cristata*. The remaining nine species all belong to the family Muridae, including the gerbil *Tatera* and the mole rat *Tachyoryctes pliocaenicus*. The sub-family Murinae make up the remainder of the mammalian fauna discovered at Hadar, with seven genera; *Acomys*, *Golunda*, *Millardia*, *Mus*, *Oenomys*, *Praomys* and *Saidomys*.

Table 5.1 Mammalian faunal list from Hadar (Turner *et al.*, 1999)

Primates	<i>Giraffa jumae</i>
<i>Australopithecus afarensis</i>	<i>Giraffa gracilis</i>
<i>Theropithecus darti</i>	<i>Giraffa cf. pygmaeus</i>
<i>Parapapio cf. jonesi</i>	<i>Damalops ?paleindicus</i>
<i>Parapapio</i> sp.	Alcelaphini indet.
<i>Rhinocolobus cf. turkanaensis</i>	<i>Dorcadoxa porrecticornis</i>
Colobinae indet	<i>Kobus cf. kob</i>
Carnivora	<i>Kobus</i> sp. A
<i>Enhydriodon</i> sp.	<i>Kobus</i> sp. B
<i>Dinofelis</i> cf. sp.	<i>Kobus</i> sp. C
<i>Megantereon cultridens</i>	<i>Gazella</i> sp.
<i>Panthera</i> sp.	<i>Raphicerus ?sp.</i>
<i>Felis</i> sp.	<i>Madoqua cf. aviflumis</i>
<i>Crocuta crocuta</i>	<i>Tragelaphus nakuae</i>
<i>Chasmaporthetes</i> sp.	Tragelaphini sp.
<i>Canis</i> cf. <i>mesomelas</i>	<i>Ugandax cf. gautieri</i>
Proboscidea	<i>Ugandax</i> sp.
<i>Deinotherium bozasi</i>	<i>Pelorovis ?sp.</i>
<i>Loxodonta adaurora</i>	<i>Aepyceros</i> sp.
<i>Elephas ekorensis</i>	<i>Makapania</i> cf. sp.
<i>Elephas recki</i>	Rodentia
<i>Mammuthus</i> sp.	<i>Xerus ?sp.</i>
Perrisodactyla	<i>Tatera</i> sp. A
<i>Hipparion afarense</i>	<i>Acomys coppensi</i>
<i>Ceratotherium praecox</i>	<i>Golunda gurai</i>
<i>Ceratotherium simum</i>	<i>Millardia taiebi</i>
<i>Diceros bicornis</i>	<i>Mus</i> sp.
Artiodactyla	<i>Oenomys tiercelini</i>
<i>Nyanzachoerus kanamensis</i>	<i>Praomys</i> sp.
<i>Notochoerus euilus</i>	<i>Saidomys afarensis</i>
<i>Kolpochoerus afarensis</i>	<i>Tachyoryctes pliocaenicus</i>
<i>Hexaprotodon</i> cf. <i>protamphibius</i>	<i>Xenohystrix crassidens</i>
<i>Sivatherium maurusium</i>	<i>Hystrix cristata</i>

Due to the relative fragileness of their bones, birds do not usually preserve well in the fossil record. At Hadar, however, there are a number of bird taxa present. These include varieties of ostrich *Struthio*, grebe *Podiceps*, cormorant *Phalacrocorax*, stork *Leptoptilus* and goose *Plectropterus*.

Table 5.2 Non-mammalian fauna from Hadar (Johanson *et al.*, 1982)

AVES	<i>Bitis</i> sp.
aff. <i>Struthio</i> sp.	<i>Crocodylus</i> sp.
<i>Podiceps</i> cf. <i>sufficolis</i>	OSTEICHTHYES
<i>Phalacrocorax</i> sp.	Siluridae gen. et sp. indet.
<i>Leptoptilus</i> cf. <i>falconeri</i>	GASTROPODA
cf. <i>Plectropterus</i>	indet.
REPTILIA	BIVALVIA
<i>Geochelone</i> sp.	indet.
<i>Trionyx</i> sp.	OSTRACODA
<i>Python</i> sp.	indet.
<i>Varanus</i> sp.	Potamidae gen. et sp. indet.

Reptiles are also represented by a number of species at Hadar including the tortoise *Geochelone* and the turtle *Trionyx*. Snakes are represented by the genera *Python* and *Bitis*, while the monitor lizard *Varanus* and crocodile *Crocodylus* have also been discovered.

The remaining fauna has either yet to be, or is unable to be identified beyond the family level. This includes a fish Siluridae, a gastropod Gastropoda, a bivalve Bivalvia and two crustaceans, Ostracoda and Potamidae.

5.4 Discussion

The faunal remains discovered at Hadar suggest that trees were probably present. A number of monkey species have been discovered, including two colobus monkeys which, although larger than modern species, appear to be indicative of well wooded habitats since all extant colobus monkeys inhabit forests (Kingdon, 1997). In addition a number of browsing species including giraffids and the rhinoceroses *Diceros bicornis* (Kingdon, 1997) suggest the presence of trees.

A permanent body of water is indicated at Hadar by the presence of otters, hippos, crocodiles, fish, turtles, crustaceans and bivalves. The avian fauna also is indicative of water. The grebe *Podiceps*, for example, a weak flier but excellent underwater diver, is fully

adapted to a waterside existence (Gooders, 1975). It lives in freshwater lakes and marshes and builds its nest in vegetation on the water (Perrins and Middleton, 1985; Campbell and Lack, 1985). The cormorant *Phalacrocorax* is also a specialist aquatic bird which dives for fish along coasts as well as in freshwater lakes and swamps (Perrins and Middleton, 1985; Gooders, 1975). The stork *Leptoptilus* is often associated with wetlands such as marshes in arid regions (Perrins and Middleton, 1985; Campbell and Lack, 1985). The goose *Plectropterus* belongs to the family Anatidae, members of which are essentially aquatic (Campbell and Lack, 1985).

The number of bovids dependant on water, including five members of the tribe Reduncini (Kingdon, 1997) and three buffaloes (Estes, 1997) suggests a large body of permanent water, while the tribe Tragelaphini, with two members present, probably indicates that dense cover was available locally (Kingdon, 1997).

There are three genera of pig present in the Hadar formations, including *Nyanzachoerus kanamensis* which may have been a swamp specialist (Bishop, 1999). It has been suggested that Pliocene suids were generally adapted to closed environments (Bishop, 1999). The sabre-toothed cats, *Dinofelis* and *Megantereon*, may have also preferred closed habitats (Lewis, 1997). The hyaenids and the jackal *Canis*, on the other hand, are perhaps more indicative of open habitats (Kingdon, 1997). The Antilopini *Gazella* may be an indicator of local dry areas and the presence of the ground squirrel *Xerus* and the gerbil *Tatera* may also suggest dry conditions (Kingdon, 1997). The ostrich *Struthio* is also probably indicative of open, arid habitats (Perrins and Middleton, 1985; Campbell and Lack, 1985).

Studies of pollen indicate that a high proportion of plants from the family Cyperaceae and the genus *Typha* occur at Hadar. The abundance of these aquatic plants (Willis, 1966) suggests “the proximity of marshy, freshwater conditions and periodic flooding” (Bonafille, 1995: 303).

Taken together, the floral and faunal remains at Hadar suggest a rich habitat in which a large body of water most probably existed, along with arboreal habitats, marshlands, open grasslands and possibly mixed bush and scrubland and more arid regions.

Chapter 6

Laetoli

6.1 Introduction

Laetoli is a mid-Pliocene Tanzanian site famous for the fossilised animal trails found within its deposits. Unlike many other east African fossil sites the sediments at Laetoli were deposited in non-lacustrine and non-fluvial environments, resulting instead from the accumulation of air-fall and wind reworked deposits (Harris, 1987). As a result many of the fossil remains are fragmentary. Hominid remains from the Laetoli area are conventionally placed within the species *Australopithecus afarensis* (Johanson and Edey, 1981).

6.2 Methods

Laetoli is made up of a number of units and beds. The remains of *Australopithecus afarensis* come from the Upper Laetoli Beds and it is therefore the fauna from this bed that have been listed here. The lists were compiled using Harris (1987) for the non-mammalian fauna and Turner *et al.* (1999) for the mammals.

6.3 Results

The Upper Laetoli Beds have revealed a rich faunal assemblage (Tables 6.1, 6.2 and 6.3). Apart from the hominid *Australopithecus afarensis* there are three cercopithecids; *Parapapio*, *Papio*, and *Paracolobus*, along with the strepsirrhine *Galago sandimanensis*.

Carnivores are richly represented at Laetoli including four mongoose species; *Helogale paleogracilis*, *Herpestes paleoserengensis*, *Herpestes ichneumon* and *Mungos dietrichi*, plus the civet *Viverra leakeyi* and the honey badger *Mellivora capensis*. Also present is the weasel *Propoecilogale*.

Large carnivores are particularly well represented. Two large extinct sabre-toothed felids are present, *Homotherium crenatidans* and *Megantereon cultridens*, as well as the modern felids *Panthera leo*, *P. pardus* and *Acinonyx jubatus*. An unidentified *Panthera* species is also present. Two hyaenids have been discovered, the spotted hyaena *Crocuta crocuta* and the

extinct *Chasmaporthetes*. Two species of *Canis* have been reported and three genera of fox; *Vulpes*, *Otocyon* and *Megacyon*.

Table 6.1 Mammalian fauna (excluding Artiodactyla) from Laetoli (Turner *et al.*, 1999)

Primates	Proboscidea
<i>Australopithecus afarensis</i>	<i>Deinotherium bozasi</i>
<i>Parapapio ado</i>	<i>Loxodonta exoptata</i>
cf. <i>Papio</i> sp.	Rodentia
<i>Paracolobus</i> sp.	<i>Xerus</i> sp. indet.
Colobinae sp.	<i>Xerus janenschi</i>
<i>Galago sandimanensis</i>	<i>Paraxerus</i> sp.
Carnivora	<i>Saimys</i> sp.
<i>Helogale paleogracilis</i>	Muridae indet.
<i>Herpestes paleoserengensis</i>	<i>Saccostomus major</i>
<i>Herpestes ichneumon</i>	<i>Dendromus</i> sp.
<i>Mungos dietrichi</i>	<i>Steatomys</i> sp.
<i>Viverra leakeyi</i>	<i>Tatera</i> cf. <i>inclusa</i>
<i>Mellivora capensis</i>	<i>Mastomys cineris</i>
<i>Propoecilogale bolti</i>	<i>Thallomys laetolilensis</i>
<i>Homotherium crenatidans</i>	<i>Pedetes laetoliensis</i>
<i>Megantereon cultridens</i>	<i>Heterocephalus quenstedti</i>
<i>Panthera leo</i>	<i>Xenohystrix crassidens</i>
<i>Panthera pardus</i>	<i>Hystrix leakeyi</i>
<i>Panthera</i> sp.	<i>Hystrix makapanensis</i>
<i>Acinonyx jubatus</i>	Insectivora
<i>Crocuta crocuta</i>	<i>Elephantulus</i> sp.
<i>Chasmaporthetes</i> sp.	<i>Rhynchocyon pliocaenicus</i>
<i>Canis</i> cf. <i>brevirostris</i>	<i>Myosorex</i> sp.
<i>Canis</i> sp.	<i>Suncus</i> sp.
cf. <i>Otocyon</i> sp.	<i>Chrysochloris</i> sp.
<i>Megacyon</i> ?sp.	Chiroptera
<i>Vulpes</i> sp.	<i>Eptesicus</i> sp.
Perrisodactyla	Lagomorpha
<i>Hipparion</i> sp.	<i>Pronolagus</i> sp.
<i>Ceratotherium praecox</i>	<i>Serengetilagas praecapensis</i>
<i>Diceros bicornis</i>	Hyracoidea
<i>Ancylotherium hennigi</i>	<i>Procavia</i> cf. <i>antiqua</i>

The large elephant *Deinotherium bozasi* as well as *Loxodonta exoptata* have both been discovered in the Upper Laetoli Beds, along with two rhinoceroses *Ceratotherium praecox* and *Diceros bicornis*, the extinct horse *Hipparion*, as well as the extinct *Ancylotherium hennigi*, a massive browser with long hooved-forelimbs and short clawed-hindlimbs (Benton, 1990).

The Rodentia include three species of Sciuridae, the gundi *Saimys*, seven murid rodent species including the genera *Saccostomus*, *Dendromus*, *Steatomys*, *Tatera*, *Mastomys* and *Thallomys*, the spring hare *Pedetes*, the naked mole rat *Heterocephalus* and three porcupines in two genera, *Xenohystrix crassidens*, *Hystrix leakeyi* and *Hystrix makapanensis*. Two elephant shrews, *Elephantulus* and *Rhynchocyon*, the mouse shrew *Myosorex*, and the pygmy shrew *Suncus* occur in the Upper Laetoli Bed deposits, as does the golden mole *Chrysochloris*, two lagomorphs, *Serengetilagas* and *Pronolagus*, and the rock hyrax *Procavia*. The bat *Eptesicus* is also present

Three pigs in three genera *Notochoerus*, *Kolpochoerus* and *Potamochoerus* occur, as well as four giraffid species in two genera; *Sivatherium* and *Giraffa*, as well as the camel *Camelus*.

Table 6.2 Artiodactyla from Laetoli (Turner *et al.*, 1999)

Suidae	<i>Parmularius pandatus</i>
<i>Notochoerus euilus</i>	Alcelaphini indet.
<i>Kolpochoerus afarensis</i>	<i>Praedamalis deturi</i>
<i>Potamochoerus porcus</i>	<i>Brabovus nanincisivus</i>
Giraffidae	Hippotragani indet.
<i>Sivatherium maurusium</i>	<i>Redunca</i> cf. sp.
<i>Sivatherium</i> sp.	<i>Gazella janenski</i>
<i>Giraffa stillei</i>	<i>Gazella</i> cf. <i>granti</i>
<i>Giraffa</i> cf. <i>jumae</i>	<i>Raphicerus</i> ?sp.
Camelidae	<i>Madoqua aviflumnis</i>
<i>Camelus</i> sp.	<i>Tragelaphus</i> sp.
Bovidae	<i>Simatherium kohllarseni</i>
<i>Damiliscus</i> ?sp.	Cephalophini indet.
<i>Damalops</i> cf. <i>palaeindicus</i>	

Fifteen bovids have been identified in the Upper Laetoli Bed deposits (Table 6.2): Four species from the tribe Alcelaphini, three from Hippotragani, a member of the tribe Reduncini, four species of Antilopini, a representative of the tribe Strepsicerotini, a buffalo *Simatherium* and the forest duiker Cephalophini.

Non-mammalian faunal remains have also been recovered from the Upper Laetoli Beds including birds, reptiles, gastropods and evidence of burrowing insects and termites (Table 6.3). The birds include remains of ostrich *Struthio*, vulture *Torgos*, a large and a small species of francolin *Francolinus*, a guinea fowl *Numida*, a dove *Streptoptelia* and an owl *Bubo*.

Table 6.3 Non-mammalian fauna from Laetoli (Harris, 1987)

AVES	GASTROPODA
<i>Struthio</i> sp.	<i>Edouardia laetoliensis</i>
<i>Torgos</i> sp.	<i>Subulona pseudinvoluta</i>
<i>Francolinus</i> spp.	<i>Pseudoglessula</i> cf. <i>gibbonsi</i>
<i>Numida</i> sp.	<i>Euonyma leakeyi</i>
<i>Streptoptelia</i> sp.	<i>Achatina</i> ? <i>zanzibarica</i>
<i>Bubo</i> sp.	<i>Burtoa nilotica</i>
REPTILIA	<i>Trochonanina</i> sp. A
<i>Geochelone laetoliensis</i>	<i>Trochonanina</i> sp. B
<i>Geochelone brachyularias</i>	Urocyclinae sp. A
<i>Python sebae</i>	Urocyclinae sp. B
cf. <i>Ramphiophis</i> sp.	Urocyclinae sp. C
<i>Bitis arietens</i>	INSECTA
<i>Naja robustus</i>	Sphecidae indet.
	Termitidae indet.

The Reptilia include two tortoises, *Geochelone laetoliensis* and *G. brachyularias*, and four snakes; the python *Python sebae*, the puff adder *Bitis arietens*, a large cobra *Naja robustus* and the colubrid snake *Ramphiophis*.

There is a relatively large assemblage of terrestrial gastropods at Laetoli including six snails; *Edouardia*, *Subulona*, *Pseudoglessula*, *Euonyma*, *Achatina* and *Burtoa*. There have been five slug taxa identified, two placed in the genus *Trochonanina* and three identified to the subfamily level of Urocyclinae.

As well as the fossilized remains discussed above, trace fossils in the form of termitaries suggest the presence of termites (Sands, 1987), and a burrowing wasp belonging to the Sphecidae family (Ritchie, 1987).

6.4 Discussion

One of the striking features of the Laetoli deposits, particularly compared to other sites, is the lack of aquatic elements such as fish, crocodiles and hippopotamus. This is a point emphasized by Harris, who concludes that the area of the Upper Laetoli Bed deposits was “a savanna ecosystem broadly comparable to that of today” (1987: 526).

The rich diversity of the faunal assemblage, however, suggested to Andrews (1989: 179) that the environmental conditions of the Upper Laetoli Beds “might be regarded as being even more wooded than the most extreme of Serengeti habitats today.” Indeed, the presence of six primate species, two giraffe genera, the browsing rhinoceros *Diceros bicornis* (Kingdon, 1997) and the chalicothere *Ancylotherium*, a browser often associated with forest species (Young, 1981), all point to the presence of well wooded to forested regions. The python *Python sebae* is recognized as being strongly associated and probably dependant on water for thermoregulatory and hunting purposes (Meylan, 1987).

Also indicative of moister and more heavily wooded conditions are the snails and slugs. “Taking the molluscan assemblage as a whole,” writes Verdcourt (1987: 450),

“and assuming all the components were living *in situ* and not partly washed down from some other locality, the evidence suggests that the vegetation could have been grassland with scattered trees or denser woodland with at least a narrow belt of evergreen riverine forest; either continuous woodland or continuous evergreen forest does not satisfy the facts. I estimate a rainfall of 625-1000 mm but if the evergreen forest was narrow and supported by a permanent river then it could have been near the lower level; many of the species could not, however, have existed in grassland with scattered trees nor in woodland.”

There is a high number of burrowing animals in the assemblage indicating the possibility that perhaps there is a taphonomic bias in favor of burrowing animals. It is perhaps possible that the fossilised remains include animals that lived in burrows and the remains of their prey. Dogs, foxes, hyaenids, mongooses and porcupines are all well represented and are all known to transport food into underground dens or burrows (Macdonald, 2001; Kingdon, 1987). Leopards and other cats are known to transport their prey for up to a hundred meters (Brain, 1981) and therefore it is possible that some remains may be of animals that have been hunted in one location, transported to another location, and perhaps scavenged upon and transported to underground dens and burrows by scavengers such as hyaenids, porcupines and other rodents.

There seems little doubt that at least some open grasslands or woodlands existed at Laetoli, the high number of grazing bovids (Alcelaphini) would appear to support this conclusion (Kingdon, 1997). The presence of two species of the ground squirrel *Xerus* and the spring hare *Pedetes* are indicative of relatively dry, open habitats, while the bush squirrel *Paraxerus* is indicative of more closed habitats (Kingdon, 1997). The mouse shrew *Myosorex* often inhabits swampy conditions (Kingdon, 1997). Another indication that water existed locally is the presence of the Egyptian mongoose *Herpestes ichneumon*, which is “water dependant and a good swimmer” (Kingdon, 1997: 240).

Relatively arid regions are suggested by the presence of the camel (Kingdon, 1997), as well as the tribes Hippotragini and Antilopini (Macdonald, 2001). There also appears to have been at least some relatively well forested areas, judging by the presence of the duiker Cephalophini (Kingdon, 1997), and most probably nearby water or at least thick cover since the buffalo *Simatherium* is dependant on water (Estes, 1991) and the genus *Tragelaphus* is usually dependant on water and thick cover (Kingdon, 1997).

Fossil pollen samples from the Upper Laetoli Beds shows that grasses were predominant and by far the highest component belonged to the family Gramineae (Bonnefille and Riollet, 1987). Although this family contains grasses that grow in arid regions such as savannas and even deserts, they also grow in wet areas including brackish waters along the coasts and fresh waters of lakes and rivers (Willis, 1966). Unfortunately, as Bonnefille (1995: 303) points out, “it is not possible to distinguish between them.” The Upper Laetoli Beds also contain pollen from the plants *Typha* and Cyperaceae, although in much smaller quantities than the Gramineae, indicating that at least some water was present locally (Willis, 1966).

The picture, therefore, at Laetoli seems to be one in which relatively dry habitats, possibly both open and closed, existed along with areas of relatively thick vegetation including evergreen forest. Water seems to have been present locally. Perhaps the area had a relatively low annual rainfall, or else an annual dry season, with a river or stream fringed with gallery forest and occasional swampy areas along its margins.

Chapter 7

Sterkfontein

7.1 Introduction

Apart from the East African Rift Valley, the other major hominid bearing fossil localities of Pliocene age in Africa occur in South Africa, including sites such as Taung, Makapansgat, Krombaai, Swartkrans and Sterkfontein. These sites differ generally from those in East Africa in that they are mainly cave deposits and therefore have different depositional processes. As a result, dating of the fossil remains has been notoriously difficult. The site chosen for this survey is Sterkfontein Member 4, from which a number of hominid specimens recognized as *Australopithecus africanus* have been recovered. This member has been estimated at between about 2.5 and 3.3 million years old (Tobias, 1976).

7.2 Methods

The fossil list was taken from Turner *et al.* (1999).

7.3 Results

The Sterkfontein fossil assemblage is rich in primate and carnivore remains (Table 7.1). *Australopithecus afarensis* is the only non-cercopithecoid primate represented. The other primates include four species of *Parapapio* including *jonesi*, *whitei*, *broomi* and an indeterminate species. There are also two *Papio* species, *hamadryas* and *izodi*, as well as *Cercopithecoides williamsi*.

Carnivores are represented by three genera of saber toothed felids, *Homotherium crenatidans*, *Dinofelis barlowi* and *Megantereon cultridens*. The lion *Panthera leo* and leopard *Panthera pardus* were also present at the time of the Sterkfontein Member 4 accumulations. Also well represented are hyaenids, including *Pachycrocuta brevirostris*, *Parahyaena*, *Chasmaporthetes nitidula* and the spotted hyaena *Crocuta crocuta*. The black backed jackal *Canis mesomelas* was present during Member 4 times as well.

A single elephant species *Elephas recki* has been discovered at Sterkfontein as well as two species of *Equus* including the now extinct giant cape horse *Equus capensis*. Suids are represented by the genus *Metridiochoerus* and there are ten bovid species present. These include two species of *Hippotragus*, two species of *Redunca*, two species of *Antidorcas*, *Megalotragus kattwinke*, *Tragelaphus cf. angastii*, *Makapania broomi* and an indeterminate species of *Syncerus*.

Table 7.1 Fauna from Sterkfontein (Turner *et al.*, 1999)

MAMMALIA	<i>Hippotragus cookei</i>
Primates	<i>Redunca darti</i>
<i>Australopithecus africanus</i>	<i>Redunca cf. arundinum</i>
<i>Parapapio jonesi</i>	<i>Antidorcas recki</i>
<i>Parapapio whitei</i>	<i>Antidorcas cf. bondi</i>
<i>Parapapio broomi</i>	<i>Tragelaphus cf. angastii</i>
<i>Parapapio sp.</i>	<i>Syncerus sp.</i>
<i>Papio hamadryas</i>	<i>Makapania broomi</i>
<i>Papio izodi</i>	Rodentia
<i>Cercopithecoides williamsi</i>	<i>Dendromus cf. mesomelas</i>
Carnivora	<i>Tatera cf. brantsii</i>
<i>Homotherium crenatidans</i>	<i>Aethomys cf. namaquensis</i>
<i>Dinofelis barlowi</i>	<i>Dasmys sp.</i>
<i>Megantereon cultridens</i>	<i>Mastomys sp.</i>
<i>Panthera leo</i>	<i>Rhabdomys sp.</i>
<i>Panthera pardus</i>	<i>Mystromys antiquus</i>
<i>Pachycrocuta brevirostris</i>	<i>Proodontomys cookei</i>
<i>Crocuta crocuta</i>	<i>Otomys gracilis</i>
<i>Parahyaena sp.</i>	<i>Graphiurus cf. monardi</i>
<i>Chasmaporthetes nitidula</i>	<i>Cryptomys robertsi</i>
<i>Canis mesomelas</i>	<i>Hystrix africae australis</i>
Proboscidea	Insectivora
<i>Elephas recki</i>	<i>Elephantulus broomi</i>
Perrisodactyla	<i>Macroscelides proboscideus</i>
<i>Equus capensis</i>	<i>Myosorex cf. cafer</i>
<i>Equus sp.</i>	<i>Myosorex robinsoni</i>
Artiodactyla	<i>Chlorotalpa sp.</i>
<i>Metridiochoerus sp.</i>	Hyracoidea
<i>Megalotragus kattwinke</i>	<i>Procavia antiqua</i>
<i>Hippotragus equinus</i>	<i>Procavia transvaalensis</i>

The small mammal fauna includes a variety of species from two main groups; rodents and shrews. The rodents are mainly from the murid family and include the genera *Dendromus*, *Tatera*, *Aethomys*, *Dasmys*, *Mastomys*, *Rhabdomys*, *Mystromys*, *Proodontomys* and *Otomys*.

Other rodents include the dormouse *Graphiurus*, the mole rat *Cryptomys* and the porcupine *Hystrix*.

The Insectivora include the elephant shrews, *Elephantulus broomi* and *Macroscelides proboscideus*, and two species of the mouse shrew *Myosorex*. The golden mole *Chlorotalpa* and two species of the rock hyrax *Procavia* have also been identified.

No non-mammalian fauna has been recovered from the Member 4 deposits at Sterkfontein.

7.4 Discussion

Perhaps the most striking feature of the Sterkfontein Member 4 assemblage is the lack of non-mammalian fauna. This may be the result of either taphonomic or collection biases. Brain has noted that the high percentage of cranial remains compared to non-cranial remains may be the result of the “rather haphazard collecting procedures” practiced between 1936 and 1947 (1981: 209). He notes that collectors, including Robert Broom, were mainly interested in bones that “were potentially capable of yielding specific identification” (1981: 209). This, combined with the site’s mining history and the fact that casual visitors often left with fossil souvenirs, meant that ideal scientific controls were not always in place at Sterkfontein. Regardless, there are inferences that can be made when the fossil assemblage is looked at in entirety.

Noticing the high ratio of carnivores to ungulates, Brain concluded that much of the large mammalian fossil assemblage may have been the result of carnivorous activity. If this is the case, the high number of primate species, including the australopithecines, might represent part of the accumulated debris of a number of large carnivorous felids and hyaenids. In fact, when the bone assemblage is examined in terms of number of individuals, as opposed to number of taxa present, 69.8% are primates (Brain, 1981). This possibly indicates that primates, including *Australopithecus africanus*, were preferentially preyed upon by at least some of the large carnivores that existed within the area. Although baboons are well adapted to living in open grasslands, they also usually require trees for shelter. The variety of primate species at Sterkfontein is an indicator, therefore, that there were numerous trees present within the vicinity.

Compared to other sites there are relatively few pachyderms, with only one elephant, one pig and no hippopotamus or rhinoceros species present. Whether this is because they were poorly represented within the local fauna or because they were rarely hunted by the (supposed) carnivorous assemblage accumulators is unclear. Two equid species including the large *Equus capensis* could be seen as evidence of open grasslands.

Bovids are relatively well represented at the species level including two antelope species from the genus *Hippotragus*, which could be indicative of relatively open, arid habitats (Macdonald, 2001). Also perhaps indicative of open grasslands are the gazelles *Antidorcas recki* and cf. *bondi*, though it is worth noting that Bishop (1999) believes it possible that *Antidorcas recki* could have been a swampy bush inhabitant. The buffalo *Syncerus* could be indicative of a number of habitats though its need for water and some cover (Kingdon, 1997) suggests that these were present locally.

Megalotragus was a large hartebeest that may have preferred grasslands that were not too dry and not too moist (Macdonald, 2001). On the other hand, two species of *Redunca* probably infer that water was close by (Estes, 1997). Meanwhile *Tragelaphus* cf. *angastii* may have preferred waterside vegetation or marshland since Kingdon (1982) believes it was similar to the sitatunga *Tragelaphus spekei*, a marshland inhabitant (Kingdon, 1997).

The variety of small mammalian fauna is perhaps suggestive that there were a variety of habitats available at Sterkfontein during Member 4 times. Brain notes that most of the small mammal fauna from the cave sites of South Africa may have been deposited in the form of owl pellets, and therefore may be subject to a particular bias (Brain, 1981). Nevertheless we can deduce by the presence of certain taxa that particular habitats may have existed locally.

Rock hyraxes prefer rocky outcrops (Kingdon, 1997), as does the bush rat *Aethomys* (Kingdon, 1997). The gerbil *Tatera* is well adapted to arid, savanna conditions (Kingdon, 1997). The rodent *Myodomys* is today found in grassy flats and dry sandy areas (Kingdon, 1997) supporting the idea that dry, grassy plains existed locally. The golden mole, *Chlorotalpa* is also perhaps indicative of open, arid regions, with a preference for sandy habitats (Kingdon, 1997).

A number of species, such as the porcupine and the shrews, are difficult to use as habitat indicators because they today occur in a variety of habitats from dense forest to open savannas, though the variety of shrews and elephants shrews, with three genera, would seem to indicate that at least some cover did exist, whether forest or leafy undergrowth. The elephant shrews *Macroscelides* and *Elephantulus* probably are indicative of drier, though nevertheless relatively thick vegetation (Kingdon, 1997), while two species of the mouse shrew *Myosorex* probably indicate that swampy regions occurred locally (Kingdon, 1997). The rodents *Mastomys* and *Rhabdomys* today inhabit various habitats and therefore could be indicative of a number of habitats.

Dendromus is an arboreal rodent, though it is known to spend a lot of time on the ground (Macdonald, 2001), and the dormouse *Graphiurus* is also arboreal and indicative of dense woodlands, thickets or forests, though rocky habitats are also preferred (Kingdon, 1997). *Dasmys* and *Otomys* are both known to inhabit the swampy fringes of wetlands and waterways (Kingdon, 1997) and therefore their presence may indicate that swampy conditions prevailed locally.

Although the Member 4 accumulation at Sterkfontein has certain taphonomic biases associated with it, it nevertheless does give some indication of the type of habitats that may have prevailed locally. There are indications that relatively dry, open habitats may have existed within the vicinity, while there are also indications of trees and relatively closed habitats and indications of nearby water and perhaps associated swampy areas.

Chapter 8

East Turkana

8.1 Introduction

The Turkana Basin in the African Rift Valley is an area rich in fossil remains. Fed by rivers such as the Omo, the Turkana Basin has often been associated with a large lake. The basin covers an area of 146,000 square kms (Feibel, 1999). The sediments are mainly fluvial and lacustrine and are interspersed with numerous volcanic tuffs which are used as stratigraphic

markers. Sites from the eastern side of Lake Turkana (formerly Lake Rudolf) are known collectively as the Koobi Fora formations, and include sites from Ileret in the north to Allia Bay in the south. The members included in this survey are those that contain fossils attributed to *Homo ergaster*: the Upper Burgi, KBS and Okote members. These range in age from 1.9 to 1.4 million years (Schwartz and Tattersall, 2003). Also discovered within these members are fossils attributed to *Paranthropus boisei*, which occurs throughout, *Homo habilis*, from the Upper Burgi and KBS formations, and *Homo rudolfensis*, which also occurs throughout (Turner *et al.*, 1999).

8.2 Methods

Fossil lists were drawn up using lists compiled by Turner *et al.* (1999) for the mammalian fauna and Feibel *et al.* (1991) for the non-mammalian fauna.

8.3 Results

East Turkana has a rich record of mammalian and non-mammalian fauna (Tables 8.1, 8.2 and 8.3). As well as *Homo ergaster* there are two other species of *Homo*, *rudolfensis* and *habilis*, and an indeterminate member of the genus *Homo* recorded from East Turkana. The other hominid present is *Paranthropus boisei*.

Non-hominid primates are also well represented at East Turkana with *Theropithecus oswaldi* along with species from the genera *Papio*, *Gorgopithecus*, *Cercocebus*, *Cercopithecus*, *Cercopithecoides* and *Colobus*. An indeterminate species from the family Colobinae has also been discovered.

Table 8.1 Mammalian fauna (excluding Artiodactyla) from East Turkana (Turner *et al.*, 1999)

PRIMATES	PERRISODACTYLA
<i>Paranthropus boisei</i>	<i>Hipparion hasumense</i>
<i>Homo habilis</i>	<i>Hipparion ethiopicum</i>
<i>Homo rudolfensis</i>	<i>Hipparion cornelianum</i>
<i>Homo ergaster</i>	<i>Hipparion sp.</i>
<i>Homo sp.</i>	<i>Equus koobiforensis</i>
<i>Theropithecus oswaldi</i>	<i>Equus cf. tabeti</i>
<i>Papio sp.</i>	<i>Equus cf. burchelli</i>
<i>Gorgopithecus major</i>	<i>Equus cf. grevyi</i>
<i>Cercocebus sp.</i>	<i>Equus sp.</i>
<i>Cercopithecus cf. aethiops</i>	<i>Ceratotherium simum</i>

<i>Cercopithecoides</i> sp.	<i>Diceros bicornis</i>
<i>Colobus</i> sp.	RODENTIA
Colobinae indet.	<i>Jaculus orientalis</i>
CARNIVORA	<i>Saccostomus</i> sp.
<i>Homotherium crenatidans</i>	<i>Tatera</i> sp. A
<i>Dinofelis barlowi</i>	<i>Arvicanthis</i> sp.
<i>Dinofelis</i> cf. <i>piveteaui</i>	<i>Aethomys</i> sp.
<i>Megantereon cultridens</i>	<i>Mastomys minor</i>
<i>Panthera</i> cf. <i>leo</i>	<i>Mus</i> sp.
<i>Crocota crocuta</i>	<i>Thallomys quadrilobatus</i>
<i>Hyaena hyaena</i>	<i>Hystrix</i> sp.
<i>Canis mesomelas</i>	<i>Thryonomys</i> sp.
<i>Lycaon ?pictus</i>	INSECTIVORA
PROBOSCIDEA	<i>Crocidura</i> cf. <i>dolichura</i>
<i>Deinotherium bozasi</i>	<i>Crocidura</i> cf. <i>nana</i>
<i>Loxodonta adaurora</i>	CHIROPTERA
<i>Elephas recki</i>	<i>Scotophilus</i> sp.
	<i>Nycteris</i> sp.

Carnivores include the large sabre-toothed felids *Homotherium crenatidans*, two species of *Dinofelis* and *Megantereon cultridens*. A lion *Panthera* is represented, as are the hyaenids *Crocota crocuta* and *Hyaena hyaena*. The black backed jackal *Canis mesomelas* and the African hunting dog like *Lycaon* also occur within the Koobi Fora formations.

Three species of proboscids in three genera are present at East Turkana; *Deinotherium bozasi*, *Loxodonta adaurora* and *Elephas Recki*. The rhinoceroses *Ceratotherium simum* and *Diceros bicornis* are present as well as four species of suid in three genera; *Notochoerus*, *Kolpochoerus* and two species of *Metridiochoerus*. *Hexaprotodon* and two species of *Hippopotamus* are also present.

Hipparion species are well represented with four species, while the genus *Equus* has five species recorded from East Turkana. Giraffids are also well represented with three species of *Giraffa* and *Sivatherium maurusium* present. The camel *Camelus* also occurs within the Koobi Fora formations.

In terms of the number of species, the bovids, with twenty four, are the largest group in the Koobi Fora formations. The Alcelaphini tribe contributes seven of these including a species of *Rabaticeras*, two species of *Megalotragus* and four species of *Parmularius*. *Aepyceros*,

placed within its own tribe by some authors (Estes, 1991) and within the Alcelaphini by others (Kingdon, 1997), is also present at East Turkana. The Hippotragini are represented by *Hippotragus gigas* and *Oryx*.

Table 8.2 Artiodactyla from East Turkana (Turner *et al.*, 1999)

Suidae	<i>Parmularius angusticorn</i>
<i>Notochoerus scotti</i>	<i>Parmularius</i> sp.
<i>Kolpochoerus limnetes</i>	<i>Rabaticeras</i> sp.
<i>Metridiochoerus andrewsi</i>	<i>Hippotragus gigas</i>
<i>Metridiochoerus compactus</i>	<i>Oryx</i> sp.
Hippopotamidae	<i>Kobus</i> cf. <i>kob</i>
<i>Hexaprotodon karumensis</i>	<i>Kobus ancystrocera</i>
<i>Hippopotamus gorgops</i>	<i>Kobus ellipsiprymnus</i>
<i>Hippopotamus aithiopicus</i>	<i>Kobus</i> cf. <i>leche</i>
Giraffidae	<i>Menelika lyrocera</i>
<i>Sivatherium maurusium</i>	<i>Redunca</i> sp.
<i>Giraffa jumae</i>	<i>Gazella</i> sp.
<i>Giraffa gracilis</i>	<i>Antidorcas recki</i>
<i>Giraffa pygmaeus</i>	<i>Madoqua</i> sp.
Camelidae	<i>Tragelaphus nakuae</i>
<i>Camelus</i> sp.	<i>Tragelaphus strepsiceros</i>
Bovidae	<i>Pelorovis turkanensis</i>
<i>Megalotragus isaaci</i>	<i>Pelorovis oldowayensis</i>
<i>Megalotragus kattwinke</i>	<i>Pelorovis</i> sp.
<i>Parmularius eppi</i>	<i>Aepyceros</i> sp.
<i>Parmularius altidens</i>	

The Reduncini are well represented with four species of *Kobus* plus *Menelika lyrocera* and *Redunca*, while the tribe Antilopini has two genera present; *Gazella* and *Antidorcas*. *Madoqua* is the sole representative of the Neotragini tribe while two Tragelaphini species from the genus *Tragelaphus* also occur. The Bovini tribe has three species of the giant buffalo *Pelorovis* recorded from East Turkana.

The small mammal assemblage includes ten rodents including the desert jerboa *Jaculus orientalis*, a porcupine *Hystrix* and the cane rat *Thryonomys*. The remaining seven rodent taxa belong to the family Muridae: *Saccostomus*, *Tatera*, *Arvicanthis*, *Aethomys*, *Mastomys*, *Mus* and *Thallomys*. Two species of shrew from the genus *Crocidura* occur in the Koobi Fora deposits and there are also two bats, *Scotophilus* and *Nycteris*.

Table 8.3 Non-mammalian fauna from East Turkana (Feibel *et al.*, 1991)

REPTILIA	<i>Cleopatra ferruginea</i>
<i>Geochelone cf. brachygularis</i>	<i>Cleopatra</i> sp. B
<i>Trionyx triunguis</i>	<i>Melanoides tuberculata</i>
<i>Pelusios adansoni</i>	<i>Melanoides</i> sp. B
<i>Varanus</i> sp.	<i>Melanoides</i> sp. C
<i>Crocodylus cataphractus</i>	BIVALVIA
<i>Crocodylus iloidi</i>	<i>Pleiodon</i> sp. A
<i>Euthecodon brumpti</i>	<i>Caelatura</i> sp. B
OSTEICHTHYES	<i>Aspatharia arcuta</i>
<i>Syndontis</i> sp.	<i>Mutela nilotica</i>
<i>Lates</i> sp.	<i>Mutela</i> sp. B
<i>Gymnarchus niloticus</i>	<i>Corbicula consobrina</i>
<i>Labeo</i> sp.	<i>Eupera</i> sp. B
<i>Barbus</i> sp.	OSTRACODA
<i>Distichodus</i> sp.	<i>Cypris</i> sp.
<i>Hydrocynus</i> sp.	<i>Hemicypris</i> sp.
<i>Sindacharax</i> sp.	<i>Megalocypris durbani</i>
<i>Tetraodon</i> sp.	<i>Sclerocypris clavularis</i>
BRACHIOPTERYGII	<i>Sclerocypris jenkinae</i>
<i>Polypterus</i> sp.	<i>Sclerocypris</i> sp.
<i>Hyperopisus</i> sp.	<i>Plesiocypridopsis newtoni</i>
CHONDRICHTHYES	<i>Potamocypris worthingtoni</i>
<i>Dasyatis africana</i>	<i>Ilyocypris gibba</i>
GASTROPODA	<i>Darwinula stevensoni</i>
<i>Valvata</i> sp. A	<i>Cyprideis torosa</i>
<i>Bellamya unicolor</i>	<i>Gomphocythere angulata</i>
<i>Bellamya</i> sp. B	<i>Limnocythere africana</i>

The non-mammalian fauna of Koobi Fora includes reptiles, fish, gastropods, bivalves and crustaceans (Table 8.3). The reptiles include a tortoise *Geochelone* and two turtles, *Trionyx triunguis* and *Pelusios adansoni*. The monitor lizard *Varanus* also occurs and there are three Crocodylia; *Crocodylus cataphractus*, *Crocodylus iloidi* and *Euthecodon brumpti*.

Fish are relatively well represented and include the genera *Syndontis*, *Lates*, *Gymnarchus*, *Labeo*, *Barbus*, *Distichodus*, *Hydrocynus*, *Sindacharax*, *Tetraodon*, *Polypterus* and *Hyperopisus*. In addition there is a stingray *Dasyatis africana* that occurs in the Koobi Fora formations.

The Gastropoda include eight species from four genera; *Valvata*, *Bellamyia*, *Cleopatra* and *Melanoides*. The Bivalvia have seven species in six genera; *Pleiodon*, *Caelatura*, *Aspatharia*, *Mutela* (two species), *Corbicula* and *Eupera*.

There have also been thirteen species of Ostracoda identified from the East Turkana formations including the genera *Cypris*, *Hemicypris*, *Megalocypris*, *Sclerocypris* (three species), *Plesiocypridopsis*, *Potamocypris*, *Ilyocypris*, *Darwinula*, *Cyprideis*, *Gomphocythere* and *Limnocythere*.

8.4 Discussion

Perhaps not surprisingly, on account of the nature of the deposits, there are a high number of aquatic species within the Koobi Fora formations, particularly fish, shellfish and crustaceans. This is despite an initial lack of interest in this type of material from fossil collectors. For example, Harris noted that the “lower vertebrate material has received little attention to date and is certainly under-represented [...] no systematic attempt has yet been made to collect fish remains *per se* [...] a small number of avian postcranial elements have been collected but have not yet been studied” (1978: 51-52).

Of the mammalian fauna, there are indications that relatively open, possibly dry, grasslands existed locally. The camel, for example, is today able to exist in desert type conditions (Macdonald, 2001) and the jerboa is also well adapted to desert living (Kingdon, 1997). The large number of *Equus* species may also be an indicator of relatively dry grasslands while the Hippotragini species, particularly *Oryx*, would also seem to indicate relatively dry, open conditions (Macdonald, 2001).

The seven Alcelaphini species (eight if *Aepyceros* is included) are indicative of open grasslands, but according to Kingdon (1982), these tribes are unable to survive in truly arid habitats, being dependant to a greater or lesser degree on the presence of water or at least moist foods.

At least some of the species of primate present at Koobi Fora appear to have been terrestrial; the large bodied *Theropithecus oswaldi*, seemingly too heavy to spend significant amounts of time in the trees, may have been a waterside inhabitant (Martin, 1990). *Papio* could indicate

open grassland, but even savanna dwelling baboons today require trees for shelter and refuge from predators (if cliffs are not available). The *Colobus* species and *Cercopithecoides* are, on the other hand, probably indicative of well forested areas.

Giraffids are probably indicative of woodlands, while rhinoceroses, particularly the browsing from *Diceros bicornis* (Kingdon, 1997), elephants and, according to Bishop (1999), suids, might all be indicative of relatively closed habitats. The acacia rat *Thallomys* is also an indicator that at least acacia trees were present. Possible swampy conditions are indicated by the presence of the cane rat *Thryonomys*, which today lives in the long reeds surrounding African watercourses (Macdonald, 2001). At least some of the Reduncini species are also likely to be indicative of swampy lake margins (Estes, 1991), and it is possible that the giant buffalo *Pelorovis*, of which at least two species have been identified, was an inhabitant of swampy habitats since modern buffaloes prefer areas with water and cover (Kingdon, 1997). *Tragelaphus* are also indicative of well vegetated possibly swampy habitats (Estes, 1991).

Clearly the hippopotami are an indication that there was a large body of permanent water, while the fact that the two genera, *Hexaprotodon* and *Hippopotamus*, were both present could indicate that both closed and open habitats existed locally at the water's edge (Kingdon, 1997).

Of the non-mammalian fauna, the only possibly non-aquatic elements are the tortoise *Geochelone* and the monitor lizard *Varanus*, though monitors are often semi aquatic (Young, 1991). The variety of crocodiles, fish, fresh water gastropods, bivalves and ostracods points to a diverse aquatic community and an extensive and well established wet land environment.

Chapter 9

West Turkana

9.1 Introduction to site

Opposite the Koobi Fora formations on the western side of Lake Turkana are the Nachukui formations of West Turkana. These deposits are also of fluvial and lacustrine origin (Schwartz and Tattersall, 2003) and contain the hominid species *Homo ergaster* and

Paranthropus boisei. The Nattoo and Nariokotome members are examined here. These members are dated, based on potassium argon dating of associated tuffs, at between about 1.33 and 1.64 million years old (Schwartz and Tattersall, 2003).

9.2 Methods

The mammalian list was compiled using Turner *et al.* (1999), and the non-mammalian fauna was compiled using Feibel *et al.* (1991). Fauna associated with the fossil WT 15 000 (Walker, 1993) is also included. Although *Homo ergaster* and *Homo erectus* are both listed as present (see table 9.1), there is some controversy as to whether only one species is present and should be called either *Homo erectus* or *Homo ergaster*, or whether there are indeed more than one species present (Schwartz and Tattersall, 2003).

9.3 Results

Table 9.1 shows the mammalian and table 9.2 the non-mammalian fauna discovered at the West Turkana members of Nattoo and Nariokotome. As mentioned, although the list infers the presence of two species of *Homo*, *ergaster* and *erectus*, it is assumed that these probably represent the same species (Groves, personal communication). *Paranthropus boisei* is also present in these members. The only other primate is the large bodied, presumably terrestrial, gelada *Theropithecus oswaldi*.

Carnivores are represented by four species in four genera (Table 9.1). The elephant *Elephas recki* is present as are the extinct horse *Hipparion ethiopicum* and two species from the family Equidae. *Diceros bicornis* and an indeterminate rhinoceros genus are also listed as present. Six suid species occur in the Nattoo and Nariokotome members, two species in the genus *Kolpochoerus*, three species of *Metridiochoerus* and the bush pig *Potamochoerus porcus*. There are also four hippopotami, three in the genus *Hippopotamus* and *Hexaprotodon karumensis*. Two giraffids, *Sivatherium maurusium* and a species of *Giraffa* also occur.

Bovids are well represented in the Nattoo and Nariokotome members with 16 species in 11 genera. The tribe Alcelaphini has three genera represented; *Connochaetes*, *Damiliscus* and *Megalotragus*, while three species of *Kobus* are present along with *Menlika lyrocera*. Two

gazelles (Antilopini), three species of Tragelaphini, two buffaloes (Bovini), an impala (Aepycerotini) and an indeterminate species of the tribe Caprini also occur at West Turkana.

Table 9.1 Mammalian fauna from West Turkana (Turner *et al.*, 1999; Walker *et al.*, 1993)

Primates	<i>Potamochoerus porcus</i>
<i>Paranthropus boisei</i>	<i>Hexaprotodon karumensis</i>
<i>Homo erectus</i>	<i>Hippopotamus gorgops</i>
<i>Homo ergaster</i>	<i>Hippopotamus aithiopicus</i>
<i>Theropithecus oswaldi</i>	<i>Hippopotamus amphibius</i>
Carnivora	<i>Sivatherium maurusium</i>
<i>Felis caracal</i>	<i>Giraffa</i> sp.
<i>Crocuta crocuta</i>	<i>Connochaetes</i> sp.
<i>Canis mesomelas</i>	<i>Damiliscus</i> sp.
<i>Lycaon ?pictus</i>	<i>Megalotragus</i> sp.
Proboscidea	<i>Kobus kob</i>
<i>Elephas recki</i>	<i>Kobus ellipsipyymnus</i>
Perrisodactyla	<i>Kobus leche</i>
<i>Hipparion ethiopicum</i>	<i>Menlika lyrocera</i>
<i>Equus</i> sp.	<i>Gazella praethomsoni</i>
Equidae indet.	<i>Gazella</i> sp.
<i>Ceratotherium simum</i>	<i>Tragelaphus scriptus</i>
<i>Diceros bicornis</i>	<i>Tragelaphus strepsiceros</i>
Rhinocerotidae indet.	<i>Tragelaphini</i> sp.
Artiodactyla	<i>Syncerus</i> cf. <i>caffer</i>
<i>Kolpochoerus limnates</i>	<i>Pelorovis</i> sp.
<i>Kolpochoerus majus</i>	<i>Aepyceros melampus</i>
<i>Metridiochoerus compactus</i>	Caprini indet.
<i>Metridiochoerus hopwoodi</i>	Lagomorpha
<i>Metridiochoerus modestus</i>	<i>Lepus capensis</i>

No rodents or insectivores have been located within these formations and the Lagomorph *Lepus capensis* is the only small mammal.

Non-mammalian fauna includes mainly fish and crustaceans with a reptile *Varanus* and two fresh water sponges also present (Table 9.2).

There are eleven species of fish including eight species of Osteichthyes, two species of Brachiopterygii and a fresh water ray, *Dasyatis africana*. The crustaceans are mainly non-marine Ostracoda and include six genera.

Table 9.2 Non-mammalian fauna from West Turkana (Feibel *et al.*, 1991; Walker, 1993a)

REPTILIA	BRACHYOPTERYGII
<i>Varanus niloticus</i>	<i>Polypterus</i> sp.
<i>Trionyx</i> sp.	<i>Hyperopisus</i> sp.
Pelomedusidae spp.	GASTROPODA
OSTEICHTHYES	<i>Pila ovata</i>
<i>Syndontis</i> sp.	OSTRACODA
<i>Lates</i> sp.	<i>Hemicypris</i> sp.
<i>Gymnarchus niloticus</i>	<i>Sclerocypris clavularis</i>
<i>Labeo</i> sp.	<i>Ilyocypris gibba</i>
<i>Barbus</i> sp.	<i>Darwinula stevensoni</i>
<i>Distichodus</i> sp.	<i>Cyprideis torosa</i>
<i>Hydrocynus</i> sp.	<i>Limnocythere africana</i>
<i>Sindacharax</i> sp.	DEMOSPONGIAE
<i>Clarias</i> sp.	Spongillidae indet.
<i>Clarotes</i> sp.	Potamolepidae indet.
CHONDRICHTHYES	
<i>Dasyatis africana</i>	

9.4 Discussion

The small number of smaller mammals from West Turkana is interesting because fauna in the form of fish and crustaceans have been recovered, suggesting that preservation and collection biases may not be responsible. The non-mammalian fauna is dominated by aquatic elements. Ostracoda are small crustaceans that are almost entirely aquatic. The six genera associated with the Nattoo and Nariokotome members are generally fresh water types although *Cyprideis torosa* can tolerate brackish waters (Anderson, 1998).

There is a relatively diverse range of fish at West Turkana. The birchir *Polypterus* is a nocturnal predatory fish that inhabits the shores, banks and flood plains of lakes and rivers (Moyle and Cech 1982), while the eel *Gymnarchus niloticus* can tolerate turbid waters and is often associated with swamps (Le Danois, 1959). Catfish are also associated with swampy waters (Moyle and Cech, 1982). The Nile perch, carp and characins are all fresh water types found today in lakes and rivers across Africa (Moyle and Cech, 1982). The fresh water ray *Dasyatis africana* indicates that a large body of permanent water existed at the time of the deposits (Le Danois, 1959) and its presence encouraged Brown and Feibel (1991) to conclude that a fluvial connection with the Indian Ocean may have existed at various times within the lake's history, including specifically about 1.9 million years ago.

Fresh water sponges are a further indication that a large body of water may have existed at the time of deposition. The only possibly non-aquatic element within the non-mammalian fauna is the monitor lizard *Varanus*, though monitors are often semi-aquatic (Young, 1981).

Primates include the hominids *Homo ergaster* and *Paranthropus boisei*, as well as the gelada *Theropithecus oswaldi*, which may have been a waterside dweller (Martin, 1990). Extant geladas are grass feeders (Kingdon, 1997) therefore it seems possible that there may have been grasslands within the vicinity of West Turkana. The large size of *T. oswaldi* is a possible indicator that it didn't use trees. Geladas today rely on cliffs for shelter instead of trees, but the large size of *T. oswaldi* may have meant it could deter potential predators without requiring the refuge of trees or cliffs. This species shows a trend towards larger size and increased complexity and hypsodonty of the cheek teeth according to the fossil record (Harris, 1978) and the fact that it may have been a waterside dweller (Martin, 1990) suggests it could have eaten the grasses associated with the water's edge.

The carnivores include mainly medium sized predators; the lynx *Felis caracal*, African wild dog *Lycaon*, the black backed jackal *Canis mesomelas* and the spotted hyaena *Crocuta crocuta*. All these species are found today in relatively dry grass and woodlands (Kingdon, 1997) though the spotted hyaena is also known from forest edges (Macdonald, 2000). The equids are indicative of open grassland and the giraffes and the elephant might suggest relatively open woodland, though elephants could also indicate water and forests (Kingdon, 1997). Swampy conditions are indicated by the high number of rhinoceroses which readily enter swamps (Estes, 1991) and pigs, which generally prefer habitats which offer concealment and food, including marshes and swamps (Estes, 1991). The three *Hippopotamus* species are an indication of water and grasslands while *Hexaprotodon* might indicate well vegetated or forested swampy regions (Kingdon, 1997).

Of the bovid species, the gazelles are the most indicative of dry habitats (Macdonald, 2001). The tribe Alcelaphini, with three species, indicates grasslands that are not too dry and not too moist (Kingdon, 1982) and the *Tragelaphus* species indicate closed habitats, possibly close to water (Estes, 1991). The buffaloes could be indicative of swampy vegetation since buffaloes today often live in swamps (Estes, 1991). Certainly the fact that four species of the tribe

Reduncini, including four *Kobus* species, are present, indicates the presence of grass or scrub land close to water (Macdonald, 2001).

The overall picture, therefore, is of a large body of water, probably a lake, with swampy bush and scrubland close by, as well as woodlands and grasslands extending from the waters edge to more arid regions some distance away.

One possible explanation for the accumulated assemblages is that they were deposited in shallow waters some distance from the shoreline. This might explain the presence of fish and crustaceans as well as the large mammals which could have waded into the lake in search of food or for some other reason, to wallow, for example. Smaller mammals may be less common in the assemblage because, assuming they did reside locally, they may have generally stayed closer to the shoreline.

Chapter 10

Olduvai Gorge

10.1 Introduction

Olduvai Gorge is a 150 to 250 foot valley cutting through the Serengeti Plain of Tanzania, exposing sediments laid down during the Pleistocene, when a broad, shallow basin was in existence (Hay, 1971). The gorge is divided into a number of beds, the lowest of which, Bed 1, is estimated to be between about 1.9 and 1.75 years old (Schwartz and Tattersall, 2003). It contains two species of hominid, *Paranthropus boisei* and *Homo habilis* (Turner *et al.*, 1999). Bed II, dated to between about 1.75 and 1.4 million years old (Schwartz and Tattersall, 2003), contains *P. boisei*, *H. habilis* and a species referred to as *H. erectus*, but which might belong to an altogether different species (Groves, personal communication). Bed II is examined here.

10.2 Methods

The Mammalian fauna was compiled using Turner *et al.*, (1999) and the non-mammalian fauna was compiled using the data compiled by Leakey (1971).

10.3 Results

A rich mammalian fauna has been recorded from the Bed II deposits of Olduvai Gorge (Tables 10.1 and 10.2). Apart from the three hominids, *H. erectus*, *H. habilis* and *P. boisei*, there are three other primates: *Parapapio*, *Cercopithecoides* and *Colobus*.

The carnivorous fauna is relatively modern with the spotted and striped hyaena, leopard, lion and cheetah all present. There is also an otter *Lutra maculicollis*, a civet *Pseudocivetta ingens* and a marsh mongoose *Atilax*. There is an elephant *Elephas recki*, the black and white rhinoceroses, *Hippopotamus gorgops* and six pigs belonging to the genera *Kolpochoerus* (two species) and *Metridiochoerus* (four species).

There is a camel *Camelus*, two giraffes *Giraffa*, the zebra *Equus burchelli* and the 'primitive' horse *Hipparion lybicum*. A relatively high proportion of the fauna are bovids. These include species in seven tribes. The largest tribe, with eleven species, is the Alcelaphini, with the genera *Connochaetes* (four species), *Damiliscus* (two), *Megalotragus* and *Parmularius* (two) all present. The Antilopini (*Gazella* and *Antidorcas*) and the Reduncini (*Kobus* and *Redunca*) have four species each. Two buffaloes, *Syncerus* and *Pelorovis*, two Tragelaphini, *Tragelaphus* and *Taurotragus*, as well as *Hippotragus gigas* and the impala *Aepyceros melampus* are present at Olduvai Gorge.

Table 10.1 Mammalian fauna (excluding Artiodactyla) from Olduvai Gorge (Turner *et al.*, 1999)

PRIMATES	PROBOSCIDEA
<i>Paranthropus boisei</i>	<i>Elephas recki</i>
<i>Homo habilis</i>	RODENTIA
<i>Homo erectus</i>	<i>Dendromys</i> sp. 2
<i>Parapapio</i> sp.	<i>Tatera gentryi</i>
<i>Cercopithecoides kimeui</i>	<i>Arvicanthis primaevus</i>
<i>Colobus</i> sp.	<i>Arvicanthis</i> cf. <i>niloticus</i>
CARNIVORA	<i>Mastomys minor</i>
<i>Atilax</i> sp.	<i>Mus petteri</i>
<i>Pseudocivetta ingens</i>	<i>Oenomys olduvaiensis</i>
<i>Lutra maculicollis</i>	<i>Thallomys quadrilobatus</i>
<i>Panthera leo</i>	<i>Zelotomys leakeyi</i>
<i>Panthera pardus</i>	<i>Otomys petteri</i>
<i>Acinonyx jubatus</i>	<i>Pedetes</i> sp.
<i>Crocuta crocuta</i>	<i>Thryonomys</i> sp.

<i>Hyaena hyaena</i>	INSECTIVORA
PERRISODACTYLA	<i>Rhynchocyon pliocaenicus</i>
<i>Hipparion lybicum</i>	? <i>Crocidura</i> sp.
<i>Equus burchelli</i>	LAGOMORPHA
<i>Ceratotherium simum</i>	<i>Serengetilagus praecapensis</i>
<i>Diceros bicornis</i>	

Ten of the twelve rodent species at Olduvai Gorge belong to the family Muridae, the exception being the cane rat *Thryonomys* and the spring hare *Pedetes*. Of the murid rodents the sub family Murinae is the best represented with seven species in six genera (see Table 10.1). Other non-Murinae species within the Muridae family include the tree mouse *Dendromus*, the gerbil *Tatera gentryi* and the grooved tooth rat *Otomys petteri*.

Other mammals present at Olduvai Gorge during Bed II times include the lagomorph *Serengetilagus*, the elephant shrew *Rhynchocyon* and a shrew with *Crocidura* affinities.

Table 10.2 Artiodactyla from Olduvai Gorge (Turner *et al.*, 1999)

Suidae	<i>Connochaetes</i> sp.
<i>Kolpochoerus limnetes</i>	<i>Damiliscus niro</i>
<i>Kolpochoerus majus</i>	<i>Damiliscus agelaius</i>
<i>Metridiochoerus andrewsi</i>	<i>Megalotragus kattwinke</i>
<i>Metridiochoerus compactus</i>	<i>Parmularius angusticorn</i>
<i>Metridiochoerus hopwoodi</i>	<i>Parmularius rugosus</i>
<i>Metridiochoerus modestus</i>	<i>Hippotragus gigas</i>
Hippopotamidae	<i>Kobus sigmoidalis</i>
<i>Hippopotamus gorgops</i>	<i>Kobus kob</i>
Giraffidae	<i>Kobus ellipsiprymnus</i>
<i>Giraffa jumae</i>	<i>Redunca</i> sp.
<i>Giraffa gracilis</i>	<i>Gazella</i> sp.
Camelidae	<i>Antidorcas recki</i>
<i>Camelus</i> sp.	<i>Antidorcas</i> sp.
Bovidae	Antilopini indet.
<i>Beatragus antiquus</i>	<i>Tragelaphus</i> cf. <i>scriptus</i>
<i>Sigmoceros</i> sp.	<i>Taurotragus arkelli</i>
<i>Connochaetes taurinus</i>	<i>Syncerus acoelotus</i>
<i>Connochaetes africanus</i>	<i>Pelorovis oldowayensis</i>
<i>Connochaetes gentryi</i>	<i>Aepyceros melampus</i>

The non-mammalian fauna of Olduvai Gorge includes a bird, reptiles, fish, a bivalve, gastropods and an amphibian (Table 10.3). The bird is an ostrich *Struthio*, the amphibian is unclassified and the bivalve is a fresh water clam *Corbicula africana*.

Reptiles are relatively well represented and include a turtle *Chelonia*, a python, a colubrid snake, a puff adder *Bitis* and two crocodiles including the Nile crocodile *Crocodylus niloticus*.

Table 10.3 Non-mammalian fauna from Olduvai Gorge (Leakey, 1971)

AVES	OSTEICHTHYES
<i>Struthio</i> sp.	<i>Clarias</i> sp.
REPTILIA	<i>Tilapia</i> sp.
<i>Chelonia</i> indet.	GASTROPODA
<i>Python</i> sp.	Gastropoda indet.
Colubridae indet.	<i>Lymnea natalensis</i>
<i>Bitis</i> sp.	<i>Bulinus tropicus</i>
<i>Crocodylus niloticus</i>	<i>Anisus natalensis</i>
<i>Crocodylus</i> sp.	BIVALVIA
AMPHIBIA	<i>Corbicula africana</i>
Anura indet.	

There are two genera of fish present during Olduvai Gorge Bed II times; the catfish *Clarias* and the cichlid *Tilapia*. Four Gastropods were also present including the fresh water snails *Lymnea*, *Bulinus* and *Anisus* (Brown, 1980).

10.4 Discussion

There was sufficient available water at Olduvai Gorge during Bed II times for species of otter, hippopotamus, crocodile, fish and shellfish to survive. There is also some indication that more open, arid country may have existed in the vicinity, since camels are well adapted to arid conditions (Macdonald, 2001). Gazelles are well adapted to exploit arid zone regions (Kingdon, 1997), while the gerbil *Tatera* and the springhare *Pedetes* prefer sandy grassy plains (Kingdon, 1997).

Grasslands are suggested by the large number of bovids, specifically the eleven species of the tribe Alcelaphini. All species of this tribe are dependant to a greater or lesser degree on water or at least moist foods (Kingdon, 1982), and need to drink daily (Estes, 1991). They are unable to colonize truly arid land (Kingdon, 1997), instead preferring to graze in open woodlands, moist grasslands and the zone in between (Macdonald, 2001).

Antidorcas recki, often inferred to be a plains dweller due to its resemblance to the modern species *A. marsuplias*, might have preferred a bush or swamp habitat according to “ecomorphic analysis” of its “metapodial functional anatomy”, according to Bishop (1999: 221).

The cheetah and the lion, as well as the hyaenids, are all indicative of relatively open arid regions (Macdonald, 2001).

Four species of Reduncini confirm the presence of nearby water and indicate that nearby grasslands and cover in the form of scrub or woodland may also have existed (Este, 1991). The presence of *Tragelaphus* and *Taurotragus* is also indicative of dense cover, while the buffaloes, including the giant buffalo *Pelorovis*, may have preferred swampy regions as their modern equivalents do (Estes, 1991).

Trees are indicated by the presence of three non-hominid primate species, at least two of which, *Cercopithecoides* and *Colobus*, were likely at least to have been partly arboreal if their living relatives are a guide (Macdonald, 2001). The leopard, *Panthera pardus*, lives in a wide range of habitats today but usually prefers areas with some amount of cover (Estes, 1991). Giraffes are an indication that woodland existed and elephants perhaps indicate forest, while six pig species are indicative of closed habitats (Bishop, 1999). *Oenomys*, a climber, suggests trees or at least thick vegetation were present (Kingdon, 1997).

Papyrus swamps and possibly dense reed thickets are suggested by the presence of the marsh mongoose *Atilax*, which makes use of these habitats (Kingdon, 1997), while the cane rat *Thryonomys* and the grooved tooth rat *Otomys* are known to inhabit marshy grasslands (Kingdon, 1997).

The ostrich prefers arid regions while crocodiles suggest water, as do fish, with catfish able to tolerate poorly oxygenated waters (Moyle and Cech, 1982) and cichlids often found in lakes (Moyle and Cech, 1982). Of the fresh water snails, one, *Lymnea natalensis*, needs permanent water to survive while another, *Bulinus tropicus*, is found in small water bodies (Brown, 1980). The amphibian and bivalve both suggest the presence of water.

The overall picture, therefore, is of a body of water supporting various types of vegetation, including possibly forest, scrubby bush land and swampy grasses. Areas of open grassland are likely to have occurred within the vicinity, with probably moist grassland closer to the waters edge and more arid grasslands further away. Woodlands also appear to be present.

Chapter 11

Humpata, Southern Angola

11.1 Introduction to site

The Humpata plateau, on average 1750 meters above sea level, is relatively flat except for where streams have cut into the dolomite and underlying sandstones. Two valleys in the plateau, the Cangalongue and Cudeje, have caves and fissures along their margins which contain fossil faunal assemblages estimated to be of Plio-Pleistocene age (Pickford *et al.*, 1992). No hominid remains have so far been located from any sites within the Humpata region.

11.2 Methods

Faunal lists were compiled based on the lists provided in the paper by Pickford *et al.* (1992). The classification of taxa has been to the genus level only, and in some cases only the class is indicated. Specimens identified to the genus level, for example *Tatera*, have been recorded on the data set as *Tatera* sp., whereas those identified to the family level have been recorded under the family name only, for example Mustelidae.

11.3 Results

A fauna consisting mainly of mammals has been identified at Humpata, though a few reptiles, a bird, an amphibian and a number of gastropods have also been discovered (Table 11.1). The mammals include three monkeys from three genera; *Cercopithecoides*, *Parapapio* and *Dinopithecus*. The carnivores have been identified to the family level and include the Mustelidae, Vivveridae, Canidae and Hyaenidae.

Large mammals are present in the form of the families Rhinocerotidae and Equidae, while the Suidae are represented by the genus *Metridiochoerus*. There are two bovids present, the genus *Connochaetes* and the tribe Hippotragini.

Rodents are particularly well represented in the Humpata deposits with nineteen different taxa in seven families. The families include the Dendromuridae (three genera), Gerbillidae (*Tatera*), Bathyergidae (*Cryptomys*), Gliridae (*Graphiurus*), Otomyinae (*Otomys*) and Hystricidae (*Hystrix*). The family Muridae has the most genera represented with eleven (see table 11.1).

Three genera of bat have been discovered at Humpata; *Rhinolophos*, *Miniopterus* and *Nycteris*. The lagomorph *Serengetilagus* has also been recorded. Shrews have been identified to the genus level, *Crocidura*, and the family Macroscelidae is also present. Two genera of hyrax have also been identified from Humpata; *Procavia* and *Gigantohyrax*.

Table 11.1 Fauna from Humpata, Southern Angola Plio-Pleistocene in age (Pickford *et al.*, 1992).

MAMMALIA	<i>Petromyscus</i>
Primates	<i>Tatera</i>
<i>Cercopithecoides</i>	<i>Otomys</i>
<i>Parapapio</i>	<i>Cryptomys</i>
<i>Dinopithecus</i>	<i>Graphiurus</i>
Carnivora	<i>Hystrix</i>
Mustelidae	Macroscelidea
Vivveridae	Macroscelidae
Canidae	Insectivora
Hyaenidae	<i>Crocidura</i>
Perrisodactyla	Hyracoidea
Rhinocerotidae	<i>Procavia</i>
Equidae	<i>Gigantohyrax</i>
Artiodactyla	Lagamorpha
<i>Metridiochoerus</i>	<i>Serengetilagus</i>
Bovidae	Chiroptera
Hippotragini	<i>Rhinolophos</i>
<i>Connachaetes</i>	<i>Miniopterus</i>
Rodentia	<i>Nycteris</i>
<i>Uranomys</i>	AMPHIBIA
<i>Acomys</i>	Amphibia
<i>Dasmys</i>	REPTILIA
<i>Aethomys</i>	Chelonia

<i>Thallomys</i>	Lacertidae
<i>Zelotomys</i>	Ophidea
<i>Mus</i>	AVES
<i>Pelomys</i>	Aves
<i>Malacomys</i>	MOLLUSCA
<i>Praomys</i>	<i>Achatina</i>
<i>Grammomys</i>	<i>Edouardia</i>
<i>Dendromus</i>	<i>Thapsia</i>
<i>Steatomys</i>	Subulinidae

There have been bird fossils found at Humpata but no determination lower than the class level has been made. Similarly, there have been amphibian remains discovered but no lower classification. The Reptilia have been identified to the order level (Chelonia), as well as to the sub order level, Lacertidia and Ophidia.

Four mollusks have also been discovered, one identified as belonging to the family Subulinidae, and three identified to the genera level; *Achatina*, *Edouardia* and *Thapsia*.

11.4 Discussion

Unfortunately, not many inferences can be made with some of the taxa because of the lack of specific classification. Generalising about the habitat of a particular sub-order of reptiles, such as snakes, for example, is extremely difficult since snakes inhabit a variety of habitats. The same applies for the Aves class. Though not specifically classified, the Amphibia are an indication that at least some water was present nearby. The mollusks are not dissimilar to those found at Laetoli, and these were said to be indicative of fairly well wooded to forested habitats (Verdcourt, 1987).

The primates are all cercopithecids and include the baboon *Parapapio*, *Cercopithecoides* and *Dinopithecus*. Baboons are able to inhabit open habitats but need either cliffs or trees for shelter. The carnivores, identified to the family level, include a hyaenid, a canid, a mustelid and a viverrid. Hyaenas and dogs tend to prefer more open habitats, though some hyaenas inhabit forest edges (Macdonald, 2001). Mustelids include genera that are semi-arboreal (martens), semi aquatic (otters), burrowing (badgers), and savanna adapted (zorilla), therefore it is probably not wise to try to infer anything from their presence at Humpata.

Similarly, the viverrid (civets, genets and mongooses) have species that live in the savanna (meerkats), are arboreal (linsang), semi-aquatic (otter civet) and are burrowers (mongooses).

The rock hyraxes suggest rocky outcrops, and the hare *Serengetilagas* may indicate open grassland (Kingdon, 1997). Compared to other sites there are relatively few bovids; a member of the tribe Hippotragini, an unspecified member of the family Bovidae and the wildebeest *Connachaetes*, which inhabits grasslands and open woodlands that are neither too moist nor too dry, with access to water and short herbs (Kingdon, 1997). There is a rhinoceros, an equid, and the suid *Metridiochoerus*. This could mean any of a range of habitats with the equid possibly indicating open grass or woodlands (Estes, 1991), the rhinoceros indicating woodlands, grasslands or possibly wetlands (Estes, 1991), and the suid *Metridiochoerus* perhaps indicating possible closed habitats (Bishop, 1999). The shrew *Crocidura* survives in a range of habitats (Kingdon, 1997), while elephant shrews are often found in more arid conditions but still require thick undergrowth (Kingdon, 1997).

There are three bat species present, and since the assemblages are from cave deposits it is possible that the bats inhabited these caves (Macdonald, 2001). The overwhelming majority of species are Rodentia. The Rodentia include indicators of dry habitats, such as the gerbil *Tatera*, and possibly swampy conditions *Dasmys* and *Otomys* (Kingdon, 1997).

Possibly the area included a river or stream, fringed in some places by rocky valley walls that included caves and possibly by gallery forest and reeds, with grasslands and woodlands in the vicinity.

Part 3

Chapter 12

Comparison of sites

12.1 Introduction

The aim of this study is to make ecological inferences from faunal associations. In the previous section the associated fauna from each site was listed and possible ecological factors discussed. In this section the sites are compared and discussed within an ecological framework. A discussion examining three models of hominid evolution will then be conducted in light of these comparisons. Finally, in consideration of the discussion and other available data, a possible evolutionary scenario, drawing on various elements of the models discussed, will be proposed.

12.2 Methods

Graphs and tables have been constructed in an attempt to compare the fauna found at different sites. As not all taxa have been classified to the species or genus level, and in some cases not below the class level, there is necessarily some inconsistency with the classification of certain taxa for some of the tables. Scientific names have been used wherever possible, except where it is felt that more general common names may be clearer and easier to make sense of.

No non-mammalian faunal list for Langebaanweg was included in this survey due to unavailability, and therefore Langebaanweg is not included in any of the graphs or tables showing non-mammalian fauna. Sterkfontein has no non-mammalian fauna, but unlike Langebaanweg, this is because no non-mammalian fauna has been recovered from the site. Nevertheless, Sterkfontein is excluded from the graphs and tables showing non-mammalian fauna.

12.3 Results

The data show a number of patterns, though the significance of these is difficult to ascertain given the lack of control for many of the methods, e.g., collecting, classifying and inferring behaviour. Nevertheless, there is a clear indication as to the types of animals, mammals in particular, that were present in Africa during the period from the late Miocene to the early Pleistocene.

12.3.1 Mammalian taxa

Carnivores, primates, pigs, horses and bovids occur at every site. Elephants occur at all but one site, Humpata (Angola), while rhinoceroses occur at all but two sites, Toros-Menalla (Chad) and Humpata. Giraffes occur at all sites except Sterkfontein and Humpata. Hippopotami occur at all sites except Laetoli, Sterkfontein and Humpata. Of the smaller mammals, rodents are the most numerous occurring at all sites except West Turkana.

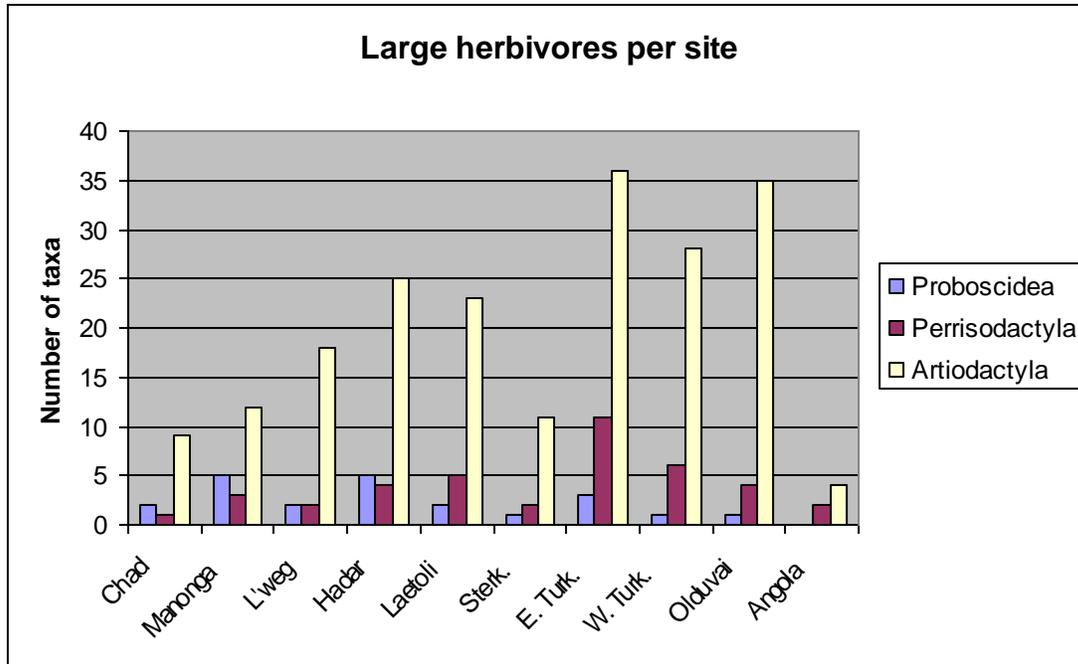
Table 12.1 Number of mammalian taxa per site

Taxa	T-M	MV	L'weg	Had	Laet	Ster.	ET	WT	OG	Ang
Carnivora	5	1	18	8	20	10	9	4	8	4
Primates	2	1	1	6	6	8	13	4	6	3
Proboscidea	2	5	2	5	2	1	3	1	1	
Rhinocerotidae		1	1	3	2		2	3	2	1
Equidae	1	2	1	1	1	2	9	3	2	1
Chalicotheridae					1					
Bovidae	5	7	11	17	15	10	24	16	25	3
Giraffidae	1	2	3	4	4		4	2	2	
Camelidae					1		1		1	
Hippopotamidae	1	2	1	1			3	4	1	
Suidae	1	1	3	3	3	1	4	6	6	1
Anthracotheriidae	1									
Lagomorpha			1		1			1	1	1
Insectivora			6		5	5	2		2	2
Rodentia	3	1	15	12	16	12	10		12	19
Chiroptera					2		2			3
Hyracoidea			1		1	2				2
Tubulidentata	1									

Rare mammalian fauna include the chalicotheriid *Ancylotherium*, which occurs only at Laetoli, and the anthracotheriid *Libycosaurus*, which occurs only at Chad (Toros-Menalla). Aardvarks are also found only at Chad. Camels are found only at three sites, Laetoli, East

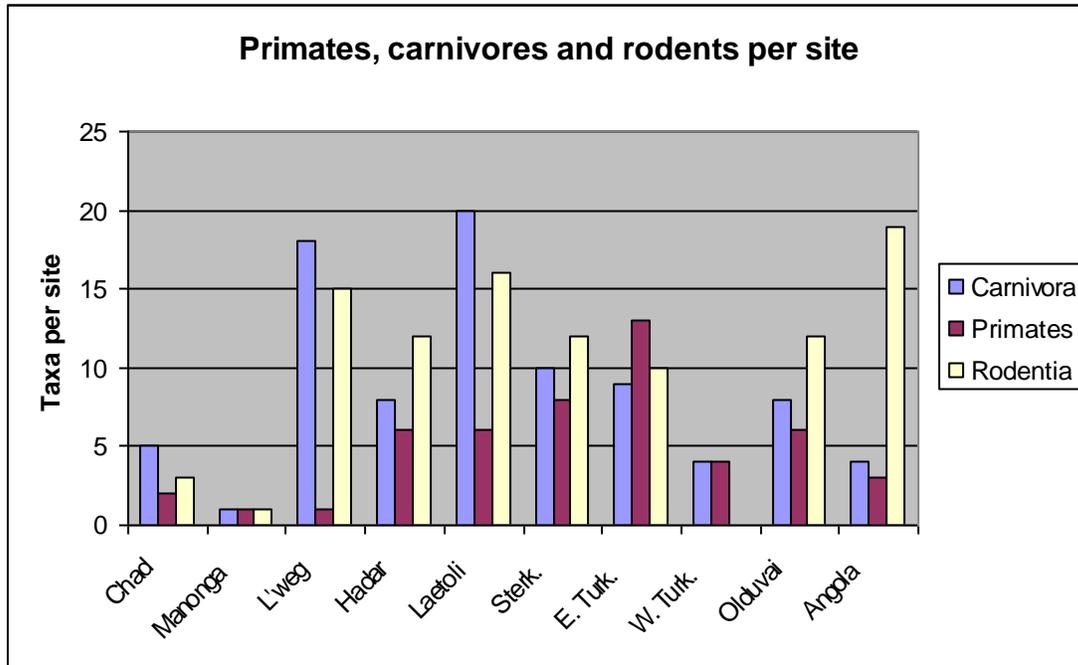
Turkana and Olduvai Gorge, while bats are found only at Laetoli, East Turkana and Angola (Humpata).

Figure 12.1



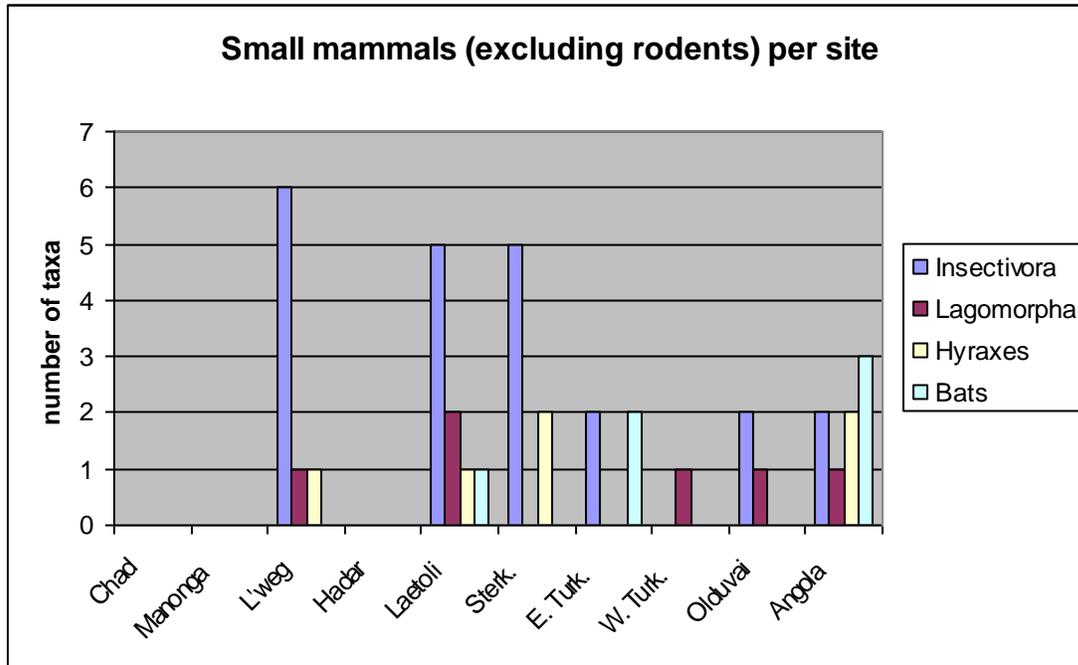
The order Artiodactyla is the most abundant herbivorous mammal group at every site, with a general trend of increasing numbers through time with the notable exception of Sterkfontein and Angola. The order Perrisodactyla is most diverse at East and West Turkana, while the Proboscidea are represented at all sites except Angola, with their highest numbers at Manonga Valley and Hadar.

Figure 12.2



Carnivores dominate the assemblages of Langebaanweg and Laetoli, and are well represented at Hadar, Sterkfontein, East Turkana and Olduvai Gorge, while relatively poorly represented at Manonga Valley. Rodents are particularly well represented at Angola, Langebaanweg, Laetoli, Hadar, Sterkfontein and Olduvai Gorge, while they are relatively poorly represented at Toros-Menalla and Manonga Valley, and are absent from West Turkana. Primates are well represented at East Turkana and Sterkfontein, while at Hadar, Laetoli and Olduvai Gorge there are also relatively high primate numbers. Langebaanweg and Manonga Valley have relatively low primate numbers.

Figure 12.3



The most common small mammals, apart from rodents, are the Insectivora, occurring at six sites including Langebaanweg, Laetoli and Sterkfontein where they are relatively well represented. Bats, which require sheltered roosting places, are found at Laetoli, East Turkana and Angola. Lagomorpha are found at Langebaanweg, Laetoli, West Turkana, Olduvai Gorge and Angola. Hyraxes, good indicators of rocky terrain, are found at Langebaanweg, Laetoli, Sterkfontein and Angola.

12.3.2 Non-mammalian fauna

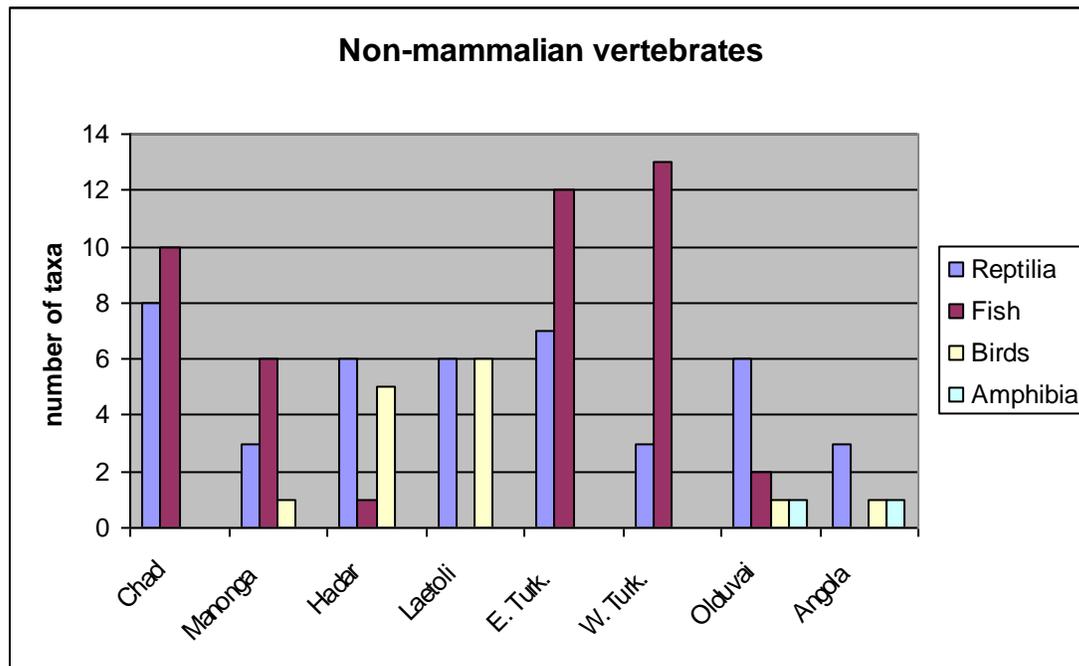
Non-mammalian faunal comparisons are complicated by the fact that Langebaanweg, where it is known non-mammalian fauna have been discovered, has no listing, and therefore is not considered within this discussion. Sterkfontein has no recorded non-mammalian fauna, though this is not due to a lack of data, rather because no non-mammalian faunal remains have been discovered. Neither Sterkfontein nor Langebaanweg are included in tables, graphs or discussion of non-mammalian fauna.

Table 12.2 Non-mammalian fauna per site

Taxa	Chad	M.V.	Hadar	Laet.	E.T.	W.T.	O.G.	Angola
Reptilia	8	3	6	6	7	3	6	3
Fish	10	6	1		12	13	2	
Aves		1	5	6			1	1
Amphibia							1	1
Crustacea			2		13	6		
Bivalves		1	1		7		1	
Gastropods		6	1	11	8	1	4	4
Sponges						2		
Insects	2	1		2				

Reptiles, gastropods and fish are the best represented non-mammalian faunal groups, occurring everywhere (not including Sterkfontein and Langebaanweg) except Chad (no gastropods) and Laetoli and Angola (no fish). Sponges are rare, occurring only at West Turkana, and amphibians occur only at Olduvai Gorge and Angola.

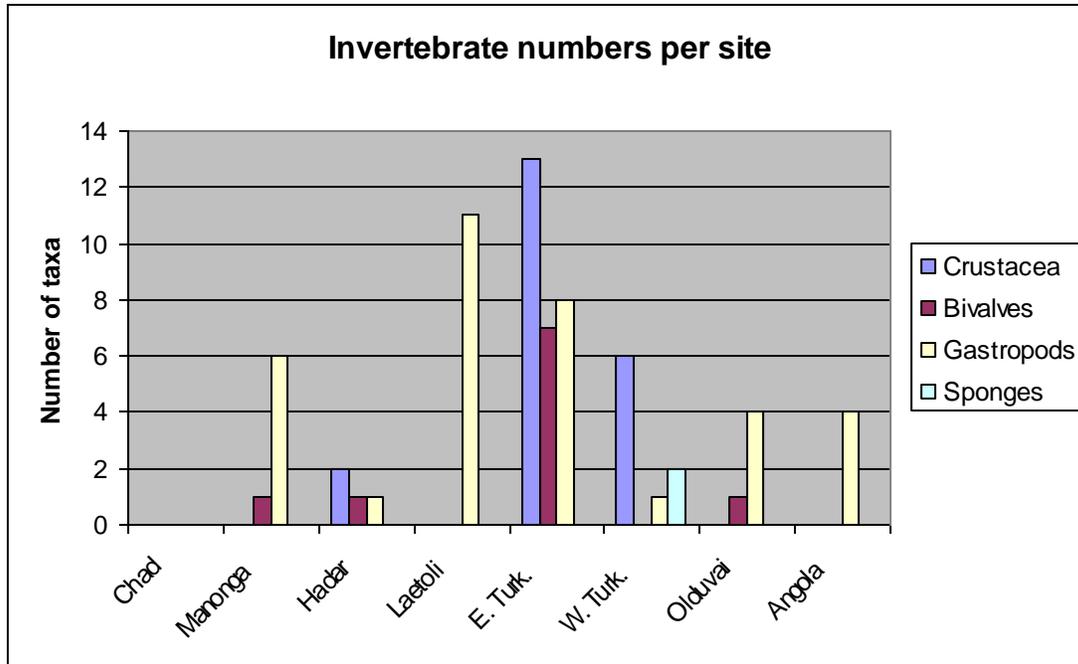
Figure 12.4



Reptiles occur at all sites, with six or more taxa present at five sites, including eight different taxa at Chad. Fish are present everywhere except Laetoli and Angola, occurring at high levels at East Turkana, West Turkana and Chad (Figure 12.4). Birds are relatively well represented

at Hadar and Laetoli, but poorly represented everywhere else, while amphibians are rare, occurring only at Olduvai Gorge and Angola.

Figure 12.5



Crustaceans are found at three sites; Hadar, West Turkana and East Turkana, and are particularly well represented at East Turkana. Bivalves are found at Manonga Valley, Hadar and East Turkana, where again they are well represented. Gastropods are well represented at Manonga Valley, Laetoli, East Turkana, Olduvai Gorge and Angola. Note that the gastropods from Laetoli and Angola are non-aquatic forms, while the Manonga Valley, Hadar, East Turkana, West Turkana and Olduvai Gorge forms are all either aquatic or semi-aquatic (Brown, 1980; Verdcourt, 1987) Sponges are found only at West Turkana.

12.3.3 Bovids

Bovids are the most highly represented group in terms of the number of taxa. There are 13 tribes of bovid present at the various sites (Table 12.2).

The most common tribe, occurring at all sites except Chad, is the tribe Alcelaphini, which makes up the majority of the bovids at Manonga Valley, is present at Angola, and makes up almost half of the bovid assemblage at Olduvai Gorge, which has 25 bovid taxa present. The

tribe Reduncini occurs at all sites except Laetoli and Angola, with the highest occurrences at Hadar, East Turkana and West Turkana. Antilopini occur at all sites except Manonga Valley and Angola. Olduvai Gorge has the highest number of Antilopini taxa present.

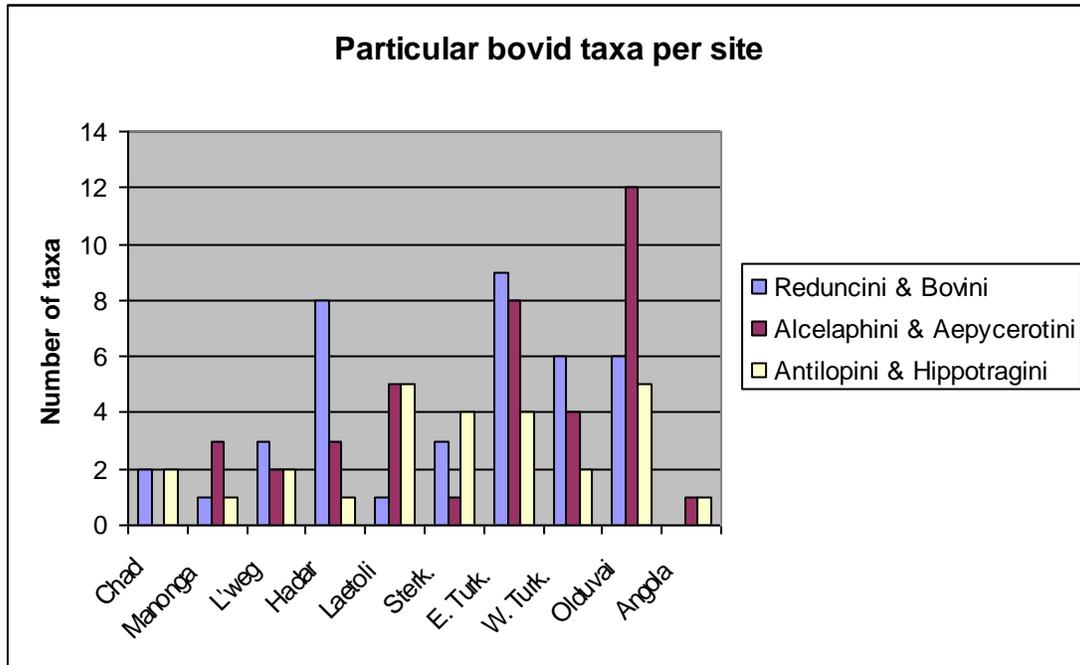
Table 12.3 Total number of bovid taxa at each site

Tribe	Chad	M.V.	L'weg	Had.	Laet.	Ster.	E.T.	W.T.	O.G.	Ang.
Alcelaphini		3	2	2	4	1	7	3	11	1
Hippotragini	1	1			3	2	2		1	1
Reduncini	1	1	2	5		2	6	4	4	
Peleini					1					
Antilopini	1		2	1	2	2	2	2	4	
Neotragini			1	2	2		1			
Boselaphini			1							
Tragelaphini			1	2	1	1	2	3	2	
Bovini	1		1	3	1	1	3	2	2	
Cephalophini					1					
Aepycerotini				1	1		1	1	1	
Ovibovini	1		1	1		1				
Caprini								1		
N = Bovids per site	5	5	11	17	16	10	24	16	25	2

Rarely occurring tribes include the Peleini, which occurs only at Laetoli; Boselaphini, which occurs only at Langebaanweg; Cephalophini, occurring only at Laetoli; and Caprini, occurring only at West Turkana. The tribe Ovibovini is found at four sites; Chad, Langebaanweg, Hadar and Sterkfontein. Laetoli is the only site with two tribes (Cephalophini and Peleini) that do not occur at any other sites.

Bovids are often grazers and therefore can be good indicators of open grasslands. Some tribes are better adapted to arid condition than others (Kingdon, 1997). Figure 12.6 shows combined totals of two tribes considered to be well adapted to arid conditions (Antilopini and Hippotragini), two tribes that prefer habitats that are neither too dry nor too moist (Alcelaphini and Aepycerotini), and two tribes that are dependant to a greater or lesser degree on permanent water (Reduncini and Bovini) (Kingdon, 1997; Macdonald, 2001).

Figure 12.6



The results show that the Alcelaphini and Aepycerotini tribes (preferring grasslands that are neither too dry nor too wet), are numerous at Laetoli, East Turkana, West Turkana and especially at Olduvai Gorge. Water dependant tribes (Reduncini and Bovini) are well represented at Hadar, East Turkana, West Turkana and Olduvai Gorge. Arid adapted taxa (Antilopini and Hippotragini) are prominent at Laetoli, Sterkfontein, East Turkana and Olduvai Gorge. Only at Sterkfontein do the dry adapted species have the highest combined total. At Laetoli the dry adapted species have the same number as the ‘not too dry not too wet’ taxa. The water dependant taxa have the highest numbers at Langebaanweg, East Turkana, West Turkana and especially at Hadar. The Alcelaphini and Aepycerotini have the highest numbers in Manonga Valley and Olduvai Gorge.

12.3.4 Carnivores

Hyaenids are the most common carnivore; occurring at all sites except Manonga Valley (Table 12.4). Felids are the next most common, occurring at all sites except Angola and Manonga Valley. Canids occur at all sites except Chad, Olduvai Gorge and Manonga Valley.

Table 12.4 Total number of carnivores per site

Family	Chad	MV	Lang	Had	Laet	Ster	ET	WT	OG	Ang
Herpestidae			1		4				1	
Viverridae		1	2		1				1	1
Mustelidae	1		3	1	2				1	1
Felidae	1		6	4	6	5	5	1	3	
Hyaenidae	3		4	2	2	4	2	1	2	1
Canidae			1	1	5	1	2	2		1
Ursidae			1							
Total	5	1	18	8	20	10	9	4	8	3

Herpestidae (mongooses) are relatively rare within the site assemblages, occurring at Langebaanweg, Olduvai Gorge and Laetoli, though there are four species present at Laetoli. The Viverridae (genets and civets) occur at Langebaanweg, Laetoli, Olduvai Gorge, Angola and Manonga Valley, while the Mustelidae (weasels and otters) occur at Chad, Langebaanweg, Laetoli, Olduvai Gorge and Angola.

The rarest carnivore family is the Ursidae (bear), found only at Langebaanweg.

12.3.5 Felids

There is a trend amongst the felids of a general reduction over time of the number of sabre-toothed varieties, of which five different genera occur in this study. Except for Manonga Valley, which has no felids present within its assemblage, all pre-Pleistocene sites contain at least one sabre-toothed cat. Chad has one genus *Machairodus*, Hadar and Laetoli have two genera, Sterkfontein has three and Langebaanweg four. Of the Pleistocene sites, only East Turkana records saber toothed cats, though this site has three genera (*Homotherium*, *Dinofelis* and *Megantereon*).

The genus *Panthera* is the most common felid, occurring at half the sites; Hadar, Laetoli (three species), Sterkfontein (two species), East Turkana and Olduvai Gorge (two species). It does not occur at the oldest sites of Chad, Manonga Valley and Langebaanweg.

The rarest Felid genus is the sabre-toothed *Adelphailurus*, which occurs only at Langebaanweg. *Machairodus* occurs only at Chad and Langebaanweg, and the cheetah *Acinonyx* occurs only at Laetoli and Olduvai Gorge.

Table 12.5 Number of felid taxa per site

Genus	Chad	M.V	Lang	Had	Laet	Ster	ET	WT	OG	Ang
<i>Adelphailurus</i>			1							
<i>Machairodus</i>	1		1							
<i>Homotherium</i>			1		1	1	1			
<i>Dinofelis</i>			1	1		1	2			
<i>Megantereon</i>				1	1	1	1			
<i>Panthera</i>				1	3	2	1		2	
<i>Acinonyx</i>					1				1	
<i>Felis</i>			2	1				1		
Total	1	0	6	4	6	5	5	1	3	0

12.3.6 Primates

Primates occur at every site and there are sixteen genera plus a family and a sub-family recorded (Table 12.5). Four hominid genera are present. The genera *Homo* and *Paranthropus* are found at the same sites; East and West Turkana and Olduvai Gorge; and at these sites no other hominid genera occur. No hominids are recorded from Manonga Valley, Langebaanweg or Angola.

Table 12.6 Total number of primate taxa per site (*plus the sub-family Colobinae and the family Cercopithecidae)

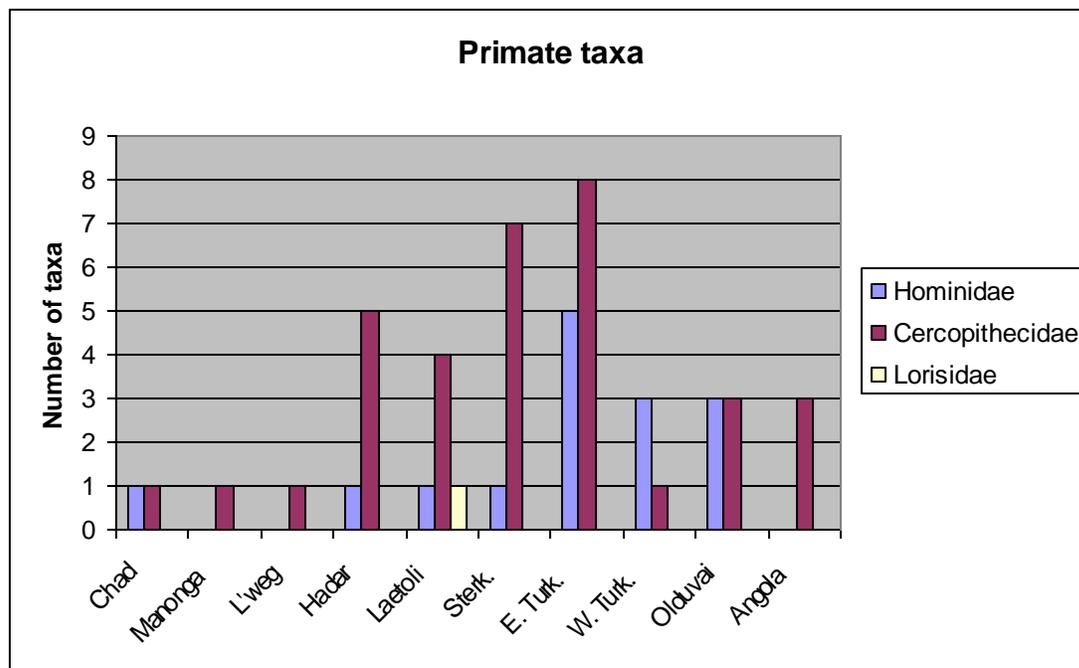
Genus*	Chad	MV	Lang	Had	Laet	Ster	ET	WT	OG	Ang
<i>Sahelanthropus</i>	1									
<i>Australopithecus</i>				1	1	1				
<i>Paranthropus</i>							1	1	1	
<i>Homo</i>							4	2	2	
<i>Theropithecus</i>				1			1	1		
<i>Parapapio</i>				2	1	4			1	1
<i>Papio</i>					1	2	1			
<i>Gorgopithecus</i>							1			
<i>Cercocebus</i>							1			
<i>Cercopithecus</i>							1			
<i>Cercopithecoides</i>			1			1	1		1	1
<i>Dinopithecus</i>										1
<i>Colobus</i>							1		1	
<i>Rhinocolobus</i>				1						
<i>Paracolobus</i>					1					
Cercopithecidae		1								
Colobinae	1			1	1		1			
<i>Galago</i>					1					
Total	2	1	1	6	6	8	13	4	6	3

The genera *Parapapio* and *Cercopithecoides* are the most common primate genera, occurring at half the sites each. *Parapapio* is found at Hadar (two species), Laetoli, Sterkfontein (four species), Olduvai Gorge and Angola. *Cercopithecoides* occurs at Langebaanweg, Sterkfontein, East Turkana, Olduvai Gorge and Angola.

East Turkana has the most primate taxa with thirteen taxa in nine genera plus the sub-family Colobinae. Manonga Valley has one primate identified as belonging to the family Cercopithecidae present. Langebaanweg has only the genus *Cercopithecoides* present.

Four genera are found at only one site. The hominid *Sahelanthropus* is found only at Chad, *Rhinocolobus* occurs only at Hadar, *Paracolobus* is present only at Laetoli and the bush baby *Galago*, the only galagid in the survey, is present only at Laetoli.

Figure 12.7



Monkeys (Cercopithecidae) occur at every site in the survey, and are particularly well represented at sites of middle Pliocene (Hadar, Laetoli and Sterkfontein) and Pleistocene (East Turkana, Olduvai Gorge and Angola) age. Hominids are represented by one taxa at the sites of Chad, Hadar, Laetoli and Sterkfontein, and by three or more taxa at East Turkana, West Turkana and Olduvai Gorge, but are absent from Angola, Manonga Valley and

Langebaanweg. Hominids are more numerous than cercopithecids, in terms of the number of taxa, only at the site of West Turkana.

12.3.7 Reptiles

Langebaanweg is not included in this summary because no data was available. All other sites except Sterkfontein contain reptiles (Table 12.7). Turtles or tortoises occur at all sites, with the family Testudinidae occurring at Chad, Hadar, Laetoli, East and West Turkana, and the family Trionychidae occurring at Chad, Manonga Valley, Hadar and East Turkana. Snakes have been discovered at Chad, Hadar, Laetoli, and Olduvai Gorge. The monitor lizard Varanidae is found at Chad, Hadar, East and West Turkana.

Table 12.7 Reptile taxa

Family	Chad	MV	Had	Laet	ET	WT	OG	Ang
Trionychidae	1	1	1		1			
Testudinidae	1		1	2	1	1		
Pelomedusidae		1			1	1		
Lacertidae								1
Boidae	1		1	1			1	
Colubridae	1			1			1	
Viperidae			1	1			1	
Elipidae				1				
Varanidae	1		1		1	1		
Crocodylidae	1	1	1		2		2	
Tomistomidae	1				1			
Gavialidae	1							
Chelonia							1	1
Ophidea								1
Total	8	3	6	6	7	3	6	3

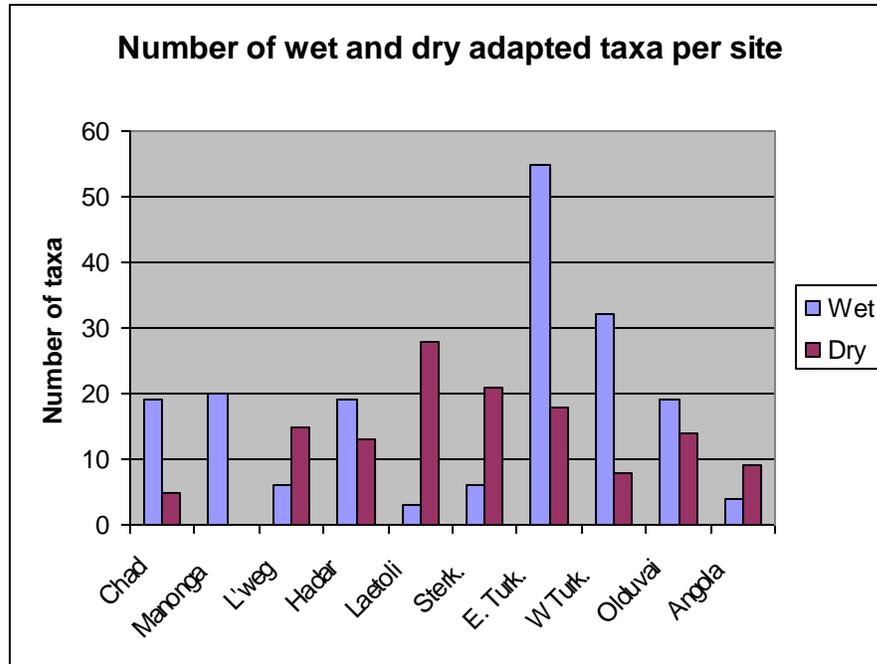
Crocodyles occur at all sites except Laetoli, West Turkana and Angola. The family Crocodylidae is the most common, occurring at Chad, Manonga Valley, Hadar, East Turkana and Olduvai Gorge. The family Tomistomidae occurs only at Chad and East Turkana while the family Gavialidae is restricted to Chad.

12.3.8 Dry and wet adapted species

Figure 12.8 shows the results of a survey of each site in which dry and wet adapted species were counted. Taxa were determined to be arid adapted if closely related extant species were adapted to arid environments and had a preference for these habitats, while taxa were

determined to be wet adapted if closely related extant species were adapted to wet environments and had a preference for these habitats (see appendix 2).

Figure 12.8



Taphonomic processes appear to be influential with the sites mostly associated with water deposited sediments (Chad, Manonga Valley, Hadar, East Turkana, West Turkana and Olduvai Gorge) all having higher numbers of water adapted taxa than arid adapted, while the cave and terrestrial deposits of Laetoli, Sterkfontein and Angola all show greater numbers of arid adapted taxa.

With this in mind, the data show that *Sahelanthropus* probably lived in the vicinity of a relatively wet environment, with fish, crocodiles, turtles, otters, hippos, waterbucks and the water dependent python all present. *Australopithecus* lived in comparatively drier environments, sharing the landscape with baboons, hyaenids, dogs, camels, gazelles, ground squirrels and arid adapted rodents and hares at Laetoli; and with baboons, horses, dogs, hyaenids, arid adapted rodents and rock hyraxes at Sterkfontein. *Homo* and *Paranthropus* appear to have inhabited relatively wet environments, with various hippopotamus and water dependant bovids such as the lechwe, plus cane rats, fish, aquatic turtles, crocodiles, aquatic snails, mollusks and freshwater crustaceans occurring at East Turkana; fish, crustaceans,

sponges, aquatic snails, fresh water turtles, hippos and waterbucks at West Turkana; and otters, the marsh mongoose, swamp rats, hippos, waterbucks, fish, crocodiles, amphibians, freshwater gastropods and mollusks at Olduvai Gorge.

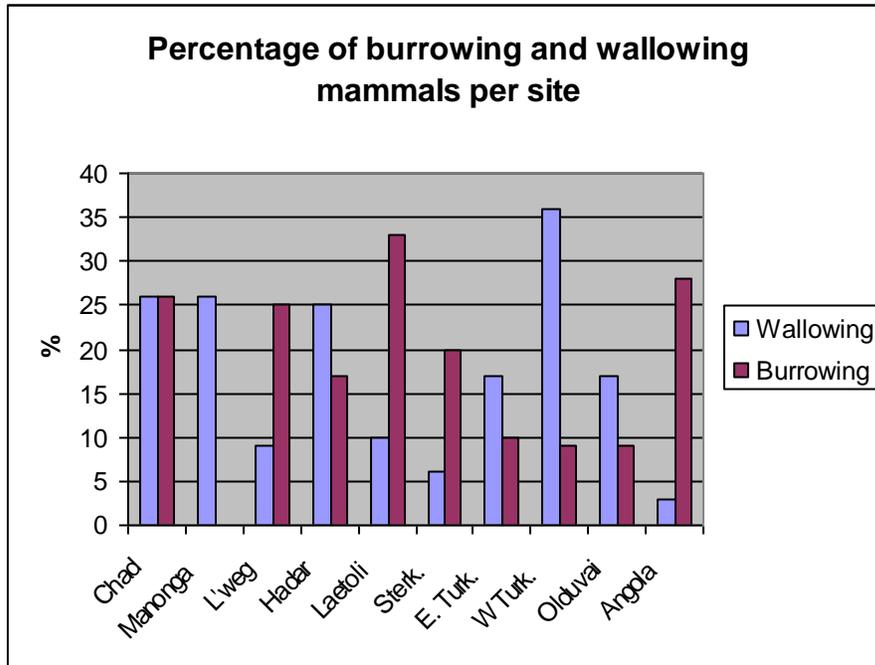
Manonga Valley has no arid adapted taxa and also has no hominids present. The Angolan site of Humpata, relatively dry in comparison to the similarly aged East and West Turkana and Olduvai Gorge sites, has no hominids present.

Although Sterkfontein and Laetoli, where the *Australopithecus* species *africanus* and *afarensis* occur, are relatively dry, there are indications that water was present in the form of the water dependant Egyptian mongoose, mouse shrew and python at Laetoli; and swamp rats, reed bucks and mouse shrews at Sterkfontein; and certainly Hadar was a relatively wet habitat with swamp pigs, otters, hippos, kobs, aquatic birds, aquatic turtles, crocodiles, fish, mollusks, bivalves and crustaceans all present. Conversely, at Chad, where *Sahelanthropus* occurs, there were dry elements such as hyaenids, antelopes and ground squirrels; and where *Paranthropus* and *Homo* occur there were arid elements including at Olduvai Gorge; baboons, hyaenids, horses, camels, gazelles and arid adapted rodents and hares; at East Turkana baboons, hyaenids, dogs, horses, camels, gazelles, and arid adapted rodents; and at West Turkana hyaenids, dogs, horses and gazelles.

Possibly wet habitats in otherwise dry landscapes were the most favourable for late Miocene to early Pleistocene African hominids, which might explain why Manonga Valley, with no arid habitat indicators, has no hominids.

Figure 12.8 shows the percentage of mammals that have a tendency to wallow and the percentage of mammals that are burrowing mammals at each site. Wallowing mammals are those that have relatives today that are known to wallow (elephants, rhinoceroses, pigs, hippopotami and buffaloes) while burrowing animals include those that have relatives today that live underground and/or use burrows and dens for shelter such as moles, foxes, mongooses, porcupines and hyaenids.

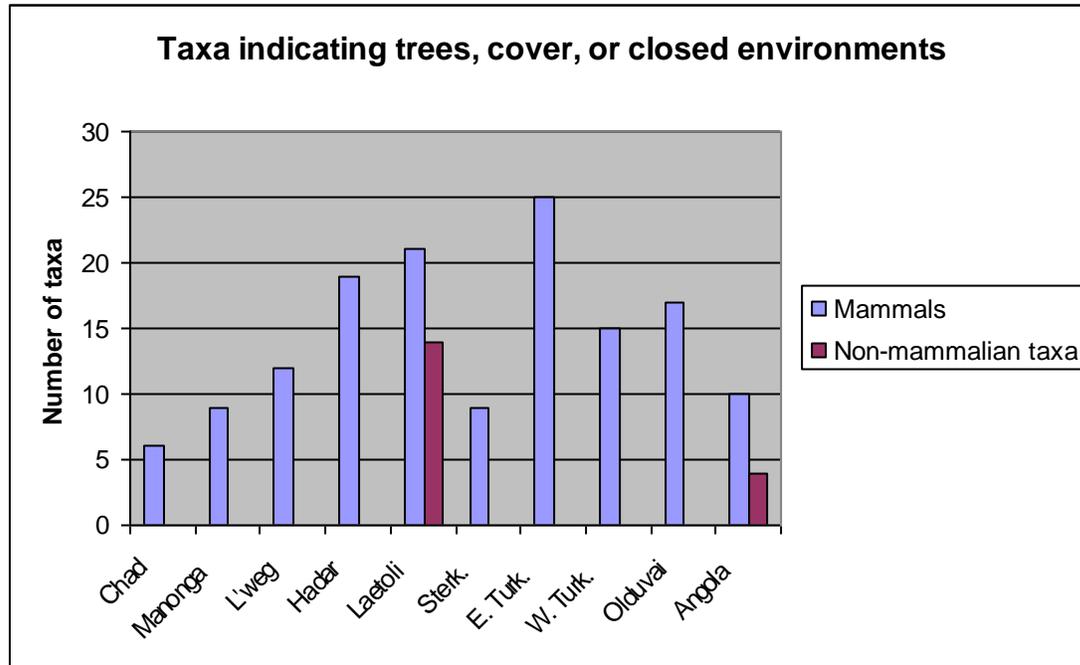
Figure 12.9



The results show that at Laetoli there is a high percentage of burrowing mammals, and since the sediments at this site were the result of volcanic activity, it seems possible that animals living under ground may have been more likely to be preserved than other taxa. Angola also has a high percentage of burrowing animals compared to wallowing mammals, an indication perhaps that relatively dry conditions prevailed there.

West Turkana has a much higher percentage of wallowing mammals than burrowing mammals, an indication perhaps that wet conditions prevailed there. Manonga Valley, Hadar, East Turkana and Olduvai Gorge all have higher percentages of wallowing mammals than burrowing mammals. Chad has the same number of wallowing and burrowing mammals. Sterkfontein and Langebaanweg have higher percentages of burrowing mammals than wallowing mammals.

Figure 12.10



At every site there is some indication of trees, cover or closed environments. Taxa used to indicate trees, cover or closed environments were those that were considered either to be arboreal, or browsers, or whose preference was for closed as opposed to open habitats, or dense cover (see Appendix 3). The sites with the highest number of mammals indicating trees, cover or closed environments were East Turkana, Laetoli, Hadar, Olduvai Gorge and West Turkana. If non-mammalian taxa are added to the mammalian totals then Laetoli has the highest number of taxa indicating trees, cover or closed environments. This is mainly on account of the high number of gastropods at Laetoli, all of which have a preference (or indeed are dependant on) habitats with trees, such as wooded or forested regions (Verdcourt, 1987).

Although baboons (including the gelada) are excellent climbers, they are not included here as taxa indicating trees because some extant populations (e.g., *Papio hamadryas*, *Theropithecus gelada*) inhabit relatively treeless regions, making use of cliff edges for shelter instead of trees. The site of Sterkfontein, therefore, with four *Parapapio* and two *Papio* taxa, is possibly more wooded than the results here indicate, because at least some of these taxa may have preferred environments with trees.

Chapter 13

Models of hominid evolution in light of the data

13.1 The savanna or terrestrial model in light of the data

The term 'savanna' has often been used in relation to hominid evolution (Clark, 1980; Wheeler, 1993); however, this term can mean a wide variety of different habitat types. Harris defines savanna habitats as "that part of the tropical world that experiences a dry season of 2.5 to 7.5 months' duration" (1980a:3). This prolonged dry season checks the growth of plants, so that only plants that can tolerate prolonged periods of low rainfall can survive. There are areas within savannas, of course, however, where permanent water occurs in the form of rivers, lakes, swamps and coasts, and therefore in these places less arid adapted vegetation, including evergreen forests, can occur.

Many authors have emphasised the role of the open, arid savanna, including Vrba, who wrote: "The human family was among the 'founder members' and for most of its history an endemic part of an African savanna biota." (1985: 63). Hominids, Vrba suggests, "underwent a significant ecological 'switch,' in terms of *vegetation cover* and *year round availability of moisture*" (1985: 68; emphasis added).

Vrba studied the faunal remains of bovids, particularly antelopes, and suggested a link between global climatic events which resulted in lower rainfall, causing forest contractions and grassland expansions, and the rapid extinction and replacement of various bovid species (Vrba, 1995; but see also Hill, 1995). The data presented here (see Figure 12.8, for example) confirms that while grasslands may have expanded through the period from the late Miocene to the early Pleistocene, these grasslands, at least in the areas where the remains of *Homo* and *Paranthropus* have been discovered, appear to have been relatively moist, as well as arid.

Clark suggests that "progressive expansion of grasslands [...] made available 'empty niches' into which hominids could expand" (1980: 43). He argues that in order to compete successfully with other carnivores early hominids might have been "middle-of-the-day

scavengers” (1980: 44). The idea of scavengers on the open savanna is rejected by Verhaegen, however, who notes that “there was no empty niche of migrating scavengers to be occupied by hominid ancestors. Not only vultures but also canid, felid and hyaenid carnivores were much better preadapted for such a niche” (1987: 305).

Clark also suggests that a “diversity of plant foods in the savanna” (1980: 44) would have been of great importance to hominids, including “deeply buried food items such as tubers, roots, rhizomes, and corms” (1980: 44). The idea of scavenging carcasses and collecting plants from the open savanna does not appeal to Sikes, however, who suggests that:

“Not only are edible plant foods, including underground storage organs, scattered in diffuse patches in more open habitats, but competition for carcasses is more intense and the remains are subject to rapid decay under the tropical sun.” (1999: 311).

And she adds,

“foraging by sweating hominids may have been riskier away from water or arboreal refuge, for predator escape and sleeping accommodations, offered by wooded habitats” (1999: 311).

The results of this study show that at every site at which hominids existed in Africa, a number of other animals, presumably well adapted to life on the savannas (bovids, dogs, large cats, hyaenids, baboons, rodents), were also present. Early *Homo* species were presumably capable tool makers and users, and therefore it could be argued that this may have enabled them to survive on the open, arid savanna more efficiently than other animals. Yet evidence of stone tools generally comes from waterside locations, rather than arid habitats away from water (Roe, 1994; Isaac, 1997; Semaw *et al.*, 1997).

Possibly, exploitation of open savannas by *Homo* and other hominids may have been restricted to waterside locations such as were present, according to the data presented here, at Olduvai Gorge and the Turkana Basin. At the waterside there would have been more shelter, a better supply of food in the form of fruit, edible herbs and other vegetation, a higher concentration of small mammals, birds and reptiles, eggs, fish, crustaceans and shellfish, than in the more arid, open regions of the savanna (Stewart, 1994; O’Brien and Peters, 1999).

“The savanna-water interface –along the coast, around lakes, along stream courses, and around swamp margins–” Harris wrote, “has played a critical role in the human ecology of savanna environments” (1980b: 31). The opportunity to scavenge or hunt large mammals may have also been greater at the water’s edge, where many mammals would have congregated to drink.

13.2 The semi-aquatic or waterside model in light of the data

The semi-aquatic model (Morgan, 1997) is based primarily on comparative data. Hardy (1960) noticed similarities between humans and animals that spend a lot of time in the water. For example, he noted that the combination of nakedness and subcutaneous fat, seen only in humans amongst primates, was also seen in other mammals that spend considerable time in the water, such as dolphins, dugongs and hippopotami. (It has been noted that humans have as much hair as chimpanzees (Oxnard, personal communication), yet numerous hypotheses purporting to explain the evolution of nakedness in humans (e.g., Newman, 1970; Pagel and Bodmer, 2003) appear to suggest that in terms of functionality, at least, many researchers agree humans are relatively naked compared to chimps).

The comparative approach of the aquatic hypothesis has been criticised because not all aquatic mammals (e.g., otters and seals), are naked (Groves, personal communication) and features such as bipedalism are not typical of aquatic mammals (Langdon, 1997). Furthermore, not all naked animals are aquatic, though some, such as elephants, do show indications suggesting possible aquatic ancestry (Gaeth *et al.*, 1999; West *et al.*, 2003). The aquatic hypothesis has been criticised for not being compatible with the fossil record. For example, Langdon notes that bipedalism, one of the features said to be explained by a possible aquatic phase (Morgan, 1997), first appeared in the fossil record “more than four million years ago and appears to have been evolutionarily static until *Homo* significantly reconfigured the postcrania about two million years ago” (Langdon, 1997: 491). If an aquatic phase was responsible for the origins of bipedalism, Langdon argues, a different event and a different explanation would be required for the evolution of the modern human gait.

13.3 Trees and water?

Recently, Verhaegen *et al.* (2002) proposed that human ancestors may have been climbers and waders (aquarboreal) in flooded forests such as swamp or mangrove forests, learning to

use tools to remove and crack open hard shelled fruits, nuts and shellfish, as capuchin monkeys are known to do (Fernandes, 1991). According to this scenario human ancestors may have eventually become waterside omnivores, improving the efficiency of their bipedal gait by wading in water and walking on land, and improving the efficiency of their underwater swimming abilities in order to collect shellfish and aquatic plants.

Langdon's proposal, that "at least two different events with two different explanations are required to achieve the modern human gait" (Langdon, 1997: 491), could possibly be accommodated by the aquarboreal model. The first event, leading to short-legged bipedalism (*Australopithecus*), could have been an adaptation to flooded forests, where climbing and wading in shallow water would have been of optimum importance. The second event, leading to a (relatively) linear body build and longer-legged bipedalism, could have been an adaptation to a waterside existence where swimming, diving, wading and terrestrial walking were more important than climbing. For the data to support this model, we would expect to see a combination of trees and water at hominid sites where short-legged bipedalism combined with arboreal adaptations occurred, and a more expansive body of water wherever relatively longer-legged, linear, non-arboreal hominids were present.

13.4 Anatomy of fossil hominids

13.4.1 *Sahelanthropus*

Postcranial remains for *Sahelanthropus* have not been described. There have, however, been tentative claims, based on the fact that the basicranial and facial morphology of *Sahelanthropus* are similar to later fossil hominids considered to be bipedal, that *Sahelanthropus* too may have been bipedal (Brunet *et al.*, 2002; but see also Wolpoff, *et al.*, 2002). Since it lived close to the estimated time when chimps, gorillas and humans separated (Chen and Li, 2001), there is reason to speculate that it may have been an efficient climber. Its fossil remains were discovered in association with aquatic (fish), amphibious (otters), swamp dwelling (*Gymnarchus*), arboreal (Colobinae) and arid adapted (ground squirrel) fauna. The possibility, therefore, that it may have been aquarboreal (climbing and wading) can not be disregarded, just as the possibility that it may have been predominantly terrestrial in open habitats cannot.

13.4.2 *Australopithecus*

There is general agreement that the *Australopithecus* locomotor repertoire probably included climbing (Collard and Wood, 1999) and a form of bipedalism that was very different to that of *Homo sapiens* (Stern and Susman, 1983). It has been suggested that the bipedalism of *Australopithecus* may have been ideally suited to wading in shallow water (Kuliukas, 2002). The data presented here show that at the sites where *Australopithecus* fossils have been found, Hadar, Laetoli and Sterkfontein, there were trees present (Colobinae at Laetoli and Hadar, *Cercopithecoides* at Sterkfontein) as well as water (fish at Hadar, swamp rats at Sterkfontein and the Egyptian mongoose at Laetoli). It is therefore possible that *Australopithecus* could have inhabited forests in which climbing and wading in shallow water were potentially important activities.

Direct evidence of bipedalism occurs at Laetoli in the form of footprints preserved in tuffs. These tuffs, according to Andrews, “provide evidence of association of animals preferring more closed conditions than were present perhaps at other stages of the Laetoli succession” (Andrews, 1989: 180). Though the area where the tuffs were accumulated was relatively unvegetated, Andrews suggests this may have been “because of some local edaphic feature” (Andrews, 1989: 180). As for the anatomy of the footprints, one set of tracks is said to have possibly been made by an animal with possibly an African ape-like foot morphology and stride, while another set is said to resemble ursid (bear) tracks (Tuttle, 1987).

The faunal data show that the habitat of *Australopithecus* could have allowed it to have been a climber, a wader or a terrestrial biped, or possibly a combination of these.

13.4.3 *Homo habilis* and *rudolfensis*

Post cranial skeletal data for *habilis* suggests it may have spent time in the trees (Collard and Wood, 1999). For *rudolfensis*, post cranial skeletal remains are rare, and its locomotion style is therefore open to speculation. Nevertheless, it has been proposed that *rudolfensis* may have had the ability to move effectively in trees (Collard and Wood, 1999). *Colobus* species at the Turkana Basin and Olduvai Gorge suggest that well wooded to forested areas existed where *habilis* and *rudolfensis* existed, while swampy vegetation is indicated by the presence of the cane rat *Thryonomys* at East Turkana and Olduvai Gorge, and the swamp snail *Pila ovata* at West Turkana. It is possible, therefore, that early *Homo* species such as *habilis* and

rudolfensis were tree dwellers in relatively swampy regions, capable of climbing and wading. The possibility that they were capable terrestrial bipeds is not ruled out by the data.

13.4.4 *Paranthropus*

Paranthropus is also considered to have had not only bipedal abilities but also tree climbing abilities (Collard and Wood, 1999). The robust size of some of these individuals, however, may have limited the effectiveness of their arboreal activity in at least some individuals. Like *Homo habilis* and *rudolfensis*, *Paranthropus* remains have been discovered in areas where both trees and water were present (see above). Possibly, they may have evolved from tree dwelling *Australopithecus* ancestors, becoming better adapted to more open regions, “but always near wetlands” (Aiello and Andrews, 2000: 27), and possibly always near trees since arboreal capabilities appear to have been retained (Sikes, 1999). Possibly, the larger male adults built nests on the ground in reed beds (indicated by the presence of the cane rat *Thryonomys*, discovered at Turkana and Olduvai Gorge, which inhabits swampy reed beds), thereby allowing a more robust build (as a result of not being reliant on trees). Recently, there have been reports from the Congo Basin of the discovery of nests (possibly made by an as yet unidentified population of chimpanzees) made in swamps both on the ground and in trees in the same area, suggesting the possibility that large males may have nested on the ground, while juveniles may have nested in trees (Young, 2004).

With thick enamel, huge molars and powerful chewing muscles, *Paranthropus* was perhaps well adapted to eating the vegetation associated with reed beds such as Gramineae (Verhaegen, 1992) and sedges such as *Typha* (cattails or bullrush). Early stone tools from Olduvai Gorge, according to Binford, “seem to relate to the immediate lakeside setting, and phytoliths derived from aquatic tuberous plants, ‘cattails’ in American terms, have been recovered from these tools (Isaac pers. comm., 1985)” (Binford, 1989: 27). Studies of early stone tools from the Turkana Basin indicate “these implements were used to cut the highly siliceous stems of grasses or reeds” (Keeley and Toth, 1981). While it is almost impossible to know whether the tools referred to here were made by *Paranthropus* or *Homo*, it is not difficult to imagine *Paranthropus* exploiting food from trees such as fruit, as well as from shallow waters, as *Gorilla* (Fay *et al.*, 1990; Nishihara, 1995) and *Pan* (Kano and Mulavwa, 1984) species do today.

The faunal data shows that open, arid grasslands probably existed within the vicinity of where *Paranthropus* fossils have been discovered, and therefore the idea that it may have been a bipedal terrestrialist cannot be ruled out.

13.4.5 *Homo ergaster*

Post cranial remains for *Homo ergaster* are relatively well known and it is generally agreed that climbing abilities in this species were relatively limited (Collard and Wood, 1999). Although clearly more human-like than ape-like in terms of limb proportions, there are nevertheless a number of differences when *Homo ergaster* is compared with *Homo sapiens*. The thorax, for example, was more tapering than in *Homo sapiens*, affecting the position of the shoulder joints, which, according to Tattersall, would have been “not at all favourable in a striding biped that swings its arms for balance” (Tattersall, 1995: 188).

The size of the thoracic vertebral canal in *Homo ergaster* was not enlarged as it is in *Homo sapiens*, and since it has been proposed that “improvements in the control of bipedalism might be responsible for the later enlargement” (Walker, 1993b: 428), the implication is that *ergaster* may have had relatively poor control of bipedalism.

Differences in the pelvis and the femoral neck structure of *ergaster* when compared with *Homo sapiens* (Groves, 1989) might possibly indicate differences in locomotion efficiency. Marchal placed ‘*erectus* like’ forms and Neandertals together in one group, with *Homo sapiens* in another, “on the basis of pelvic bone morphology” (Marchal, 2000: 362). And on the basis of their pelvic morphology Yoel Rak concluded that, compared to *Homo sapiens*, who are greatly adapted to walking, there was “very little doubt that Neandertals were less efficient” (Shreeve, 1995: 188). It follows, therefore, that if Neandertal and ‘*erectus* like’ pelvises are more similar to each other than either is to *Homo sapiens*, and Neanderthals are less efficient walkers than *Homo sapiens*, then ‘*erectus* like’ forms, including *ergaster*, might have been less efficient walkers as well.

The only possible direct evidence we have of bipedalism in *Homo ergaster* are footprints dated to about 1.5-1.6 mya from the Turkana Basin, which correspond to a time when both *Homo ergaster* and *Paranthropus* were present. As with the stone tools, it is difficult to determine who may have made these prints.

“The length of the stride of the hominid is about 80cm, less than that of modern humans with feet of comparable size during normal walking. This, along with the orientation of the feet, seems to indicate a hesitant, somewhat sideways progression across a slippery surface with one misstep (L4) into a deep hippopotamus track, which may have been concealed by turbid water” (Behrensmeyer and Laporte, 1981).

The size and shape of the skull of *Homo ergaster* was different to *Homo sapiens*. Examination of the *Homo* fossil crania OH 9 (Olduvai Gorge) and KNM-ER 3733 (East Turkana), reveals the shared characteristic of a flattened and stretched basicranium. “It is most likely”, wrote Maier and Nkini, “that this character is correlated with the specific elongation of the braincase and with a peculiar poise of the head” (1985: 252).

The generally more robust, and therefore heavier, skeleton of *Homo ergaster* (Walker, 1993b: 425), compared to *Homo sapiens*, combined with the differences listed above, are difficult to immediately account for in terms of adaptations to savanna living, where large, fast, carnivorous mammals were present. *Homo ergaster* was different in a number of ways to other savanna inhabitants (antelopes, dogs, hyaenas, baboons, ground squirrels), which are generally fast quadrupeds with a covering of sun protective fur. Though models have been put forward to explain the evolution of bipedalism and nakedness on a savanna setting (e.g., Wheeler, 1991), none have so far proved attractive enough to have been widely accepted by the scientific community (Morgan, 1997). The data certainly show that early *Homo* inhabited areas where savanna habitats were within the vicinity (camels at East Turkana and Olduvai Gorge, gazelles at West Turkana) so the idea of terrestrial bipedalism can certainly not be ruled out based on the faunal associations alone.

On the other hand, the robust skeleton of *ergaster* and other early *Homo* species may have been a distinct advantage in a species that needed to stay submerged for lengthy periods while collecting shellfish or aquatic vegetation. Slow diving mammals such as dugongs which feed on sea grasses have heavy bones. The elongation of the braincase and unusual poise of the head might have given *ergaster* a more streamlined profile making it easier to swim head first through water. *Homo ergaster* is found in association with shellfish at East Turkana (*Mutela*) and Olduvai Gorge (*Corbicula*) and with the swamp snail *Pila ovata* at

West Turkana. In fact, apart from *Pila ovata*, the best preserved faunal remains associated with the WT 15000 (*Homo ergaster*) fossil at West Turkana are “all aquatic animals” (Walker, 1993a: 52).

Also associated with *Homo ergaster* at East and West Turkana is the stingray *Dasyatis*, which probably migrated from the Indian Ocean via a fluvial connection, possibly about 1.9 million years ago (Brown and Feibel, 1991). It is not impossible, therefore, that *Homo ergaster* may have had its origins in east African coastal forests, and was able to migrate into the Turkana Basin along the same fluvial connection as *Dasyatis*, exploiting resources from the water’s edge along the way.

It has been suggested that tropical shellfish and fish would be the ideal food for fueling and building a large brain (Broadhurst *et al.*, 1998). An external nose with downward oriented nostrils would have allowed swimming and diving in water without the risk of water entering the airways (Morgan, 1972). Human speech, according to this hypothetical ‘diving for shellfish’ model, might have evolved as more efficient breath hold diving abilities developed, and increased muscular control of the lips, tongue, jaw and larynx evolved, in association with an expanding neo cortex, to assist diving and the consumption of slippery foods such as shellfish underwater (Verhaegen and Munro, 2004). This ‘diving for shellfish’ model could also help explain the drastic and abrupt reduction in the human muscles involved in mastication (Stedman *et al.*, 2004), the improved capacity for amino-acid catabolism (Clark *et al.*, 2003) and why so many genes in which *Homo* differs from *Pan* are involved in olfaction (Gilad *et al.*, 2003). After all, shellfish, rich in amino acids, can be swallowed without mastication and a sense of smell is not required for their procurement, (Verhaegen, personal communication).

Whereas *Paranthropus* may have required well vegetated wetlands, and in particular reed-beds, in order to survive (for shelter and food), *Homo* may have been adapted to a more omnivorous waterside existence, and therefore, rather than being restricted to a particular type of wetland, may have been able to move along rivers and around coasts (Sauer, 1962), eventually reaching places as far away as the island of Flores, an oceanic island east of Wallace’s Line, which would have required a journey from one coast to another in order to be reached (Tobias, 2003).

Chapter 14

Summary and conclusion

14.1 Conclusion

The aim of this thesis has been to examine the faunal remains of ten African sites, and to use the data to build a possible picture of the environment of a number of African hominids, namely; *Sahelanthropus*, *Australopithecus*, *Paranthropus* and *Homo*. Three models of human evolution; the aquatic, the terrestrial and the aquarboreal, have been briefly discussed in light of the results.

In Part II each of the ten sites was examined individually, with lists compiled and an ecological discussion undertaken. The results showed that at every site, except Manonga Valley, there was some indication that arid habitats were present. Since Manonga Valley was a non-hominid site, all hominid sites were found to have arid elements. The results also showed that at every site there were indications of wet habitats, and also indications of trees in the form of either woodland or forest.

Part III involved a comparison of the sites, with tables and graphs constructed to give an overview of the data. The results showed that a number of taxonomic groups were common throughout the range of sites (e.g., bovids), whereas others were rare (e.g., bears were restricted to Langebaanweg). Although all hominid sites showed indications of dry habitats, the sites of Laetoli and Sterkfontein, where the *Australopithecus* species *afarensis* and *africanus* occur, had a greater proportion of arid-adapted taxa than the other hominid sites. Humpata and Langebaanweg, both non-hominid sites, also had a greater number of arid adapted taxa as a proportion of their respective assemblages than water-adapted taxa. Manonga Valley, as already mentioned, had no arid-adapted taxa.

The faunal assemblages of all sites suggested the presence of water, though at some sites water-dependant taxa were relatively rare. These sites were Laetoli, Sterkfontein, Angola and Langebaanweg. The sites with higher numbers of water adapted taxa than arid adapted, according to the data, were, in order, East Turkana and West Turkana, followed by Manonga

Valley, Chad, Hadar and Olduvai Gorge. With regard to hominids, this suggests that the genera *Homo* and *Paranthropus* inhabited environments with high numbers of water adapted taxa, while *Sahelanthropus* also inhabited environments with high numbers of water-adapted taxa, and *Australopithecus* inhabited environments that had both high (Hadar) and relatively low (Laetoli and Sterkfontein) numbers of water adapted taxa. It should be kept in mind that taphonomic processes probably have influenced the numbers and types of taxa preserved from site to site.

The data show that trees, cover or closed environments occur at every examined site. The site with the highest relative number of taxa indicating trees, cover or closed environments was Laetoli, which had a number of gastropods associated with woodland and evergreen forest habitats, as well as a number of browsers, arboreal primates and rodents. East Turkana, Hadar, West Turkana and Olduvai Gorge all had high numbers of taxa indicating trees, cover or closed environments. These results show that at each site there may have been suitable habitats for a hominid with arboreal adaptations, though of course it does not automatically follow that hominids were necessarily arboreal just because trees may have been present.

Part IV included a discussion of three models of hominid evolution; namely the savanna, the aquatic and the aquarboresal models, and a brief review of the anatomical data with regard to locomotion was undertaken. While the faunal data are not inconsistent with the savanna model, nor do they offer solid support for the open, arid version of this model. *Homo* sites, rather than containing many arid adapted taxa, consistently have higher numbers of water adapted taxa. Moreover, other animals within the assemblages seem better adapted for the niches offered by open, arid habitats.

The skeletal differences of *Homo ergaster*, when compared with *Homo sapiens*, are not easily explained by an arid, savanna dwelling lifestyle, which is not to say there is a lack of hypotheses to try to explain these differences (e.g., see Walker, 1993b). It seems more likely, considering the available data, that savanna wetlands such as lakes, swamps, gallery forests and coastlines may have had a more significant influence on hominid evolution than open, arid, savanna environments.

The data are not inconsistent with the waterside model. All hominids are found at sites where water was present. *Homo*, in particular, is associated with comparatively wet habitats where shellfish, fish, aquatic plants and apparently large permanent bodies of water were present. The data suggest that a river may have connected Lake Turkana to the Indian Ocean shortly before *ergaster* first appeared there. The differences of the *Homo ergaster* skeleton compared to *Homo sapiens* are possibly explained by a model that has the species spending at least part of its time in the water.

The waterside scenario, for example, is arguably a more satisfactory model, when compared to the dry savanna model, for explaining such human features as nakedness, subcutaneous fat, external nose, large brain, tool use, speech, reduced masticatory abilities, improved capacity for amino acid catabolism and reduced olfactory abilities. The recent discovery of *Homo floresiensis* on the island of Flores, in association with “fish, frogs, tortoises, varanids, birds, rodents and bats” (Morwood, *et al.*, 2004) does little to contradict the idea of a waterside phase in human evolution. If anything, it strengthens the proposition since it demonstrates the importance of oceanic islands in the diversification of the *Homo* genus. Stone tools discovered on Flores dated at over 800 thousand years old (Morwood *et al.*, 1998) demonstrate that at least by this time humans had been living along tropical coast lines and were able to cross significant water barriers. More detailed examination of the faunal associations of *Homo floresiensis* will no doubt give us a better understanding of how this species may have lived.

The waterside theory alone, however, can not explain the evolution of the australopithecine style of bipedalism, or the evolution of the modern human gait. Mammals that spend considerable time in the water are generally quadrupedal (otters, hippos) or else have limbs of reduced length (whales, dugongs, seals), whereas humans are bipedal and have long legs.

The aquarboreal model of hominid evolution (Verhaegen *et al.*, 2002) proposes that human and chimp ancestors lived in flooded forests where they waded and climbed. In this model the type of bipedalism seen in species such as *Australopithecus afarensis* may be the result of an adaptation by an already arboreal primate (with flexible hips and shoulders), to an environment where wading in shallow water may have been required. Since *Pan* and *Gorilla* are known to enter swamps (Kano and Mulavwa, 1984; Fay, *et al.*, 1989) and wade bipedally

in shallow water (Kuliukas, 2002), the idea of a common ancestor also having this ability should not be difficult to imagine. The data presented here show that there were most probably trees and water present at every hominid site examined, meaning it is possible that *Sahelanthropus*, *Australopithecus*, *Paranthropus*, *Homo habilis* (and possibly *Homo rudolfensis*?) were all aquarboreal hominids (that is, climbing with bipedal-wading abilities). Of course, the presence of trees and water does not, in itself, prove that these species were aquarboreal, just as the presence of arid habitats does not necessarily prove they were adapted to the arid savanna.

The aquarboreal model proposes that when *Homo* became less dependant of trees, possibly as a result of the same climatic shifts which influenced the evolutionary changes seen in bovids, suids, equids and proboscideans between 3 and 2 million years ago (Rozzi *et al.*, 1999), they may have become more efficient swimmers and divers (Schagatay, 1996), and because their ancestors were already capable bipeds, they may have continued to wade bipedally and become more efficient bipeds on land.

The conclusions offered here are necessarily speculative, and because the data set is limited (just ten sites) and not without flaws (identification and taphonomic problems), a certain amount of caution is needed in interpreting the results. It should be possible, however, to eliminate some of these problems in any future study by increasing the number of sites examined. A data set of a hundred sites, for example, might allow patterns to emerge that might be of some statistical significance. What will be needed is a consistent and methodical approach, so that data sets can be confidently used to test the predictions of different evolutionary models. This thesis, in that context, could be viewed as a preliminary study that offers a potential framework, as well as an opportunity to avoid the same pitfalls, to any researchers who may feel inclined to undertake a more expansive study.

I predict that a more extensive examination and comparison of the faunal assemblages from a greater number of sites, including both hominid and non-hominid, and from a wider timeframe, and incorporating sites not only from in Africa but also outside Africa, will offer possible new insights into hominid evolution.

References*

- Aiello, L. & Andrews, P. (2000) The Australopithecines in Review. *Human Evolution* **15**: 17-38.
- Anderson, D. (1998) *Invertebrate Zoology*, Melbourne: Oxford University Press.
- Andrews, P. (1989) Palaeoecology of Laetoli. *Journal of Human Evolution* **18**: 173-81.
- Behrensmeyer, A. & Laporte, L. (1981) Footprints of a Pleistocene hominid in northern Kenya. *Nature* **289**: 167-9.
- Benton, M. (1990) *Vertebrate Palaeontology*, London: Unwin Hyman.
- Binford, L. (1989) Isolating the transition to cultural adaptations: an organizational approach. In E. Trinkaus (ed.), *The Emergence of Modern Humans: Biocultural Adaptations in the Later Pleistocene*, pp. 18-41. Cambridge: Cambridge University Press.
- Bishop, L. (1999) Suid Paleoeology and Habitat Preferences at African Pliocene and Pleistocene Times. In T. Bromage & F. Schrenk (eds.), *African Biogeography, Climate Change & Human Evolution*, pp. 226-52. New York: Oxford University Press.
- Bonnefille, R. (1995) A Reassessment of the Plio-Pleistocene Pollen Record of East Africa. In E. Vrba, G. Denton, T Partridge & L. Burckle (eds.), (1995) *Paleoclimate and Evolution, with Emphasis on Human Origins*, pp. 297-310. New Haven and London: Yale University Press.
- Bonnefille, R. & Riollet, G. (1987) Palynological spectra from the Upper Laetoli Beds. In M. Leakey & J. Harris (eds.), *Laetoli: A Pliocene Site in Northern Tanzania*, pp. 52-61. Oxford: Clarendon Press.
- Brain, C. (1981) *The Hunters or the Hunted?* Chicago: University of Chicago Press.
- Broadhurst, C., Cunnane, S. & Crawford, M. (1998) Rift Valley fish and shellfish provide brain-specific nutrition for early *Homo*. *British Journal of Nutrition* **79**: 3-21.
- Brown, D. (1980) *Freshwater Snails of Africa and their Medical Importance*, London: Taylor & Francis.
- Brown, F. & Feibel, C. (1991) Stratigraphy, Depositional Environments and Palaeogeography of the Koobi Fora Formation. In J. Harris (ed.), *Koobi Fora Research Project Volume 3 The Fossil Ungulates: Geology, Fossil Artiodactyls, and Palaeoenvironments*, pp. 1-30. Oxford: Clarendon Press.
- Brown, P. *et al.*, (2004), A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature*, **431**: 1055-61.

- Brunet, M. *et al.* (2002) A new hominid from the Upper Miocene of Chad. Central Africa, *Nature* **418**: 145-51.
- Cadman, A. & Rayner, R. (1989) Climatic change and the appearance of *Australopithecus africanus* in the Makapansgat sediments. *Journal of Human Evolution* **18**: 107-13.
- Campbell, B. & Lack, E. (1985) *A Dictionary of Birds*, Calton: T. & A. D. Poyser.
- Chen, F. & Li, W. (2001) Genomic divergences between humans and other hominoids and the effective population size of the common ancestor of humans and chimpanzees. *American Journal of Human Genetics* **68**: 444-56.
- Clark, A. *et al.* (2003) Inferring nonneutral evolution from human-chimp-mouse orthologous gene trios. *Science* **302**: 1960-3.
- Clark, J. (1980) Early Human Occupation of Africa Savanna Environments. In D. Harris (ed.), *Human Ecology in Savanna Environments*, pp. 41-71. London: Academic Press.
- Collard, M. & Wood, B. (1999) Grades among the African Early Hominids. In T. Bromage & F. Schrenk (eds.), *African Biogeography, Climate Change & Human Evolution*, pp. 316-27 New York: Oxford University Press.
- Coppens, Y. (1999) Introduction. In T. Bromage & F. Schrenk (eds.), *African Biogeography, Climate Change & Human Evolution*, pp.13-8. New York: Oxford University Press.
- Dart, R. (1925) *Australopithecus africanus*: The Man-Ape of South Africa. *Nature* **115**: 195-9.
- Denys, C. (1999) Of Mice and Men: Evolution in East and South Africa during Plio-Pleistocene Times. In T. Bromage & F. Schrenk (eds.), *African Biogeography, Climate Change & Human Evolution*, pp. 226-52. New York: Oxford University Press.
- Erlandson, J. (2001) The Archaeology of Aquatic Adaptations: Paradigms for a New Millennium. *Journal of Archaeological Research*. **9**: 287-350.
- Estes, R. (1991) *The Behavioural Guide to African Mammals*, Berkeley: University of California Press.
- Fay, M. (1989) Gorillas (*Gorilla gorilla gorilla*) in the Likouala Swamp Forest of North Central Congo: Preliminary Data on Populations and Ecology. *International Journal of Primatology* **10**: 477-87.
- Feibel, C. (1999) Basin Evolution, Sedimentary Dynamics, and Hominid Habitats in East Africa: An Ecosystem Approach. In T. Bromage & F. Schrenk (eds.), *African Biogeography, Climate Change & Human Evolution*, pp. 276-81. New York: Oxford University Press.

- Feibel, C., Harris, J. & Brown, F. (1991) Palaeoenvironmental Context for the Late Neogene of the Turkana Basin. In J. Harris (ed.), *Koobi Fora Research Project Volume 3 The Fossil Ungulates: Geology, Fossil Artiodactyls, and Palaeoenvironments*, pp. 321-70. Oxford: Clarendon Press.
- Fernandes, M. (1991) Tool use and predation of oysters by the tufted capuchin in brackish water mangrove swamp. *Primates* **32**: 529-31.
- Gaeth, A., Short, R. & Renfree, M. (1999) The developing renal, reproductive, and respiratory systems of the African elephant suggest an aquatic ancestry. *Proceedings of the National Academy of Sciences of the U.S.A.* **96**(10): 5555-8.
- Gentry, A. (1980) Fossil Bovidae (Mammalia) from Langebaanweg, South Africa. *Annals of the South African Museum* **79**: 213-337.
- Gilad, Y. (2003) Human specific loss of olfactory receptor genes. *Proceedings of the National Academy of Sciences of the U.S.A.* **100**: 3324-7.
- Gooders, J. (1975) *Birds: an illustrated survey of the bird families of the world*, Melbourne: Landsdowne Press.
- Groves, C. (1989) *A Theory of Human and Primate Evolution*, Oxford: Clarendon Press.
- Hardy, A. (1960) Was man more aquatic in the past? *New Scientist* **7**: 642-5.
- Harris, D. (1980a) Tropical Savanna Environments: Definition, Distribution, Diversity, and Development. In D. Harris (ed.), *Human Ecology in Savanna Environments*, pp. 3-27. London: Academic Press.
- Harris, D. (1980b) Human Occupation and Exploitation of Savanna Environments. In D. Harris (ed.), *Human Ecology in Savanna Environments*, pp. 31-39. London: Academic Press.
- Harris, J. (1978) Palaeontology. In M. Leakey & R. Leakey (eds.), *Koobi Fora Research Project Volume 1 The Fossil Hominids and an Introduction to Their Context 1968-1974*, pp. 32-63. Oxford: Clarendon Press.
- Harris, J. (1987) Summary. In M. Leakey & J. Harris (eds.), *Laetoli: A Pliocene Site in Northern Tanzania*, pp. 524-31. Oxford: Clarendon Press.
- Harrison, T. & Baker, E. (1997) Paleontology and Biochronology of Fossil Localities in the Manonga Valley, Tanzania. In T. Harrison (ed.), *Topics in Geobiology*, pp. 361-93. New York: Plenum Press.
- Hay, R. (1971) Geological Background of Beds I and II Stratigraphic Summary. In L. Leakey (ed.), *Olduvai Gorge Volume 3 Excavations in Beds I and II, 1960-1963*, pp. 9-18. Cambridge: University Press.
- Hendey, Q. (1974) The Late Cenozoic Carnivora of the South-Western Cape Province. *Annals of the South African Museum* **63**: 1-369.

Hill, A. (1995) Faunal and Environmental Change in the Neogene of East Africa: Evidence from the Tugen Hills Sequence, Baringo District, Kenya. In E. Vrba, G. Denton, T Partridge & L. Burckle (eds.), *Paleoclimate and Evolution, with Emphasis on Human Origins*, pp. 178-93. New Haven and London: Yale University Press.

Hvass, H. (1964) *Reptiles and Amphibians of the World*, London: Methuen.

Isaac, G. (ed.) (1997) *Koobi Fora Research Project Volume 5 Plio-Pleistocene Archaeology*, Oxford: Clarendon Press.

Jablonski, N. & Chaplin, G. (1993) Origin of habitual terrestrial bipedalism in the ancestor of the Hominidae. *Journal of Human Evolution* **24**: 259-80.

Johanson, D. & Edey, M. (1981) *Lucy: The Beginnings of Humankind*, London: Granada.

Johanson, D. & Taieb, M. (1978) Plio-Pleistocene hominid discoveries in Hadar, central Afar, Ethiopia. In C. Jolly (ed.), *Early Hominids of Africa*, pp. 29-44. London: Duckworth.

Johanson, D., Taieb, M. & Coppens, Y. (1982) Pliocene Hominids From the Hadar Formation, Ethiopia (1973–1977): Stratigraphic, Chronologic, and Paleoenvironmental Contexts, With Notes on Hominid Morphology and Systematics. *American Journal of Physical Anthropology* **57**: 373-402.

Kappelman, J., Plummer, T., Bishop, L., Duncan, A. & Appleton, S. (1997) Bovids as indicators of Plio-Pleistocene paleoenvironments in East Africa. *Journal of Human Evolution* **32**: 229-56.

Kano, T. & Mulavwa, M. (1984) Feeding ecology of the Pygmy Chimpanzees (*Pan paniscus*) of Wamba. In R. Susman (ed.), *The Pygmy Chimpanzee: Evolutionary Biology & Behaviour*, pp. 233-274. New York: Plenum Press.

Keeley, L. & Toth, N. (1981) Microwear polishes on early stone tools from Koobi Fora, Kenya. *Nature* **293**: 464-5.

Kingdon, J. (1982) *East African Mammals: An Atlas of Evolution in Africa*, London: Academic Press.

Kingdon, J. (1997) *The Kingdon Field Guide to African Mammals*, London: Academic Press.

Kuliukas, A. (2002) Wading for Food: The Driving Force of the Evolution of Bipedalism? *Nutrition and Health* **16**: 479-94.

Langdon, J. (1985) Fossils and the Origin of Bipedalism. *Journal of Human Evolution* **14**: 615-35.

Langdon, J. (1997) Umbrella hypotheses and parsimony in human evolution: a critique of the Aquatic Ape Hypothesis. *Journal of Human Evolution* **33**: 479-94.

- Leakey, M. (1971) List of Identified Faunal Remains From Known Stratigraphic Horizons in Beds I and II. In L. Leakey (ed.), *Olduvai Gorge Volume 3 Excavations in Beds I and II, 1960-1963*, pp. 290-4. Cambridge: University Press.
- Leakey, M. & Harris, J. (1987) *Laetoli: A Pliocene Site in Northern Tanzania*, Oxford: Clarendon Press.
- Le Danois, E. (1959) *Fishes of the World*, London: George C. Harrap & Co.
- Lewis, M. (1997) Carnivoran paleoguilds of Africa: implications for hominid food procurement strategies. *Journal of Human Evolution* **32**: 257-88.
- Macdonald, D. (2001) *The Encyclopedia of Mammals*, New York: Facts On File.
- Maier, W. & Nkini, A. (1985) The Phylogenetic Position of Olduvai Hominid 9, Especially as Determined From Basicranial Evidence. In E. Delson (ed.), *Ancestors: The Hard Evidence*, pp. 249-54. New York: Alan R. Liss.
- Marchal, F. (2000) A new morphometric analysis of the hominid pelvic bone. *Journal of Human Evolution* **38**: 347-65.
- Martin, R. (1990) *Primate origins and evolution: a phylogenetic reconstruction*, London: Chapman & Hall.
- Meylan, P. (1987) Fossil snakes from Laetoli. In M. Leakey & J. Harris (eds.), *Laetoli: A Pliocene Site in Northern Tanzania*, pp. 78-82. Oxford: Clarendon Press.
- Morgan, E. (1972) *The Descent of Woman*, New York: Stein & Day.
- Morgan, E. (1997) *The Aquatic Ape Hypothesis*, London: Souvenir Press.
- Morwood, M. *et al.* (1998) Fission-track ages of stone tools and fossils on the East Indonesian island of Flores. *Nature*, **392**: 173-6.
- Morwood, M. *et al.* (2004) Archaeology and age of a new hominin from Flores in eastern Indonesian. *Nature* **431**: 1087-91.
- Moyle, P. & Cech, J. (1982) *Fishes: An Introduction to Ichthyology*, New Jersey: Prentice-Hall.
- Nishihara, T. (1995) Feeding Ecology of Western Lowland Gorillas in the Nouabale-Ndoki National Park, Congo. *Primates* **36(2)**: 151-68.
- Newman, R. (1970) Why man is such a sweaty and thirsty naked animal: a speculative review. *Human Biology* **42**: 12-27.

- O'Brien, E. & Peters, C. (1999) Landforms, Climate, Ecogeographic Mosaics, and the Potential for Hominid Diversity in Pliocene Africa. In T. Bromage & F. Schrenk (eds.), *African Biogeography, Climate Change & Human Evolution*, pp. 115-37. New York: Oxford University Press.
- Perrins, C. & Middleton, A. (1985) *The Encyclopedia of Birds*, New York: Facts On File.
- Pickford, M., Mein, P. & Senut, B. (1992) Primate bearing Plio-Pleistocene cave deposits of Humpata, Southern Angola. *Human Evolution* **7**: 17-33.
- Pagel, M. & Bodmer, W. (2003) A naked ape would have fewer parasites. *Proceedings of the Royal Society of London. Series B, Biological Sciences* **270 Suppl. 1**: S117-9.
- Reed, K. (1997) Early hominid evolution and ecological change through the African Plio-Pleistocene. *Journal of Human Evolution* **32**: 289-322.
- Ritchie, J. (1987) Trace fossils of burrowing Hymenoptera from Laetoli. In M. Leakey & J. Harris (eds.), *Laetoli: A Pliocene Site in Northern Tanzania*, pp. 433-38. Oxford: Clarendon Press.
- Roe, D. (1994) Summary and Conclusion. In M. Leakey (ed.), *Olduvai Gorge Volume 5 Excavations in Beds III, IV and the Masek Beds, 1968-1971*, pp. 299-309. Cambridge: Cambridge University Press.
- Roede, M., Wind, J., Patrick, J. & Reynolds, V. (eds.), (1991) *The Aquatic Ape: Fact or Fiction?* London: Souvenir Press.
- Rozzi, F., Walker, C. & Bromage, T. (1999) Early Hominid Dental Development and Climate Change. In T. Bromage & F. Schrenk (eds.), *African Biogeography, Climate Change & Human Evolution*, pp. 349-63. New York: Oxford University Press.
- Sands, W. (1987) Ichnocoenoses of probable termite origin from Laetoli. In M. Leakey & J. Harris (eds.), *Laetoli: A Pliocene Site in Northern Tanzania*, pp. 409-33. Oxford: Clarendon Press.
- Sauer, C. (1962) Seashore – Primitive Home of Man? *Proceedings of the American Philosophical Society* **106 (1)**: 41-7.
- Schagatay, E. (1996) *The Human Diving Response – Effects of Temperature and Training*, Lund: University of Lund.
- Schwartz, J. & Tattersall, I. (2003) *The Human Fossil Record: Volume Two*, Hoboken: Wiley-Liss.
- Semaw, S. *et al.* (1997) 2.5-million-year-old stone tools from Gona, Ethiopia. *Nature* **385**: 333-6.
- Shreeve, J. (1996) *The Neandertal Enigma*, New York: Morrow.

- Sikes, N. (1999) Plio-Pleistocene Floral Context and Habitat Preferences of Sympatric Hominid Species in East Africa. In T. Bromage & F. Schrenk (eds.), *African Biogeography, Climate Change & Human Evolution*, pp. 301-315. New York: Oxford University Press.
- Spencer, L. (1997) Dietary adaptations of Plio-Pleistocene Bovidae: implications for hominid habitat use. *Journal of Human Evolution* **32**: 201-228.
- Stedman, H. *et al.* (2004) Myosin gene mutation correlates with anatomical changes in the human lineage. *Nature* **428**: 415-8.
- Stern, J. & Susman, R. (1983) The locomotor anatomy of *Australopithecus afarensis*. *American Journal of Physical Anthropology* **60**: 279-317.
- Stewart, K. (1994) Early hominid utilization of fish resources and implications for seasonality and behaviour. *Journal of Human Evolution* **27**: 229-45.
- Tattersall, I. (1995) *The Fossil Trail*, Oxford: Oxford University Press.
- Tobias, P. (1976) African Hominids: Dating and Phylogeny. In G. Isaac & E. McCown (eds.), *Human Origins*, pp. 377-422. Menelo Park: Staples Press.
- Tobias, P. (2003) Twenty questions about Human Evolution. *Human Evolution* **18**: 9-64.
- Turner, A. *et al.* (1999) A Locality-based Listing of African Plio-Pleistocene Mammals. In T. Bromage & F. Schrenk (eds.), *African Biogeography, Climate Change & Human Evolution*, pp. 369-399. New York: Oxford University Press.
- Tuttle, R. (1987) Kinesiological inferences and evolutionary implications from Laetoli bipedal trails G-1, G-2/3, and A. In M. Leakey & J. Harris (eds.), *Laetoli: A Pliocene Site in Northern Tanzania*, pp. 503-20. Oxford: Clarendon Press.
- Verhaegen, M. (1987) Scientific Correspondence. *Nature* **325**: 305-6.
- Verhaegen, M. (1992) Did Robust Australopithecines Partly Feed on Hard Parts of Gramineae? *Human Evolution* **7**: 63-4.
- Verhaegen, M. & Munro, S. (2004) Possible Preadaptations to Speech. A Preliminary Comparative Approach. *Human Evolution* **19**: 53-70.
- Verhaegen, M. & Puech, P-F. (2000) Hominid lifestyle and diet reconsidered: paleo-environmental and comparative data. *Human Evolution* **15**: 151-62.
- Verhaegen, M., Puech, P-F. & Munro, S. (2002) Aquariboreal ancestors? *Trends in Ecology & Evolution* **17**: 212-7.
- Verdcourt, B. (1987) Mollusca from the Laetoli and Upper Ndolanya Beds. In M. Leakey and J. Harris (eds.), *Laetoli: A Pliocene Site in Northern Tanzania*, pp. 438-50. Oxford: Clarendon Press.

- Vignaud, P. *et al.* (2002) Geology and Palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad. *Nature* **418**: 152-5.
- Vrba, E. (1985) Ecological and Adaptive Changes Associated With Early Hominid Evolution. In E. Delson (ed.), *Ancestors: The Hard Evidence*, pp. 63-71. New York: Alan R. Liss.
- Vrba, E. (1995) The Fossil Record of African Antelopes (Mammalia, Bovidae) in Relation to Human Evolution and Paleoclimate. In E. Vrba, G. Denton, T. Partridge & L. Burckle (eds.), (1995) *Paleoclimate and Evolution, with Emphasis on Human Origins*, pp. 385-424. New Haven and London: Yale University Press.
- Walker, A. (1993a) Taphonomy. In A. Walker & R. Leakey (eds.), *The Nariokotome Homo erectus Skeleton*, pp. 40-53. Cambridge: Harvard University Press.
- Walker, A. (1993b) Perspectives on the Nariokotome Discovery. In A. Walker & R. Leakey (eds.), *The Nariokotome Homo erectus Skeleton*, pp 411-30 Cambridge: Harvard University Press.
- West, J., Fu, Z., Gaeth, A. & Short, R. (2003) Fetal lung development in the elephant reflects the adaptations required for snorkeling in adult life. *Respiratory Physiology & Neurobiology* **138(2-3)**:325-33.
- Wheeler, P. (1991a) The influence of bipedalism on the energy and water budgets of early hominids. *Journal of Human Evolution* **21**: 117-136.
- Wheeler, P. (1991b) The thermoregulatory advantages of hominid bipedalism in open equatorial environments: the contribution of increased convective heat loss and cutaneous evaporative cooling. *Journal of Human Evolution* **21**: 107-116.
- Wheeler, P. (1992) The thermoregulatory advantages of large body size for hominid foraging in savannah [*sic*] environments. *Journal of Human Evolution* **23**: 351-62.
- Wheeler, P. (1993) The influence of stature and body form on hominid energy and water budgets: a comparison of *Australopithecus* and early *Homo* physiques. *Journal of Human Evolution* **24**:13-28.
- Wheeler, P. (1994) The thermoregulatory advantages of heat storage and shade-seeking behaviour to hominids foraging in equatorial savannah [*sic*] environments. *Journal of Human Evolution* **26**: 339-50.
- Willis, J. (1966) *A Dictionary of the Flowering Plants and Ferns*, Cambridge: University Press.
- Wolpoff, M., Senut, B., Pickford, M. & Hawks, J. (2002) *Sahelanthropus* or 'Sahelpithecus'? *Nature* **419**: 581-2.
- Wood, B. (2000) The History of the Genus *Homo*. *Human Evolution* **15**: 39-49.

Young, E. (2004) The beast with no name. *New Scientist* **9 October 2004**: 33-35.

Young, J. (1981) *The Life of Vertebrates*, Oxford: Clarendon Press.

* Lists with more than five authors truncated

