Molluscs as ecological indicators in palaeoanthropological contexts

Thesis submitted by

Stephen James Munro

October 2010

For the degree of Doctor of Philosophy of

The Australian National University

I declare that, except where otherwise stated, this thesis is entirely my own work. All photos were taken during a research trip to museums and universities in May 2007.

Stephen James Munro

Acknowledgements

I'd like to acknowledge my panel of supervisors: Colin Groves, whose detailed knowledge of hominine taxonomy and primatology has been invaluable, Judith Caton, who offered valuable advice and encouragement, and Robert Attenborough, whose comments and suggestions have improved this thesis immeasurably.

Apart from my supervisors perhaps the most important people in shaping this thesis were those who attended the Turkana Malacology Workshop in the Netherlands in February 2006. These included organisers Hubert Vonhof and Craig Feibel, who allowed me to attend the workshop as an observer, Dirk Van Damme and Bert Van Bocxlaer, who allowed me to study collections at their laboratory at Ghent University, Belgium, and who also provided much assistance and constructive feedback, Henning Scholz and Matthias Glaubrecht, from Humboldt University, Berlin, who assisted me in viewing collections at the Humboldt Natural History Museum and have provided much important information in numerous discussions; Frank Wesselingh, Curator of molluscs at Naturalis, Leiden, who also offered great assistance and who allowed me to use his office and photographic equipment to document specimens from the Dubois Collection, and Jose Joordens for her advice and generosity.

Thanks to Ian McDougall who alerted me to the Turkana Malacology workshop, and John de Vos who allowed me access to the Dubois Collection at Naturalis, and other staff at that Museum. I'd like to also acknowledge Jonathan Wynn and Zeresenay Alemseged who allowed me to study samples they had collected at Dikika, Ethiopia, plus the director and staff of the Ethiopian National Museum for their kindness and assistance while studying the samples there.

Thanks to the Australian National University, who provided a scholarship, and the staff and students of the School of Archaeology and Anthropology, especially Dave McGregor and Liz Walters. I'd also like to thank Matthew Higgins, Mathew Trinca and Peter Stanley from the National Museum of Australia, where I was given the opportunity to complete this thesis on a Curatorial Fellowship at the Centre for Historical Research. Finally I'd like to acknowledge the enormous support of my family and friends, too numerous to mention.

This thesis is dedicated to the memory of my mother, who nurtured my love of natural history:
Marie-Louise Maidment-Laurent - 1941–1999.

Abstract

One method of investigating the palaeoecology of a site is to analyse the associated faunal remains. In palaeoanthropology faunal analysis is not uncommon, but on most occasions only a fraction of the overall fauna is analysed, often only large mammals. This discrepancy is addressed in this thesis. Here, the molluscan fauna from a range of sites is analysed from an ecological perspective, and the results compared to the palaeoecological results based on other faunal data, including, when available, small mammals, birds, reptiles, fish and amphibians. The aim of this study is to investigate whether the molluscs add anything to the overall palaeoecological picture of a site. The data are analysed from a palaeoanthropological perspective, with different hominine groups of sites compared from a palaeoecological perspective, based on the molluscan data. At the same time the value of molluscs as palaeoecological indicators is measured against data from other sources, such as other faunal data. The results show that molluscs are capable of adding important new and corroborating data that could be used to test established palaeoecological reconstructions of the past. The data support the idea that open habitats may have played an important role in the evolution of the genus *Homo*, but they also strongly suggest the presence of permanent water, whether in open or closed habitats.

Abstract

One method of investigating the palaeoecology of a site is to analyse the associated faunal remains. In palaeoanthropology faunal analysis is not uncommon, but on most occasions only a fraction of the overall fauna is analysed, often only large mammals. This discrepancy is addressed in this thesis. Here, the molluscan fauna from a range of sites is analysed from an ecological perspective, and the results compared to the palaeoecological results based on other faunal data, including, when available, small mammals, birds, reptiles, fish and amphibians. The aim of this study is to investigate whether the molluscs add anything to the overall palaeoecological picture of a site. The data are analysed from a palaeoanthropological perspective, with different hominine groups of sites compared from a palaeoecological perspective, based on the molluscan data. At the same time the value of molluscs as palaeoecological indicators is measured against data from other sources, such as other faunal data. The results show that molluscs are capable of adding important new and corroborating data that could be used to test established palaeoecological reconstructions of the past. The data support the idea that open habitats may have played an important role in the evolution of the genus *Homo*, but they also strongly suggest the presence of permanent water, whether in open or closed habitats.

Table of contents

Table of contents cont.

Table of contents cont.

Table of contents cont.

Table of contents cont.

Table of contents cont.

Table of contents cont.

Table of contents cont.

Table of contents cont.

List of Figures

List of figures cont.

List of figures cont.

List of figures cont.

List of figures cont.

List of figures cont.

List of Tables

List of tables cont.

List of tables cont.

1 Introduction

The past few decades have witnessed significant changes in the way researchers view the past, including human origins. These changes have been brought about by a combination of new technologies, new discoveries and new interpretations of old data. Advances in molecular studies, for example, have allowed researchers to compare the DNA of various human populations, including fossil species, to map likely phylogenetic pathways and to date speciation events. The development of dating technologies have allowed new chronologies of hominin dispersal events to be developed, challenging previously held models, and discoveries of new hominine genera such as *Sahelanthropus*, *Orrorin* and *Ardipithecus* have added much more detail to this early period of hominine evolution.

Perhaps the most unexpected recent discovery is that of the diminutive human fossil species *Homo floresiensis*, on the Indonesian island of Flores at a time when modern humans had already spread well past Wallace's Line into Sahul. Earlier and subsequent discoveries have confirmed that the island of Flores, east of Wallace's Line and therefore only reachable via a deep sea crossing, was first inhabited by hominins at least a million years ago (Brumm et al. 2010), much earlier than had previously been predicted.

While it was once thought that *Homo erectus*–like species were essentially modern human–like from the neck down, new discoveries and new interpretations of old material suggest this most probably is not the case. The idea that all early and middle Pleistocene hominin fossils could be placed in the single species *Homo erectus* has long been disputed.

While these advances in technology, new discoveries and new interpretations of old data have been important in challenging old ideas about human evolution, they have also introduced the need for new hypotheses to try to make sense of these new data and interpretations. This thesis, by focusing on a not previously well-studied area - the molluscs - aims to provide additional data to help evaluate and test hypotheses relating to human evolution.

1.1 Investigating the past

One way of better understanding human evolution is to reconstruct the type of ecological conditions human ancestors were exposed to at certain times in the past. Within the field of palaeoanthropology, various data have been used in an attempt to reconstruct the palaeoecological settings of early hominines. Anatomical studies of fossil bones, analysis of archaeological remains and genetic and molecular data, chemical analysis of bones and teeth, tooth wear analysis and pollen studies have all been employed to try to build a clearer picture of the types of habitats, environmental conditions and ecological characteristics human populations may have been exposed to during their evolution.

Analysis of the fauna associated with hominin sites has been used to reconstruct hominin palaeoecologies (Hernandez Fernandez & Vrba 2006). This approach looks at the fauna associated with a site and attempts to build a palaeoecological picture by comparing these with present day animals. The idea is that closely related or morphologically similar species will have similar ecological requirements. Although there are limitations to this method, it remains an effective way of interpreting past habitats. For example, if a fossil species resembles a modern species known to be a grazer, then it is a good indication that grasslands were present. In the same way, if species with arboreal adaptations are found at a site, it can be inferred that trees were present. This approach has limitations which are discussed in Chapter 2.

Faunal analysis in the context of palaeoanthropology is not uncommon. These studies have tended to focus on particular sub-sets of the fauna, often ignoring others. Vertebrates, for example, are more commonly employed in faunal analysis than invertebrates, and the most common vertebrates studied are usually mammals, especially large mammals. Micromammals, birds, reptiles and fish are less commonly studied in terms of palaeoecological reconstruction, as the following literature review shows.

1.2 Faunal analysis of hominine sites

When a new fossil or archaeological site is announced there is often also a description of the palaeoecology based on the make-up of the associated fossil fauna, often presented as a faunal list. These reports and lists vary in detail and scope and are too numerous to review completely here, but the following examples are as representative as I could find in my searches.

The report on the site of Asa Koma Member, a Late Miocene Middle Awash fossil locality, discusses the palaeoenvironment based solely on vertebrate faunal remains and only mammals are specifically referred to (WoldeGabriel et al. 2001). Su et al. (2009) examine the palaeoenvironment of sections of the Adu-Asa and Sagantole Formations, focusing their study on large mammals, with a few paragraphs dedicated to small mammals, fish and birds. No invertebrates are referred to, although invertebrates are known from these formations (WoldeGabriel et al. 2009).

Johanson et al. (1982), in their discussion on the palaeoenvironment of Hadar, refer primarily to the mammalian fauna, even though their taxonomic lists include birds, reptiles, fish and invertebrates. Alemseged et al. (2005), describing the palaeoenvironment of the Basal member of the Hadar Formation at Dikika, refer to mammals, fish and reptiles, but not to the gastropods that are reported in the stratigraphic section.

The palaeoecology of Kanapoi (*Australopithecus anamensis*) was discussed in palaeoecological terms by M.G Leakey et al. (1995). The discussion came under the heading 'palaeoecology and fauna', though the only faunal elements referred to are mammals. The paper notes that fish and reptiles were common at Kanapoi, but these are not identified or included in the faunal list, and nowhere in the paper are they discussed in detail. Invertebrates were also present at Kanapoi according to the section on geological context and dating, but these were not referred to in the discussion on palaeoecology.

The palaeoenvironment of Alia Bay from East Turkana is discussed by Coffing et al. (1994), who include fish, reptiles and mammals in their faunal list and these are also referred to in the discussion on possible environmental characteristics, but no invertebrates are referred to.

M.G. Leakey et al. (2001), announcing the discovery of the new hominid species *Kenyanthropus platyops* from Lomekwi, west of Lake Turkana, discuss the palaeoecology and fauna but refer to mammalian taxa only. No faunal list is included in the report, however, and therefore whether non-mammalian vertebrate or invertebrate remains were discovered is unknown.

In a review of the palaeoenvironments of Asian hominid sites, Pope (1989) analysed only mammalian faunal remains, whereas Huffman & Zain (2003), who studied the hominin site of Mojokerto, focused not only on the mammalian fauna but also non-mammalian vertebratetes such as fish and reptiles, as well as invertebrates, including freshwater and marine gastropods and bivalves. This latter study provides one of the more detailed accounts of the available resources and likely habitats available to ancient hominin species, painting a rich picture indeed of the palaeoecology (see Chapter 6.9).

Suwa et al. (2003) discuss the palaeoenvironmental implications of the mammalian fauna from the Konso site, southern Ethiopia, but make no mention of birds, reptiles, fish or invertebrates. In an article on the Pleistocene fauna of the Asbole site in the lower Awash Valley, Ethiopia, Geraads et al. (2004) list and discuss the mammalian but no other faunal data. Whether other non-mammalian fauna from Asbole are known is not clear, but gastropods were present according to the stratigraphic sections.

At Olduvai Gorge Fernandez-Jalvo et al. (1998) discuss the rodents in relation to the changing palaeoecological conditions that occurred over time in the region; a method which Vrba (1988) had previously employed using bovids.

Schrenk et al. (1995), in an overview of the palaeoecology of the Chiwondo Beds of northern Malawi, take into account vertebrate and invertebrate faunal remains. In this case the faunal list includes mammals, fish, reptiles, gastropods and bivalves, and all of these are given consideration when the palaeoecology of the Beds is discussed.

The Daka Member of the Bouri Formation, containing a fossil hominin identified as *Homo erectus*, is discussed within a palaeoecological context using mammalian fauna by Gilbert (2008a). Although non-mammalian vertebrates are known from the Daka

Member, these are not included in the palaeoecological discussion. Birds were rare within the Member, while fish remains were not collected (apart from one almost complete cranium of a catfish) and crocodile remains were also found but not collected (Gilbert 2008b). The Daka Member contains layers rich in gastropods and bivalves (WoldeGabriel et al. 2008), but these are not identified, not included in any faunal lists, and not referred to in palaeoecological discussions.

Stanley (1992) examined the fossil record of antelopes and micromammals associated with hominin sites, but did not include birds, reptiles, fish or invertebrates.

One of the best known and most widely cited studies on the palaeoecology of extinct hominines is that of Reed (1997), who used a combination of functional morphology and ecological structural analysis to reconstruct past habitats and likely environments. Reed's study was significant in that it employed a data set of 27 sites, one of the largest known. Such a comprehensive set allowed comparisons and contrast including to non-hominine sites. Reed's faunal data consisted of large mammalian fossil remains only.

1.3 Non-mammalian faunal analysis

The above review shows that mammals, and in particular large mammals, are on many occasions the only faunal component considered in palaeoecological reconstructions. Non-mammalian vertebrates such as birds, fish, amphibians and reptiles are more rarely included in faunal lists, and reference to them in palaeoecological discussions is also less common. Those that do use more faunal representations in the data set often also paint rich pictures of the fossil locality (e.g., Tchernov 1973, M.D. Leakey 1979, Feibel et al.

1991, Vignaud et al. 2002, Louchart 2008). Invertebrates are even rarer in terms of inclusion in faunal lists and reference in relation to palaeoecological reconstruction, though again there are numerous exceptions.

It is not difficult to understand why large mammals predominate in palaeoecological discussions; they are, after all, often the most likely faunal element to be preserved at a site, particularly certain skeletal parts such as the leg bones, jaws, horns and teeth. Birds, reptiles, amphibians, smaller mammals and fish generally have more fragile bones that are under certain circumstances less likely to preserve (Andrews et al. 1979), although crocodiles and ostriches are two obvious exceptions.

Taphonomic processes might be one reason why invertebrates are not generally studied from a palaeoecological perspective in palaeoanthropological contexts. Since they lack skeletal parts, evidence of many invertebrates comes from trace fossils. The body of a wasp, for example, is unlikely to preserve as a fossil, whereas wasp nests are probably much more common (Vignaud et al. 2002), as are the nests of termites (Darlington 2005). There is one group of invertebrates, however, that does have hard parts that fossilise readily: Molluscs, including especially bivalves and gastropods, have shells that can be preserved in great numbers, and are known from probably just as many sites as vertebrates.

Though often a significant component of the fauna in certain stratigraphic sections of hominine sites, molluscs have rarely been part of a large scale palaeoecological study, in which the molluscan fauna from various different sites are compared. Indeed, it is not unusual for hominine site reports to make no mention of the molluscan fauna, either in the faunal or palaeoecological sections, despite often featuring in the geological section or stratigraphic descriptions of the same publications (e.g., Gilbert & Asfaw 2008).

Molluscs have been used to date sites (Butzer et al. 1969), to establish characteristics of palaeohabitat through chemical analysis (Hailemichael et al. 2002), and as stratigraphic markers (Asfaw et al. 2002). Yet this potentially rich source of palaeoecological data is rarely utilised in palaeoanthropological contexts. Although it is known that there were bivalves and gastropods in the Hata, Daka and Herto Members of the Bouri Formation (WoldeGabriel et al. 2008), for example, it is not known what species, genus or even family these belonged to, because samples have not been collected, and therefore no reports, descriptions or identifications have been published. Reference to the molluscs appears in geological reports, but they are not listed in faunal reports or discussed in terms of palaeoecology.

Molluscs often have very specific ecological requirements and therefore have great potential to be used as tools to help reconstruct palaeoecologies. They also preserve well and are relatively easy to identify. Terrestrial gastropods are useful indicators of rainfall, temperature and vegetation patterns (Pickford 1995), and other mollusc species have been shown to be reliable indicators of freshwater systems (De Francesco & Hassam 2009). Molluscs can provide numerous data on habitat characteristics such as water depth and velocity and the presence of certain types of substrates, particualry compared to large mammals.

1.4 Primary objective

The primary objective of this thesis is to synthesise and analyse the various data that have been collected on the molluscs associated with hominine sites, as well as to add new data through original research. The goal is to investigate whether by studying these molluscs they can add data to the likely palaeoecological setting of the sites. The sites selected for the study are primarily, but not exclusively, those that are associated with the evolution of the genus *Homo*, specifically what Groves (2009) refers to as 'erectine grade' hominin populations, characterised by individuals with low, long, flat skulls and heavy supraorbital tori, including fossils commonly referred to as *Homo erectus*, as well as *Homo ergaster* and others such as *Homo georgicus* (see Section 2.3). This grade of hominin is important from a palaeoanthropological point of view because it marks the first appearance in the fossil record of a number of derived *Homo* features — such as external nose, large brain and loss of climbing features — as well as the dispersal of hominin populations to a wide geographical area including Europe and eastern Asia.

This thesis aims to extend the faunal data set for fossil and archaeological sites associated with the evolution of 'erectine grade' and other hominine fossils, so that they include not only vertebrates but also molluscs. The data set surveyed comes from a subset of sites that is one of the largest (33) known for studies of this kind. Turner et al. (1999) provide a larger set of sites (49), but this is restricted to mammals, and is presented as a set of data only, with no linked analysis or discussion.

The basic method employed in the study is to examine which sites associated with human evolution had associated mollusc fossil faunas, determine what taxa were present, and analyse what this reveals about the palaeoecology of hominine fossil and archaeological sites by comparing the known ecological traits of extant taxa to their fossil counterparts. The results are then compared to what was already known about hominine fossil and archaeology sites to determine the extent to which molluscs add information.

1.5 Palaeoecology

Palaeoecology is the study of ancient ecologies; the relationship between plants, animals and their environments. The palaeoecology of a species overlaps with but also differs in some respects from the palaeoenvironment of a species, in that it includes the interaction of various plants and animals, rather than just the physical environment. While palaeoenvironments include physical aspects of the habitats of a species, such as substrate, topography and climate, palaeoecology is concerned also with the interaction amongst organisms, such as predator-prey relationships, parasites, plant food availability and other aspects of the biosphere (Behrensmeyer et al. 2007).

Palaeoecology in the context of human evolutionary studies is often concerned with how open or closed (i.e., how forested) the palaeoenvironment might have been, how much grass cover there was, how dry the climate was, what bovid taxa were present etc. (see e.g., Stanley 1992, Vrba 1985). These ecological characteristics are important because human evolution is often seen as being associated with the opening up of previously forested landscapes (see e.g., Tappen 1995, Plummer et al. 2009, Cerling et al. 2010, White et al. 2010).

Researchers have also long focused on large mammal butchering sites and examined human palaeoecology from the perspective of answering questions about whether humans were more likely to have been hunting or scavenging large mammals (Harris 1992). While these questions too are important, it could be argued that placing too much emphasis on these aspects of the palaeoecology of humans might limit researchers' ability to properly appreciate other aspects of the palaeoecology, such as access to shelter and the availability of particular plant, non-mammalian vertebrate and invertebrate food resources.

In this thesis I attempt to expand the available palaeoecological data set, so that researchers can better ask, for example, what was the likely temperature of the region, the annual rainfall, was their marked seasonality, and what type of vegetation cover was there. These are all questions that might be more easily answered with a better understanding of the local molluscan fauna.

1.6 Hominine nomenclature and phylogeny

One basic problem in discussing human evolution is trying to identify within the fossil record which species belong to which clade. According to molecular studies the minimum divergence date of the lineages leading to *Homo* and *Pan* may be as recent as between ~3 and 5 Ma (Stauffer et al. 2001, Patterson et al. 2006, Hobolth et al. 2007). If this is correct then there must be some doubt as to whether species such as *Sahelanthropus tchadensis* (c. 6–7 Ma: Brunet et al. 2002), *Orrorin tugenensis* (c. 5.7–6 Ma: Senut et al. 2001), *Ardipithecus kadabba* (c. 5.5–5.8 Ma: Haile-Selassie et al. 2004) and even *Ardipithecus ramidus* (4.4 Ma: White et al. 2009) are ancestral to humans to the exclusion of chimpanzees (see e.g., Sarmiento 2010). In fact it is more likely that these fossil species are side-branches of the lineages leading to extant hominine species, but to which extant lineage they are most closely related, is probably difficult to determine without extracting molecular data, due to the fragmented nature of much of the fossil material and the effects of parallelism and convergence on evolutionary change.

In terms of hominoid taxonomy the terminology in this thesis is adapted from Groves (1989). Humans (genus *Homo*) belong to the primate superfamily Hominoidea, which also includes the great apes (*Pan*, *Gorilla* and *Pongo*) and the lesser apes (*Hylobates*, *Hoolock*, *Nomascus* and *Symphalangus*).

The Hominidae includes the great apes to the exclusion of the gibbons; that is humans, chimpanzees, gorillas and orang utans. The term hominid, sometimes used to describe fossil taxa belonging to descendants of the earliest human ancestors after the human-chimpanzee split, in this study describes all great apes (including *Pongo*) and their ancestors up until the time of the split from the lesser apes.

The Hominidae separated into two subfamilies: the Ponginae (orang utans); and the Homininae (humans, gorillas and chimps) most probably some time in the Middle Miocene. The African great apes and humans, therefore, are hominines, while orang utans are pongines.

The Homininae split some time in the late Miocene into the Gorillini (gorillas), and the clade that gave rise to the Panini (chimps and bonobos) and the Hominini (humans).

Members of the Hominini (genus *Homo*) are known as hominins, while the Panini (chimpanzees and bonobos) are panins and the Gorillini (gorillas) are gorillins.

Interestingly, almost every fossil hominine ever found in Africa less than c. 7 Ma is considered a hominin, with virtually no panins and very few gorillins recognised in the fossil record (Sarmiento 2010). The earliest fossil assigned to the tribe Panini is only 500 ka, discovered at a site at which fossil humans were also found, in the Rift Valley (McBrearty & Jablonski 2005). Other less well known and discussed examples of non-hominin hominine fossils include 6 Ma gorilla-like teeth from the same deposits from which *Orrorin* was discovered (Pickford & Senut 2005), and the apparently gorilla-like *Chororapithecus* from late Miocene deposits in Ethiopia (Suwa et al. 2007).

It is beyond the scope of this thesis to discuss the merits and limitations of the various hypotheses regarding the phylogeny and taxonomy of fossil hominine species, except to emphasise that hominine is used here to identify fossils that may be ancestral or related to ancestors of the three surviving genera of Homininae (*Pan*, *Homo*, *Gorilla*), and that hominin refers to fossil that are considered part of the human clade (e.g., *Homo erectus*). To avoid confusion, whenever possible I will refer to the specific fossils, e.g. *Homo ergaster* (KNM-WT 15000), or the locations (Daka, Sangiran, Sterkfontein Member 4).

In Chapter 2 the selected sites are presented along with the rationale for site selection, an overview of the material used in the study is put forward, and the method used to analyse the data is outlined and discussed.

2 Methods and material

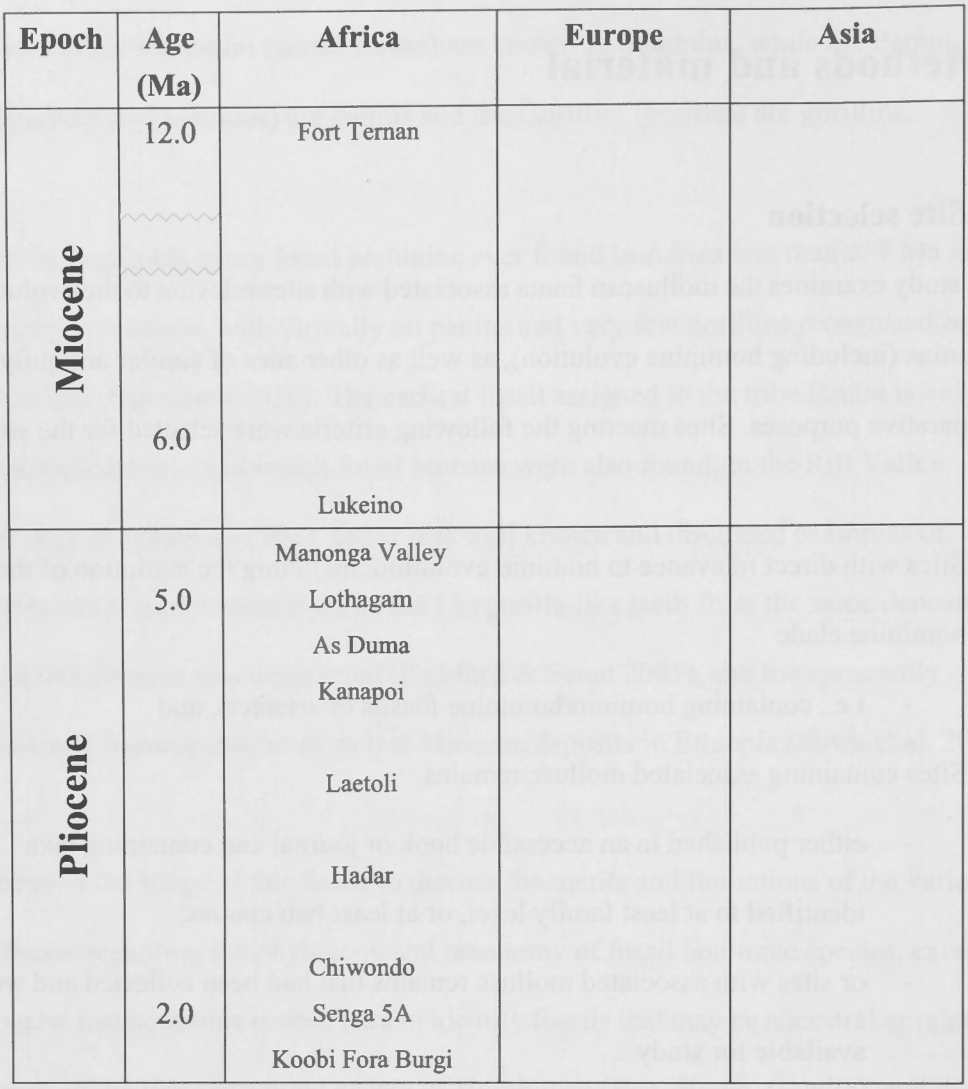
2.1 Site selection

This study examines the molluscan fauna associated with sites relevant to the evolution of hominins (including hominine evolution), as well as other sites of similar antiquity for comparative purposes. Sites meeting the following criteria were selected for the study:

1. Sites with direct relevance to hominin evolution, including the evolution of the hominine clade
    - i.e., containing hominin/hominine fossils or artefacts, and
2. Sites containing associated mollusc remains
    - either published in an accessible book or journal and containing taxa identified to at least family level, or at least two classes;
    - or sites with associated mollusc remains that had been collected and were available for study

A total of 29 sites meet those criteria and therefore were chosen for the study (Figures 2.1.1 & 2.1.2). Non-hominine sites were also included to allow comparisons between hominine and non-hominine sites. Non-hominine sites meeting the following criteria were selected:

1. Sites containing non-hominoid catarrhine (i.e., Old World monkey) fossil remains
2. Sites containing identified molluscan fossil fauna as per the above criteria
3. Sites in areas and times where hominines are thought likely to have been present



Epoch	Age (Ma)	Africa	Europe	Asia
Miocene	12.0	Fort Ternan		
	6.0			
		Lukeino		
Pliocene		Manonga Valley		
	5.0	Lothagam		
		As Duma		
		Kanapoi		
		Laetoli		
		Hadar		
		Chiwondo		
	2.0	Senga 5A		
		Koobi Fora Burgi		

Figure 2.1.1: Miocene and Pliocene sites included in the study arranged according to chronology and region

Two sites meet these criteria and therefore were included in the study: Manonga Valley, an early Pliocene east-African site containing cercopithecids but no hominines or artefacts; and Humpata, a Plio-Pleistocene south-west African site containing cercopithecids but no hominines or artefacts. One older site, Fort Ternan was included for comparative reasons. Fort Ternan, a mid-Miocene east-African site, has yielded hominoid remains of a number of taxa, but none that have been identified as members of the hominine clade.

Epoch	Age (Ma)	Africa	Europe	Asia
Pleistocene		Olduvai Gorge Bed I	Dmanisi	Pabbi Hills
	1.8	Koobi Fora KBS	Erk-el-Ahmar	Mojokerto
		Humpata		Nihewan
		Olduvai Gorge Bed II	Ubeidiya	Trinil
	1.0	Buia		Yuanmou
		Daka		
		Olorgesailie		
		Olduvai Gorge Bed IV		
			Pakefield	Soa Basin
	0.6	Bodo		
			Ceprano	
	0.18			
		Omo Kibish		

Figure 2.1.2: Pleistocene sites included in the study arranged according to chronology and habitat

The time frame of selected sites, mid-Miocene to mid-Pleistocene, brackets the origins of the genus *Homo*, and includes the emergence and dispersal of 'erectine grade' populations. Hominin sites include those that contain hominin fossils as well as those that include artefacts presumed to have been made by hominins. Other hominine sites are considered relevant to hominin evolution since hominins evolved from hominine ancestors, so that other hominines, if not ancestral to hominins, are at least closely related to the hominin clade. Hominine sites could include fossils not ancestral to hominins, but which are part of the larger clade to which hominins belong.

Sites such as Toros-Menalla (*Sahelanthropus*), Taung (*Australopithecus*) and Ain Hanech (early Pleistocene stone artefact site) are not included in the study because, even though they are relevant to hominine evolution, they have no molluscan faunal remains associated with them according to the published material. Although these sites do not contribute to the study's data set, they are nevertheless reviewed in Chapter 10. Sites such as Orce (Gibert et al. 2004), Longgupo (Huang et al. 1995) and Sahabi (Boaz et al. 1979), some of which contain molluscs and all of which have been claimed to have yielded hominine remains, are not included here because of concerns as to whether they are in fact hominine sites (White et al. 1983, Etler et al. 2001, Moya-Sola & Kohler 1997). These sites are also reviewed in Chapter 10. The site of Aramis, which meets the criteria for inclusion in this study, is not included because it was published after the sites for this study had already been finalised. It is instead reviewed and discussed in Chapter 10.

2.2 Material

The mollusc faunal lists were compiled through literature searches, by communications with researchers associated with particular sites, and by studying mollusc collections stored at Naturalis (The National Museum of Natural History), Leiden, The Netherlands, Museum für Naturkunde (Museum of Natural History), Berlin, Germany, Ethiopian National Museum, Addis Ababa, and Ghent University, Belgium.

Literature searches were conducted to determine whether mollusc remains were associated with a site, and in cases in which molluscs did exist, lists of the taxa present were compiled.

Collected assemblages were examined to determine which taxa were present. Morphological descriptions were made of each taxon and photographs were taken whenever possible.

At Naturalis collections from Trinil, Java were examined, at the Museum für Naturkunde, Berlin, collections from the Turkana Basin, Kenya, were examined, at Ghent University, Belgium, assemblages from Lukeino, Lothagam, Kanapoi, Hadar, Omo Kibish, the Turkana Basin and the Chiwondo Beds were examined, and at the Ethiopian National Museum an assemblage from Dikika, Ethiopia, was examined.

2.3 Methods

A number of methods of varying complexity can be used to interpret palaeoecologies using faunal data (Andrews 1995). Most of these rely on comparisons of fossil fauna with closely related extant forms. Reed (1997) identifies five distinct methods by which fossil fauna can be used to reconstruct some of the ecological characteristics of a site:

- Taxonomic uniformitarianism (e.g. Vrba 1974)
- Functional or ecological morphology (e.g. Bishop 1999)
- Species diversity indices (e.g. Rose 1981)
- Faunal resemblance indices (e.g. Van Couvering & Van Couvering 1976)
- Ecological structure analysis (e.g. Andrews 1989)

In this study a combination of taxonomic uniformitarianism, faunal resemblance, and ecological structural analysis are used to help determine the likely palaeoecological characteristics of a site. Since the available data are limited in many cases to the identification of specific taxa without abundance ratio data, species diversity indices are not always possible. Functional or ecological morphological methods rely on morphological descriptions or photographs, and since these are not consistently available for the data set in this study, this method can not be used comprehensively, though it is used for individual sites and taxa when available.

Although doubts have been raised as to whether extant taxa can be used as models to infer habitats for extinct relatives (Solounias & Dawson-Saunders 1988), these concerns are more likely to apply to taxonomic groups that have undergone periods of substantial morphological and habitat change (such as certain mammal lineages) than to more ecologically stable taxa such as molluscs, which have been shown to be reliable bioindicators of past environmental conditions (De Francesco & Hassan 2009). Indeed, this is an advantage of using molluscs as indicators of past ecologies rather than mammals such as bovids, for example, which have in some cases undergone significant evolutionary change over a relatively short period (Vrba 1999).

In order to compare the different sites, the molluscan taxa from each site are listed and information about the environmental and ecological requirements of closely related extant taxa are specified and discussed. Characteristics of the morphology, where relevant, are also considered from a palaeoecological view point. A preliminary reconstruction of aspects of the palaeoecology and palaeoenvironment of each site is presented based on the mollusc taxa present. These interpretations are examined in light of other data including, primarily, other faunal remains, as well as pollen, soil, geographical and geological studies.

A certain amount of caution is required when interpreting results of faunal analysis and palaeoecological reconstruction because of the various taphonomic processes which influence a sites faunal make-up. In an attempt to minimise the effects of taphonomic bias, each site is placed within a context which includes relevant taphonomic information, so that it can be determined how likely it was that a fossil assemblage derived from the actual location or from any distance away.

It should be noted too that the method used here, to compare fossil remains from different sites collected in different contexts, has a number of limitations. The study relies to some extent on published faunal lists of a particular member, but contextual information such as abundance ratios and collecting methods are not always available, and therefore some caution is needed when interpreting the results.

Taphonmy is another limiting factor in this type of study. The fossilisation process alone introducies some bias in the range of faunal communities available to sample. The listing of fauna for a stratigraphic member also means fine scale differences in stratigraphic horizons and facies might be overlooked, and restraint therefore is needed in assuming that all the animals at a site necessarily co-inhabited.

Following the individual site studies, a comparison of the molluscan fauna from each site is undertaken, involving direct comparison of the taxa associated with all sites in the study, with tables, graphs and discussion designed to highlight and analyse trends and correlations. In order to compare the various data, the molluscs and sites are divided into groups based on taxonomy (e.g. genus, family) as well as ecology, e.g.:

- Terrestrial/open
- Terrestrial/forested
- Amphibious
- Aquatic/freshwater
- Aquatic/marine

The sites are also divided into various sub-groups according to whether they are classified as:

- Non-hominine
- Non-'erectine grade' hominine
- 'Erectine grade' hominine

By dividing the sites and the molluscs into these groups it should be possible to compare the data to determine whether there are any similarities or differences in terms of the molluscan fauna associated with the various groups of sites. This could then lead to insights about the palaeoecological characteristics of the different groups of sites. The ecological data associated with the molluscs for each site can potentially provide information about the characteristics of a particular site, including temperature, type of vegetation, whether or not a water body was present, and if so, its salinity, depth, velocity and duration, as well as the types of vegetation and fish which may have been present and the likely substrates available.

Analysis and case studies, beyond the treatment given to sites analysed in Chapters 5–7, are provided for the sites of Dikika, from the Hadar and Busidima Formations in Ethiopia (Chapter 4). The Dikika molluscs come from samples associated with the juvenile fossil specimen *Australopithecus afarensis*, and have not previously been studied.

The present study attempts to draw inferences from the molluscan remains associated with deposits which have also yielded hominine fossil remains and artefacts. Since taphonomical processes influence the make-up of a fossil assemblage, a certain level of caution needs to be exercised when analysing data of this type. The presence of a molluscan taxon at a site can almost always be taken as confirmation that that mollusc existed in that location at the time of deposition, but the absence of a taxon does not necessarily mean that that taxon was absent. Although fossil faunal assemblages offer researchers sometimes only brief glimpses into the past, they nevertheless provide some of the best evidence for reconstructing past ecologies. Indeed, Behrensmeyer (1991) has argued that broad-scaled palaeoecological reconstructions based on the presence of taxa are likely to be accurate despite the taphonomic history of the assemblage.

In this chapter a rationale for how the sites in the study were selected has been put forward, as well as an explanation of how the molluscan data were collated and the methods used to synthesise and analyse the data. The following chapter reviews the mollusc taxa most commonly encountered in this study.

3 Molluscs associated with hominine sites

3.1 Introduction

Of the more than one million animal species that exist on Earth today, less than 5% are vertebrates, the other 95% being invertebrates (Anderson 1998). Yet as shown in Chapter 1, most palaeoanthropologists examining faunal remains in relation to palaeoecological reconstructions focus only on vertebrates. This is understandable to some extent given that vertebrates are usually larger and possess bones that are more easily fossilised in most cases than the soft tissue and fragile exoskeletons of most invertebrates.

Insects and other arthropods are rarely discovered at hominine sites, some exceptions being traces of burrows revealing the presence of termites at Laetoli (Darlington 2005), remains of dung beetle brood balls at Toros-Menalla (Vignaud et al. 2002), crabs at Hadar (Johanson et al. 1982) and various insect remains at Pakefield (Parfitt et al. 2005).

The Phylum Mollusca, unlike many other invertebrates, includes classes that have hard parts that fossilise readily, making them in some cases so visible and widespread in the fossil record that the beds in which their remains are found are sometimes used as stratigraphic markers (e.g., Taieb et al. 1976).

Molluscs have been found at numerous sites at which hominine and early hominin fossils and artefacts have been found, yet except for occasional reference in relation to taphonomy or chronology, these are rarely considered in terms of faunal presence or in the context of palaeoecology (see e.g., Fleagle et al. 2008). The molluscs most commonly associated with hominine sites in this study are gastropods and bivalves (a single scaphopod species is also known), and, probably due to the location of most of these sites, the molluscs are generally freshwater, amphibious or terrestrial, with marine taxa occurring at only a few sites.

This chapter reviews the ecological characteristics of the mollusc groups most commonly encountered at the sites in this study. It is not intended as a comprehensive overview of the phylum Mollusca, or as a definitive statement on the phylogeny, taxonomy or nomenclature of the molluscs. It is rather an introduction to the main taxa encountered within this study, giving an overview of their basic biology, including aspects of their reproduction, diet, habitat and habits. The overview focuses on aspects of the biology of each taxon that might be relevant in describing the palaeoecology of the sites at which they are found.

3.2 Molluscs

The phylum Mollusca is one of the most widespread and diverse groups of animals known. In general, molluscs have a body plan that contains a head, a ventral foot, a dorsal visceral mass and a shell secreting integument known as the mantle (Anderson 1998). They are predominantly marine creatures.

There are several classes of Mollusca including the Scaphopoda (tooth or tusk shells), Polyplacophora (chitons, with a shell composed of eight plates) and the Cephalopoda (octopus, squid etc.), the latter including species that lack an external shell and that have developed elaborate sense organs and jet propulsion, allowing them to hunt mobile prey. Although all classes of mollusc have marine representatives, and most are made up exclusively of marine species, there are two exceptions: The Bivalvia, which contain numerous freshwater as well as marine species; and the Gastropoda, which contain marine, freshwater, amphibious and terrestrial species. These two groups are well represented at hominine sites, and because they contain species which have specific requirements in terms of diet, substrate, physical environment, climate and other ecological factors, they are a potentially useful tool for investigations into palaeoecology.

3.3 Bivalvia

- **Introduction**

The Bivalvia, also known as the Lamellibranchia or Pelecypoda, are an abundant and diverse class, with over 8000 extant species and thousands of extinct species having been described. The shells of dead bivalves can be found littered over ancient and modern shorelines throughout the world.

- **Palaeontology**

The earliest bivalves known are Cambrian, but they became diverse in the early Ordovician, and much more common in the Mesozoic (like the gastropods). From the early Tertiary onwards bivalves became the dominant hard-shelled shallow marine fauna (Clarkson 1993). As discussed earlier, the vast majority of bivalves are marine, but there are also a few freshwater groups, most notably the Unionoida and some members of the Veneroida. There are no terrestrial bivalves.

- **Morphology**

Bivalve shells are extremely varied in shape, but typically they are laterally compressed, with two valves hinged together dorsally by elastic ligament and shell teeth. The shells are held shut by the use of adductor muscles. Bivalves have a rudimentary head without eyes and a foot which is typically laterally compressed, usually without a sole. Whereas all other classes of mollusc have a radula (an anatomical structure used for feeding), bivalves do not. Bivalves generally have a large mantle cavity, with the posterior edges of the mantle often fused to form inhalant and exhalant siphons (Brusca & Brusca 1990).

The ancestral bivalve was probably a burrowing form (infaunal — buried in sediment), whereas today there is a diversity of species including those that attach themselves to surfaces by flexible byssal threads, those that rigidly attach themselves to hard surfaces by cementation, or bore into rock, shells or wood, or simply rest on the surface of the sediment (epifaunal — living on the sediment). Other bivalves can swim using jet propulsion (Harper et al. 2000).

- **Taxonomy**

Bivalve classification has been in a state of flux for a number of decades and it is difficult to find any two authors who utilise exactly the same system of classification or nomenclature (Brusca & Brusca 1990). Difficulties in classification arise particularly when dealing with fossil species, because the soft parts (often the most useful and stable characters for identification) do not generally fossilise, and the shell microstructure can be difficult to determine because the aragonitic part has often recrystallised or dissolved. Parallel evolution can also cause difficulties in determining taxonomic relationships (Clarkson 1993).

Taxonomically stable characters include shell microstructure, dentition and (to some extent) hinge structure, gill type, stomach anatomy and the nature of the labial palps (Moore 1969). Shell shape is often closely related to life habits, and is therefore an unstable character for identification, useful only at lower taxonomic levels (Clarkson 1993). Since the focus in this study is on what molluscs can reveal about the palaeoecology of the sites at which they are found, ecological characteristics of each taxon are given precedence over precise nomenclature and phylogeny, though every effort has been made to present these accurately.

- **Ecology**

Bivalves are essentially aquatic animals, with no member of their class able to respire, feed or remain active outside water. Many species, however, are able to survive temporary periods of exposure to air; most notably intertidal mussels and oysters that sometimes spend several hours a day out of water. These species reduce moisture loss to a minimum by closing their valves hermetically (Moore 1969).

Bivalves are generally suspension feeders, although the superfamily Nuculoidea contains deposit feeders, which collect organic particles from the sediment, and the order Septibranchia are carnivorous. The suspension feeders can be grouped into seven ecomorphological categories (Clarkson 1993):

1) infaunal shallow burrowing
2) infaunal deep burrowing
3) epifaunal — attached by byssus threads to the substratum
4) epifaunal — cemented to the rock
5) free-lying
6) swimming
7) boring and cavity-dwelling

The bivalves associated with the sites in this study come most commonly from two Orders: The Unionoida and Veneroida.

3.3.1 Unionoida

The Unionoida, also known as freshwater or pearly mussels, or naiads (Figure 3.3.1), have specific habitat preferences, making them a useful source of palaeoenvironmental data (Warren 1991). They can be divided into two superfamilies: The Unionoidea and the Etherioidea. The former contains the families Unionidae and Margaritiferidae, while the latter contains four families: The Hyriidae, Etheriidae, Mycetopodidae and Iridinidae (Graf & Cummings 2007). These families contain a diversity of genera whose range together encompasses every continent except Antarctica.

Figure 3.3.1: Unionoid bivalve (naiad, freshwater or pearly mussel), genus *Chambardia*, Koobi Fora Formation (scale 10mm)

Although aerial dispersal by birds is theoretically possible for members of the Unionoida, their large size, dioecious reproduction and reliance on fish hosts during a larval stage of the life cycle, makes their chances of survival after transport less likely than some other molluscs. For this reason unionoid bivalves are generally characterised by relatively large, stable drainage systems, as opposed to transient water bodies which are more easily colonised by, for example, pisidiid clams (Burky 1983).

The parasitic stage of the Unionoida life cycle, which involves attachment by the glochidial (or lasidial in the Iridinidae) larvae onto a vertebrate (usually fish) host, limits the types of water bodies within which these mussels can survive, to those water bodies that can support and be traversed by specific types of fish. Fuller (1974) lists the hosts of some of the Nearctic unionids, including Salmonidae (salmon, trout), Cyprinidae (carp), Percidae (perch) and Ictaluridae (a family of North American catfish). During this stage of their life cycle, the mussels gain all of their nutrition from their host, and also disperse to wherever the fish may carry them. This means they can disperse upstream, but it also means they are blocked when the fish are blocked by travelling upstream, by waterfalls, dams and other impediments.

Although unionoid bivalves are often described as exclusive suspension feeders (Burky 1983), some studies suggest they may also deposit feed (Raikow & Hamilton 2001). The diet of unionoids includes detritus (Fuller 1972), as well as bacteria and micro-eukaryotes such as phytoplankton (Christian et al. 2004). Unionoids are generally shallow water inhabitants and, while they do not cope well in areas where macrophytes form too dense a cover (Burlakova & Karatayev 2007), their occurrence has been found to be correlated positively with certain macrophytes such as *Potamogeton*, the roots of which may provide a stable mud substrate for unionoid bivalves, and the stems of which may offer protection from predators (Korzeniak et al. 2004). The order Unionoida contains species that reside in the bottom sediments of permanent water bodies with adequately flowing water to allow feeding and dispersal, but not too rapid so that sediments are shifted and substrates disturbed or buried.

Order	**Superfamily**	**Family**	**Genus**
Unionoida			
	Etherioidea		
		Etheriidae	
			Etheria
		Iridinidae	
			Chambardia
			Iridina
			Pleiodon
			Aspatharia
	Unionoidea		
		Unionidae	
			Coelatura
			Unio
			Pseudodon
			Elongaria
			Lamellidens

Figure 3.3.2: Taxonomic diagram of the main superfamilies, families and genera of the order Unionoida encountered in this study

A number of Unionoida families contain genera that are associated with hominine sites including from the Unionidae and Iridinidae (Figure 3.3.2). The Iridinidae, an endemic African family, and Etheriidae are generally inhabitants of tropical freshwaters (Strayer

2008). The Unionidae appear in the African fossil record relatively recently compared to the Iridinidae, their entry into Africa possibly coinciding with the closure of the Tethys Sea, which brought Africa and Eurasia together (Kat 1987). Freshwater mussels occur most commonly in streams, rivers and lakes and have been an important food resource for human populations for millennia (Morrison 1942, Bowler et al. 1970, Parmalee & Klippel 1974, Waselkov 1987, Claassen 1998, Ersoy & Sereflisan 2010).

- **Life cycle**

Most members of the Unionoida have a parasitic larval stage which involves attachment of the larvae — of which there are two types: glochidia, associated with the Unionidea, and lasidia, generally associated with the Etherioidea — to a vertebrate host, usually a fish, although amphibians have also been shown to be successful, albeit very occasional, hosts (Watters & O'Dee 1998). After hatching from fertilized eggs, which are incubated within the parent shell in a brood pouch, the larvae are expelled and require contact with fish hosts to continue their life cycle. Although it was once though that chance encounters with fish were required for the larvae of mussels to infect a host, recent research reveals that at least some freshwater mussels have evolved various strategies to attract potential hosts to their larvae (Strayer et al. 2004, Grabarkiewicz & Davis 2008). The glochidia or lasidia, on contact with a fish host, attaches itself to the gills and generally becomes a cyst-enclosed parasite — the Iridinidae attaches via a tubular appendage forming a haustorium (Graf & Cummings 2006a) — extracting nourishment from the host.

Eventually, the larvae grow into minute complete mussels, at which stage they pierce the skin of the fish and drop to the bottom (Moore 1969). This reliance on fish hosts is important from a palaeoecological point of view, and therefore in the context of this study, because it implies that wherever unionoid or etherioid populations are found, there must also have been suitable fish hosts present.

- **Dispersal**

One advantage to the Unionoida of their parasitic larval association with fish is that it allows individuals to disperse against the flow of rivers and streams. The parasitic larval stage, therefore, as with parental care by brooding, can be seen as an adaptation to reproduction in the flowing waters of freshwater river and stream habitats (Graf & Cummings 2006b). Whereas marine bivalves release their gametes directly into the water where fusion can take place and prevailing currents facilitate dispersal, such a method employed in a freshwater river or stream would lead to the developing zygotes and veligers being transported back to salt water, to which freshwater mussels are intolerant.

Because of their reliance on fish hosts for distribution, unionoid bivalves are restricted to permanent drainage systems with a relatively longer duration than transient water bodies that last only seasonally or intermittently. Unable to cross terrestrial barriers and intolerant of salt water, unionoids and etherioids generally are strictly continental taxa confined to stable freshwater environments (Graf & Cummings 2006b). Once established within a drainage system unionoid and etherioid bivalves are able to disperse to any part of the system to which their fish hosts are able to navigate. This means natural barriers such as waterfalls or other impediments to fish movements will also affect unionoid and etherioid dispersal.

- **Shell morphology**

The shape of an individual unionoid shell can be influenced by the type of environmental conditions it is exposed to. Good (2004), for example, describes how high stream velocity can result in ecophenotypes of medium size, lanceolate form and with very thick shells, whereas low stream velocity ecophenotypes are of large maximum sizes, with ovate shell shape and thinner shells. Harman (1970) found that given the same general habitats unionoids living in warm waters generally grew faster and attained larger sizes than those living in cold waters. The type of substrate a mussel lives on can also influence its shell shape, with individuals living in sandy substrates generally more compressed, with thicker and bigger shells than those living in muddy substrates (Hinch et al. 1986). Species with shells marked by tubercles and ridges are more likely to come from lakes and rivers than small streams (Moore 1969). Scholz & Hartman (2007) note that the shape of unionoid bivalves, including their outline, can be strongly influenced by environmental factors, including were individuals are positioned in relation to the headwaters of a particular drainage system.

These factors are important from a palaeoecological point of view, and demonstrate that unionoid shell morphology can provide potential information regarding the palaeoecology of a particular site. In this study ecomorphological factors will be considered wherever possible, depending on the availability of morphological descriptions, photographs or access to original material.

- **Predators**

Unionoids, like many bivalves, are preyed upon by a diverse range of predators, including certain gastropods, fish, turtles, crabs, birds and mammals such as otters and rats (Smith 2001). They are also an important food resource for many modern human populations (Mitchell 1839, Van Damme 1984, Strayer 2008).

- **Etherioidea: Etheriidae**

One of the more distinctive families of unionoid bivalve is the Etheriidae, which contains a number of 'cementing' genera including *Etheria* (fresh water oysters), which are well known from a number of Plio-Pleistocene African fossil sites. Unlike the more common unionoid form, etheriids are inequivalve and irregular in shape (Figure 3.3.3). These 'oyster-like' bivalves are covered with a dark periostracum and can grow to very large size with lengths of more than 40cm being recorded for some individuals (Yonge 1962).

Instead of living within sediments of relatively slow flowing waters as most unionoids do, etheriids inhabit turbulent waters by cementing themselves to a hard surface. Unlike true oysters (Ostreidae) which usually attach by a specific valve, *Etheria* attaches by either valve. Attachment is accompanied by lateral compression and dorsoventral extension of the visceral mass and gills. The young postlarval bivalve enters a crevice and attachment by periostracal adhesion occurs (Yonge 1962).

Figure 3.3.3: Internal and external view of an *Etheria* valve, Lothagam (scale 10mm)

- **Taxonomy**

Within the Etheriidae four genera are recognised: *Etheria* (cemented bivalve from Africa), *Acostaea* (a South American cemented bivalve), *Bartlettia* (a crevice dwelling bivalve from South America) and *Pseudomulleria* (a cemented bivalve from India) (Graf & Cummings 2007). Although there have been claims based on DNA comparisons that the Etheriidae do not form a monophyletic clade (Bogan & Hoeh 2000), more recent analysis suggests the Etheriidae is monophyletic (Graf & Cummings 2007). Cementation in the Unionoida appears to have arisen at least twice (Graf & Cummings 2007).

- **Ecology**

Etheriids generally require swiftly running water, probably comparable with the actual Omo River today. They are widespread throughout tropical Africa including the basins of the Nile, Lake Tanganyika, Lake Victoria, Lake Chad, the Niger and Senegal, parts of the rivers of Angola, and in north Madagascar. In the Congo River *Etheria* shells have been found in association with the rocky sections of rapids and the waterfalls of fair-sized streams, forming banks in stony and generally turbulent places, often three metres and more below the surface (Yonge 1962). Where extensive reefs occur they are indicative of large rivers with considerable water flow, even during dry seasons, though *Etheria* can also occur in smaller aggregates in lakes, or loose single specimens, in which case they develop large spines on both valves (Van Bocxlaer & Van Damme 2009).

Etheria is collected for its meat in certain regions of the Congo (Pain & Woodward 1961), and eaten usually after drying and smoking (Yonge 1962). Van Damme (1984) also reports that *Etheria* were collected for food by the Bakongo and Mangbetu along the Congo River.

- **Fossil record**

Etheria is known from the Miocene and Plio-Pleistocene of Africa (Van Damme 1984). It is possible that the turbulent habitats that freshwater oysters prefer may have made it less likely that their fossils have been preserved (Yonge 1962). Feibel et al. (1991) note that *Etheria elliptica* (an indicator of perennial water flow) has been found in fluvial deposits of the Turkana Basin. Henning Scholz (personal communication) cautions that while *Etheria* reefs occur in the Turkana Basin their stratigraphic history is sometimes difficult to determine, because of their habit of cementing onto hard surfaces. It is possible, for example, that they might cement themselves to ancient shell beds, giving the appearance that they are as old as the particular shell bed they are cemented to, whereas they may be considerably younger.

3.3.2 Veneroida

The order Veneroida includes mainly marine bivalves, but also groups which have evolved brackish and freshwater varieties, including the superfamily Corbiculoidea, which contains the families Corbiculidae and Sphaeriidae, which contain genera found at a number of hominine sites (Figure 3.3.4).

- **Corbiculidae**

The Corbiculidae are a family of infaunal suspension feeders known variously as fingernail and pea clams. One of the most widespread genera is *Corbicula* (Figure 3.3.5), whose native range encompasses tropical and sub-tropical regions throughout Africa, mainland Asia, the Malay Archipelago, the Philippines, New Guinea and eastern Australia (Morton 1986). It is an important component of the benthic community of both lotic (flowing) and lentic (stagnant) environments (McMahon 1983).

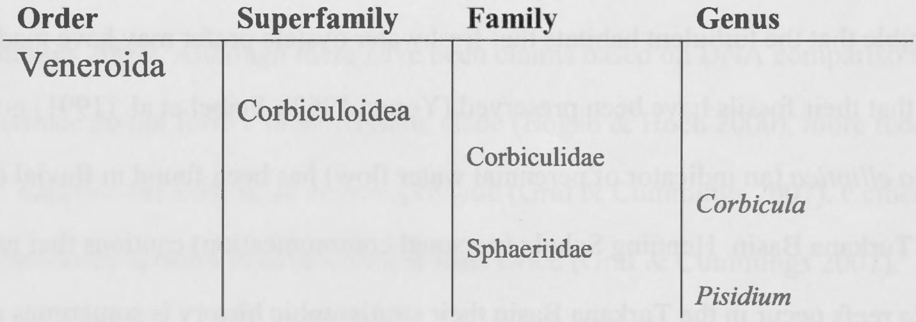


Figure 3.3.4: Taxonomic diagram of the Veneroida families and genera commonly found in this study

Corbicula is probably a relatively late addition to the molluscan fauna of Africa, dating to the mid to late Pliocene (Van Damme 1984). It is not found in the lower zone of the Omo Group (Gautier 1976), and first appears in the lower Burgi Member (late Pliocene), in the Koobi Fora Formation (Williamson 1982). Recently it has been introduced to North America where it has become an invasive pest because of its ability to tolerate various different ecological circumstances, and it has also invaded a number of European waterways (Ciutti & Cappelletti 2009).

- **Habitat**

The genus *Corbicula* can inhabit a wide variety of substrata including bare rock, loose gravel, sand, and even silts and muds, but achieves its highest population density and greatest success in well-oxygenated substrates such as coarse sand, gravel or sand-gravel mixtures.

Corbicula africana is restricted to flowing waters or shallow lakeshore habitats it tropical and sub-tropical regions (McMahon 1983), while *Corbicula fluminalis* is an estuarine species common in the open water riverine portions of large estuaries such as that of the Pearl River in China. *Corbicula* has a preference for sandy, well oxygenated sub-strata and flowing water, and a high tolerance for salinity fluctuation but not for fluctuations in temperature (McMahon 1983). The preference of *Corbicula* species in general is for well oxygenated sandy strata, meaning that in lakes and other generally lentic environments it is usually restricted to shallow near shore waters and well oxygenated sediments. *Corbicula* is relatively intolerant of exposure to air and cold waters (McMahon 1983).

Figure 3.3.5: *Corbicula* from the Burgi Member of the Koobi Fora Formation (scale 5mm)

- **Life cycle**

Within the Corbiculidae a wide range of reproductive strategies is known, from development via free swimming veliger larvae, to prolonged incubation of juveniles, and even within the genus *Corbicula* a variety of strategies are known (Korniushin & Glaubrecht 2003). Viviparity within the corbiculids has evolved independently on at least one occasion, and both oviparity and euviviparity are known to exist within the genus *Corbicula* (Glaubrecht et al. 2006). The freshwater *Corbicula fluminea*, a brooding species, releases highly advanced benthic juveniles that bypass the free swimming larval stage. When released, the juveniles sink and settle on the substratum, using their foot to crawl. They can anchor themselves to the substratum with a mucilaginous byssal thread that facilitates burrowing and resists against passive current dispersal (McMahon 1983). On the other hand the brackish water *Corbicula fluminalis* develops via a free swimming larval stage. There is some speculation as to whether this diversity of lifecycle processes in the Corbiculidae is caused by the wide ecological spectrum of the family (Korniushin & Glaubrecht 2003). In terms of palaeoecology at least some of these reproductive strategies provide opportunities for rapid colonization and population growth (Byrne et al. 2000).

- **Predators**

The Corbiculidae are a major food resource for a variety of fish, including carp and catfish, as well as crayfish, birds and raccoons (McMahon 1983, Sickel 1986). They are a good source of protein and are utilised extensively as both a human and domestic animal food resource in Southeast Asia, where they are today the subject of intense aquaculture (McMahon 1983).

- **Sphaeriidae**

The family Sphaeriidae in the order Veneroida contains some of the smallest known bivalves (fingernail clams). They have a worldwide distribution (except Antarctica) and are almost totally restricted to freshwater habitats with only a few species able to tolerate slightly brackish water conditions in estuaries (Korniushin 2002). They often dominate in small springs, swamps and temporary pools, where they are largely responsible for the quality of water (Korniushin & Glaubrecht 2002).

The genus *Pisidium* also has a worldwide distribution (Korniushin & Glaubrecht 2002), and is characterised by small, colourless, orbicular bivalves, usually less than a centimetre long, and these are found burrowing shallowly in nearly all types of freshwater habitats (Morton 1979). It is likely that sphaeriid clams can disperse between unconnected waterways by the attachment of newborn clams to the legs of insects and the legs and feathers of birds (Burky 1983). Only one of these hermaphroditic and viviparous clams is necessary to establish a new population and since they are smaller than unionoids and don't have a parasitic stage, they are much better suited to establishing populations in relatively small transient bodies of water (Burky 1983). This is important from a palaeoecological perspective since the presence of these bivalves and the absence of unionoids could indicate the presence of an unstable, relatively newly formed or even ephemeral water body.

While bivalves are one of the few mollusc classes to have adapted to freshwater as opposed to marine habitats, there is only one class of mollusc that has invaded terrestrial habitats: The Gastropoda.

3.4 Gastropoda

The class Gastropoda comprises between 40 000 and 100 000 extant species (Brusca & Brusca 1990, Ponder & Lindberg 1997) and these include all marine, freshwater and terrestrial snails and slugs. Because many gastropods have a hard external shell, they are not uncommon in fossil assemblages, and since individual gastropod taxa have specific ecological requirements they are an important potential indicator of past environments (De Francesco & Hassan 2009).

Gastropods are asymmetrical molluscs with a true head more or less continuous with the elongated body. They usually have tentacles, eyes and other sense organs, including a mouth with a rasping jaw (the radula) composed of a multitude of tiny teeth which scrape against a horny upper plate. Some gastropods have a tubular extension of the mouth, called a proboscis. Gastropods feed in a variety of ways, some for example being carnivorous, feeding on the flesh of other gastropods or bivalves after drilling a neat, round hole by rasping away at the shell and injecting a muscle relaxant so that the shell can be opened. Many gastropods feed on detritus or decayed material (Clarkson 1993), and others are feeders on macrophytes and terrestrial vegetation.

- **Taxonomy**

For a number of years the Gastropoda were divided into three subclasses: The Prosobranchia, Opisthobranchia and Pulmonata. Anderson (1998) recognised only two subclasses, the Prosobranchia and the Heterobranchia. Ponder & Lindberg (1997), on the other hand, recognised two alternative subdivisions of the Gastropoda, the Orthogastropoda and Eogastropoda, rejecting the Prosobranchia as a polyphyletic taxon.

Clade	Clade/Informal Group*	Superfamily	Family	Genus
Neritimorpha				
	Cycloneritimorpha			
		Neritoidea		
			Neritidae	
				Theodoxus
Caenogastropoda				
	Sorbeoconcha			
		Cerithioidea		
			Thiaridae	
				Melanoides
	Architaenioglossa*			
		Ampullarioidea		
			Ampullariidae	
				Pila
		Viviparoidea		
			Viviparidae	
				Bellamya
Heterobranchia				
	Basommatophora*			
		Lymnaeoidea		
			Lymnaeidae	
				Lymnaea
		Planorboidea		
			Planorbidae	
				Bulinus
	Stylommatophora			
		Achatinoidea		
			Achatinidae	
				Achatina
			Subulinidae	
				Homorus

Figure 3.4.1: Taxonomic classification of molluscs (based on Bouchet & Rocroi 2005)

While the Prosobranchia is no longer valid in terms of phylogenetic groupings, as a descriptive term 'prosobranch' remains useful in differentiating gastropods with gills from 'pulmonate' gastropods which have lungs. Here, I follow as closely as possible the classification of Bouchet & Rocroi (2005, Figure 3.4.1), while acknowledging that the classification of the gastropods remains in a state of flux.

The classification system of Bouchet & Rocroi (2005) uses unranked clades below the class level and above the level of superfamily, and these include the Neritimorpha, Caenogastropoda and Hertobranchia.

3.4.1 Neritimorpha

The Neritimorpha includes the clade Cycloneritimorpha, which includes the family Neritidae containing the genus *Theodoxus* (Figure 3.4.1). This mainly European snail is found in a variety of water bodies and includes species such as *Theodoxus niloticus* which inhabits slow flowing rivers (Tchernov 1973), as well as species that inhabit more open turbulent water bodies, and species such as *Theodoxus jordani* which inhabits lentic water bodies (Brown 1980).

Tolerant of both fresh and brackish water, *Theodoxus* is also found in habitats with rocky bottoms (Preston 1915). Although this genus generally lives in gently running freshwater, it has given rise to a number of species that live in fast streams with the shell flattened and elongated (Morton 1979). Plaziat & Younis (2005) remark how exceptionally widespread this genus is in lakes, marsh channels, fluviatile channels and estuaries of southern

Mesopotamia. Its distribution suggests an association with the breakup of the ancient Tethys Sea (Bunje & Lindberg 2007).

3.4.2 Caenogastropoda

The clade Caenogastropoda includes more than 85 families containing mainly marine species, though a number of clades in the group also contain freshwater genera. For example the Sorbeoconcha contains the widespread family Thiaridae, the Architaenioglossa contains the Ampullariidae and the Viviparidae, and the Littorinimorpha contains the Bithyniidae.

- **Thiaridae**

The Thiaridae is a family of viviparous snails from the superfamily Cerithioidea that inhabit freshwater and brackish water bodies in tropical and sub-tropical regions worldwide (Glaubrecht 2006). Dispersal of the species in this family is facilitated by the fact that they are all parthenogenetic, so only a single individual is needed to colonise a new area. Although known to inhabit lentic habitats, the Thiaridae are often associated with lotic (flowing) waters and their shells can often be seen to reflect that, being well sculptured. One of the most widespread genera in this family is *Melanoides*.

  - ***Melanoides***

Probably the most common thiarid in this study, *Melanoides* is native to a large part of tropical Africa, the eastern Mediterranean, India, Southeast Asia, Malaysia, southern China, north to the Ryukyu Islands of Japan and south and east through the Pacific Islands to northern Australia and the New Hebrides (Pace 1973). It has a distinctive high, often slender spiral with transverse and vertical ridges forming tubercles (Figure 3.4.2). Recently the species *Melanoides tuberculata* has been introduced into Florida and is now widely distributed throughout that state and is also now known in South America, demonstrating its abilities to successfully colonise new regions.

- **Habitat**

Melanoides has been found living in a wide variety of mainly freshwater habitats, including shallow seepage, irrigation channels, streams, rivers and lakes. It is absent from habitats that regularly dry out, but tolerant of moderate salinity (Brown 1980). It is known to inhabit both lentic and lotic waterways and is found in waterways where other species are unable to survive: "The Awash River itself is inhospitable for most molluscs because of its irregular flow and heavy silt load, and apparently *Melanoides tuberculata* is the only gastropod tolerant of these conditions" (Brown 1980: 311).

In a study by Supian & Ikhwanuddin (2002), *Melanoides tuberculata* was found in abundance and dominated the fast flowing upper and middle parts of the Mahua stream in Malaysia; in the Baiayo River it dominated the middle stream, being less frequent, though still abundant in the upper stream. Both these rivers flow over rock and gravel beds. They are shallow and fast flowing with many rapids. Boulders and rocks mostly line the riverbanks and both rivers are generally clear.

- **Morphology**

Melanoides has a medium to large sized shell, reaching 50mm in height, with a high slender spire and characteristic sculpturing or transverse ridges and tubercles. The cosmopolitan species *Melanoides tuberculata* is viviparous and parthenogenetic, though some isolated populations in the Levant have been found to include males (Livshits et al. 1984).

3.4.2: *Melanoides* specimens from different Formations of the Dikika region, Ethiopia (scale 5mm)

- **Distribution and ecology**

Of the about thirty *Melanoides* species recognised in Africa, only *Melanoides tuberculata* is widespread, the majority of other species being restricted to Lake Malawi and the Congo Basin (Brown 1980). *Melanoides tuberculata* is infrequently encountered in West Africa and virtually absent from the Congo Basin (Ndifon & Ukoli 1989).

The dispersal of snails into newly established water bodies appears primarily to occur through flooding, although birds and human agency (Wright 1977) are also likely to play a role (Ndifon & Ukoli 1989). An association between certain snails, including *Melanoides*, and various aquatic or sub-aquatic macrophytes has been suggested by some studies (Ndifon & Ukoli 1989).

Melanoides tuberculata is usually associated with environments of low salinity, but can tolerate salinities of up to 23% (Plaziat & Younis 2005). It dwells on sub-aquatic soft bottoms, often concealed in the sediment where its sinuous track is a characteristic token of its presence in freshwater lakes. Empty shells float easily and consequently accumulate on the shores of lakes. Strongly affected by water flow and rainfall distribution, *Melanoides tuberculata* has low reproduction rates, low mortality rates, and a long life span (Giovanelli et al. 2005).

- **Ancestry**

Melanoides, according to Tchernov (1973), was part of an ancient group which inhabited the eastern periphery of the Miocene Tethys Sea. *Melanopsis* and *Melanoides* are widespread today in many isolated springs including in the desert. Most of the Jordan Valley was part of the Tethys during the Pliocene.

- **Viviparidae**

The Viviparidae are a family of relatively large freshwater snails, found world wide except in South America, in temperate and tropical zones. The family includes the genus *Bellamya*, common to tropical freshwater habitats of Africa and Asia including lakes, rivers and slowly running streams, but never habitats that regularly dry out (Brown 1980, Balaparameswara Rao & Subba Rao 1985). Medium sized with dextral shells, generally with a conical spire and circular aperture (Figure 3.4.3), *Bellamya* are viviparous, with the female carrying the developing young in the lower part of the oviduct.

The Viviparidae are known to feed on a wide selection of food resources. Brown (1980) reports they can graze on algae growing on any submerged surface, as well as being detritivorous (feeding on fine particulate organic matter and the bacteria and microorganisms within). They also filter feed on suspended matter, competing with clams and mussels. Some species of this family are regularly consumed by human populations, but they can also act as intermediate hosts for trematode worms including *Echinostoma*, leading to infection in humans if the snails are not properly cooked (Sulianti 2008). These snails are also preyed upon by fish, birds, mammals and other molluscs.

Figure 3.4.3: *Bellamya* from the Galana Boi Formation, Turkana Basin (scale 10mm)

- **Ampullariidae**

The Ampullariidae are a family of tropical and subtropical freshwater snails, unable to tolerate winter temperatures of less than ten degrees. Genera of this family include *Lanistes* and *Pila*, both genera often associated with marshes or swamps. They have dextral shells and are typically medium to very large in size (figure 3.4.4). Due to their ability to breathe air and to close the aperture, *Pila ovata* is common to temporary water bodies in some regions, able to tolerate periods of dryness (Beadle 1981). These snails often inhabit papyrus swamps in East Africa, and are abundant on stony beaches in Lake Victoria (Brown 1980). They are common in the mat or in anoxic pools of water in the dense papyrus swamps of Uganda (Beadle 1981). They are a popular food resource in Africa and Asia and commonly occur in lentic situations.

Unlike many other snails, the Ampullariidae are either male or female, so that at least two individuals are needed for reproduction. They generally lay their eggs above the waterline, although *Pila ovata* from Lake Victoria deposits egg clusters amongst stones or within crevices in the earth (Brown 1980), whereas *Lanistes* deposits its eggs on aquatic vegetation (Van Damme 1984).

Figure 3.4.4: *Lanistes* from the Galana Boi Formation, Turkana Basin (scale 10mm)

3.4.3 Heterobranchia

The Heterobranchia is one of the main clades of the Gastropoda, and includes the largest number of species of any clade, including marine, freshwater and terrestrial inhabitants. It is divided into three informal groups: The lower Heterobranchia, Opisthobranchia, and Pulmonata.

- **Pulmonata**

The Pulmonata is an informal group which consists of terrestrial and amphibious gastropods. The taxa belonging to the latter group are secondarily freshwater dwelling, having shifted from their original aquatic existence, to a more terrestrial existence, back to a more aquatic existence (McMahon 1983).

- **Anatomy/morphology**

Pulmonate gastropods do not possess gills, and since the whole mantle surface acts as a lung it needs to be kept permanently moist. Most pulmonates have retained the ancestral mollusc shell, although most slugs have lost it or retain a reduced internal shell. Pulmonates generally do not have an operculum.

- **Ecology**

Water dwelling pulmonates are generally able to tolerate greater variations in temperature than prosobranch gastropods, which characteristically inhabit larger, more stable bodies of water. In order to survive periods of forced aerial exposure, pulmonates burrow into cool, moist substrates, or inhabit areas of dense vegetation (McMahon 1983).

Important as a potential food resource and used as ornaments by some human populations today, certain pulmonates such as *Biomphalaria* and *Bulinus* are also known to be intermediate hosts of parasites such as *Schistosoma*, which can infect humans and domestic animals who enter waters where they live (Brown 1978). The Pulmonata clade is divided into two informal groups: The Eupulmonata, which includes the Stylommatophora, and the Basommatophora.

- **Basommataphora**

- **Ancestry**

Whereas the freshwater Bivalvia and gill-bearing ‘prosobranch’ gastropods are descendants of marine ancestral forms, the freshwater pulmonates of the suborder

Basommatophora appear to have readapted to aquatic life from a more terrestrial existence.

- **Ecology**

Because these gastropods breathe air, they necessarily exploit mainly the edges of rivers and lakes where waters are shallow, rarely descending below four metres. They also inhabit small and temporary ponds, marshes and streams, where water fluctuations are common and desiccation is sometimes experienced (McMahon 1983).

Basommatophora are essentially benthos of the euphotic zones, and thus marginal in most lakes. In lotic habitats they generally live on rocks, or other hard surfaces, whereas in lentic (stagnant water) habitats they are usually found in greater densities living on emergent or submerged plants. They do not appear to feed directly on these plants, however, consuming instead the *aufwuchs* which coat these substrates in suitably lit depths (Russell-Hunter 1978).

The hermaphrodite Basommatophora produce eggs and sperm simultaneously and can self-fertilise, although the presence of copulatory organs in some populations appears to allow cross fertilization (Brown 1980). Due to their ability to survive periods of dryness, and because gulls, geese, reedbirds, waders and insects such as water beetles are all capable of acting as agents for dispersal, pulmonate gastropods are often the only mollusc species inhabiting transient water bodies (for a review of aerial dispersal methods in molluscs see Wesselingh et al. 1999).

Freshwater bodies, unlike seas and oceans, are transient, and exhibit a high degree of small-scale, short-term isolation. The transient nature of most freshwater environments, resulting in a high degree of short term, small scale isolation of populations, results in rates of evolutionary change which are very different from the evolution of similar animals in marine or terrestrial habitats, and even in the few ancient lakes of unusual permanence (Russell-Hunter 1978). Some freshwater drainage systems, however, are relatively long lived compared to the temporary pools that can form due to seasonal or occasional flooding events, and it is these ephemeral water bodies that pulmonate gastropods, of all the molluscs, are best suited to exploit.

From a palaeoecological point of view this is important because the presence of pulmonate gastropods within a fossil assemblage to the exclusion of bivalves or prosobranch gastropods could indicate a water body of a temporary nature, which could reflect seasonal rainfall patterns.

There are many families belonging to the Basommatophora, including two that are common to a number of sites in this study: the Planorbidae and Lymnaeidae.

- **Lymnaeidae**

The Lymnaeidae contain a number of genera of small to large freshwater pulmonates, including some that are common to a number of hominine sites including the genus *Lymnaea* (Figure 3.4.5).

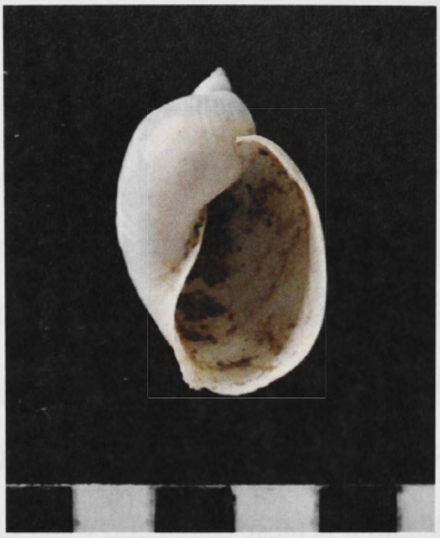


Figure 3.4.5: *Lymnaea* from the Dikika region, Ethiopia (scale 5mm)

This genus has a small to medium sized dextral shell with a pointed spire generally not much higher than the aperture. Species of this genus, such as *Lymnaea natalensis*, are commonly found in permanent water bodies, including reservoirs and drains, and can survive in very shallow water that is constantly seeping, but rarely in seasonally filled pools. They have a high requirement for oxygen and a general intolerance of desiccation, though aestivation up to six months has been reported (Brown 1980). *Lymnaea* can lay more than a hundred eggs in a capsule at a time.

- **Planorbidae**

The Planorbidae form a large family of small to medium sized mainly freshwater pulmonates that include the characteristic subfamily Planorbinae of discoid gastropods such as the genera *Biomphalaria* (Figure 3.4.6), *Gyraulus* and *Planorbis*, and the subfamily Bulininae, which includes the genus *Bulinus*.

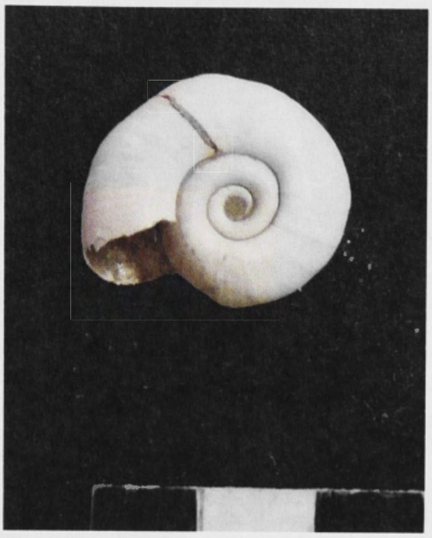


Figure 3.4.6: *Biomphalaria* from Dikika, Ethiopia (scale 5mm)

- ***Gyraulus***

Gyraulus is a small discoid planorbid that is most often associated with aquatic vegetation, marginal grass or stones in slow flowing rivers. It is found in streams, large dams and lakes. *Gyraulus* is usually absent from habitats which regularly become dry.

- ***Bulinus***

Bulinus is a medium sized gastropod with a sinistral shell possessing a highly variable spire in terms of shape and height relative to the aperture (Figure 3.4.7).

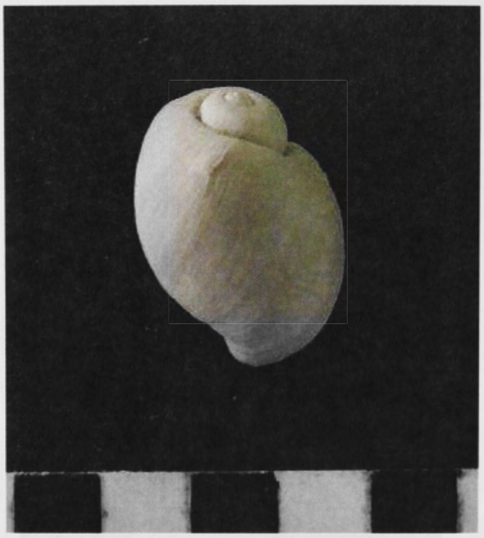


Figure 3.4.7: *Bulinus* from Dikika, Ethiopia (scale 5mm)

Bulinus generally inhabits a wide range of water bodies, including seasonal pools and lakes, though *Bulinus tropicus* is generally restricted to small lentic waterbodies and is not found in large lakes. It tolerates cold winters and hot summers. Certain species of *Bulinus* transmit the waterborne parasite *Schistosoma haematobium*. *Bulinus* is relatively unsuccessful in heavily forested regions (Brown 1980: 305).

- **Stylommatophora**

The Stylommatophora, part of the Eupulmonata clade, includes the majority of terrestrial snails and slugs. Members of the Stylommatophora differ from other members of the Pulmonata in that they possess eyes that sit on top of retractable tentacles. This group includes a large number of snail families including families that are found at a number of hominine sites, such as the Achatinidae.

- **Achatinidae**

The family Achatinidae is made up of medium to large sized tropical land snails contained in a number of genera including the largest of all land snails, *Achatina* (Figure 3.4.8).

Figure 3.4.8: *Achatina* from Chiwondo Beds, Malawi (scale 10mm)

This genus contains a number of species, such as *Achatina fulica,* which inhabits tropical and subtropical moist broad-leaf forests and tropical and subtropical dry broadleaf forests of Africa (Venette & Larson 2004). These snails tend to prefer forest habitats and are known to aestivate when living in regions that experience hot, dry months, burying themselves in soil or hiding under rocks to avoid direct sunlight. The genus *Achatina*, like a number of terrestrial snails, is an important food resource today providing valuable protein for a number of human populations (Uboh et al. 2010).

3.5 Summary

The molluscs associated with hominine sites in this study are almost exclusively either bivalves or gastropods (the exception being a single scaphopod species). The bivalves fall into two broad categories, the relatively large freshwater mussels in the order Unionoida and the relatively small freshwater bivalves in the order Veneroida.

The gastropods are varied in terms of habitat and ecology, including families that contain freshwater, amphibious and terrestrial representatives. While bivalves are restricted generally to water bodies that remain relatively permanent, and have some water movement, even if very gentle, there are gastropod species that can survive in temporary and stagnant water bodies, as well as those that can live fully independently from permanent water. Each of these groups has the potential to reveal information relevant to the palaeoecology of the sites at which they are found, as is demonstrated in the following chapters.

In Chapter 4 the results of a study into two mollusc assemblages from different stratigraphic layers of the Dikika region in the Awash Valley, Ethiopia, will be presented and analysed in light of their palaeoecological context. This will be followed by a review and synthesis of data collected from the literature and through further studies of original collections.

4 Molluscs from the Hadar and Busidima Formations at Dikika, Ethiopia

4.1 Introduction

In this chapter the molluscs associated with two hominine sites from the Hadar and Busidima Formations at Dikika, Ethiopia, are examined, especially from a palaeoecological perspective. Since the molluscs have not previously been studied, each taxon is described systematically to justify the identification assigned to it, before an analysis is undertaken from a palaeoecological perspective. This is not an attempt to officially identify these samples, but rather to try to understand them from an ecological view point.

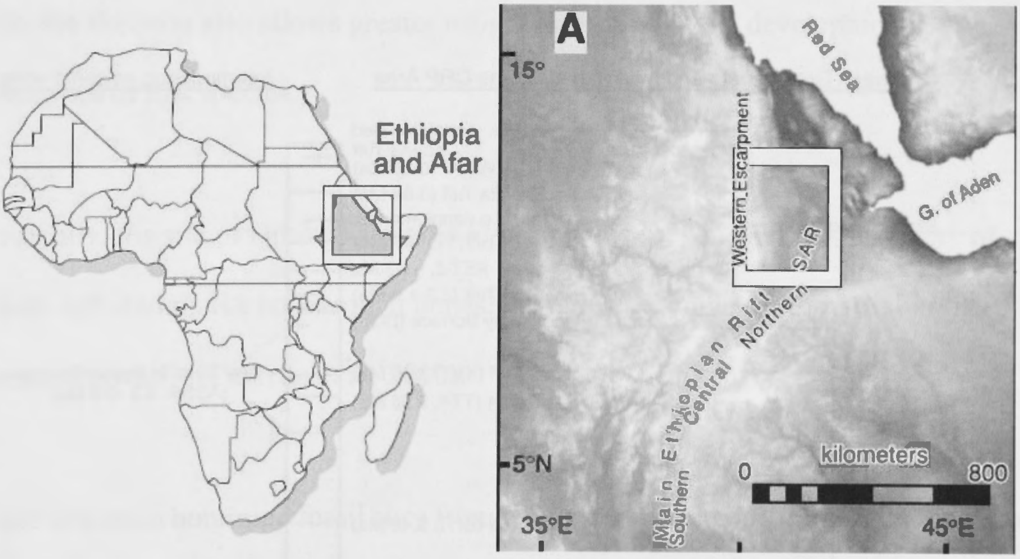


Figure 4.1.1: Map showing location of the Afar Triangle region where the Ethiopian Rift system meets the Red Sea and Gulf of Aden Rift systems. The Dikika Research Project area is signified located within the rectangle (Wynn et al. 2008)

The Dikika Site is situated in the Afar region of Ethiopia, part of the northern extension of the Ethiopian Rift Valley, which itself is part of the East African Rift (Figure 4.1.1).

Sediments from the Dikika region make up part of the Awash Group and form a nearly continuous sequence spanning a period from older than 3.8 Ma (Basal Member of the Hadar Formation) to younger than 0.15 Ma (upper part of the Busidima Formation) (Figure 4.1.2). The Hadar and Busidima Formations were deposited in distinctly different sedimentological, tectonic, and palaeoenvironmental circumstances, and are separated by a major disconformity named the Busidima Unconformity Surface (BUS), which is dated to c. 2.95 Ma (Wynn et al. 2008). Molluscs from both the Hadar and Busidima Formations were collected by the Dikika Research Project and deposited in the Ethiopian National Museum, where they were analysed for this study in 2007.

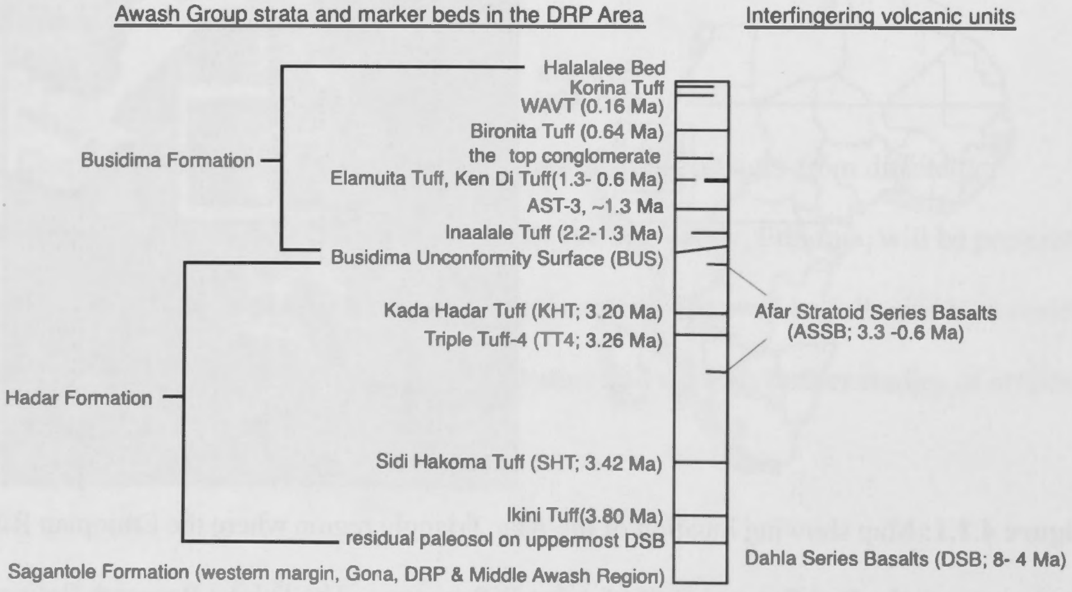


Figure 4.1.2: Stratigraphic summary of Awash Group strata exposed in the Dikika Research Project area (Wynn et al. 2008)

4.2 The Hadar Formation

The Hadar Formation is well known for yielding hominine fossils of Pliocene age, including AL 288 or ‘Lucy’ from the Kada Hadar Member, and AL 333 or ‘The First Family’ from the Denen Dora Member, both assigned to the species *Australopithecus afarensis*. Here, molluscs from the Sidi Hakoma Member of the Hadar Formation at Dikika are analysed. The site of Dikika is significant from a palaeoanthropological perspective because of the recent discovery there of the juvenile fossil DIK-1-1, also assigned to the species *Australopithecus afarensis*. Other fossils of this species have been found at Dikika in sections spanning the Basal and Sidi Hakoma Members. The skull and partial skeleton of the juvenile hominine are especially significant because of their exceptional preservation, and because they preserve many elements of the skeleton not previously known from the Pliocene fossil record (Alemseged et al. 2006). Being a juvenile, the skeleton also allows greater insight into some of the developmental characteristics of this species.

More recently, the site of Dikika has come to prominence because of the discovery of stone-tool-inflicted marks on mammal bones, the oldest example of stone-tool-assisted butchering known (McPherron et al. 2010).

There are two main hominine fossil sites from the Dikika region: DIK-2-1 from the Basal member of the Hadar Formation, ~20m below the Sidi Hakoma Tuff, with a minimum age of c. 3.4 Ma (Alemseged et al. 2005); and DIK-1-1 from the Sidi Hakoma Member, above the Basal Member, dated to c. 3.3 Ma (Alemseged et al. 2006). The cut-marked bones mentioned above lie between these two levels, within, though close to the base of the Sidi Hakoma Member. The molluscs described here come from an interval above the section in which the Dikika hominine fossils were discovered, and are part of the Sidi Hakoma gastropodite (SH-g), a geological marker often used for chronological comparisons (Wynn et al. 2008, Figure 4.2.1).

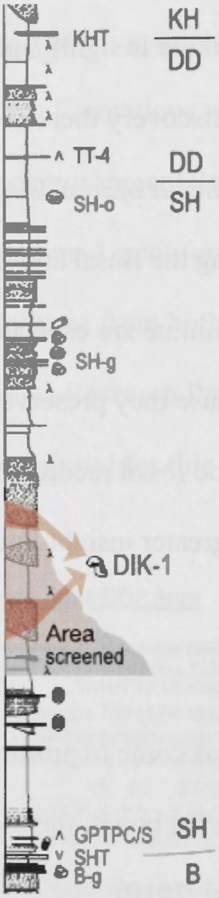


Figure 4.2.1: Stratigraphic section showing position of the Sidi Hakoma Gastropodite (SH-g) in relation to the DIK-1 hominin fossil location (Wynn et al. 2006)

Three samples were collected from the Sidi Hakoma Member. In the following sections the molluscs from each sample are described and provisionally identified.

4.2.1 Sample E02-1032

This sample contains at least two genera, and possibly three (Table 4.2.1). According to Jonathan Wynn (personal communication), the bivalve *Corbicula* may have also been present in these beds, but no individuals were collected for these samples.

Table 4.2.1: Mollusc taxa from sample E02-1032, Sidi Hakoma gastropodite

Taxon	**Palaeoecology**	**Reference**
Melanoides	Wide variety of brackish and freshwater environments, except papyrus swamps and waters that regularly dry out — tropical	Van Damme 1984; Brown 1980
Bellamya	Lakes, large slow flowing rivers and streams — tropical	Van Damme 1984
? *Cleopatra*	Stagnant or slowly flowing waters, incl. small and seasonal streams — tropical	Brown 1980

- ***Melanoides***

The specimens assigned to *Melanoides* in this sample have spiral ridges and ribs forming a familiar *Melanoides* pattern (Figure 4.2.2). Most specimens are well preserved, although some are preserved as internal structures only so that they are smooth with small gaps between the whorls (Figure 4.2.3). Although generally well preserved, many specimens are nevertheless damaged, with aperture and spire damage most common. This genus is known from Hadar and other Pliocene sites in East Africa, such as the Turkana Basin. They are medium sized, ranging from 26 to 13mm in height, and between 5 and 8mm in width.

Figure 4.2.2: *Melanoides* from sample E02-1032, Hadar Formation, Dikika (scale 5mm)

Figure 4.2.3: *Melanoides* endocast from Sample E02-1032, Hadar Formation, Dikika (scale 5mm)

- ***Bellamya***

The non-*Melanoides* specimens fall into two morphological groups characterised by size and shape. The larger specimens are here assigned to *Bellamya*, a genus which is today widespread in Africa, and which is known from other Hadar Formation deposits (Van Damme 1984). These are often not perfectly preserved (Figure 4.2.4).The smaller specimens are here assigned to *Cleopatra*, and are treated under that heading below.

Figure 4.2.4: *Bellamya* specimens from sample E02-1032, Hadar Formation, Dikika (scale 5mm)

The *Bellamya* specimens are medium to large sized (16–30mm) gastropods. Although reminiscent of *Bellamya unicolor* from Ethiopia (Brown 1980: p.38; Fig. 19b), the shells of these individuals also have some resemblance to *Cleopatra* (see Brown 1980: p. 106; Fig 60d), although the aperture in these Dikika specimens is generally more circular, rather than the oval shape of certain *Cleopatra* specimens (Brown 1980). While most of the shells have rounded whorls, there are a small number that have a slight angle, forming a ridge at the base of the body whorl, as seen for example in *Bellamya crawshayi* (Brown 1980: p.40; Fig. 20e).

- ***Cleopatra***

There is some variation in the smaller forms and it is possible that more than one species (or even genus) is represented. The shape of the aperture is generally more oval shaped than round, and in this respect these specimens are more similar to *Cleopatra* (e.g. *Cleopatra bulimoides*) than *Bellamya*.

4.2.2 Sample E02-1031

The molluscs from this sample come from a few metres lower than sample E02-1032. The sample contains a large number of what could be *Bellamya* and *Cleopatra* specimens and a smaller number of *Melanoides* (Table 4.2.2). The fossilisation process has preserved two groups. A group of relatively small specimens without much adhering matrix, with no visible deformation and with a clean whitish finish, and larger, *Bellamya*-like specimens, characterised by matrix filling, indeed with the matrix often protruding from where the aperture would have been had it been preserved. These larger shells are often fragmentary, but are held together and more or less in shape by the internal matrix. Deformation of the shells has occurred most probably since burial. Some of the fossils preserve the internal shell structure only, giving the shells a tubular spiral appearance.

The *Melanoides* specimens are similar in terms of their preservation to the smaller *Cleopatra* shells. The different forms of preservation may represent different substrates:

possibly a muddy substrate associated with the *Bellamya* fossils and a sandier substrate associated with the *Melanoides* and *Cleopatra* fossils.

Table 4.2.2: Mollusc taxa from sample E02-1031, Sidi Hakoma gastropodite

Taxon	**Palaeoecology**	**Reference**
Melanoides	Wide variety of brackish and freshwater environments, except papyrus swamps and waters that regularly dry out, tropical	Van Damme 1984; Brown 1980
Bellamya	Lakes, large slow flowing rivers and streams – tropical	Van Damme 1984
Cleopatra	Stagnant or slowly flowing waters, incl. small and seasonal streams – tropical	Brown 1980

- ***Melanoides***

The specimens assigned to *Melanoides* have both transverse and spiral ridges, forming prominent tubercles (Figure 4.2.5). *Melanoides* is widespread today throughout East Africa, and has been identified in African deposits since at least the early Pliocene. The specimens in this sample are generally medium sized (10-20mm), whereas some modern *Melanoides tuberculata* can grow up to 50mm.

Figure 4.2.5: *Melanoides* (right) from E02-1031 compared to *Melanoides* (left) from E02-1032 (scale 5mm)

- ***Bellamya***

The largest specimens assigned to *Bellamya* are fragmented, making measurements difficult but they are medium to large sized (20 to 40mm). One of the specimens filled with matrix also contains a small *Melanoides* specimen, demonstrating that these genera co-existed. While these individuals are almost certain to belong to *Bellamya*, and strongly resemble *Bellamya unicolor*, identification to species level will require a larger sample size.

Figure 4.2.6: *Bellamya* (left two specimens) & *Cleopatra* (right two specimens) from sample E02-1031 (scale 5mm)

- ***Cleopatra***

A number of specimens in the sample are better preserved than the *Bellamya* specimens as well as being free of adhering matrix (Figure 4.2.6). These specimens have medium sized conical to ovate shells with fine transverse ridging. The whorls are smoothly rounded with the slightest carination on only a few individuals, and then only restricted to the body whorl. The aperture of most of these individuals is distinctly higher than wide, and given this, and the general measurements and morphology, these specimens are assigned to the genus *Cleopatra* (possibly *bulimoides*), which is widespread in the region today.

Distinguishing between *Bellamya* and *Cleopatra* on the basis of fossil shells alone can be difficult. In order to test the idea that two species are represented by the non-*Melanoides* specimens in sample E02-1031, measurements of length and width of the shell and aperture of each specimen were plotted on a graph (Figure 4.2.7).

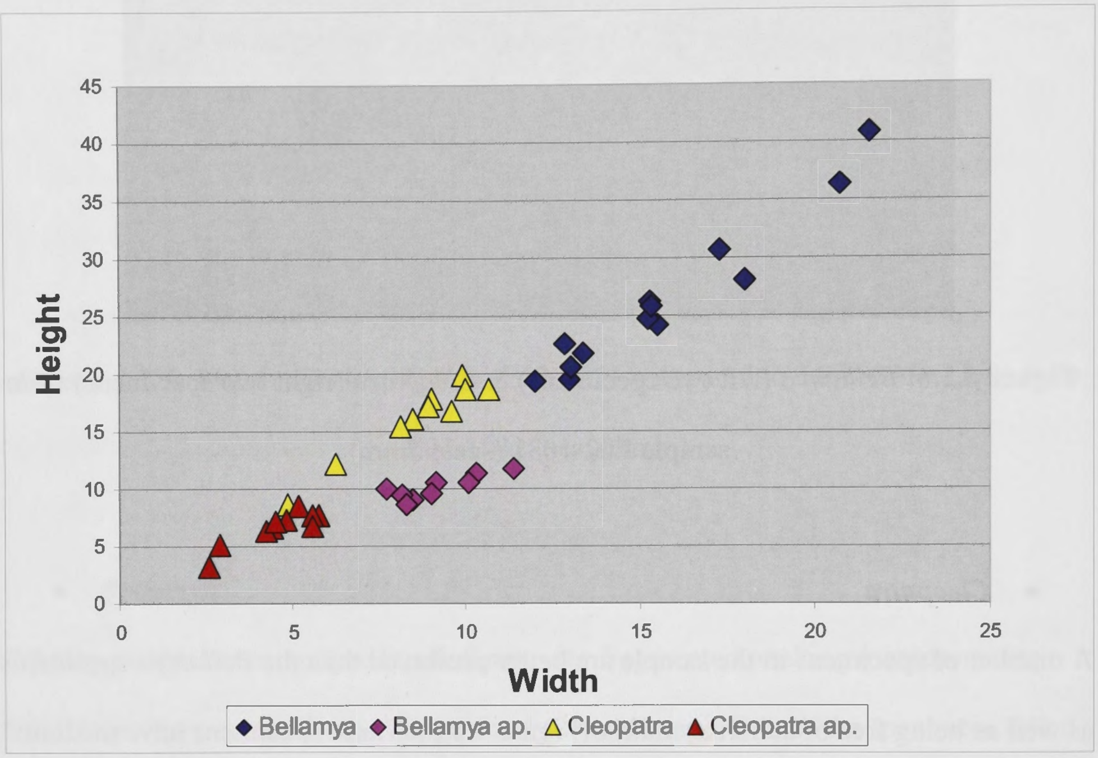


Figure 4.2.7: Shell and aperture (ap.) measurements (mm) of specimens assigned to *Cleopatra* and *Bellamya* from sample E02-1031

Although the results are not conclusive, there is some support for the idea of two morphological groups, which may represent two different taxa. The aperture measurements in particular cluster in two distinct groups, and the relationship of the aperture measurements to the shell measurements are different for the two groups of specimens, supporting the idea of two morphological groups. It is probable on what we know that these two morphological groups represent populations of *Bellamya* and *Cleopatra*.

4.2.3 Sample E02-1031B

This sample comes from the same layer as E02-1031, which is part of the Sidi Hakoma gastropodite, and contains several mollusc specimens (Table 4.2.3). The sample consists of a single bivalve with both valves present, but because the valves were open when preservation took place it has filled with matrix, which includes specimens of what appear to be *Bellamya, Cleopatra* and *Melanoides*. The bivalve shell itself is relatively large (71 x 44mm).

Table 4.2.3: Mollusc taxa from sample E02-1031B, Sidi Hakoma gastropodite

Taxon	**Palaeoecology**	**Reference**
Chambardia	Freshwater unionoid mussel of the family Iridinidae, lakes and rivers — tropical	Van Damme 1984
? *Melanoides*	Wide variety of brackish and freshwater environments, except papyrus swamps and waters that regularly dry out — tropical	Van Damme 1984; Brown 1980
? *Bellamya*	Lakes, large slow flowing rivers and streams — tropical	Van Damme 1984
? *Cleopatra*	Stagnant or slowly flowing waters, incl. small and seasonal streams — tropical	Brown 1980

The bivalve is identified as *Chambardia*, a genus of the African family Iridinidae. The fossil itself has only part of the shell preserved, including the umbo and most of the posterior hinge area. The right valve preserves about two thirds of the shell (Figure 4.2.8) while the left valve has about one quarter preserved. The general form of the shell is well preserved, however, because the internal matrix remains complete, forming an endocast of the original shape. The matrix is a fine grained, dark brown silt or mudstone containing the shells described above, though because these shells are mostly embedded in matrix, precise identification is difficult.

Figure 4.2.8: *Chambardia* specimen from sample 1031B (scale 5mm)

The specimen possesses an umbo which is not particularly strong or with prominent sculpture, and which is positioned three quarters of the way towards the anterior margin. The shell is inequilateral, equivalve and oval to elongate (Figure 4.2.8). No hinge teeth are visible and radial grooves run parallel to the ventral margin from the umbo.

4.3 Sample comparisons: E02-1031 and E02-1032

Samples EO2-1031 and EO2-1032 contain similar taxa, including *Melanoides*, *Bellamya* and *Cleopatra*. Morphologically there are not many differences between the specimens in each of the genera in samples E02-1031 and E02-1032. In terms of proportion, *Melanoides* makes up more than half of the individuals in sample EO2-1032, whereas in sample EO2-1031 *Melanoides* makes up less than a third (Figure 4.3.1).

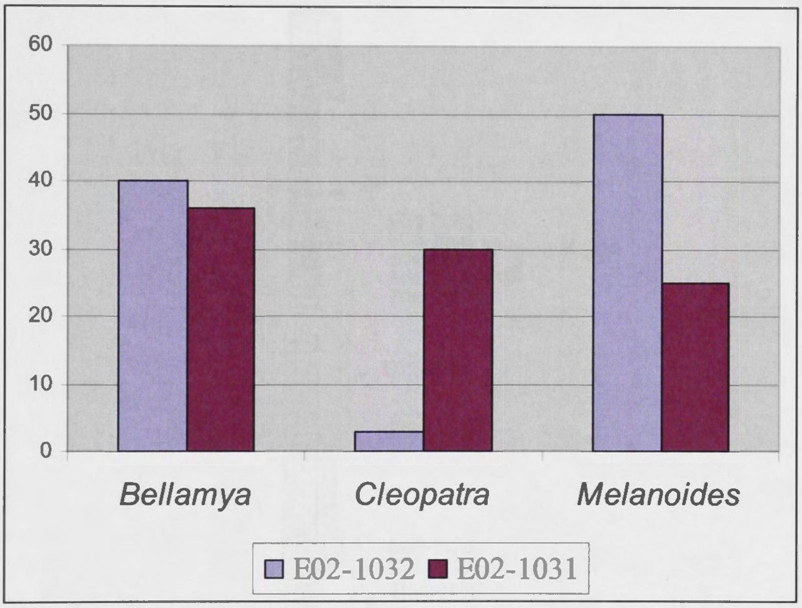


Figure 4.3.1: Number of specimens of each taxon per sample

Cleopatra is poorly sampled in EO2-1032 (3 of 93), whereas in EO2-1031 it makes up a third of all specimens. Preservation seems to be similar in both samples, with the *Bellamya* specimens generally poorly preserved in terms of completeness, matrix attachment and signs of distortion. The *Cleopatra* specimens are generally better preserved, as are those of *Melanoides*.

The significance of this is difficult to determine given the small data set, though it is possible that the differences in preservation are related to the sediment in which the specimens were preserved.

4.4 Busidima Formation

The Busidima Formation lies in a half graben of the Rift Valley, above the Hadar Formation from which it is separated by the Busidima Unconformity Surface (BUS, see Figure 4.1.2). The sediments of the Busidima Formation have yielded a vertebrate fossil faunal assemblage known as the "Asbole fauna" as well as Middle Stone Age artefacts.

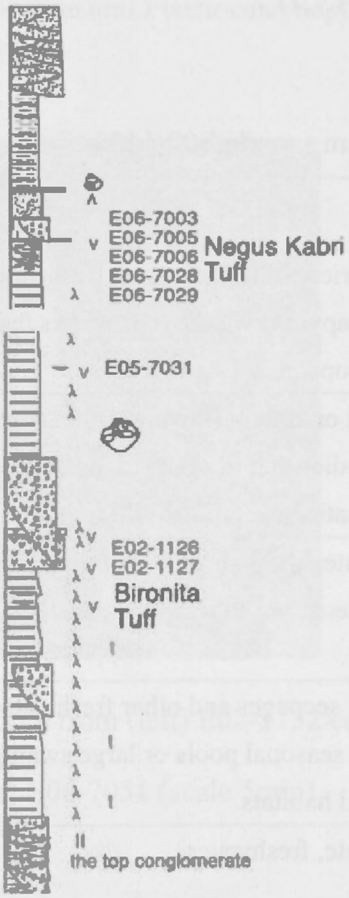


Figure 4.4.1: Stratigraphic section of the Busidima Formation showing the location the mollusc samples and an MSA archaeological site in relation to the Bironita and Negus Kabri Tuffs (Wynn et al. 2008)

The mollusc samples in this study come from above the Negus Kabri Tuff, which lies above a Middle Stone Age archaeological site which itself lies well above the Bironita Tuff (Figure 4.4.1).

4.4.1 Sample E02-1132

This sample was collected from a deposit near the top of the Busidima Formation, and is estimated to be late Pleistocene in age (Wynn et al. 2008). The sample includes a number of molluscan taxa (Table 4.4.1).

Table 4.4.1: Molluscs from sample E02-1132

Taxon	**Ecology**	**Reference**
Melanoides tuberculata	Wide variety of brackish and freshwater environments, except papyrus swamps and waters that regularly dry out — tropical	Van Damme 1984, Brown 1980
Bulinus	Stagnant or slowly flowing freshwaters, including water bodies that dry out seasonally, often associated with aquatic vegetation	Brown 1980
Lymnaea	Pulmonate, all kinds of slow moving and stagnant freshwaters, rare in temporary water bodies	Brown 1980, Van Damme 1984
Biomphalaria pfeifferi	Streams, seepages and other freshwater bodies, not found in seasonal pools or large swamps – prefers unshaded habitats	Brown 1980, Loreau & Baluku 1991
Planorbinae indet.	Pulmonate, freshwater	
Gastropoda indet.	Gastropod	

- ***Melanoides tuberculata***

The *Melanoides* specimens from this sample are most likely *Melanoides tuberculata*. The shells are dextral, often decollate and feature finely sculptured spiral ridges with less prominent transverse ridges (Figure 4.4.2). They range in size from small to medium. *Melanoides* is widespread in Africa, with endemic forms found in a few very long-lived lakes as well as the Congo basin (Brown 1980), but *Melanoides tuberculata* is the most widespread. *Melanoides* is known from the Awash Valley, and is one of the most widespread taxa in east African Pliocene and Pleistocene deposits.

Figure 4.4.2: *Melanoides tuberculata* from (left) E02-1132 compared to specimen from (right) E06-7051 (scale 5mm)

- ***Bulinus***

This taxon is identified as *Bulinus*, a small to medium sized pulmonate gastropod with a sinistral shell with fine transverse ridges. The body whorl dominates the shell outline with the spire made up of only a slight coil of one or two whorls, but these hardly add to the height of the shell (Figure 4.4.3).

Figure 4.4.3: *Bulinus* specimens from Dikika sample E02-1132 (scale 5mm)

A columella fold is present but weak, with a ridge running along the lower part of the parietal wall before, in most specimens, merging with the shell body. The specimens resemble *Bulinus abyssinicus* in size and shape (Brown 1980: p. 184; Fig. 103f), and since this species is found today along marshes of the Awash River, assignment to this species would seem warranted.

- ***Lymnaea***

Specimens assigned to the genus *Lymnaea* are dextral with a large aperture, and range in size from small to medium, but accurate measurement is difficult due to the fragile and fragmentary condition of many of the shells. No specimens are completely undamaged. In many cases they are decollate and the aperture margins of most are damaged. Some smaller specimens are reminiscent of *Lymnaea columella*, while some of the larger individuals resemble *Lymnaea peregra* (Brown 1980: p.139; Fig. 77b).

- ***Biomphalaria pfeifferi***

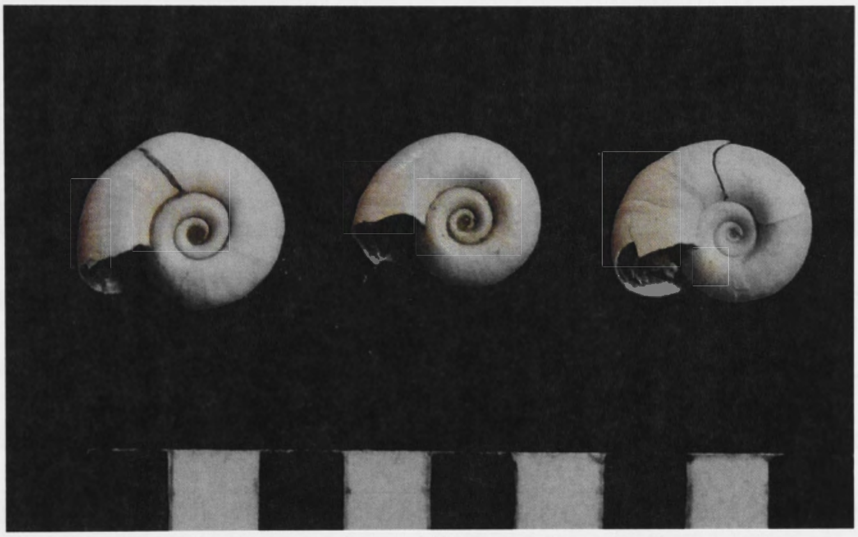


Figure 4.4.4: *Biomphalaria pfeifferi* from E02-1132 (scale 5mm)

Specimens assigned to the species *Biomphalaria pfeifferi* are small to medium in size, and have a particularly large outer whorl, with the next whorl perhaps only one quarter of the size (Figure 4.4.4). These specimens have a large and relatively wide aperture (viewed in cross-section).The whorls are evenly convex and in some individuals there is a tendency for the last whorl to descend at the opening, although in general the cross-section view shows that the whole shell resides in a nearly horizontal plane, with the lower part of the opening slightly lower than the lower part of the body of the shell itself. The lower lip of the aperture noticeably overlaps the upper lip when viewed from above.

- **Planorbinae indet.**

The sample also includes a number of smaller Planorbinae specimens, which are reminiscent of *Gyraulus*, though there is also a possibility that they represent some other species, such as *Ceratophallus*, or juvenile *Biomphalaria.* It is perhaps even possible that more than one species is represented. These specimens range in size from 1 to 3mm.

- **Gastropoda indet.**

A few very small gastropods, almost too small to measure, which might possibly include a juvenile *Lymnaea* were also found in the sample. These are about 1mm in width. There is a possibility that a juvenile *Melanoides* specimen might have been present amongst these specimens, but this is difficult to know without comparisons. These specimens possess the kind of sculpture associated with *Melanoides* (ridges forming tubercles), but are somewhat *Cleopatra*-like in overall form. They are more strongly sutured than mature *Melanoides*.

4.4.2 Sample E06-7051

Sample E06-7051 was collected from the same bed as E02-1132, but from a slightly different sampling area and in a different year (Jonathan Wynn personal communication). The sample includes several gastropod taxa (Table 4.4.2). Most probably the deposits are about 0.1 Ma.

Table 4.4.2: Molluscs from sample E06-7051

Taxon	Ecology	Reference
Melanoides tuberculata	Wide variety of brackish and freshwater environments, except papyrus swamps and waters that regularly dry out — tropical	Van Damme 1984, Brown 1980
Bulinus	Stagnant or slowly flowing waters, including water bodies that dry out seasonally, often associated with aquatic vegetation	Brown 1980
Lymnaea	Pulmonate, all kinds of slow moving and stagnant waters, rare in temporary water bodies	Brown 1980, Van Damme 1984
Biomphalaria pfeifferi	Streams, seepages and other water bodies, not found in seasonal pools or large swamps	Brown 1980
Gyraulus	Generally stagnant or slowly flowing freshwaters often associated with aquatic vegetation	Brown 1980
Gastropoda indet.	Gastropod	

- ***Melanoides tuberculata***

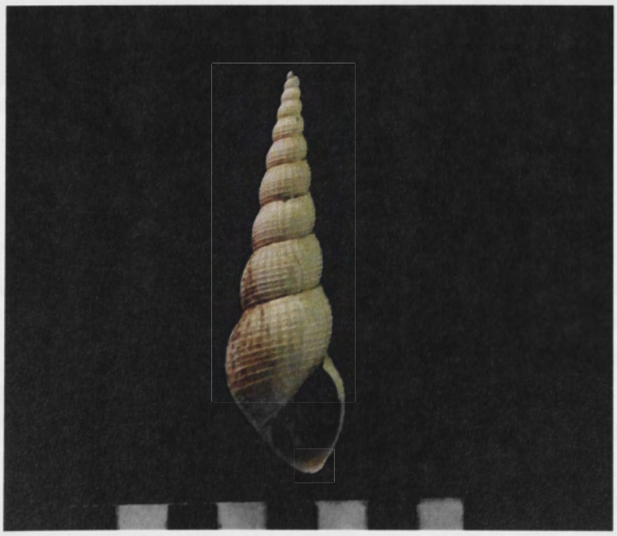


Figure 4.4.5: *Melanoides tuberculata* from sample E06-7051 (scale 5mm)

Specimens assigned to *Melanoides tuberculata* include the largest *Melanoides* individual (40mm) found in all the Dikika samples (Figure 4.4.5). The specimens range in size from medium to large and all have well preserved spiral ridges with not so prominent transverse ridges.

- ***Lymnaea***

Specimens assigned to the genus *Lymnaea* have dextral shells, with large apertures and prominent body whorls, with the upper two whorls forming a small point (Figure 4.4.6).

Figure 4.4.6: *Lymnaea* from Dikika sample E06-7051 (scale 5mm)

The specimens are most reminiscent of *Lymnaea peregra* (Brown 1980: p.139; Fig 77b), although variation in *Lymnaea natalensis* could accommodate these individuals as "considerable variation is seen both between and within populations" (Brown 1980: 136). These gastropods are medium sized.

- ***Bulinus***

Most specimens assigned to the genus *Bulinus* in this sample consist of the body whorl and a large aperture, with the upper one or two whorls hardly adding to the height of the individual. One exception exhibits two to three whorls clearly spiraling higher, so that in some respects it is more reminiscent of the condition in *Lymnaea* (Figure 4.4.7). In this specimen the upper whorls contribute an extra 4mm to the individual's height, whereas similar sized specimens within the sample have upper whorls contributing less than 0.5mm.

Figure 4.4.7: *Bulinus* specimens from sample E06-7051 (scale 5mm)

Overall these specimens most resemble *Bulinus africanus* or *Bulinus abyssinicus* (Brown 1980: 184; Figures 130a, f). The specimens have fine transverse grooves running down the body whorl. They are small to medium sized.

- ***Biomphalaria***

The specimens assigned to *Biomphalaria* are medium sized. Their shape, particularly when viewed in cross section (horizontally with opening in front), and dimensions and reminiscent of *Biomphalaria pfeifferi* (Brown 1980: p. 172; Fig. 98c), to which they will probably be assigned. This species has a widespread distribution in Africa today, including the present Awash Valley.

- ***Gyraulus***

In terms of dimensions, the largest of the specimens assigned to *Gyraulus* in this sample are similar to the dimensions given in Brown (1980) for *Gyraulus mauritanus*. Morphologically they look similar to *Gyraulus costulatus* (Brown 1980: p. 163; Fig 92c).

- **Gastropoda indet.**

One specimen of gastropod with very small proportions (c. 1.5 x 0.85mm) has sculptures that resemble *Melanoides*, and therefore might be a juvenile of this genus. Since adults are known from this sample, this might be correct. A larger sample set would be needed to confirm this, however.

4.5 Sample comparisons: E02-1132 and E06-7051

EO2-1132 and EO6-7051 have a similar taxonomic makeup. They both contain *Melanoides*, *Bulinus*, *Lymnaea*, *Biomphalaria* and a smaller discoid member of the Planorbidae, possibly *Gyraulus*. The main difference in relative abundance between these samples is that in EO2-1132 *Biomphalaria* is very common (one third of total specimens), whereas in EO6-7051 it makes up only one eighth of the total sample (Figure 4.5.1). In EO2-1132 *Melanoides*, *Lymnaea* and *Bulinus* are represented roughly equally, whereas in EO6-7051 *Bulinus* is more prevalent, making up one third of the total collection.

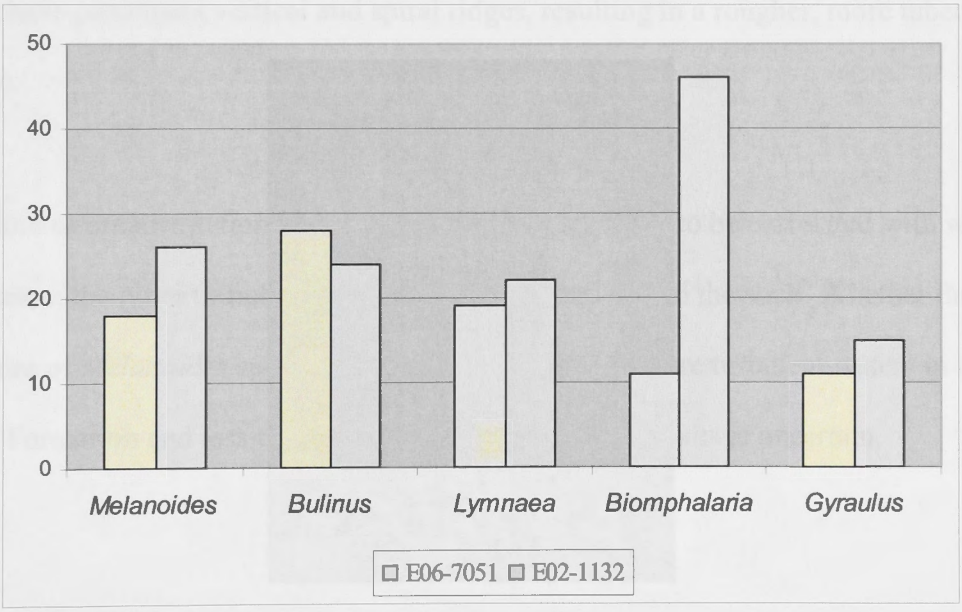


Figure 4.5.1: Number of specimens of each taxon per sample

In terms of preservation EO6-7051 specimens are much better preserved so that the entire shell is often present, whereas most of the EO2-1132 specimens are fragmentary. *Biomphalaria* specimens in both samples are morphologically similar. *Bulinus* specimens are morphologically similar, although preservation is better in EO6-7051. The *Lymnaea* specimens of EO6-7051 and EO2-1132 are similar in morphological terms but differ in size, and as with the *Bulinus* and *Melanoides* specimens, preservation is noticeably better in sample EO6-7051. *Melanoides* specimens from E02-1132 and E06-7051, apart from size, are not substantially different, although there are variations in colour and ridge formation (Figure 4.5.2).

Whether the preservation differences between sites is significant, and what significance that might have with regard to ecology is difficult to speculate on with such a small data set.

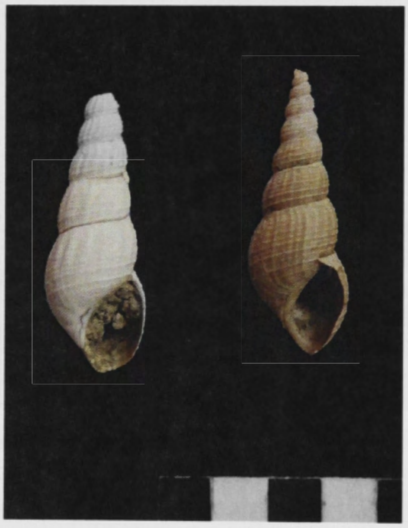


Figure 4.5.2: *Melanoides tuberculata* from samples E02-1132 & E06-7051 (scale 5mm)

4.6 Sample comparisons: Busidima and Hadar Formations

The only genus common to all samples is *Melanoides* (Figure 4.6.1). There are clearly two morphological groups present for this genus. Those belonging to the younger Busidima Formation appear to represent *Melanoides tuberculata*, and those belonging to the older Hadar Formation are probably some other species. The *Melanoides* specimens from sample EO6-7051 are relatively large compared to specimens from other samples. Specimens from EO2-1032 and EO2-1031 have more strongly sculptured shells with spiral and vertical ridges producing prominent tubercles. In samples EO6-7051 and EO2-1132 the spiral ridges, while relatively fine, are more prominent than the vertical ridges, resulting in an overall smoother surface than those of EO2-1031 and EO2-1032, which have prominent vertical and spiral ridges, resulting in a rougher, more tuberculed surface.

Sculpture or ornamentation in some aquatic molluscs tends to be correlated with water turbulence: the more turbulent the water the more sculptured the shell. Whether the sculpture of *Melanoides* specimens from Dikika reflects more turbulent waters in the Hadar Formation and less turbulent water in Busidima deposits is uncertain.

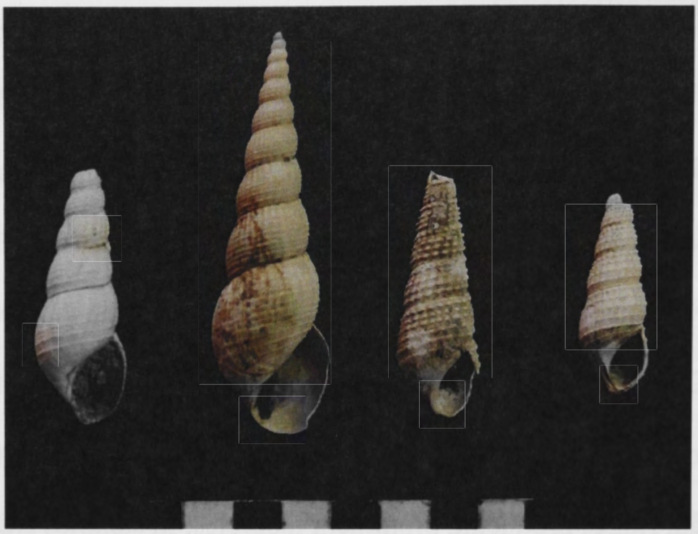


Figure 4.6.1: Largest *Melanoides* specimens from samples (left to right) E02-1132, E06-7051, E02-1032 and E02-1031 (scale 5mm)

The samples from the Hadar and Busidima Formations preserve very different molluscan communities (Figure 4.6.2). The older Hadar Formation has a faunal composition which includes the prosobranch gastropods *Bellamya*, *Melanoides* and *Cleopatra* as well as the iridinid bivalve *Chambardia*, while the younger Busidima Formation includes only one prosobranch taxon, *Melanoides*, as well as the pulmonate gastropods *Bulinus*, *Lymnaea*, *Biomphalaria* and at least one other smaller species of discoid Planorbidae, possibly *Gyraulus,* as well as some very small unidentified gastropod specimens.

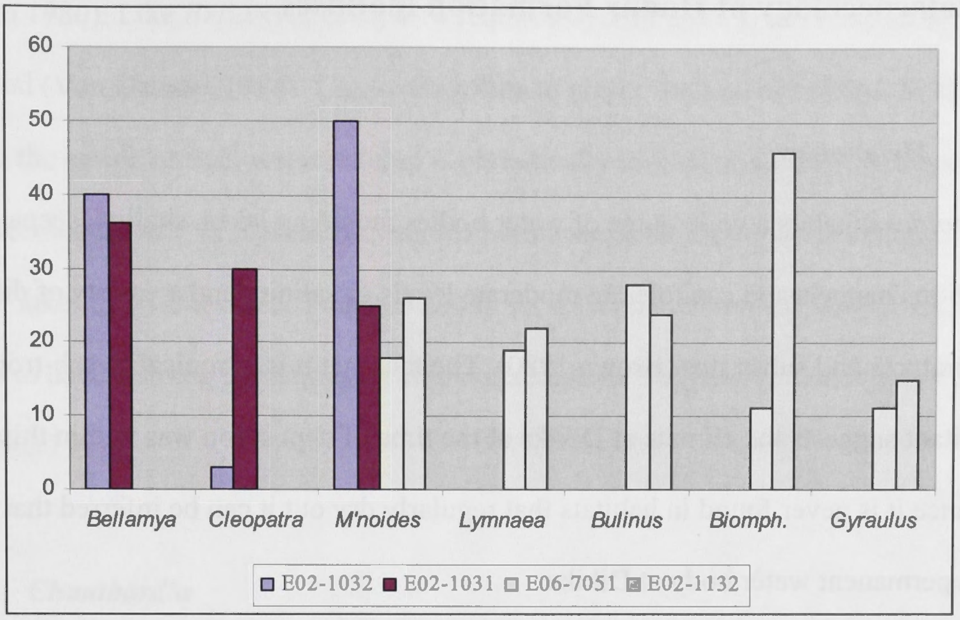


Figure 4.6.2: Number of specimens of each taxon included in samples from the Hadar (E02-1032 & E02-1031) and Busidima Formations (E06-7051 & E02-1132)

Bellamya is found in permanent lakes and rivers, whereas many pulmonates are able to inhabit ephemeral water bodies. The data therefore seem to indicate the presence of two different palaeoecologies.

4.7 Palaeoecology of Hadar Formation molluscs

- ***Melanoides***

Melanoides inhabits a wide range of water bodies including lakes, shallow seepages and irrigation channels and can tolerate moderate levels of salinity and a variety of different temperatures and substrates (Brown 1980). The fact that it is a tropical to sub-tropical inhabitant suggests the climate at Dikika at the time of deposition was within this range, and since it is never found in habitats that regularly dry out it can be inferred that there was a permanent water body at Dikika.

- ***Bellamya***

Most common in tropical freshwater lakes, rivers and slowly flowing streams, *Bellamya* never occurs in habitats that regularly become dry (Brown 1980). Because it is monoecious, viviparous and large as an adult, it generally requires freshwater connections for dispersal, as opposed to *Melanoides*, which can apparently be dispersed via bird carriage (Van Damme 1984). There is some evidence that *Bellamya* prefers lake bottoms free of dense vegetation (Songtham et al. 2005), although at least one species, *Bellamya capillata*, has been found to have a strong association with the macrophyte *Vallisneria aethiopica* (Kautsky & Kiibus 1997.

- ***Cleopatra***

Cleopatra prefers slowly flowing waters with sandy or especially muddy substrates (Van Damme & Pickford 2003) in tropical habitats, and also inhabits seasonal streams and residual pools as well as forest streams but rarely water bodies that regularly become dry

(Brown 1980). Like *Bellamya*, *Cleopatra* requires hydrographical connections for dispersal (Van Damme 1984). *Cleopatra* seems to prefer shallow or holomictic lakes (where the entire vertical water column is periodically mixed) and is rare, and known to have become extinct, in meromictic (with a permanently stratified water column) or mature lakes (Van Damme & Pickford 2003). At least one species of *Cleopatra* has been shown to have a strong association with the macrophyte *Vallisneria aethiopica* (Kautsky & Kiibus 1997).

- ***Chambardia***

This genus belongs to the family Iridinidae, a unionoid bivalve, and generally prefers fluviatile environments in tropical habitats (Van Damme 1984). All bivalves require permanent water for growth, feeding and reproduction, and unionoid bivalves rely on fish for dispersal during their parasitic larval stage (Moore 1969). Given that the shell is more ovate than lanceolate, the water velocity may have been moderate rather than high (Good 2004).

4.7.1 Summary

The presence of *Bellamya*, *Melanoides*, *Cleopatra* and *Chambardia* strongly indicate a body of permanent freshwater since all are usually associated with habitats that do not regularly become dry. The combination of taxa indicates a perennial river network, as well as the long term relatively wet conditions that would enable such a system to evolve and endure. It can be confidently asserted too that the habitat was tropical since each of the taxa present are known to inhabit tropical waters, and genera such as *Bellamya*, *Chambardia* and *Cleopatra* are generally restricted to the tropical zone.

The empty shells of *Bellamya* and *Melanoides* float (Plaziat & Younis 2005) and consequently it is not uncommon for these taxa to accumulate on beaches due to current action and they sometimes can represent high lake shore deposits (Gautier 1970).

Since *Cleopatra* requires relatively shallow waters and freshwater mussels have their greatest distribution in relatively shallow waters as well, there was most likely shallow water habitats at Dikika during the Hadar Formation.

4.8 Other palaeoecological data: Hadar Formation

Faunal remains are relatively uncommon from the hominine fossil site DIK-2, from the Basal Member of the Hadar Formation, but fauna collected include fish, crocodilians, hippopotamids, a tortoise, a small carnivore, some bovid and equid fossils as well as *Australopithecus afarensis.* These vertebrates suggest “rather open environments in the proximity of water” or more precisely, “a woodland-grassland landscape, close to water and/or with frequent flooding” (Alemseged et al. 2005: pp. 503,505).

Table 4.8.1: Vertebrate fauna from DIK-1 locality and surroundings (Wynn et al. 2006)

PISCES	**PROBOSCIDEA**
Clarias sp.	*Elephas* cf. *recki brumpti*
REPTILIA	*Elephas* cf. *ekorensis*
Elapidae cf. *Naja* sp.	**PERISSODACTYLA**
Crocodylus cf. *niloticus*	*Ceratotherium mauritanicum*
Centrochelys sp.	*Hipparion* cf. *hasumense*
RODENTIA	**ARTIODACTYLA**
Golunda cf. *gurai*	*Hexaprotodon afarensis*
Acomys coppensi	*Kolpochoerus afarensis*
Millardia taiebi	*Notochoerus euilus*
Pelomys sp.	*Nyanzachoerus kanamensis*
Saidomys cf. *afarensis*	*Giraffa* cf. *jumae*
PRIMATES	*Sivatherium maurusium*
Australopithecus afarensis	*Tragelaphus* aff. *Nakuae*
Theropithecus darti	*Ugandax* sp.
Cercopithecidae indet.	*Praedamalis* cf. *howelli*
CARNIVORA	*Damalops* sp.
Herpestidae indet.	*Aepyceros* sp.
Canidae indet. aff *Nyctereutes* sp.	*Gazella* sp.
Enhydriodon sp.	

The DIK-1 locality, from below the Sidi Hakoma gastropodite, has a more extensive fossil faunal record (Table 4.8.1). The abundance of fish (mostly catfish), and the presence of hippopotamids, crocodilians and giant tortoises associated with DIK-1 indicate a mesic, deltaic environment with permanent water in the vicinity (Wynn et al. 2006).

The three suid genera include *Notochoerus*, probably adapted to closed habitats (Bishop 1999), *Kolpochoerus*, a water-dependent suid (Harris & Cerling 2002), and *Nyanzachoerus kanamensis*, which, according to ecomorphological studies was a swamp specialist (Bishop 1999).

The combination of the impala *Aepyceros*, the most common antelope at DIK-1 and a good indicator of the presence of C_3 vegetation (bushes, shrubs, vines), and grazers such as *Damalops*, as well as the grazing rhinoceros *Ceratotherium*, suggests a combination of open and closed habitats (Wynn et al. 2006). Two monkeys including *Theropithecus* were present, and although the modern gelada is known from grasslands in Ethiopia, this combination of monkeys is probably a good indicator that at least some cover was available. The most common carnivore is the large otter *Enhydriodon* (Wynn et al. 2006), indicating that permanent water was an element of the local environment.

Palynological studies at Hadar show that *Typha* and Cyperaceae were abundant locally in the Sidi Hakoma Member, with Gramineae predominant regionally (Bonnefille 1995). This indicates that areas of open grassland and marshy wetlands were part of the environment in at least some parts of the Awash Valley in the late Pliocene.

The faunal and palynological data support the molluscan evidence in indicating a permanent drainage system in which aquatic animals could survive. The combination of data indicate a drainage system including slowly running rivers with marshy wetlands probably lining the waterways in places, and a combination of relatively open and closed habitats.

4.9 Palaeoecology of Busidima Formation molluscs

- ***Bulinus***

This genus contains species that are able to aestivate and therefore is capable of inhabiting seasonal pools and streams and is perhaps the most characteristic gastropod of African freshwater habitats. It can survive in cool highland areas as well as hot tropical lowlands (Brown 1980). *Bulinus* contains a number of species that require or are often associated with vegetation (Table 4.9.1).

Table 4.9.1: Palaeoecological characteristics of the genus *Bulinus*

Species	**References to vegetation in habitat description (Brown 1980)**
abyssinicus	Marshes associated with the Awash river
globosus	Rich aquatic vegetation
jousseaumei	Abundant on water-lily leaves
ugandae	Reed swamp — in the fringe of papyrus swamp
hightoni	With aquatic plants including water-lilies
angolensis	Aquatic vegetation
depressus	Rotted vegetation
guernei	Streams flowing amongst clumps of grass — pools containing water-lilies
hexaploidus	Abundant aquatic vegetation
octoploidus	Rich vegetation in the residual pools which remain dry through the dry season
forskali	Margins of lakes and permanent swamps
rohlfsi	Weedbeds of *Ceratophyllum* provide especially favourable conditions
succinoides	Living upon *Vallisneria* plants at a depth of about 3 meters
trigonus	Papyrus thicket
obtusipira	Common in rice fields
crystallinus	Rotting vegetation
cernicus	Watercress bed

Bulinus is also sometimes found in water bodies that lack higher plants, and around rocky or stony areas. It is generally not found in rapidly flowing water, and requires vegetation, rocks or other features to protect it from currents when they are present. *Bulinus* is not very successful in forested regions (Brown 1980: 305).

- ***Lymnaea***

The most common species of this genus, *Lymnaea natalensis*, is generally intolerant of desiccation and is commonly associated with permanent water bodies including drains, reservoirs and very shallow though constantly seeping water (Brown 1980). It appears to have a strong association with the macrophyte *Vallisneria aethiopica* (Kautsky & Kiibus 1997). Another species, *Lymnaea truncatula*, is particularly common in cool, humid conditions. *Lymnaea* can apparently tolerate enormous differences in temperature.

- ***Biomphalaria***

This genus is known from various permanent freshwater bodies and is a relatively recent immigrant to Africa, arriving possibly via bird carriage from South America sometime within the last million years according to molecular studies. It is only known from the last 250ka in the north African fossil record (Van Damme, personal communication).

Although *Biomphalaria pfeifferi* is generally absent from seasonal pools and extensive papyrus swamps (Van Damme 1984), it appears to have a strong association with the macrophyte *Vallisneria aethiopica* (Kautsky & Kiibus 1997). The different African species of *Biomphalaria* have a number of different habitat characteristics (Table 4.9.2).

Table 4.9.2: Palaeoecological characteristics of *Biomphalaria*

Species	**Habitat description (Brown 1980)**
pfeifferi	Streams, seepages, hard rock formations in rivers
choanomphala	Gravel and soft sedimentary rocks, stones
smithi	Vegetation growing on sand at depths down to 4m
stanleyi	Vegetation on sand in a few feet of water
barthi	Lakes
alexandrina	Dense aquatic vegetation
angulosa	Kalenga Swamp, dries out in the dry season
tchadiensis	Lake Chad
camerunensis	Shallow water shaded by palm trees…abundant vegetation including papyrus
sudanica	Swamps which are sufficiently permanent to support a rich aquatic vegetation…papyrus swamp with *Pila ovata*

- ***Gyraulus***

This genus is known from a variety of vegetation rich water bodies (Table 4.9.3) but is usually absent from water bodies that seasonally dry out (Van Damme 1984). *Gyraulus* can tolerate relatively stagnant water and feeds on algae and detritus.

Table 4.9.3: Palaeoecological characteristics of *Gyraulus*

***Gyraulus* species**	**Habitat description (Brown 1980)**
ehrenbergi	Amongst dense vegetation in drains in the delta region of Egypt
costulatus	Aquatic vegetation, marginal grass, and stones in slow flowing rivers
connollyi	Vegetation and stones in rivers and streams
cockburni	Obtained from water plants

4.9.1 Summary

The molluscan samples from the Busidima Formation in the Dikika region are characterised, apart from *Melanoides*, by pulmonate gastropods such as *Lymnaea*, *Bulinus*, *Biomphalaria* and *Gyraulus*. These freshwater pulmonate snails as a group are "especially associated with small water bodies which may be filled only seasonally" (Brown 1980: p. 10). The Planorbidae in particular are:

> "conspicuous in the innumerable small and more or less seasonal pools and watercourses, and their success in such habitats is due partly to their abilities to satisfy their needs for oxygen despite stagnant conditions, and to survive in a dormant state the intermittent disappearance of water" (Brown 1980: 10).

Since *Melanoides* and most pulmonates are capable of dispersal via bird carriage (Van Damme 1984) it is possible that the Dikika region during deposition of these Busidima Formation molluscs was characterised by isolated waterbodies that seasonally became dry. Given that *Melanoides* requires permanent water, it is possible that the ancestral Awash River meandered through the region, flooding seasonally and leaving residual temporary wetlands that were than populated by the pulmonate gastropods associated with these samples.

The absence of *Bellamya* or any unionoid bivalves suggests that this was not the margin of a larger river or lake system. It seems probable that there was ample vegetation to support the planorbids and the *Lymnaea* species. The presence of *Bulinus* and *Biomphalaria* could indicate that at least part of the region was not heavily forested

(Brown 1980) and therefore open grass or wetlands were probably present. *Vallisneria*, a plant often associated with more than one of the mollusc taxa found in the Busidima Formation samples, is a tropical to sub-tropical adapted aquatic plant that does not grow in cold habitats.

4.10 Other palaeoecological data: Busidima Formation

The section of the Busidima Formation from which the molluscs described here were recovered has not been well studied, and no other faunal material has so far been described. The Asbole fauna (Table 4.10.1) comes from below this section and may be closer in age to 0.6 Ma (Geraads et al. 2004).

Table 4.10.1: Mammals from Asbole, Busidima Formation (Geraads et al. 2004)

PRIMATES	*Oryx* sp.
Colobus sp.	*Kobus kob*
Cercopithecus sp.	*Redunca* sp.
Papio sp.	cf. *Connochaetes* sp.
Theropithecus oswaldi	*Damaliscus niro*
Homo sp. (based on Acheulean industry?)	*Gazella* cf. *thomsoni*
RODENTIA	*Gazella* aff. *granti*
Thryonomys cf. *swinderianus*	**CARNIVORA**
Tachyoryctes sp.	*Ichneumia* aff. *albicauda*
Hystrix cristata	*Herpestes* cf. *ichneumon*
Otomys sp.	*Hyaena hyaena*
Arvicanthis cf. *niloticus*	*Crocuta crocuta*
ARTIODACTYLA	*Felis* cf. *libyca*
Hippopotamus cf. *amphibius*	*Panthera* cf. *leo*
Metridiochoerus modestus	*Canis* cf. *aureus*
Kolpochoerus majus	*Mellivora capensis*
Giraffa cf. *camelopardalis*	**PERISSODACTYLA**
Tragelaphus scriptus	*Diceros* cf. *bicornis*
Taurotragus sp.	*Ceratotherium simum*?
Bos sp.	*Equus* sp.
Pelorovis sp.?	**PROBOSCIDEA**
Syncerus sp.?	*Elephas recki recki*

Middle Stone Age tools are known from the section containing the mollusc samples, while Acheulean Industry artefacts are associated with the Asbole fauna. The sedimentological data suggest more open and well drained grass dominated flood plains compared to the reed bed, marsh and woody vegetation environments of the delta plains in the Hadar Formation (Wynn et al. 2008). The Busidima Formation preserves fossil palm wood and is characterized by slow and episodic deposition in a predominantly fluvial environment (Wynn et al. 2008).

Overall the fauna from Asbole suggests humid bushy landscapes associated with a permanent water source (Geraads et al. 2004). The Egyptian mongoose *Herpestes ichneumon* prefers habitats close to water, the cane rat *Thryonomys* inhabits grasses and reeds fringing lakes and rivers, and the most dominant ungulates of the Asbole fauna are reduncines, especially *Kobus*, which are known to live in edaphic grasslands. *Kolpochoerus*, a water dependent suid, is also present, and *Hippopotamus* cf. *amphibius* indicates that both permanent water and open grasslands occurred locally.

A significant part of the area must have been forested since there is an abundance of colobus monkeys and a number of browsing animals which prefer cover. Open landscapes must have also been present, as shown by the alcelaphines, antilopines and *Oryx* (Geraads et al. 2004), but overall there is an absence or rarity of taxa indicating open savanna, and a similar absence or rarity of aquatic taxa such as hippopotamids, crocodilians and fish (Alemseged & Geraads 2000).

The faunal data from the Busidima Formation derives from a period from the Middle Pleistocene, during which time it appears there was a moderate water presence in the area as well as habitats with sufficient cover to support populations of browsing animals and arboreal monkeys. This combination of fauna is possible suggestive of a permanent flowing rivers, with an associated gallery forest, in an otherwise seasonally dry habitat. Unfortunately no molluscs are known from this period.

The molluscs from the late Pleistocene section of the Busidima Formation examined here suggest a relatively open habitat with isolated pools, probably formed after seasonal flooding along the flood-plains of a permanent river, almost certainly the ancestral Awash River. This is in agreement with sedimentological studies of the Busidima Formation which indicate more open, well-drained, grass-dominated floodplains (Wynn et al. 2008). The combination of molluscs points to a relatively warm tropical or sub-tropical climate.

4.11 Summary

The Dikika fossil sites of the Hadar Formation are important in palaeoanthropological terms because they sample deposits from a time (3.4Ma) which had previously yielded only meagre hominine remains (Alemseged et al. 2005). The fact that DIK-1 is an exceptionally well preserved juvenile fossil featuring parts of the skeleton previously unknown in the Pliocene fossil record adds to this importance. Gastropod beds have long been known from the Hadar Formation and these have been used as important stratigraphic markers (Aronson et al. 1977), as well as for chemical analysis (Hailemichael et al. 2002).

The upper sections of the Busidima Formation are in places poorly preserved, and the gastropod bed from which the mollusc samples described here were taken is apparently previously unknown. When compared, the samples clearly represent two very different depositional environments and ecologies. Because *Bellamya*, *Cleopatra* and *Chambardia* require hydrographical connections in order to disperse, it is likely that the water body associated with these deposits was connected to a larger drainage system that had been established for some time.

When other faunal data are taken into consideration, it is apparent that both open and closed habitats were present locally in the Dikika region during deposition of these sections of the Hadar Formation, and that some type of permanent water body also existed. The idea that there may have been a lake, river or slow moving stream is supported by the presence of *Bellamya* and *Chambardia*. Unionoid bivalves and

Cleopatra are restricted to relatively shallow water habitats, so their presence at Dikika suggests that shallow waters were locally present.

Australopithecus therefore had numerous habitats available for exploitation, including gallery forest, open grasslands, and shallow wetlands.

The Busidima Formation mollusc samples contain *Melanoides tuberculata* as well as air-breathing pulmonate genera including *Lymnaea*, *Bulinus*, *Biomphalaria* and possibly *Gyraulus*. *Melanoides* is an indicator of permanent water, as is, to a lesser extent, *Lymnaea*, whereas *Bulinus* and *Biomphalaria* are both capable of surviving in more ephemeral water bodies. Although *Bulinus* is not usually successful in forested regions, it is often associated with rich vegetation, and in order to survive dry periods it usually requires the protection of dense vegetation. *Biomphalaria* and *Gyraulus* are also often associated with rich vegetation and since *Lymnaea* is often associated with very shallow water bodies it is possible that this mollusc community signifies some type of shallow marshland environment.

Together, *Melanoides tuberculata*, *Biomphalaria pfeifferi*, *Bulinus truncatus* and *Lymnaea natalensis* make up the most common community of gastropods found in Holocene deposits of the Sahara, which may be an indication of their collective dispersal abilities and the fact that they are capable of surviving in isolated water bodies.

The hominins responsible for the stone tools at Busidima may therefore have come across shallow wetlands rich in vegetation, in otherwise relatively open habitats with seasonal rainfall and a nearby permanent river.

This chapter has demonstrated that molluscan assemblages can be used to make certain inferences about the ecological characteristics of the various sites. In the following three chapters the molluscan fauna from sites ranging in age from Miocene to mid-Pleistocene, and encompassing Africa, Europe and Asia, will be examined and the palaeoecological interpretations compared to the results of palaeoecological studies using other data.

5 Molluscs from African Mio-Pliocene sites

In the previous chapter mollusc samples from Pliocene and Pleistocene stratigraphic layers of the Hadar and Busidima Formations of the Awash Group at Dikika, Ethiopia, were analysed, provisionally identified and placed within a palaeoecological framework. The older molluscs, associated with layers from which the early hominine fossil species *Australopithecus afarensis* has been recovered, suggest a large, tropical, freshwater drainage system with lakes and slow moving rivers, while the younger molluscs, associated with stratigraphic layers containing Middle Stone Age artefacts, suggest a warm tropical to sub-tropical climate with temporary water-bodies and relatively areas of still or stagnant water, dense vegetation, relatively open habitats and a nearby permanent water source, probably the ancestral Awash River.

In this chapter the molluscs from a number of other hominine and non-hominine sites from the Mio-Pliocene of Africa are examined and the palaeoecological evidence they provide compared to what is known using other sources such as vertebrate faunal remains, palynological studies and geological data.

The sites are examined in chronological and geographical order, beginning with the middle Miocene site of Fort Ternan. Each site is given similar treatment with details of the site's age, stratigraphy and taphonomy given in the introduction. For palaeoanthropological comparisons all fossil primates are identified, and all archaeological contexts described. The mollusc taxa from each site are listed, discussed and placed within a palaeoecological context. Finally, the palaeoecology of each site is discussed with a comparison of what is known through non-molluscan data, primarily non-molluscan fauna, and what the molluscan data reveal.

5.1 Fort Ternan

5.1.1 Introduction

Fort Ternan is an East African site located in western Kenya, south of Lake Turkana and about 20kms east of the north eastern part of Lake Victoria (Figure 5.1.1).

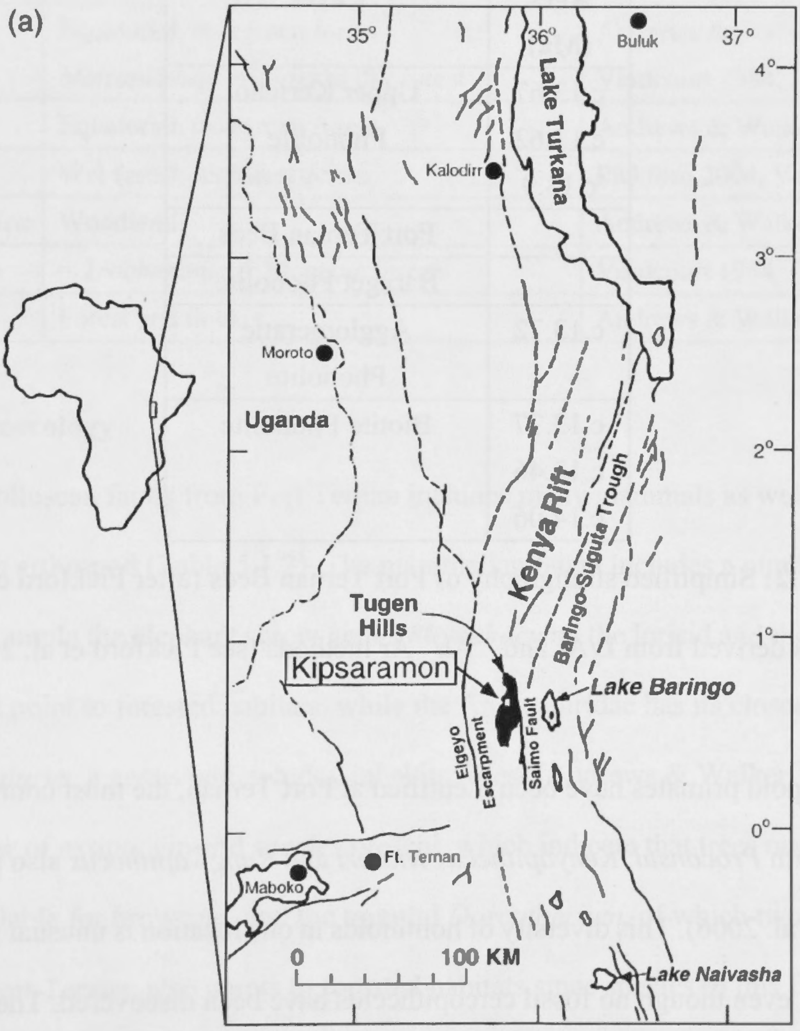


Figure 5.1.1: Map showing location of Fort Ternan (bottom left), Kenya (Behrensmeyer et al. 2002).

The sediments of Fort Ternan are estimated to be between 13 and 14 Ma and consist of sediments associated with a large volcano including sub-aerial accumulations of volcanic ash and palaeosols containing fossils that may have accumulated through water action (Andrews & Walker 1976). The Beds sit above the Agglomeratic Phonolite and below the Upper Kericho Phonolite (Figure 5.1.2).

Ages (Ma)	**Layer**
c.13.67 c.13.62 c.13.9	Upper Kericho Phonolite
	Fort Ternan Beds
	Baraget Phonolite
c.13.72	Agglomeratic Phonolite
c.13.77 c.13.46 c.14.06	Biotite Phonolite

Figure 5.1.2: Simplified stratigraphy of Fort Ternan Beds (after Pickford et al. 2006). Ages derived from L/Ar and ^{40}Ar/^{39}Ar methods (see Pickford et al. 2006).

Four anthropoid primates have been identified at Fort Ternan, the most common being *Simiolus*, with *Proconsul*, *Kenyapithecus wickeri* and *Rangwapithecus* also present (Pickford et al. 2006). This diversity of hominoids in one location is unusual from today's perspective, even though no fossil cercopithecids have been discovered. The only other primate identified from Fort Ternan is a lorisid (Andrews & Walker 1976). No artefacts are known from Fort Ternan, and the age of the site almost certainly predates the emergence of the Homininae (Easteal & Herbert 1997).

5.1.2 Molluscs

Six molluscan genera from six separate families have been identified from Fort Ternan (Table 5.1.1). These are all terrestrial gastropods with *Maizania* the only prosobranch gastropod and all the others pulmonates.

Table 5.1.1: Molluscs from Fort Ternan (Andrews & Walker 1976)

Taxon	Palaeoecology	References
Maizania	Equatorial, evergreen forest *Maizania lugubrioides* in dry forest	Andrews & Walker 1976, Verdcourt 1984, Pickford 2004
Homorus	Equatorial, evergreen forest	Andrews & Walker 1976
Cerastua	Wet forest; highland genus	Pickford 2004, Verdcourt 1984
Burtoa nilotica	Woodland	Andrews & Walker 1976
Trodonania	= *Trochonanina*? Montane forests	Verdcourt 1984
Gulella	Forest and thicket	Andrews & Walker 1976

5.1.3 Palaeoecology

The non-molluscan fauna from Fort Ternan includes many mammals as well as reptiles, birds and an arthropod (Table 5.1.2). The mammalian fauna includes a number of forest taxa. For example the elephant shrew genus *Rhynchocyon*, the lorisid and the diversity of anthropoids point to forested habitats, while the Anomaluridae has its closest affinities with *Anomalurus*, a genus which today inhabits forest (Andrews & Walker 1976). There are a number of extinct giraffid species present, which indicate that trees must have been locally available for browsing, and the tragulid *Dorcatherium*, of which two species are present at Fort Ternan, also points to forested habitats since species of this family today are restricted to forested habitats (Chua et al. 2009).

Table 5.1.2: Non-molluscan fauna from Fort Ternan beds (Andrews & Walker 1976, Pickford et al. 2006).

MACROSCELIDEA	**PERISSODACTYLA**
Rhynchocyon	*Chilotheridium pattersoni*
PRIMATES	*Paradiceros mukirii*
Kenyapithecus wickeri	*Chalicotherium rusingense*
Proconsul sp. ?	**ARTIODACTYLA**
Rangwapithecus sp.	*Listriodon bartulensis* (suid)
Simiolus	*Albanohyus* sp. (suid)
Lorisinae	*Kenyapotamus ternani*
RODENTIA	*Dorcatherium chappuisi*
Leakeymys ternani	*Dorcatherium piggoti*
Anomaluridae cf. *Anomalurus*	*Kipsigicerus labidotus*
Sciuridae	*Gazella* sp.
Pedetidae	*Oiocerus tanycerus*
Phyomyidae	*Climacoceras gentryi*
CARNIVORA	*Palaeotragus primaevus*
Hyainailourus sulzeri	*Samotherium africanum*
Percrocuta tobieni	*Gentrytragus gentryi*
Agnotherium antiquum	**ARTHROPODA**
Mustelidae	Potamidae (freshwater crab)
Viverridae	**REPTILIA**
TUBULIDENTA	Chamaeleodontidae
Orycteropus sp.	*Crocodylus* sp.
PROBOSCIDEA	**AVES**
Afrochoerodon sp.	*Struthio* cf. *asiaticus*
Deinotherium giganteum	Falconidae

In addition there are certain faunal indications of more open habitats. The antelope *Gazella* is an inhabitant today of relatively arid grasslands while the ostrich *Struthio* inhabits semi-desert to woodland environments. Signs of cursorial adaptations in some of the artiodactyls signify open or lightly wooded habitats (Churcher 1970, Gentry 1970).

Evidence of water at Fort Ternan comes from the ancient hippopotamid *Kenyapotamus*, the freshwater crab Potamidae and the crocodilian *Crocodylus* (Andrews & Walker 1976). The picture therefore is of a landscape including some forests but also some more open habitats with water in the form of a lake or possibly a river.

The molluscan fauna is indicative of forest cover since *Maizania* and *Homorus* in particular are today restricted to evergreen forest. No aquatic molluscs or clear examples of open terrain molluscs have been discovered (Andrews & Walker 1976). As a whole, the gastropod assemblage strongly suggests the presence of evergreen forest at Fort Ternan (Andrews & Walker 1976), though woodland, dry forests and montane forests are all also possible given the presence of certain molluscan genera. The habitat was most likely tropical, since terrestrial prosobranch gastropods such as *Maizania* are today generally found in tropical habitats.

5.1.4 Conclusion

The molluscan fauna at Fort Ternan offer support to the conclusions based on other data that equatorial forested habitats probably prevailed. The molluscan data do not reflect the idea of open habitats. The diversity of snails suggests that the forested area may have been relatively large and diverse; encompassing different types of forest such as wet, dry and montane, as well as woodland, as opposed to a thin strip of gallery forest lining a lake or river. These forests would have provided foraging opportunities and shelter to the Fort Ternan hominoids.

5.2 Lukeino

5.2.1 Introduction

The Lukeino Formation is situated immediately east of the Tugen Hills, Kenya, which is south of Lake Turkana and northeast of Lake Victoria (Figure 5.2.1).

Figure 5.2.1: Map showing location of Tugen Hills, Kenya, immediately west of the Lukeino Formation (Sawada et al. 2002).

Significantly younger than Fort Ternan, Lukeino has yielded some of the earliest fossil hominine evidence known. Radio-isotopic age estimates on volcanogenic crystals, and age determinations on lavas both overlying and underling the sediments, indicate an age of between 6.2 and 5.65 Ma (Figure 5.2.2). This date is consistent with bio-chronology estimates based on fauna, especially the suids and proboscideans (Pickford & Senut 2001).

Age (Ma)	**Formation**	**Hominine levels**
c.5.14 c.5.65 c.5.92 c.5.65	Kaparaina Basalts	
c.5.62 c.6.06	Lukeino Formation	Kapcheberek Kapsomin Cheboit Aragai
c.6.2 c.6.31 c.6.36	Kabernet Trachytes	

Figure 5.2.2: Simplified stratigraphic column for Lukeino (after Pickford & Senut 2001)

Some of the fossils from Lukeino are coated with algae, while others have cracks, apparently from desiccation. Tooth marks on the bones and the fact that the assemblage is dominated by small to medium sized bovids and small colobines indicate that a large predator, possibly a leopard-like cat, may have been one of the accumulating agents. The hominine fossils come from shallow lake deposits at Kapsomin and fluvial, floodplain deposits at Cheboit, Kapcheberek and Aragai (Pickford & Senut 2001).

Remains at Lukeino include a number of primates such as a galagid, a colobine monkey (Colobinae) and at least one hominine, *Orrorin tugenensis*, which is considered by some (Senut et al. 2001) to have possessed bipedal features and arboreal adaptations. *Orrorin* was probably comparable in size to a female chimpanzee (Pickford & Senut 2001). Pickford & Senut (2005) believe, on the basis of fossilised teeth, that a gorillin may have been present at Lukeino. No artefacts have been discovered in association with the Lukeino Formation.

5.2.2 Molluscs

Fossil mollusc remains from Lukeino were studied at Ghent University in May 2007 (Table 5.2.1).

Table 5.2.1: Molluscs from Lukeino

Taxon	**Palaeoecology**	**References**
Iridina subelongata	Iridinidae: tropical freshwater lakes and rivers, parasitic on fish at larval stage	Van Bocxlaer & Van Damme 2009
Iridina moharensis	Iridinidae: tropical freshwater lakes and rivers, parasitic on fish at larval stage	Van Bocxlaer & Van Damme 2009
Melanoides	Wide variety of brackish and freshwater environments, except papyrus swamps and waters that dry out regularly	Van Damme 1984, Brown 1980

The Lukeino assemblage includes two species of the family Iridinidae preserved as endocasts. At Kaptabuyan *Iridina subelongata* was preserved in shallow yellow clayey sandstone, with the largest specimen measuring 70 x 29mm (Figure 5.2.3).

From the locations of Ngembo Kuprelach, Cheboit and Sangorok, endocast specimens assigned to *Iridina moharensis* have been discovered, formed from dark orangey brown fine-grained sandstone, possibly chemically discoloured (Figure 5.2.4). These specimens reached maximum measurements of 71 x 21mm. From Kapsomin, medium sized *Melanoides* shells encrusted with algal growth were also discovered.

Figure 5.2.3: *Iridina subelongata* from Kaptabuyan, Lukeino (scale 5mm)

Figure 5.2.4: *Iridina moharensis* from Cheboit, Lukeino (scale 5mm)

5.2.3 Palaeoecology

The Lukeino Formation has a diverse range of associated vertebrate taxa including fish, reptiles, birds and mammals (Table 5.2.2). The fauna provides evidence for a diversity of habitats.

Pickford & Senut (2001) argue that open woodlands were present on the basis of the number of impalas preserved in the deposits. Forested areas were most likely present since colobus monkeys have been discovered. In addition there were two species of hippopotamid, suggesting two separate econiches. Today, there are two extant hippopotamid genera and these are characterised by different habitat preferences, with *Hippopotamus* preferring open habitats, and the smaller *Choeropsis* associated with generally closed habitats. The large and small hippopotamid species found at Lukeino might indicate the existence of both closed and more open habitats.

The presence of three crocodilian species, two hippopotamids, three families of fish, three turtle families, an otter from the family Lutrinae, the cane rat *Thryonomys* (which inhabits waterside reed beds) and the waterbuck *Kobus*, together indicate permanent water, fringed by grassy wetlands, including at least some stands of longer reeds. Muddy substrates are indicated by the presence of the turtle families.

The gastropod *Melanoides* requires permanent water but can survive in a wide variety of habitats including moderately saline waters as well as lentic and lotic habitats. *Iridina* species belong to the family Iridinidae, and these strongly indicate a large permanent

Table 5.2.2: Vertebrate fauna from the Lukeino Formation (Pickford & Senut 2001)

PISCES	**PROBOSCIDEA**
Cichlidae Indet.	*Anancus kenyensis*
Cyprinidae Indet.	*Primelephas gomphotheroides*
Clariidae Indet.	*Stegotetrabelodon orbus*
REPTILIA	*Loxodonta* Lukeino stage
Crocodylus lloydi	*Deinotherium bozasi*
Crocodylus sp.	**TUBULIDENTATA**
cf *Euthecodon* sp.	*Orycteropus* large sp.
Pelomedusidae Indet.	*Orycteropus* small sp.
Trionychidae Indet.	**PRIMATES**
Testudinidae Indet.	Galagidae indet.
Varanus sp.	Colobinae
Ophidea Indet.	*Orrorin tugenensis*
AVES	Cf. *Gorilla*
Indet.	**PERISSODACTYLA**
RODENTIA	*Hipparion* cf *sitifense*
Hystrix sp.	*Hipparion turkanense*
Saidomys sp.	?*Diceros* sp.
Bathyergidae Indet.	*Ceratotherium praecox*
Thryonomys sp.	*Ancylotherium hennigi*
LAGOMORPHA	**ARTIODACTYLA**
Leporidae Indet.	*Hippopotamus* s.l. large sp.
CARNIVORA	*Hippopotamus* s.l. small sp.
Amphicyon sp.	*Nyanzachoerus tulotos*
Lutrinae sp.	*Giraffa* cf *jumae*
cf *Herpestes* sp.	*Cephalophus* sp.
Hyaenidae Indet.	*Kobus* aff. *Porrecticornis*
Felidae Large sp.	*Aepyceros* sp.
Felidae Small sp.	Neotragini
HYRACOIDEA	*Ugandax* cf. *gautieri*
Procaviidae Indet	*Tragelaphus* cf. *spekei*

freshwater drainage system with a tropical climate. Freshwater mussels are intolerant of salinity and since they are reliant on fish hosts for nutrition and transport during the larval stage of their life-cycle, require large permanent drainage systems for dispersal. The *Iridina* specimens are elongate, which is typical in freshwater mussels of riverine habitats (Scholtz & Hartman 2007), the lanceolate shape suggesting that the river may have flowed at some velocity (Good 2004). Since *Melanoides* can tolerate a wide range of permanent aquatic habitats including riverine habitats, the presence of these genera together are indicative of a permanent river system.

5.2.4 Conclusion

The non-molluscan fauna from Lukeino indicate the presence of forested regions, more open habitats and permanent water. The sedimentological data are indicative of lacustrine and fluvial environments. The molluscan data confirm the presence of riverine habitats and are consistent with a large permanent drainage system including a lake, relatively fast flowing rivers, and associated floodplains.

The overall picture of Lukeino is a tropical, partly forested, partly open habitat including a relatively large perennial freshwater drainage system fringed with reeds and wetlands, with at least part of the river flowing at a relatively high velocity.

Since its anatomy suggests *Orrorin* was adapted to climbing (Senut et al. 2001), it probably sheltered in the trees for which there is evidence at Lukeino. Open habitats and local wetlands could have provided extra forraging opportunities for this early hominine (Wrangham et al. 2009).

5.3 Lothagam

5.3.1 Introduction

Lothagam is a Mio-Pliocene fossil site located to the west of Lake Turkana, northern Kenya, and is part of the African Rift Valley (Figure 5.3.1).

Figure 5.3.1: Map showing location of Lothagam, northern Kenya (McDougall & Feibel 1999)

The stratigraphy of Lothagam is made up of a lower unit of mid-Miocene age known as the Nabwal Arangan Beds, overlain by the Nawata Formation of late Miocene age, which is overlain by the Plio-Pleistocene age Nachukui Formation (McDougall & Feibel 1999, Figure 5.3.2). The upper member of the Nawata Formation is between 6.5-5 Ma, while the Apak Member of the Nachukui Formation, which overlies the Nawata Formation, is c.

4.2–5 Ma (McDougall & Feibel 1999). The Lothagam deposits were laid down by a large meandering river flanked by abundant back swamps and ponds (Leakey et al. 1996).

Formation	Member	Age (Ma)
Nachukui		1.88
	Apak	4.22
Nawata	Upper	6.55
	Lower	7.44
Nabwal Arangan Beds		9.1

Figure 5.3.2: Simplified stratigraphic diagram for Lothagam

Hominoids (possibly hominines) are represented by three fossil occurrences: a lower incisor and an upper molar from the upper member of the Nawata Formation, and a mandibular fragment (KNM-LT 329) from the lower part of the Apak Member (M.G. Leakey & Harris 2003). Three cercopithecoid species are also present at Lothagam; two colobines and a papionine. No artefacts have been recovered from Lothagam (M.G. Leakey & Harris 2003).

5.3.2 Molluscs

A variety of freshwater molluscs have been discovered at Lothagam (Table 5.3.1).

Table 5.3.1: Molluscs from Lothagam

Taxon	**Palaeoenvironment**	**References**
Etheria	Flowing water in rivers and large lakes where they cement themselves to hard substrates – tropical	Van Bocxlaer & Van Damme 2009
Coelatura	Lakes and rivers	Van Damme 1984
Bellamya	Lakes, large slow flowing rivers, streams – tropical	Van Damme 1984
Ampullaria wernei	River connected swamps, floodplains and other stagnant waters, aestivate in mud – humid tropical	Cowie 2002
Lanistes carinatus	Slow streaming rivers and their swamps and floodplains, capable of aestivation humid tropical	Van Damme 1984
Melanoides	Wide range of freshwater and brackish habitats tropical to sub-tropical	Brown 1980

Numerous freshwater oyster reefs (*Etheria*) have been discovered at Lothagam, particularly in the lower Nawata and Apak members (Patterson et al. 1970, M.G. Leakey et al. 1996, Figure 5.3.3). During a visit to Ghent University fragments of *Etheria* from Lothagam were examined, some of which measured 260 by 120mm. Other mollusc species identified from Lothagam are the gastropods *Bellamya*, *Ampullaria wernei*, *Lanistes carinatus* and *Melanoides*, as well as the bivalve *Coelatura*.

Figure 5.3.3: Upper valve of *Etheria elliptica* from Lothagam, (scale 10mm)

5.3.3 Palaeoecology

Lothagam has a diverse range of associated fossilised faunal remains, including a number of mammalian taxa, especially perissodactyls and artiodactyls (Tables 5.3.2 & 5.3.3).

Table 5.3.2: Lothagam Perissodactyla & Artiodactyla (M.G. Leakey & Harris 2003)

PERISSODACTYLA	*Palaeotragus* sp.
Brachypotherium lewisi	*Giraffa stillei*
Ceratotherium praecox	*Tragelaphus kyaloae*
Diceros bicornis	*Tragelaphus nakuae*
Hippotherium cf. *H. primigenium*	*Tragelaphus* cf. *T. scriptus*
Eurygnathohippus turkanense	Traelaphini gen. and sp. indet.
Eurygnathohippus feibeli	*Simatherium* aff. *S. kohllarsoni*
Eurygnathohippus sp. (large)	Bovini gen. and sp. indet.
Eurygnathohippus sp. (small)	*Tragoportax* cf. *T. crenaicus*
ARTIODACTYLA	*Tragoportax* sp. A
cf. *Kubanochoerus* sp	*Tragoportax* sp. B
Nyanzachoerus syrticus	Boselaphini gen. and sp. indet.
Nyanzachoerus cf. *Ny. syrticus*	*Kobus presigmoidalis*
Nyanzachoerus cf. *Ny. australis*	*Kobus laticornis*
Nyanzachoerus pattersoni	*Menelikia leakeyi*
Nyanzachoerus devauxi	Reduncini gen. and sp. indet.
Nyanzachoerus jaegeri	*Praedamalis* sp
Notochoerus euilus	*Hippotragus* sp.
cf. *Potamochoerus* sp.	Hippotragini gen. and sp. Indet
Cainochoerus cf. *C. africanus*	*Damalacra* sp. A
Hexaprotodon lothagamensis	*Damalacra* sp. B
Hexaprotodon harvardi	Alcelaphini gen. and sp. indet.
Hexaprotodon sp. indet.	*Aepyceros premelampus*
Hexaprotodon cf. *Hex. protamphibius*	*Gazella* sp. indet.
cf. *Sivatherium* sp.	*Raphiceros* sp.
Palaeotragus germaini	*Madoqua* sp.

Table 5.3.3: Non-Perissodactyla & -Artiodactyla mammalian fauna from Lothagam (M.G. Leakey & Harris 2003)

RODENTIA	Melivorinae
Alilepus sp.	*Vishnuonyx angololeniss*
Serengetilagues praecapensis	*Viverra* cf. *V. leakeyi*
Leporidae sp	Viverriane gen and sp. Indet
Hystrix sp. (small)	cf. *Genetta* sp. A
Hystrix sp. (large)	cf. *Genetta* sp. B (large)
Kubwaxerus pattersoni	*Ictitherium ebu*
Abudhabia sp.	*Hyaenictitherium* cf. *H. parvum*
Karnimata jacobsis sp.	cf. *Hyaenictus* sp.
Saidomys sp.	*Ikeloyaena* cf. *I. abronia*
Paraphiomys chororensis	*Lokotunjailurus emageritus*
Paraulacodus cf. P. jahanesi	*Dinofelis* sp. A
Thryonomys cf. T. gregorianus	*Dinofelis* sp. B
Thryonomys sp. (small)	cf. *Metailurus* sp.
Muridae incertae sedis	*Leptailurus/Caracal* sp.
PRIMATES	cf. *Canis* sp.
Hominoidea indet.	**PROBOSCIDEA**
Australopithecus cf. *A. afarensis*	*Anancus kenyensis*
Parapapio lothagamensis	Gomphotheriidae gen. and sp. indet.
cf. *Parapapio* sp. indet	*Stegotetrabelodon orbus*
Theropithecus cf. *T. brumpti*	*Primelephas gomphotheroides*
Cercopithecoides kerioensis	*Primelephas* or *S. orbus*
Colobinae sp. A	*Elephas nawatensis*
Colobinae sp. B	*Elephas* cf. *E. ekorensis*
Colobinae sp. C	*Loxodonta* sp. indet.
Colobinae (large)	Elephantidae gen. and sp. Indet
Colobinae (small)	Elephantidae incertae sedis A
CARNIVORA	Elephantidae incertae sedis B
Amphicyonidae sp (large)	*Deinotherium bozasi*
Amphicyonidae sp (small)	**TUBULIDENTATA**
Ekorus ekakoran	*Leptorycteropus guilielmi*
Erokomellivora lothagamensis	*Orycteropus* sp. indet.

The abundant mammalian fauna includes evidence of both forested and more open wood or grassland habitats. The alcelaphine bovids, for example, are indicative of open habitats, as are the reduncine bovids, which are often grazers in open grasslands near water. The giant squirrel, *Kubwaxerus*, on the other hand, suggests that forested habitats were locally present, and this is supported by the presence of a number of bovids belonging to the genus *Tragelaphus*, as well as a diversity of cercopithecoid monkeys, at least some of which are likely to have been reliant on forest habitats.

The four fossil hippopotamid taxa from the Lothagam Formation have been assigned to the genus *Hexaprotodon*, which is essentially a forest dweller, and the presence of this genus is also indicative of a permanent water body. Also indicating a permanent water body is the presence of the otter *Vishnuonyx*, while the rodent *Thryonomys* suggests reed beds lining waterways.

Lothagam also preserves fish, reptiles and birds (Table 5.3.4). This non-mammalian vertebrate fauna points to a diversity of aquatic habitats. Freshwater habitats must have been present because *Polypterus* is intolerant of even slightly saline waters, *Gymnarchus* inhabits swamps and vegetated river edges, *Hydrocynus* is more likely to be found in open waters of lakes and rivers, and *Protopterus* is able to survive in habitats that seasonally dry out.

The piscivorous crocodilian taxa (including *Euthecodon* and *Eogavialis*) suggest large, permanent water bodies were present, while the diversity of turtle taxa point to habitats such as streams, rivers, lakes and ponds with both stagnant and flowing waters.

Table 5.3.4: Non-mammalian vertebrate fauna from Lothagam (M.G. Leakey et al. 1996, M.G. Leakey & Harris 2003)

OSTEICHTHYES	Testudinidae
Citharinus	*Crocodylus lloidi*
Bagrus	*Crocodylus niloticus*
Synodontis	*Crocodylus cataphractus*
Lates	*Euthecodon brumpti*
Sindacharax	*Eogavialis*
Protopterus	**AVES**
Polypterus	Struthionidae (ostrich)
Heterotis	Aepyonithidae (elephant bird)
Gymnarchus	Pelecanidae (pelican)
Hydrocynus	Anhingidae (anhinga)
REPTILIA	Ardeidae (heron)
Cycloderma debroinae	Ciconiidae (stork)
Cycloderma frenatum	Anatidae (duck)
Trionychidae	Rallidae (rail)
aff. *Erymnochelys*	Otididae (bustard)
Kenyemys williamsi	Strigidae (owl)

The Aves fauna has representatives indicative of open (ostrich) and wooded (owl) habitats, but also has a diverse wetland component. These include waders (rail, heron, stork), surface swimmers (ducks, pelicans) and divers (anhinga). These aquatic birds suggest shallow waters suitable for wading and sufficient fish stocks to support a diverse avian fauna.

The invertebrate taxa from Lothagam include the freshwater crab Potamonautidae, indicative of well oxygenated riverine habitats (Martin & Trautwein 2003). The other invertebrate fossils from Lothagam are molluscs.

The freshwater oyster specimens from Lothagam are large and typical of those derived from extensive reefs. These indicate a large tropical river with considerable rates of flow, even during dry seasons (Van Bocxlaer & Van Damme 2009). *Bellamya* is a tropical snail most commonly associated with lakes and slow flowing rivers, while the unionid bivalve *Coelatura* is usually found in large lakes and rivers (Van Damme 1984). *Melanoides* is found in a wide range of permanent water bodies (Brown 1980), while *Lanistes* and *Ampullaria* are adapted to the vegetation belts that grow around swamps and other waterways and can survive in waterbodies that seasonally become dry. The Ampullariidae are found in the humid tropics and subtropics and are limited to areas where the temperatures does not fall below 10 degrees, and rainfall is no less than 600mm annually (Cowie 2002).

5.3.4 Conclusion

The diverse and abundant vertebrate fauna at Lothagam points to both open and closed habitats as well as a permanent water body. Shallow wetlands including well vegetated water margins must have been locally present. The molluscs from Lothagam reinforce the conclusion that permanent water was present, including shallow wetland habitats and areas of marshy vegetation. The molluscs also add some extra information since it is clear that rapidly flowing water must have been present, as well as areas of more stagnant water. Since a number of the mollusc genera present are restricted to tropical habitats today, the likelihood is that at the time of deposition Lothagam had a tropical climate.

5.4 Kanapoi

5.4.1 Introduction

Kanapoi is located southwest of the Turkana Basin in northeast Kenya (Figure 5.4.1). The depositional context consists of deltaic and fluviatile sediments which accumulated during a major lacustrine stage. The hominine fossils from Kanapoi, except for a large mandible, all come from sediments deposited between about 4.17 and 4.07 Ma (M.G. Leakey et al. 1998). The mandible derives from a palaeosol just above this level, and may therefore not be much younger (Ward et al. 2001). All the hominines from Kanapoi come from floodplain palaeosols or deltaic sandstones, and many show damage caused by mammalian carnivores (M.G. Leakey et al. 1998). The interval in which the hominines are found contains claystones probably associated with deposition into the ancient Lonyuman Lake.

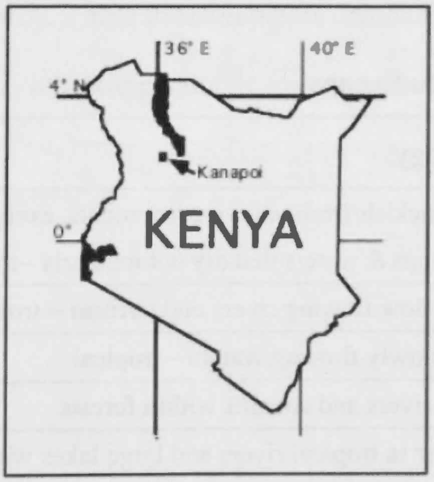


Figure 5.4.1: Location of Kanapoi fossil site, northeast Kenya (after Feibel 2003).

The hominine fossils from Kanapoi have been assigned to the species *Australopithecus anamensis* (M.G. Leakey et al. 1995). This species is reported to have been bipedal with arboreal adaptations, and it may have had a gorilla-like degree of sexual dimorphism (M.G. Leakey et al. 1998). A galagid and a number of monkeys are also known from Kanapoi. These include two species of Colobinae, a small *Parapapio* (which dominates the cercopithecoid assemblage), a monkey with affinities to *Cercopithecoides* and a *Theropithecus*-like monkey (Harris et al. 2003). No artefacts are known from Kanapoi.

5.4.2 Molluscs

Fossil Mollusca are common in the lacustrine deposits of Kanapoi (Table 5.4.1), but their state of preservation is relatively poor. Gastropods include *Melanoides*, *Bellamya*, *Cleopatra* and *Potadoma* (Craig Feibel, personal communication). Reefs of the freshwater oyster *Etheria* are also present within the Kanapoi sediment sequence (Feibel 2003).

Table 5.4.1: Molluscs from Kanapoi

Taxon	**Palaeoecology**	**References**
Melanoides	Variety of brackish/freshwater environments, except papyrus swamps & waters that dry out regularly - tropical	Van Damme 1984, Brown 1980
Bellamya	Lakes, large slow flowing rivers and streams – tropical	Van Damme 1984
Cleopatra	Stagnant or slowly flowing waters – tropical	Brown 1980
Potadoma	Abundant in rivers and streams within forests	Brown 1980
Etheria	Flowing water in tropical rivers and large lakes where they cement themselves to hard substrates	Van Bocxlaer & Van Damme 2009
Aspatharia	Iridinidae: Freshwater mussel, lakes and rivers – tropical	Van Damme 1984
Iridina	Iridinidae: Lakes, rivers, streams - tropical	Van Damme 1984

A fossil mollusc assemblage from Kanapoi was studied at Ghent University. Specimens within the assemblage included *Melanoides*, *Cleopatra* and *Aspatharia* (Figure 5.4.2).

Figure 5.4.2: *Aspatharia* cf. *rugifera* from Kanapoi (scale 10mm)

Specimens of *Iridina subelongata* were also present at Kanapoi, one of which measured 76mm in length (Figure 5.4.3). These measurements demonstrate that the mussels in this region were relatively large, indicating suitable growing conditions and a relatively long lived drainage system.

Figure 5.4.3: *Iridina subelongata* from Kanapoi (scale 10mm)

5.4.3 Palaeoecology

The associated faunal remains from Kanapoi are extensive and diverse, with mammals in particular well represented (Table 5.4.2). The mammals include both large and small taxa and indicate a mosaic setting with both open and closed habitats. Harris et al. (2003) note that grazing bovids outnumber browsing bovids two to one in terms of numbers of species, and three to one in terms of number of specimens at Kanapoi, suggesting open grasslands were present. Open grasslands are also suggested because of grazing bovids such as the Alcelaphini. Arid conditions may have also prevailed according to the presence of *Gazella* and the rodents *Tatera* and *Xerus* which are known to inhabit arid environments. On the other hand, there is likely to have been a substantial arboreal component in the area as well since a number of cercopithecoid primates are present, including two colobus monkeys, which are today associated with forest or woodland habitats, and bovids of the tribe Tragelaphini which today inhabit forests (Harris et al. 2003).

Table 5.4.2: Mammalian fauna from Kanapoi (Harris et al. 2003)

CHIROPTERA	*Elephas ekorensis*
Hipposideros spp.	*Loxodonta adaurora*
INSECTIVORA	*Loxodonta exoptata*
Myosorex sp.	**PERISSODACTYLA**
MACROSCELIDEA	*Ceratotherium praecox*
Elephantulus sp.	*Diceros bicornis*
LAGOMORPHA	*Eurygnathohippus* sp. Indet.
Leporidae indet.	**ARTIODACTYLA**
RODENTIA	*Hexaprotodon protamphibius*
Tatera sp.	*Hexaprotodon* sp.
Murini indet.	*Nyanzachoerus pattersoni*
Xerus sp.	*Notochoerus jaegeri*
cf. *Steatomys* sp.	*Notochoerus* cf. *N. euilus*
CARNIVORA	*Giraffa stillei*
Enhydriodon ekecaman	*Giraffa jumae*
cf. *Torolutra* sp.	*Giraffa* sp. Indet.
Parahyaena howelli	*Sivatherium* cf. *S. hendeyi*
Dinofelis petteri	*Tragelaphus kyaloae*
Homotherium sp.	Tragelaphini indet.
Felis sp.	*Simatherium* cf. *S. demissum*
Helogale sp.	Hippotragini indet.
Genetta sp.	*Kobus* sp.
PRIMATES	Reduncini indet.
Australopithecus anamensis	*Damalacra* cf. *D. neanica*
cf. *Galago* sp. indet.	*Damalacra* sp. A
cf. *Cercopithecoides* sp. Indet.	*Damalacra* cf. *D. acalla*
Colobinae sp. A	Alcelaphini indet.
Colobinae sp. B	*Aepyceros* sp.
Parapapio ado	*Gazella* sp.
cf. *Theropithecus* sp.	Caprini indet.
PROBOSCIDEA	*Raphiceras* sp.
Deinotherium bozasi	*Madoqua* sp.
Anancus kenyensis	

In addition, the hippopotamids are from the genus *Hexaprotodon*, which are similar in some respects to the living pygmy hippopotamus which today resides in forests, and a number of giraffids are present, meaning suitable browsing forage must have been available.

The hippopotamids are also indicative of permanent water, and this is evidenced also by the presence of two species of otter, *Enhydriodon ekecaman* and the piscivorous *Torolutra* (Petter et al. 1991). The presence of Reduncini, including the genus *Kobus*, is also indicative of permanent water since today these mammals inhabit near water environments (Macdonald 2001).

Table 5.4.3: Non-mammalian vertebrate fauna from Kanapoi (Harris et al. 2003, Stewart 2003)

OSTEICHTHYES	cf. *Semlikiichthys rhachirhinchus*
Polypterus sp.	**AVES**
Hyperopisus sp.	*Struthio* sp.
Gymnarchus sp.	Anatidae
Labeo sp.	*Mycteria* sp. (tropical stork)
Barbus sp.	*Anhinga* sp.
Distichodus sp.	**REPTILIA**
Hydrocynus sp.	*Euthecodon brumpti*
Brycinus macrolepidotus	*Rimasuchus lloydi*
Sindacharax lothagamensis	? *Crocodylus* sp.
Sindacharax mutetii	*Crocodylus niloticus*
Sindacharax howesi	cf. *Geochelone* sp.
Sindacharax sp.	*Geochelone crassa*
Bagridae/Claroteidae	Trionychidae
Clarias or *Heterobranchus*	Cyclanorbini
Synodontis sp.	*Cyclanorbis turkanensis*
Lates niloticus	*Kenyemys* sp.
Lates sp.	*Turkanemys pattersoni*

An extensive non-mammalian faunal assemblage is known from Kanapoi (Table 5.4.3). The fish fauna in many respects resembles that from Lothagam. The assemblage includes the saline intolerant *Polypterus*, for example, indicating that freshwater was locally present, and *Gymnarchus*, which indicates swamps and vegetated river edges. The fact that *Protopterus* is present suggests possible drying out of the landscape, which could indicate isolated pools on flood plains. *Hydrocynus* is likely to be found in open waters of lakes and rivers. Piscivorous and molluscivorous taxa dominate the assemblage, while herbivorous fish are rare (Stewart 2003).

Aquatic reptiles, including turtles and crocodiles are common at Kanapoi (Leakey et al. 1995), indicating extensive wetland habitats, and the fossil birds, as with the birds of Lothagam, include wetland inhabitants such as ducks, storks and darters (Harris et al. 2003). Analysis of ostrich egg shell remains indicate that these birds had a greater proportion of C_3 vegetation in their diet than ostriches today (Harris et al. 2003), an indication that there may have been more cover in the habitat than one would expect for ostriches living today.

The palaeosol and stable carbon isotope studies of Wynn (2000) indicate a range of environments at Kanapoi, from forb-dominated edaphic grasslands to gallery woodland. Reed's (1997) ecological structural analysis suggests a closed woodland habitat for Kanapoi. There is some indication of seasonality. M.G. Leakey et al. (1995: 571) favour a dry, open wood- or grassland where a "wide gallery forest would have almost certainly been present on the large river that brought in the sediments". This river was probably the Kerio (Feibel 2003).

The molluscs give further evidence regarding the palaeoecology. The gastropod, *Potadoma* is today restricted to central African rain forest habitats (Williamson 1985a), and therefore its presence at Kanapoi suggests that at least some forest was present. *Etheria* reefs indicate that there was a perennial, and at least in regions, fast flowing river. *Bellamya*, *Melanoides* and *Cleopatra* are all indicative of permanent water; *Bellamya* generally preferring slow moving rivers and large lakes in tropical habitats. *Melanoides* can tolerate a wide range of conditions, while *Cleopatra* prefers shallow waters.

The two Iridinidae bivalves, *Aspatharia* and *Iridina*, suggest that there was a large drainage system within the vicinity, and that suitable nutrition and fish hosts were available in a freshwater context. The shape of the *Iridina* specimens, more elongate than ovate, might be an indication of relatively high water velocity, which would fit with the ecological requirements of the *Etheria* bivalves. The morphology of the *Aspatharia* specimen on the other hand would seem to indicate quieter waters. *Potadoma* is often associated with fast flowing rivers and streams with gravelly or rocky substrates.

5.4.4 Conclusion

The molluscs of Kanapoi therefore reinforce the conclusions based on other data that permanent water was present, but provide much greater detail about the nature of the water body. It can be inferred, for example, that at some places the water velocity was relatively swift, and that the drainage system was relatively large and permanent. Forested waterside habitats are confirmed by the presence of *Potadoma*, and the fact that relatively shallow waters were present is indicated by the presence of *Cleopatra*. There is little doubt that Kanapoi had a tropical climate since most of the molluscs present, including *Melanoides*, *Bellamya*, *Cleopatra*, *Potadoma* and the Iridinidae are restricted today to tropical and sub-tropical habitats.

Australopithecus anamensis at Kanapoi would have had at least some gallery forest in which to shelter, associated with a large permanent river system in a possibly seasonal savanna type tropical habitat.

5.5 As Duma, Gona

5.5.1 Introduction

As Duma, Gona, is located in the Afar region of Ethiopia, near the Awash River (Figure 5.5.1), an area rich in fossil sites that have played an important role in the study of hominine evolution.

Figure 5.5.1: Map of Ethiopia showing location of Gona (Quade et al. 2004).

The As Duma Member is part of the Sagantole Formation, which lies below the Hadar Formation and above the Adu Asa Formation. The Sagantole Formation at Gona consists of the As Duma, Segala Noumou and As Aela Members, with the upper section of the As Aela Member extending into the lower part of the Hadar Formation (Figure 5.5.2). Radio-isotopic and palaeo-magnetic data suggest an early Pliocene age of between 4.51 and 4.32 Ma. The depositional environment apparently includes small-scale fluvial, lacustrine and volcanic processes and shallow marshy areas (Semaw et al. 2005).

Age (Ma)	**Member**	**Formation**	**Hominid**
3.3	As Aela	Hadar	
3.9		Sagantole	
4.1			
4.2	Segala Noumou		*Ardipithecus ramidus*
4.6			
>4.6	As Duma		
<5.2			
5.2-5.4		Adu Asa	*Ardipithecus kadabba*

Figure 5.5.2: Simplified stratigraphy of the major Formations of Gona (after Quade et al. 2008)

The As Duma Member of the Sagantole Formation is important from a hominine evolutionary perspective because it has yielded fossil specimens for the species *Ardipithecus ramidus*, including mandibular and dental remains as well as manual and pedal phalanx fragments. As Duma also contains two cercopithecoid fossils; a colobine *Kuseracolobus aramisi*, and a papionine *Pliopapio alemui* (Semaw et al. 2005). The hominine fossils show no obvious evidence of transport (Semaw et al. 2005) indicating that they were deposited *in situ*. No artefacts are known from As Duma.

5.5.2 Molluscs

The As Duma sediments contain a number of molluscs (Table 5.5.1). The gastropods include *Melanoides tuberculata*, *Bellamya unicolor* and *Cleopatra* (Semaw et al. 2005). A bivalve from As Duma has been reported (Semaw et al. 2005), but not identified. Quade et al. (2008) report the presence of unionid bivalves in the Sagantole Formation, and it is assumed here therefore that the As Duma bivalves may be unionoids. Tiny gastropods similar to *Gyraulus* are also reported from the As Duma Member (Quade et al. 2008).

Table 5.5.1: Molluscs from As Duma (Semaw et al. 2005, Quade et al. 2008)

Taxon	**Palaeoecology**	**References**
Melanoides	Wide variety of brackish and freshwater environments, except papyrus swamps and waters that dry out regularly tropical	Van Damme 1984, Brown 1980
Bellamya	Lakes, large slow flowing rivers and streams – tropical	Van Damme 1984
Cleopatra	Stagnant or slowly flowing waters – tropical	Brown 1980
cf. *Gyraulus*	Generally stagnant or slowly flowing freshwaters often associated with aquatic vegetation	Brown 1980
Unionoida	Lakes and rivers	Van Damme 1984

5.5.3 Palaeoecology

The As Duma site at Gona has a faunal assemblage which includes mammals, reptiles, birds and fish; although no bird or fish identifications have been made (Table 5.5.2).

The papionine monkey *Pliopapio* makes up 65% of the cercopithecoid assemblage, with the colobine *Kuseracolobus* making up the other 35% (Semaw et al. 2005). This could reflect an environment that included open as well as closed habitats, although White et al. (2009) argue that the postcrania of both these genera, at Aramis at least, are suggestive of predominantly arboreal adaptation.

The diets of most of the large mammals, according to stable carbon isotope data, included mostly C_4 grasses rather than C_3 plants, indicating open grassland habitats, and the bovids of the tribe Antilopini indicate open and possibly dry habitats.

Table 5.5.2: Vertebrate fauna from As Duma (Semaw et al. 2005)

CARNIVORA	*Ugandax* sp.
Hyaenidae	Bovidae indet.
Felidae (2 sizes)	cf. *Giraffa* sp.
Viverridae	*Sivatherium* sp.
PRIMATES	**PERISSODACTYLA**
Pliopapio alemui	*Eurygnathohippus* sp. A
Kuseracolobus aramisi	*Eurygnathohippus* sp. B
Ardipithecus ramidus	*Ceratotherium* sp.
PROBOSCIDEA	*Diceros* sp.
Anancus cf. *kenyensis*	**RODENTIA**
Deinotherium sp.	cf. *Hystrix* sp.
Elephantidae	*Tachyoryctes* sp.
ARTIODACTYLA	**REPTILIA**
Nyanzachoerus jaegeri	cf. Geochelone sp.
Nyanzachoerus kanamensis	Trionychidae
Kolpochoerus deheinzelini	*Varanus* sp.
Hexaprotodon harvardi	Crocodylia
Tragelaphus cf. *kyaloae*	**AVES**
Hippotraginae	Indet.
Reduncini	**OSTEICHTHYES**
Antilopini	Indet.

The presence of colobines and the forest/woodland-dwelling bovid *Tragelaphus* are an indication that closed environments were locally present. The presence of *Hexaprotodon* points to closed environments in the vicinity of water, while the water dependent bovids of the tribe Reduncini are an indication of permanent water bodies. *Nyanzachoerus* *kanamensis* – a suid adapted to swampy habitats (Bishop 1999), as well as turtles, crocodilians and fish all point to substantial and varied wetland habitats.

Celtis (hackberry) seeds and wood fragments have been found at As Duma (Semaw et al. 2005). This is similar to Aramis, where *Ardipithecus anamensis* remains (Lower Aramis Member) were discovered in association with *Celtis* seeds, as well as palm wood (WoldeGabriel et al. 2009, and see Chapter 10.3.1). According to Semaw et al. (2005) a diverse range of data (sedimentological, faunal composition, ecomorphological, stable carbon isotopic evidence from palaeosols and tooth enamel) indicate that As Duma had a moderate rainfall and woodland and woodland/grassland habitats.

The molluscs from As Duma allow a more detailed picture of the local palaeoecology. *Bellamya unicolor* is a tropical gastropod most often found in large lakes, rivers or slow moving streams (Brown 1980), while *Melanoides* has a wide tolerance range but is never found in habitats that regularly become dry. *Cleopatra* prefers sandy substrates in tropical shallow waterways. Bivalves are aquatic and generally require non-stagnant, permanent water for survival. While no identifications of the bivalves at As Duma have been published, unionoid bivalves do occur in the Sagantole Formation. Unionoid bivalves are strictly freshwater inhabitants, require large drainage areas for dispersal, and are most commonly associated with large lakes, rivers and slow flowing streams, but more information regarding the bivalves from As Duma are needed to provide more detailed palaeoecological inferences.

5.5.4 Conclusion

The molluscs from As Duma reinforce the conclusion based on other data that a permanent water source was present. Since *Bellamya* is present it can be further inferred that the water source was part of a larger tropical drainage system with connected lakes and rivers, rather than a series of isolated pools or ponds. The presence of *Cleopatra* points to relatively shallow habitats with sandy substrates and relatively slow flowing waters. This was a freshwater body according to the makeup of the gastropods. Specific identification of the bivalve could allow more detailed inferences regarding the ecology of As Duma.

5.6 Manonga Valley

5.6.1 Age and stratigraphy

The Manonga Valley is an early Pliocene site from Africa's Rift Valley, situated south of current day Lake Victoria, Tanzania (Figure 5.6.1).

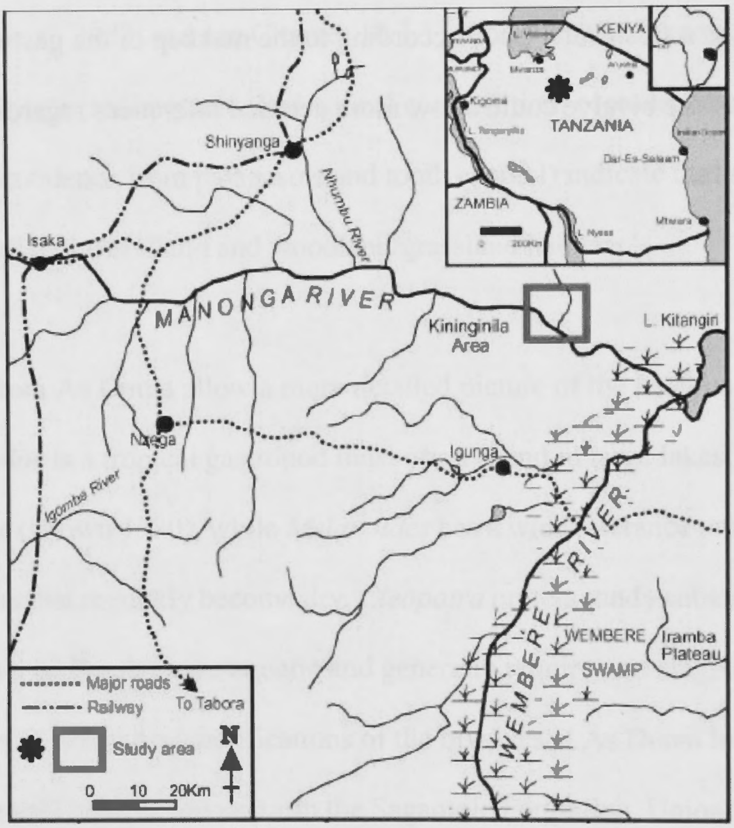


Figure 5.6.1: Map showing location of the Manonga-Wembere Valley, Tanzania (Kafumu 2004)

Deposits are known from the Wembere-Manonga Formation, and the data analysed here come from the Tinde and Kiloleli Members of the Formation (Figure 5.6.2).

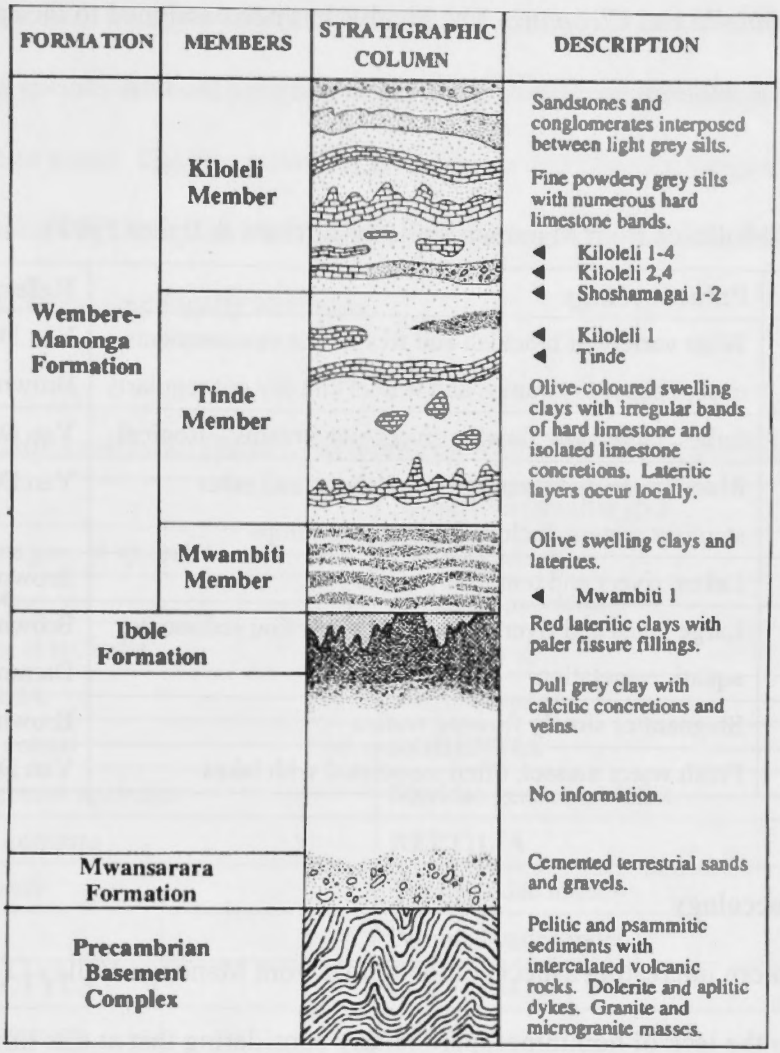


Figure 5.6.2: Schematic stratigraphic section from the Manonga Basin. Fossil sites indicated by arrows in the right hand column (Harrison et al. 1993).

The deposits are mainly of lacustrine origin (Harrison & Baker 1997). The only primate discovered at Manonga Valley is the canine of a large cercopithecid monkey.

5.6.2 Molluscs

A variety of molluscs have been discovered at Manonga Valley (Table 5.6.1) including both gastropods and a bivalve. The six gastropod genera are *Melanoides*, *Bellamya*, *Pila*, *Lanistes*, *Gabbiella* and *Cleopatra.* The bivalve has been assigned to the species *Chambardia wahlbergi.*

Table 5.6.1: Molluscs from Manonga Valley (Harrison & Baker 1997)

Taxon	**Palaeoecology**	**References**
Melanoides	Wide variety of brackish and freshwater environments, except papyrus swamps and waters that dry out regularly	Van Damme 1984, Brown 1980
Bellamya	Lakes, large slow flowing rivers and streams – tropical	Van Damme 1984
Pila	River connected swamps, flood plains and other stagnant waters, including papyrus swamps	Van Damme 1984
Lanistes	Lakes, rivers and temporary pools	Brown 1980
Gabiella	Large lakes and rivers, associated with fine sediments; aquatic vegetation	Brown 1980, Van Damme 1984
Cleopatra	Stagnant or slowly flowing waters	Brown 1980
Chambardia	Fresh water mussel, often associated with lakes	Van Damme 1984

5.6.3 Palaeoecology

One of the more interesting aspects of the faunal from Manonga Valley (Table 5.6.2), as discussed, is the lack of hominines, particularly considering that at this time hominines are known from Ethiopia, Kenya and Chad. The Carnivora and Rodentia are poorly represented at Manonga valley, unlike Kanapoi and Lothagam.

One of the more diverse mammalian orders at Manonga Valley is Proboscidea. This order has five different taxa in at least four genera, indicating that the palaeoecology of the region was notably different to anything known today. *Loxodonta* generally prefers shade and water (Kingdon 1997) and the diversity of elephants could be an indication of diverse forest regions probably with a nearby water source. The Alcelaphini, on the other hand, are generally grassland inhabitants (Kingdon 1997), indicating that at least some open areas may have been locally available. *Tragelaphus* species prefer cover and the two hippopotamid species are both assigned to the genus *Hexaprotodon*, suggesting forested habitats close to water. The two giraffids, *Sivatherium* and *Giraffa*, suggest habitats suitable for browsing (Kingdon 1997), and the presence of a cercopithecoid is an indication that trees were locally available.

Table 5.6.2: Non-molluscan fauna from Manonga Valley (Harrison and Baker 1997)

PRIMATES	Acelaphini (smaller sp.)
Cercopithecidae gen. et sp. indet.	*Praedamalis* sp.
CARNIVORA	*Kobus* cf. *subdolus*
Viverridae gen. et sp. indet.	*Aepyceros* sp.
PROBOSCIDEA	*Tragelaphus* sp.
Deinotherium bozasi	**RODENTIA**
Elephantinae gen. et sp. indet.	Muridae gen. et sp. indet.
Loxodonta cf. *exoptata*	**REPTILIA**
Elephas ekorensis	Trionychidae indet.
Anancus sp.	Pelomedusidae indet.
PERISSODACTYLA	*Crocodylus* sp.
Eurygnathohippus sp.	**AVES**
Eurygnathohippus aff. *hasumense*	indet.
Ceratotherium praecox	**OSTEICHTHYES**
ARTIODACTYLA	*Alestes* sp.
Nyanzachoerus kanamensis	*Sindacharax* sp.
Hexaprotodon harvardi	Cichlidae indet.
Hexaprotodon sp.	*Protopterus* sp.
Giraffa sp.	*Clarias* sp.
?*Sivatherium* sp.	*Lates* ?sp.
Damalacra sp.	**INSECTA**
Acelaphini (larger sp.)	Hymenoptera indet

The bovid assemblage includes the genus *Kobus* which is never found far from permanent water, while the hippopotamids, turtles, crocodiles and fish also indicate the presence of permanent water, though the presence of the lung fish *Protopterus* also indicates that shallow, swampy or marshy habitats subject to drying could also have been present. The suid *Nyanzachoerus kanamensis*, as previously mentioned, has anatomical features suggesting it was a swamp specialist (Bishop 1999).

The molluscan assemblage reinforces the idea of a permanent water body, and adds detail to the various types of sub-habitats that may have existed within and around the Manonga Valley. *Bellamya capillata*, for example, is usually found in tropical lakes, slow flowing rivers and permanent marshes (Brown 1980), while *Cleopatra* prefers shallow waters and sandy substrates in tropical regions, though the small size of the specimens in these samples suggest sub-optimal conditions (Van Damme & Gautier 1997).

The Ampullariidae, of which two species are known from Manonga Valley *Pila ovata* and *Lanistes ovum*, are found in marshy habitats that contain vegetation today, such as papyrus swamps, also in tropical regions. The bivalve *Chambardia* is today typically found in lacustrine environments (Van Damme 1984, Van Damme & Gautier 1997).

5.6.4 Conclusion

The molluscan fauna point to a large drainage area in which a large slow moving river and/or lake was present together with fringing shallow, swampy wetlands with abundant vegetation in a tropical habitat. Taken together, the faunal remains at Manonga Valley suggest a lake or river fringed by forest, with nearby open woodlands, grasslands and swampy conditions also likely. The molluscan faunal remains add weight to the non-molluscan data in terms of palaeoecological reconstruction, and add detail in terms of the types of vegetation that may have been present, the climate, types of substrate, water depths and velocity.

5.7 Laetoli

5.7.1 Introduction

Laetoli, northern Tanzania, is an important site with regard to hominine evolution because it contains both skeletal remains and footprints of early hominines. It is situated south of the Serengeti Plain, north of Lake Eyasi and west of the Ngorongoro Crater (Figure 5.7.1).

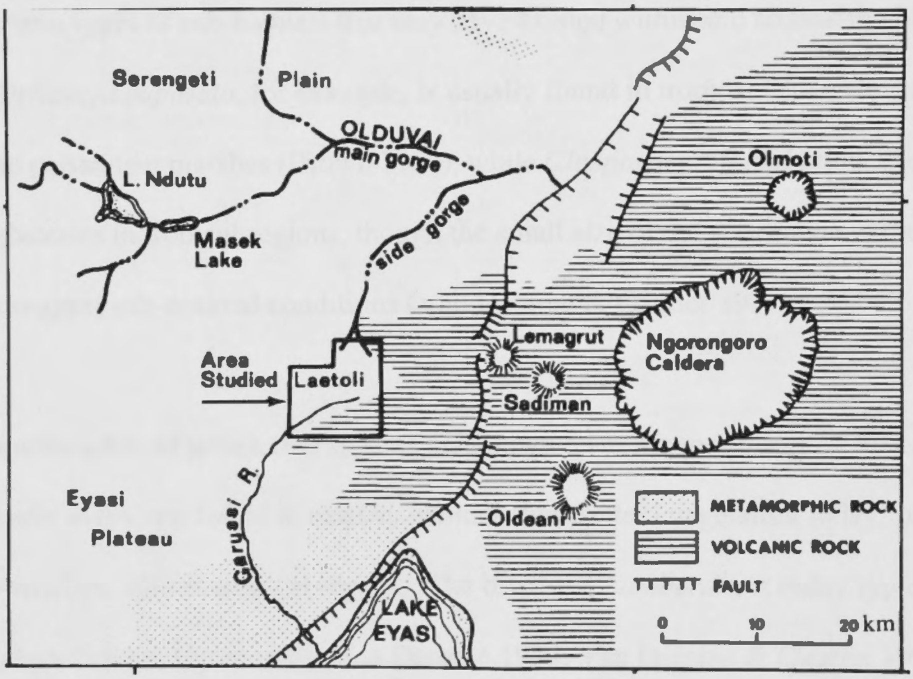


Figure 5.7.1: Map showing location of Laetoli study area (M.D. Leakey & Hay 1979)

The fossils and footprints come from the Upper Laetoli Beds, Pliocene deposits dated at between c. 3.76 and 3.46 Ma (M.D. Leakey & Harris 1987, Figure 5.7.2).

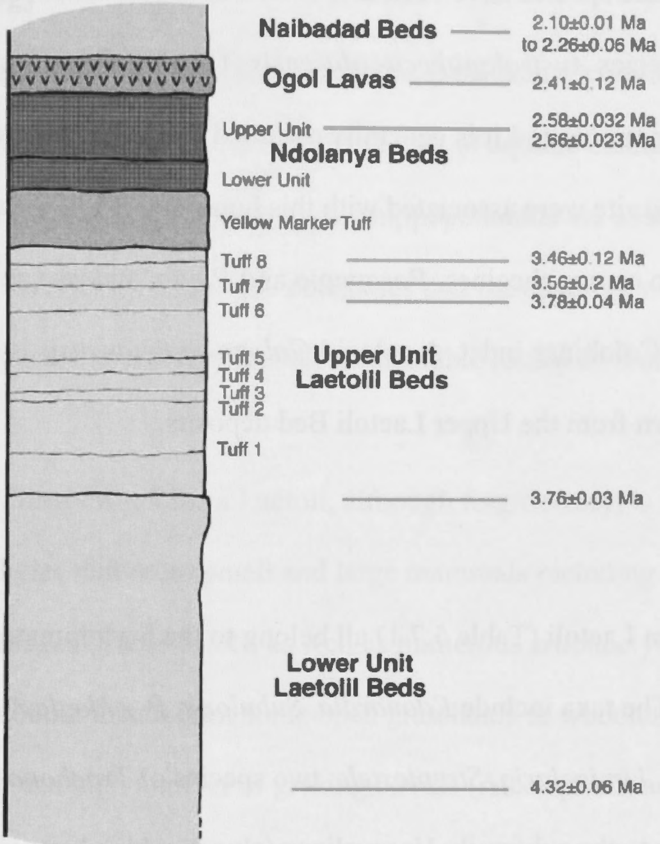


Figure 5.7.2: Generalised stratigraphic section and radiometric dates from Laetoli (Harrison & Msuya 2005)

The sediments were formed through accumulation of air-fall and wind-reworked deposits (Harris 1987). The Laetoli fossil faunal remains are derived almost entirely from surface collections and are consequently very poorly preserved. Major taphonomic processes include carnivore crushing, rodent gnawing, weathering, aeolian abrasion, root etching and invertebrate modification. The latter is the most frequent surface modification recorded at Laetoli (Kaiser 2000).

A number of primate species have been discovered at Laetoli including a hominine assigned to the species *Australopithecus afarensis*. This fossil species is known from fragmented bone remains and it is generally assumed that at least some of the fossil footprints from the site were associated with this hominine (M.D. Leakey & Hay 1979). There are also two cercopithecines, *Parapapio* and *Papio*, and two colobines; *Paracolobus* and Colobinae indet. A galagid *Galago sadimanensis* is also present. No artefacts are known from the Upper Laetoli Bed deposits.

5.7.2 Molluscs

The molluscs from Laetoli (Table 5.7.1) all belong to the Stylommatophora, a largely terrestrial clade. The taxa include *Edouardia*, *Subulona*, *Pseudoglessula*, *Euonyma*, *Achatina*, *Burtoa*, *Limicolaria*, *Streptostele*, two species of *Trochonanina* and three species belonging to the subfamily Urocyclinae (slugs), which have internal shells capable of fossilising.

Table 5.7.1: Molluscs from Laetoli (Verdcourt 1987)

Taxon	**Palaeoecology**	**References**
Edouardia	Trees in savanna and open woodland	Verdcourt 1987
Subulona	Evergreen forest	Verdcourt 1987
Pseudoglessula	Coastal scrub and woodland	Verdcourt 1987
Euonyma	Evergreen forest: 1000–2000mm annual rainfall	Verdcourt 1987
Achatina	Terrestrial, warm and humid conditions, forests including forest edge and plantations	Raut & Barker 2002
Burtoa	Woodland	Andrews & Walker 1976
Limicolaria	Generally higher rainfall areas - tropical	Verdcourt 1987
Streptostele	Evergreen forest	Verdcourt 1987
Trochonanina	Woodland to evergreen forest	Verdcourt 1987
Urocyclinae	Slugs – require adequate cover to avoid sun	Verdcourt 1987

5.7.3 Palaeoecology

One of the striking features of the Laetoli deposits, particularly compared to other East African sites, is that there is an almost complete lack of aquatic elements. Certainly perennial aquatics such as fish, crocodiles and hippopotamids are absent. This is a point emphasised by Harris (1987: 526), who concludes that the area of the Upper Laetoli Bed deposits was "a savanna ecosystem broadly comparable to that of today".

The mammalian faunal record from Laetoli, although fragmentary, is nevertheless extensive and includes numerous small and large mammals including diverse carnivore and rodent assemblages (Table 5.7.2), as well as numerous artiodactyls (Table 5.7.3). There seems little doubt that at least some open grasslands or woodlands existed at Laetoli since there is a high number of grazing bovids (Alcelaphini) as well as two species of the ground squirrel *Xerus* and the spring hare *Pedetes*. On the other hand, the rich diversity of the faunal assemblage indicates that the environmental conditions of the Upper Laetoli Beds were relatively well wooded (Andrews 1989) and other studies support also support this view (Andrews 2006, Koravic & Andrews 2007).

The presence of six primate species, two giraffids, 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 habitats. The bush squirrel *Paraxerus*, also points to more closed habitats (Kingdon 1997), and the climbing mouse *Dendromus* indicates some locally available cover. The mouse shrew *Myosorex* today often inhabits swampy conditions (Kingdon 1997).

Table 5.7.2: Non-Artiodactyla Mammalian fauna from Laetoli (Turner et al. 1999)

PRIMATES	**PROBOSCIDEA**
Australopithecus afarensis	*Deinotherium bozasi*
Parapapio ado	*Loxodonta exoptata*
cf. *Papio* sp.	**RODENTIA**
Paracolobus sp.	*Xerus* sp. indet.
Colobinae sp.	*Xerus janenschi*
Galago sadimanensis	*Paraxerus* sp.
CARNIVORA	*Saimys* sp.
Helogale paleogracilis	Muridae indet.
Herpestes paleoserengetensis	*Saccostomus major*
Herpestes ichneumon	*Dendromus* sp.
Mungos dietrichi	*Steatomys* sp.
Viverra leakeyi	*Tatera* cf. *inclusa*
Mellivora capensis	*Mastomys cinerus*
Propoecilogale bolti	*Thallomys laetolilensis*
Homotherium crenatidens	*Pedetes laetoliensis*
Megantereon cultridens	*Heterocephalus quenstedti*
Panthera leo	*Xenohystrix crassidens*
Panthera pardus	*Hystrix leakeyi*
Panthera sp.	*Hystrix makapanensis*
Acinonyx jubatus	**INSECTIVORA**
Crocuta crocuta	*Elephantulus* sp.
Chasmaporthetes sp.	*Rhynchocyon pliocaenicus*
Canis cf. *brevirostris*	*Myosorex* sp.
Canis sp.	*Suncus* sp.
cf. *Otocyon* sp.	*Chrysochloris* sp.
Megacyon ?sp.	**CHIROPTERA**
Vulpes sp.	*Eptesicus* sp.
PERISSODACTYLA	**LAGOMORPHA**
Hipparion sp.	*Pronolagus* sp.
Ceratotherium praecox	*Serengetilagus praecapensis*
Diceros bicornis	**HYRACOIDEA**
Ancylotherium hennigi	*Procavia* cf. *antiqua*

Relatively arid habitats are suggested by the presence of camels (Kingdon 1997) while the bovid tribes Hippotragini and Antilopini contain species that tend to prefer more arid habitats (Macdonald 2001). There also appear to have been at least some relatively closed areas, judging by the presence of a duiker, tribe Cephalophini (Kingdon 1997), and most probably nearby water or at least thick cover since an extinct genus of buffalo *Simatherium* is present, and buffaloes today are generally dependent on water (Estes 1991).

Tragelaphus is also usually dependent on water and thick cover (Kingdon 1997). Another indication that water may have existed locally is the presence of the Egyptian mongoose *Herpestes ichneumon*, which is "water dependent and a good swimmer" (Kingdon 1997: 240).

Table 5.7.3: Artiodactyla from Laetoli (Turner et al. 1999)

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

In regard to the absence of aquatic fauna it is interesting to note the taphonomy of the Laetoli site. There are a number of burrowing animals in the assemblage indicating the possibility of a taphonomic bias in favour of burrowing animals. It is possible that the fossilised remains include animals that lived in burrows and the remains of their prey. Dogs, foxes, hyaenas, 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 metres (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 and transported to underground dens and burrows by dogs, hyaenas, porcupines and other rodents.

The non-mammalian fauna includes birds, reptiles and insects (Table 5.7.4). The bird fossils include species such as owls and doves which require trees to roost. Guinea fowl are also present, and these birds inhabit open habitats although they too require trees to roost.

Table 5.7.4: Non-mammalian, non-molluscan fauna from Laetoli (Harris 1987)

AVES	*Geochelone brachygularias*
Struthio sp.	*Python sebae*
Torgos sp.	cf. *Ramphiophis* sp.
Francolinus spp.	*Bitis arietens*
Numida sp.	*Naja robustus*
Streptoptelia sp.	**INSECTA**
Bubo sp.	Sphecidae indet.
REPTILIA	Termitidae indet.
Geochelone laetoliensis	

The snakes are all species that are found in a range of habitats, although the python *Python sebae* is today dependent on water for thermoregulatory and hunting purposes (Meylan 1987). Tortoises live in a range of habitats and from a palaeoecological point of view are not greatly informative.

Isotopic dietary reconstuctions of herbivores at Laetoli indicate a relatively humid period with significant forest or wooded components (Kingston & Harrison 2007), while studies based on geology and geomorphology indicate low and tall woodlands and forest associations along water courses (Andrews & Bamford 2008). Fossil pollen samples from the Upper Laetoli Beds show that grasses were predominant and the largest component belonged to the family Gramineae (Bonnefille & Riollet 1987). Although this family contains grasses that grow in arid regions such as savannas and even deserts, they also contain species that grow in wet areas including brackish waters along the coasts and freshwaters of lakes and rivers (Willis 1966). Unfortunately, "it is not possible to distinguish between them" (Bonnefille 1995: 303).

The Upper Laetoli Beds contain pollen from *Typha* and Cyperaceae, although in much smaller quantities than the Gramineae, indicating that at least some water was locally present (Willis 1966). Sediment analysis indicates the existence "of a substantial amount of water in the area during and after deposition" (Musiba et al. 2007: 262).

The molluscs from the Upper Laetoli Beds add important information to the overall palaeoecological picture. *Subulona* and *Euonyma* are both typically evergreen forest inhabitants (Verdcourt 1984), as is *Streptostele*, indicating that at least some forest was locally present. *Burtoa nilotica* is a woodland species also known to inhabit evergreen forest. *Achatina* is known from a range of habitats but the majority of species are naturally confined to tropical and subtropical forested regions (Raut & Barker 2002). *Pseudoglessula* is often found in coastal scrub and woodland, *Limicolaria martensiana* is found in a range of tropical habitats but is mostly associated with higher rainfalls, and *Trochonanina* is an inhabitant of woodlands and evergreen forest. Slugs (Urocyclinae) indicate either moderate to high rainfall (875 – 3000mm) and tree cover, or a habitat in which suitable cover was available to offer protection from the direct sun (Verdcourt 1987).

5.7.4 Conclusion

The molluscan fauna indicate that Laetoli may have been a varied habitat in which at least some evergreen forest existed, along with some open landscapes such as woodland or even savanna in a tropical climate. Verdcourt (1987) estimates the rainfall at Laetoli, based on the molluscan fauna, to have been at least between 625-1000mm per annum, though he also points out that if the evergreen forest was supported by a permanent river, the rainfall could have been at the lower level of this estimate.

The molluscan fauna of Laetoli therefore add an important element to the palaeoecological picture of the Laetoli site, adding support to certain inferences based on other data about the amount of cover that must have been available, and the tropical nature of the climate. *Australopithecus afarensis* at Laetoli appears to have had at least some forest habitat in which to shelter, though fossil footprints demonstrate that they did not spend all their time in trees.

5.8 Hadar

5.8.1 Introduction

Hadar is a fossiliferous site from the Afar region of Ethiopia (Figure 5.8.1).

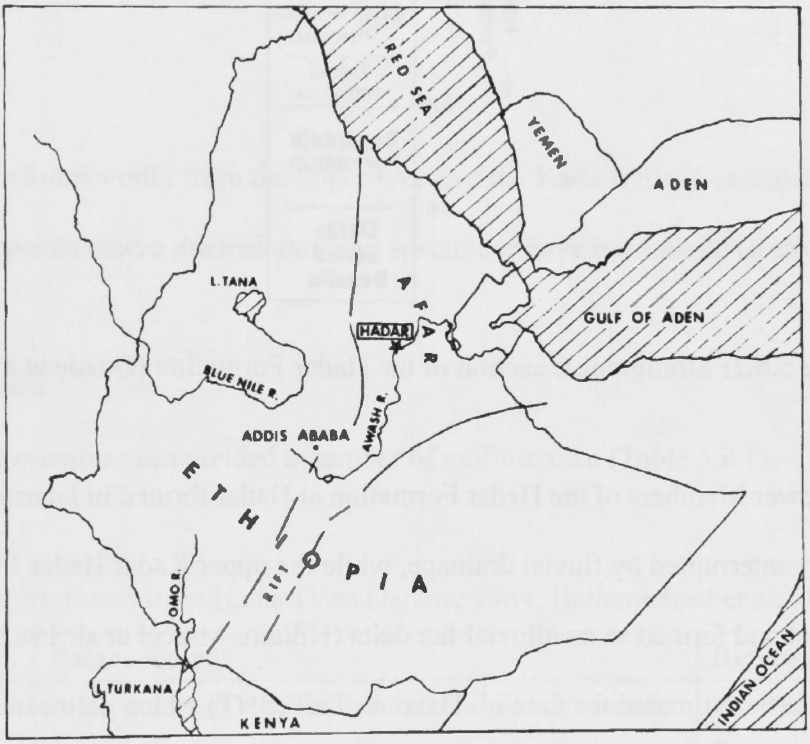


Figure 5.8.1: Map of Ethiopia showing location of Hadar (Johanson et al. 1982)

The fossils at Hadar derive from the Hadar Formation, which is made up of four Members (Figure 5.8.2). The site is located east of the Gona fossil location and north of the Dikika fossil site, which is located across the other side of the Awash River (see Chapter 4).

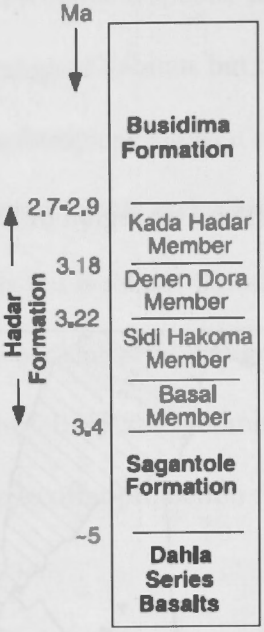


Figure 5.8.2: Stratigraphic section of the Hadar Formation (Quade et al. 2004)

The three lower Members of the Hadar Formation at Hadar formed in lacustrine habitats, occasionally interrupted by fluvial drainage, while the upper Kadar Hadar Member is quite distinct and formed as an alluvial fan delta (Hillaire-Marcel et al. 1982). A date of 3.4 Ma has been estimated for the Sidi Hakoma Tuff (SHT) which delineates the Basal Member from the Sidi Hakoma Member (Walter & Aronson 1993), while the Bouroukie Tuff 2 (BKT 2) near the top of the Kadar Hadar Member has been dated at 2.9 Ma.

A number of primates have been discovered in the Hadar Formation deposits at Hadar, one of which is the hominine *Australopithecus afarensis*. There are also at least three genera of cercopithecoid present at Hadar, *Parapapio*, *Theropithecus* and *Rhinocolobus*.

Some of the hominine fossils may have been subject to scavenging by crocodiles and fish (Aronson & Taieb 1981). The AL 288 fossil derives from a sandstone horizon characterised by superb fossil preservation which yielded delicate items such as crocodile and turtle eggs, rodent skulls and even crab claws (Johanson et al. 1978). This observation indicates that the animals died *in situ* rather than being transported any great distance.

Artefacts are known only from the upper levels of the Kada Hadar Formation and not from any deposits where *Australopithecus* specimens have been found (Kalb et al. 1982).

5.8.2 Molluscs

The Hadar Formation has yielded a number of mollusc taxa (Table 5.8.1).

Table 5.8.1: Molluscs from Hadar (Van Damme 1984, Hailemichael et al. 2002)

Taxon	**Palaeoecology**	**References**
Melanoides	Wide variety of brackish and freshwater environments, except papyrus swamps and waters that dry out regularly - tropical	Van Damme 1984, Brown 1980
Bellamya	Lakes, large slow flowing rivers and streams – tropical	Van Damme 1984
Cleopatra	Stagnant or slowly flowing shallow waters	Brown 1980
Bulinus	Stagnant or slowly flowing waters, including waterbodies that dry out seasonally, often associated with aquatic vegetation	Brown 1980
Jubaia	Fresh water river snail	Brown 1980
Corbicula	Tropical and sub-tropical fresh and brackish waters, variety of substrates, prefers well oxygenated waters and sandy substrates	McMahon 1983
Unio	Large rivers and lakes	Van Damme 1984
Chambardia	Iridinidae – Freshwater mussel, lakes and rivers	Van Damme 1984

The molluscs in this report were collected by Francoise Gasse and co-workers in the 1970s and made available to Dirk Van Damme and Achilles Gautier at Ghent University, Belgium (Van Damme 1984), where they were examined for this study. The molluscs are part of the assemblages from the Sidi Hakoma Member of the Hadar Formation, which is the same member from which the Dikika molluscs were collected (see Chapter 4). The molluscs are generally poorly preserved and often occur in hard and very heavy sediments of either mud or silt-stone (Figures 5.8.3 & 5.8.6). Genera include the gastropods *Cleopatra*, *Melanoides* (Figure 5.8.4), *Bellamya* (Figure 5.8.5), *Jubaia* and *Bulinus*, and the bivalves *Corbicula*, *Unio* and *Chambardia*.

Figure 5.8.3: Rock from Hadar with embedded *Bellamya* and *Melanoides* (scale 5mm)

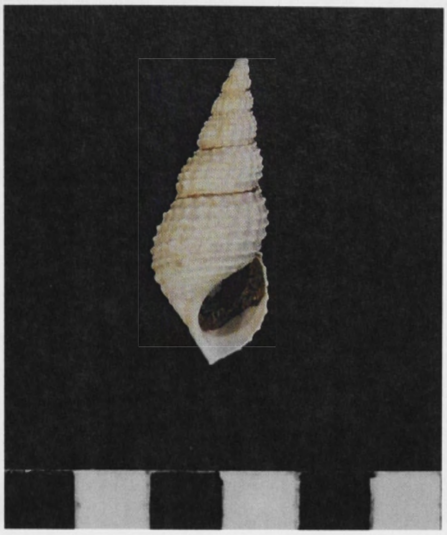


Figure 5.8.4: *Melanoides* from Hadar (scale 5mm)

Figure 5.8.5: *Bellamya* from Hadar (scale 5mm)

Figure 5.8.6: *Unio* embedded in matrix, Hadar (scale 5mm)

5.8.3 Palaeoecology

The vertebrate fauna at Hadar is diverse and includes mammals (Table 5.8.2), birds, reptiles and fish (table 5.8.3). A number of cercopithecoids have been discovered at Hadar, including two colobus monkeys which, although larger than modern species, appear to be indicative of well wooded habitats (Kingdon 1997). In addition a number of browsing species including giraffids and the black rhinoceros *Diceros bicornis* (Kingdon 1997) are present.

A number of bovids present at Hadar have modern relatives dependent on permanent water, including five species of the tribe Reduncini (Kingdon 1997) and three buffaloes (Estes 1997). The presence of members of the tribe Tragelaphini, of which two species are known, most probably indicates that dense cover was available locally (Kingdon 1997).

Table 5.8.2: Mammalian faunal list from Hadar (Turner et al. 1999)

PRIMATES	*Giraffa jumae*
Australopithecus afarensis	*Giraffa gracilis*
Theropithecus darti	*Giraffa* cf. *pygmaeus*
Parapapio cf. *jonesi*	*Damalops palaeindicus?*
Parapapio sp.	Alcelaphini indet.
Rhinocolobus cf. *turkanaensis*	*Dorcadoxa porrecticornis*
Colobinae indet	*Kobus* cf. *kob*
CARNIVORA	*Kobus* sp. A
Enhydriodon sp.	*Kobus* sp. B
Dinofelis cf. sp.	*Kobus* sp. C
Megantereon cultridens	*Gazella* sp.
Panthera sp.	*Raphicerus* ?sp.
Felis sp.	*Madoqua* cf. *aviflumnis*
Crocuta crocuta	*Tragelaphus nakuae*
Chasmaporthetes sp.	Tragelaphini sp.
Canis cf. *mesomelas*	*Ugandax* cf. *gautieri*
PROBOSCIDEA	*Ugandax* sp.
Deinotherium bozasi	*Pelorovis* ?sp.
Loxodonta adaurora	*Aepyceros* sp.
Elephas ekorensis	*Makapania* cf. sp.
Elephas recki	**RODENTIA**
Mammuthus sp.	*Xerus* ?sp.
PERISSODACTYLA	*Tatera* sp. A
Hipparion afarense	*Acomys coppensi*
Ceratotherium praecox	*Golunda gurai*
Ceratotherium simum	*Millardia taiebi*
Diceros bicornis	*Mus* sp.
ARTIODACTYLA	*Oenomys tiercelini*
Nyanzachoerus kanamensis	*Praomys* sp.
Notochoerus euilus	*Saidomys afarensis*
Kolpochoerus afarensis	*Tachyoryctes pliocaenicus*
Hexaprotodon cf. *protamphibius*	*Xenohystrix crassidens*
Sivatherium maurusium	*Hystrix cristate*

The three suid genera were probably adapted to closed habitats, and include the probable swamp specialist, *Nyanzachoerus kanamensis* (Bishop 1999). The sabre-toothed felids *Dinofelis* and *Megantereon*, according to Lewis (1997), were adapted to closed habitats. The hyaenas and the jackal *Canis* are indicative of open habitats (Kingdon 1997), while the antelope *Gazella,* the ground squirrel *Xerus* and the gerbil *Tatera* all point to dry conditions (Kingdon 1997). A permanent body of water at Hadar is suggested by the presence of the otter *Enhydriodon* and the hippopotamid *Hexaprotodon.*

The avian fauna (Table 5.8.3) suggests that there was permanent water present, since the grebe *Podiceps* is a weak flier but excellent underwater diver fully adapted to a waterside existence (Gooders 1975). This bird lives in freshwater lakes and marshes and builds its nest in vegetation on the water (Perrins & Middleton 1985, Campbell & 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 & Middleton 1985, Gooders 1975). The stork *Leptoptilus* is often associated with marshy wetlands in arid regions (Perrins & Middleton 1985, Campbell & Lack 1985). The goose *Plectropterus* belongs to the family Anatidae, members of which are essentially aquatic (Campbell & Lack 1985), while the ostrich *Struthio* is normally associated with open, arid habitats (Perrins & Middleton 1985, Campbell & Lack 1985).

A number of reptiles have also been discovered at Hadar (Table 5.8.3). These include clearly aquatic taxa such as the crocodilian *Crocodylus* and the soft shelled turtle *Trionyx*. Also present at Hadar is a catfish (Siluridae) and a crab (Potamidae), both reflecting aquatic habitats.

Table 5.8.3: Non-mammalian, non-molluscan fauna from Hadar (Johanson et al. 1982)

AVES	*Varanus* sp.
aff. *Struthio* sp.	*Bitis* sp.
Podiceps cf. *sufficolis*	*Crocodylus* sp.
Phalacrocorax sp.	**OSTEICHTHYES**
Leptoptilus cf. *falconeri*	Siluridae gen. et sp. indet.
cf. *Plectropterus*	**OSTRACODA**
REPTILIA	indet.
Geochelone sp.	**DECAPODA**
Trionyx sp.	Potamidae gen. et sp. indet.
Python sp	

Studies of pollen indicate that a high proportion of the plants that occur at Hadar come from the family Cyperaceae and the genus *Typha.* The abundance of these aquatic plants (Willis 1966) suggests "the proximity of marshy, freshwater conditions and periodic flooding" (Bonnefille 1995: 303). Bonnefille stresses the abundance of aquatic pollen, with Gramineae the dominant taxon (Alemseged et al. 2005: 503).

The molluscs from Hadar suggest a large tropical freshwater body. *Bellamya* is restricted to tropical lakes, rivers and slow moving streams, *Melanoides* inhabits a range of freshwater habitats in tropical to sub-tropical environments and *Cleopatra* prefers shallow waters with sandy substrates. *Bulinus* is a pulmonate gastropod able to aestivate, and therefore able to survive in waterways that become seasonally dry, as long as there is adequate vegetation in which to shelter. It does not usually cope well with fast running water and is most usually associated with lotic habitats that have either abundant aquatic vegetation or rocks that can provide shelter and a suitable substrate on which to feed.

Bulinus is not usually found in well forested regions, suggesting that open habitats may have been present at Hadar.

The bivalves from Hadar include the unionid *Unio* and the iridinid *Chambardia*, which require permanent water and are most often associated with lakes and rivers. The genus *Corbicula* generally requires fast flowing waters.

5.8.4 Conclusion

The molluscan fauna from Hadar adds weight to the palaeoecological reconstruction drawn from other data at Hadar, as well as providing extra detail. It can be inferred that since *Bulinus* was present there must have been relatively open regions associated with water edge habitats at Hadar, and these waters must have been relatively slow flowing with either abundant vegetation or rocky substrates with sufficient crevices to provide protection. *Corbicula*, on the other hand, requires well oxygenated waters so these conditions must also have been present at Hadar. It can be deduced that relatively shallow waters, possibly with sandy substrates, were present since these are the conditions *Cleopatra* prefers. A large permanent drainage system is also indicated because of the presence of *Chambardia* and *Bellamya*. Finally, it can be assumed that Hadar had a tropical climate because both *Bellamya* and *Melanoides* are tropical taxa, and the iridinid bivalve *Chambardia* is also restricted to tropical waters.

Australopithecus afarensis at Hadar apparently had sufficient forest in which to shelter, as well as a range of habitats including open grasslands and diverse wetlands in which to forage.

5.9 Conclusion

In this chapter African sites from the Miocene and Pliocene have been analysed in terms of the molluscs present and the palaeoecological indications of those molluscs compared to the conclusions based on other data such as non-molluscan faunal analysis, pollen studies and sedimentology.

The results demonstrate that in all cases the molluscan fauna were able to provide information that either confirmed views reached based on alternative data, or added information that was previously not well established. The kinds of information the molluscs were able to elucidate ranged from the amount of rainfall, tree cover, climate, type of water body and the existence and stability of hydrological connections.

The mollusc assemblages examined so far include those restricted to terrestrial snails (Fort Ternan and Laetoli), and others which contain mainly freshwater gastropods and bivalves. The gastropods that have most commonly occurred in the fossil assemblages so far are *Melanoides*, *Bellamya* and *Cleopatra*.

The bivalves which have occurred in the most assemblages so far examined are unionoids such as *Etheria* and *Aspatharia*, whereas veneroids have been represented at only one assemblage: *Corbicula* at the last examined site, Hadar.

Chapter 6 examines the molluscs from Plio-Pleistocene sites from Africa as well as Eurasia.

6 Plio-Pleistocene molluscs and palaeoecology

In the previous chapter the molluscs from Miocene and early to middle Pliocene sites were analysed from a palaeoecological perspective. The sites in the previous chapter had in common the presence of anthropoid primates, including in a number of sites hominines, but in none of these sites were *Homo* fossils known, nor were any artefacts known from any of the sites reviewed in the previous chapter. In addition, all sites were in Africa.

In this chapter molluscs associated with sites from the later Pliocene and early Pleistocene are surveyed. All these sites have anthropoid primates associated with them, and many have *Homo* fossils and/or artefacts associated with them as well. In this chapter sites from outside Africa are also analysed. This reflects the fact that from the late Pliocene and early Pleistocene hominins begin to appear in the fossil records of Europe and Asia as well as Africa, and stone artefacts begin to appear in areas in and outside of Africa too.

The aim of this chapter, as with Chapter 5, is to examine whether the molluscs associated with each site are able to provide additional information that would help build a picture of that site's palaeoecology.

6.1 Chiwondo Beds

6.1.1 Introduction

One of the earliest sites at which fossils belonging to the genus *Homo* have been discovered come from the Chiwondo Beds of northern Malawi (Figure 6.1.1). Lake Malawi forms part of the most southern extension of the East African Rift system.

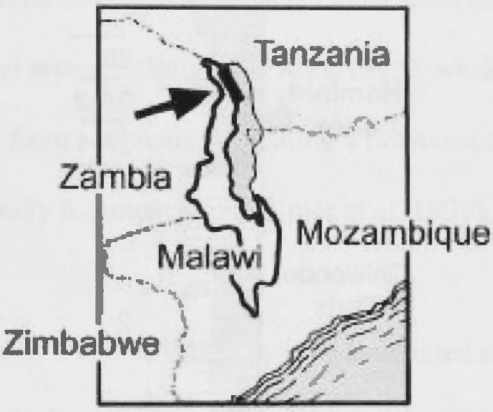


Figure 6.1.1: Map showing location of the Chiwondo Beds (indicated by rectangle and arrow), northern Malawi (after Bromage et al. 1995)

The Chiwondo Beds are divided into 4 Units (Figure 6.1.2). Unit 1 overlies Mesozoic Dinosaur Beds, and is at least older than 4.0 Ma. Unit 2 is also older than 4.0 Ma in its lower layers but somewhat younger than 4.0 Ma in its highest layers. Unit 3 is divided into two subunits; subunit 3A (in which hominine fossils have been found), which is younger than 4.0 Ma at its base and late Pliocene in age (2–2.5 Ma) at the top; and Subunit 3B, estimated to be of early Pleistocene age (2 to 1.5 Ma). Unit 4 is constrained by Units 3 and Unit 5, which belongs to the Chitimwe Beds (Betzler & Ring 1995). The major fossil bearing Units 2 and 3A have an age range estimated on the basis of the associated fauna of between 4.0 and 1.5 Ma (Bromage et al. 1995). Unit 3A, from which the hominine remains have been recovered, is estimated as being late Pliocene in age (Schrenk et al. 1995).

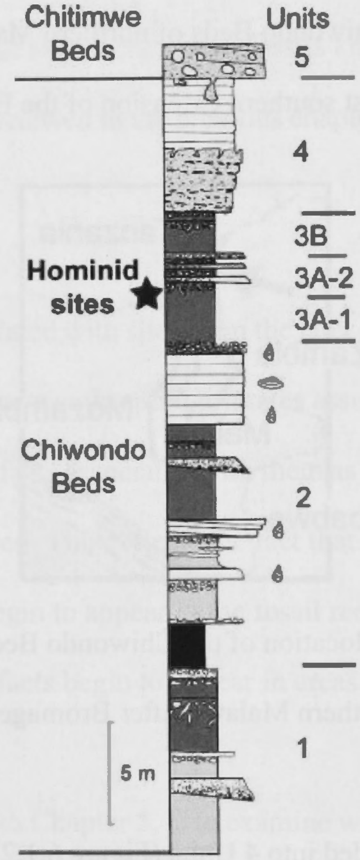


Figure 6.1.2: Generalised stratigraphic profile of the Chiwondo Beds showing position of hominin sites (Schrenk et al. 1997).

Chiwondo Bed deposits include alluvial, aeolian and lacustrine processes with evidence for braided river systems, meandering river systems, deltaic deposits, aeolian sands, alluvial fan deposits, high energy ramp associations, low energy ramp associations and diatom rich deposits (Betzler & Ring 1995).

Most fossils are poorly preserved with varying degrees of breakage and abrasion. Nearly all the fossils are fragmented, with no articulating skeletal parts recovered and mostly only the smaller and most dense skeletal elements preserved. The state of preservation led Schrenk et al. (1995: 61) to hypothesise that the accumulation process was related to "high energy beach transportation and reworking".

The *Homo* fossil discovered from sub-Unit 3A at Uraha Hill comes from an "interchannel or swamp-related alluvial setting" (Betzler & Ring 1995), while *Paranthropus boisei* remains were recovered from sediments indicating a deltaic accumulation in which all fossil bones were extremely fragmentary (Kullmer et al. 1999).

Whereas deposition in Unit 2 is dominated by lake associated sediments, Unit 3 shows a predominance of fluviatile deposition activity, with Subunit 3A featuring meandering rivers, minor lagoons and sediment accumulated in the stream-mouth bars of deltas (Betzler & Ring 1995).

A number of primate fossils have been found in the Chiwondo Beds. Apart from the two hominines, Subunit 3A has also yielded three cercopithecoids; *Theropithecus*, *Papio* and *Parapapio*.

Stone artefacts including flaked pebbles, pebble fragments, flakes and flake fragments have been discovered in the infill of a palaeogully within the Chiwondo (Kaufulu & Stern 1987).

6.1.2 Molluscs

Mollusc remains are abundant within the Chiwondo Beds (Schrenk et al. 1995, Table 6.1.1), and have been studied by Gautier (1970) and Schrenk et al. (1995).

Table 6.1.1: Molluscs from the Chiwondo Beds (Gautier 1970, Schrenk et al. 1995)

Taxon	**Palaeoecology**	**References**
Melanoides	Wide variety of brackish and freshwater environments, except papyrus swamps and waters that dry out regularly	Van Damme 1984, Brown 1980
Bellamya	Lakes, large slow flowing rivers and streams – tropical	Van Damme 1984
Lanistes	Tropical lakes, rivers and temporary pools	Brown 1980
Gabiella	Large lakes and rivers, associated with fine sediments; and aquatic vegetation	Van Damme 1984, Brown 1984
Cleopatra	Stagnant or slowly flowing shallow waters	Brown 1980
*Bulinu*s	Stagnant or slowly flowing waters, including waterbodies that dry out seasonally, often associated with aquatic vegetation	Brown 1980
Achatina	Terrestrial, warm and humid conditions, mainly confined to forests and forest margin	Raut & Barker 2002
Corbicula	Tropical and sub-tropical fresh and brackish waters, variety of substrates, prefers well oxygenated waters and sandy substrates	McMahon 1983
Chambardia	Iridinidae - Freshwater mussel, mainly rivers	Van Damme 1984
Coelatura	Large rivers and lakes, tropical	Van Damme 1984
Etheria	Flowing water in rivers and large lakes where they cement themselves to hard substrates	Van Bocxlaer & Van Damme 2009

Gautier assigned a number of the taxa to species level including *Bellamya unicolor*, *Melanoides tuberculata* and *Aspatharia* (=*Chambardia*) *nyassaensis*, and also noted that some genera, including *Bellamya* and *Melanoides*, may have been represented by more than one species. Schrenk et al. (1995) also recognise *Melanoides tuberculata*, but identify four species of *Bellamya*, though not *Bellamya unicolor*. Both Gautier (1970) and Schrenk et al. (1995) recognise the freshwater oyster as belonging to the non-tubiferous form, *Etheria elliptica* (see Section 6.1.3).

Mollusc assemblages from the Chiwondo Beds held at Ghent University were examined for this study. A number of the specimens were encased in a crusty layer of fossilised algal sediments, which represents the early stage of stromatolite formation (Figure 6.1.3).

Figure 6.1.3: Algal encrusted gastropod specimens forming stromatolites from Chiwondo Beds, Malawi (scale 5mm)

Bellamya specimens, some of quite large size (32 x 20mm), were common in the deposits, while medium sized *Cleopatra* specimens were also present. Some *Cleopatra* and *Bellamya* specimens are carinate (Figure 6.1.4), suggesting lacustrine conditions at least periodically.

Figure 6.1.4: *Bellamya* from Chiwondo Beds, Malawi (scale 5mm)

Figure 6.1.5: *Melanoides* from Chiwondo Beds, Malawi (scale 5mm)

Melanoides, many of which were encrusted (Figure 6.1.5), were present as well as the genus *Gabiella*. Other Chiwondo Bed mollusc material at Ghent University was collected by Desmond Clark in 1963 and identified by Thomas Pain, including the freshwater gastropods *Lanistes* (Figure 6.1.6) and the giant land snail *Achatina* (Figure 6.1.7).

Figure 6.1.6: *Lanistes* from Chiwondo Beds, Malawi (scale 10mm)

Figure 6.1.7: *Achatina* from Chiwondo Beds, Malawi (scale 10mm)

Bivalves included *Coelatura*, *Corbicula*, *Chambardia* (Figure 6.1.8) and *Etheria*.

Figure 6.1.8: *Chambardia* from Chiwondo Beds, Malawi (scale 5mm)

6.1.3 Palaeoecology

The vertebrate faunal remains from the Chiwondo Beds include fish, reptiles and a diverse mammalian assemblage (Table 6.1.2).

A diverse range of suids (seven species) have been identified in the Chiwondo Beds, probably indicating closed habitats (Bishop 1999), although *Phacochoerus* today is able to inhabit relatively open habitats. Bovids belonging to the genus *Tragelaphus* generally prefer habitats with some cover, and this type of habitat would also have been suitable for rhinocerotids and proboscideans, of which there were two and five species respectively. Open grasslands are likely to have existed during Chiwondo Bed times since *Gazella, Oryx* and *Connochaetes* are all present, while more arid habitats are suggested by the presence of *Camelus*.

Table 6.1.2: Vertebrate fauna from the Chiwondo Beds (Schrenk et al. 1995), including Mammals from Unit 3A (Schrenk et al. 1993, Kullmer et al. 1999).

PISCES	**ARTIODACTYLA**
Protopterus sp.	*Metridiochoerus andrewsi*
Clarias sp.	*Metridiochoerus compactus*
REPTILIA	*Phacochoerus* sp.
Trionyx sp.	*Notochoerus capensis*
Pelomedusa subrufa	*Notochoerus euilus*
Pelusios sinuatus	*Potamochoeroides shawi*
Cyclanorbis urahensis	*Kolpochoerus heseloni*
Cycloderma frenatum	*Hippopotamus* sp.
Crocodylus sp.	*Camelus* sp.
PRIMATES	*Giraffa camelopardalis*
Homo rudolfensis	*Giraffa stillei*
Paranthropus boisei	*Giraffa pygmaea*
Theropithecus sp.	*Gazella* sp. aff. *vanhoepeni*
Parapapio sp.	*Tragelaphus* aff. *angasi*
Papio sp.	*Tragelaphus* aff. *strepsiceros*
PROBOSCIDEA	*Megalotragus kattwinki*
Elephas recki	*Connochaetes* aff. *taurinus*
Elephas ekorensis	*Damaliscus* sp.
Mammuthus subplanifrons	*Syncerus* sp.
Loxodonta adaurora	*Ugandax* sp.
Deinotherium bozasi	*Kobus sigmoidalis*
PERISSODACTYLA	*Kobus* aff. *Patulicornis*
Equus sp.	*Oryx* aff. *Gazella*
Hipparion sp.	*Aepyceros* sp.
Ceratotherium aff. *Simum*	*Madoqua* sp.
Diceros bicornis	

Hippopotamids in the Chiwondo Beds point to the presence of permanent water and suitable nearby grasslands for grazing, and the bovids from the genus *Kobus* would support this view since they are dependent on water and grazing grasslands.

The two fish genera, *Protopterus* and *Clarias*, are today both associated with shallow, slow moving waters and can survive the desiccation of waterbodies, though by different methods (Bruton 1979). The presence of the crocodilian *Crocodylus* points to permanent waters. Five soft-shelled turtles (*Trionyx, Pelomedusa, Pelusios, Cyclanorbis* and *Cycloderma*) indicate permanent water with open, muddy substrates.

The molluscan fauna confirms and adds detail to the palaeoecological picture based on other fauna. The presence of *Lanistes* confirms that the environment was tropical, and that there were relatively shallow and still swampy areas (Gautier 1970) in which aquatic vegetation existed. The *Chambardia* specimens are heavily built (Figure 6.1.8) and "suggest agitated waters, such as are found near open shores" (Gautier 1970: 329).

Unionoid bivalves require perennial drainage systems rather than ephemeral streams or waterholes, and therefore the fact that *Coelatura* and *Chambardia* are both present indicates that this was a water body connected to a large perennial drainage system. The non-tubiferous *Etheria* found at Chiwondo (Figure 6.1.9) is also an indication of agitated waters, and both *Etheria* and *Chambardia* are tropical water inhabitants.

Figure 6.1.9: *Etheria* from Chiwondo Beds, Malawi (scale 5mm)

Bellamya, *Cleopatra* and *Gabiella* are all indicative of permanent freshwater habitats ranging from slow-moving rivers and lakes (*Bellamya*) to streams and shallow ponds (*Gabiella*, *Cleopatra*). *Melanoides* is known from a range of permanent freshwater habitats and therefore is not always a useful palaeoecological indicator, but where it occurs in large numbers along with other gastropod species such as *Bellamya*, as it does in the Chiwondo Beds (Gautier 1970) it can indicate an accumulation on a beach as a result of current action. *Bulinus* can tolerate seasonal pools and prefers lentic rather than lotic environments. It is usually not found in heavily forested regions suggesting at least some open habitats in Chiwondo.

The stromatolites suggest shallow, near-shore lake habitats in which some water movement was present, although fluvial formation of stromatolites in freshwater habitats is also possible (Hoffman 1973, Abel et al. 1982).

6.1.4 Conclusion

The molluscs from Chiwondo provide important palaeoecological information. For example *Lanistes* indicates the presence of relatively still, shallow waters with abundant aquatic vegetation, *Cleopatra* suggests shallow open waters, while *Bulinus* is indicative of still waters with some vegetation. *Corbicula* and *Etheria* both require well oxygenated flowing or turbulent water, while *Bellamya* and the iridinid bivalve *Chambardia* point to drainage systems with perennial connection.

The climate was likely to have been tropical since many of the molluscs are restricted today to tropical regions such as *Bellamya*, *Etheria* and *Chambardia*. Forested habitats are indicated by the presence of the terrestrial snail *Achatina*, while more open habitats are likely since *Bulinus*, which is not usually associated with forests, was present. *Bulinus* is also a well known carrier of parasites causing schistosomiasis, so its presence in the Chiwondo Beds indicates that this disease may also have been present.

The hominines at Chiwondo, *Homo* and *Paranthropus*, had a range of habitats in which to forage and shelter, including forests, open grasslands and shallow wetlands with abundant vegetation.

6.2 Turkana Basin

6.2.1 Introduction

The Turkana Basin is part of the East African Rift Valley and is situated largely in northwest Kenya, though its northern margin extends into southern Ethiopia (Figure 6.2.1). Over the past 4 million years it has been influenced for about 85% of the time by a fluvial system and for the other periods the basin has contained a series of relatively short-lived palaeo-lakes (Van Bocxlaer & Van Damme 2009).

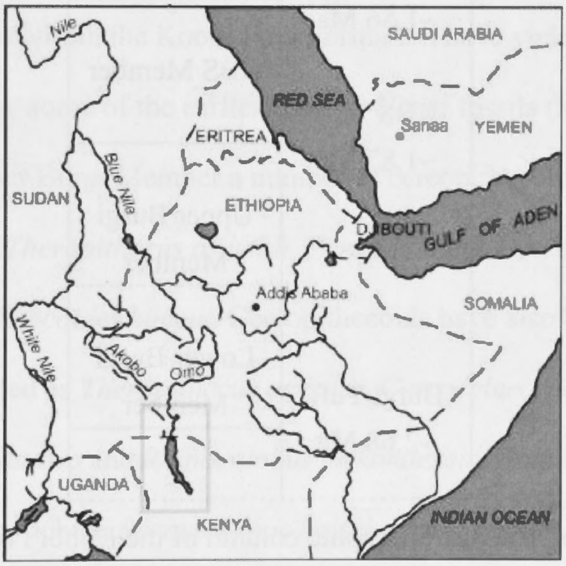


Figure 6.2.1: Map of Northeast Africa showing the location of Lake Turkana (enclosed by rectangle) (Van Bocxlaer & Van Damme 2009)

The Plio-Pleistocene sediments associated with the Turkana Basin come mainly from the Omo Group deposits, which span a period from c. 4.0 to 0.7 Ma (Feibel et al. 1989). This Group includes the Koobi Fora Formation, which is divided into a number of Members including the Burgi Member, which is separated into upper and lower divisions, the KBS

Member and the Okote Member. These Members are divided by tuffs. The Burgi Member has at its base the Burgi Tuff dated to c.2.68 Ma (Feibel et al. 1989), and is separated from the KBS Member above it by the KBS Tuff which is dated to c.1.87 Ma (McDougall & Brown 2006). The Okote Member lies above the KBS Member and is separated by the Okote Tuff dated at c.1.56 Ma (McDougall & Brown 2006, Figure 6.2.2).

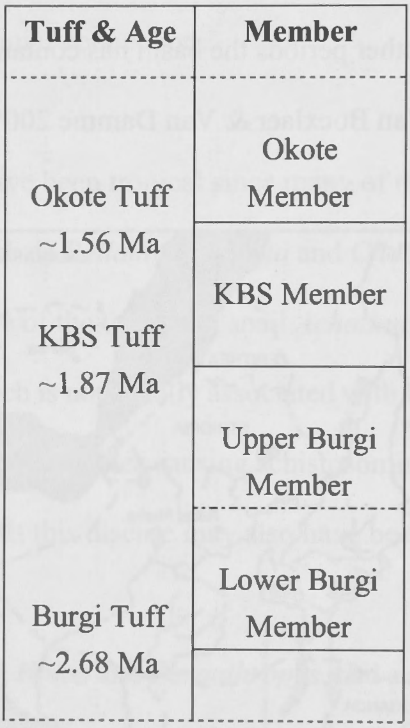


Figure 6.2.2: Simplified stratigraphic column of the Koobi Fora Formation (after McDougall & Brown 2006)

The Koobi Fora Formation is made up of alluvial, deltaic, flood plain and distributary channel deposits associated with an ancient river flowing through the proto-Bakate Gap, situated to the east of Lake Turkana and the Koobi Fora study region (Findlater 1978). Brown & Feibel (1991) identify five major depositional environments: fluvial channel, fluvial floodplain, delta, lake-margin and lake basin.

The upper Burgi Member is dominated by lacustrine (stable freshwater lake) deposits in the lower part, becoming more unstable towards the top of the Member, with deltaic deposits widespread (Feibel et al. 1991). The KBS Member is characterised by meandering fluvial and flood plain deposits associated with a fluctuating, unstable lake. On the western side of Lake Turkana, the Nachukui Formation is comparable in age with the Koobi Fora Formation, while to the north, the Shungara Formation, associated with the ancestral Omo River, is made up of Plio-Pleistocene sediments of roughly contemporary age.

A number of Members within the Koobi Fora Formation have yielded hominine fossils and artefacts, including some of the earliest known *Homo* fossils (McDougall & Brown 2006). Within the upper Burgi Member a number of cercopithecoids have been discovered, including *Theropithecus oswaldi*, *Parapapio ado*, *Cercopithecoides williamsi* and *Cercopithecoides kimeui*. Cercopithecoids have also been found within the KBS Member, identified as *Theropithecus oswaldi*, *Cercocebus*, *Cercopithecoides kimeui*, *Paracolobus mutiwa* and *Rhinocolobus turkanaensis*. Hominine remains from the Koobi Fora Formation include *Paranthropus boisei*, *Homo habilis* and/or *Homo rudolfensis*, and *Homo ergaster*.

Oldowan style artefacts are known from the top of the upper Burgi Member and from the KBS Member, though within the Turkana Basin stone tools are known from much earlier; for example from 2.34Ma deposits at Lokalalei, West Turkana (Roche et al. 1999). Recent discoveries of stone tools and evidence of animal butchering from FwJj20, a site from the upper Burgi member are discussed below.

6.2.2 Molluscs

The sedimentary layers of Koobi Fora provide an excellent record of the Plio-Pleistocene freshwater molluscs that have existed in the area over an extended period. They provide the basis for a number of papers published in the early 1980s supporting the idea of evolution by punctuated equilibrium (Williamson 1981, 1982, 1985b). Many of the conclusions from these papers have since been challenged (e.g., Boucot 1982), and Van Bocxlaer et al. (2008) argue that biological invasions, rather than evolutionary change through punctuated equilibrium, were more likely to explain the changes seen in the molluscan fauna of the Turkana Basin over time.

Following a review of Palaeoheterodont diversity by Graf & Cummings (2006b), Van Bocxlaer & Van Damme (2009) reviewed the classification of the late Cenozoic Iridinidae and Etheriidae from the Turkana Basin.

The Burgi Member of the Koobi Fora Formation includes an abundance of molluscan fauna including a number of both gastropod and bivalve taxa (Table 6.2.1). From the upper Burgi Member Feibel et al. (1991) list 13 species including the gastropod *Valvata*, two species of *Bellamya*, two species of *Cleopatra*, three species of *Melanoides*, including *Melanoides tuberculata*, as well as the bivalves *Coelatura*, *Pleiodon*, two species of *Mutela* (=*Iridina*), *Corbicula consobrina* and *Eupera*. If Williamson's (1982) zones 4 to 9 correspond with the upper Burgi Member, as Feibel et al. (1991) suggest, then *Gabbiella senaariensis* and *Bulinus truncatus* also occurred here.

Table 6.2.1: Molluscs from the Burgi Member of the Koobi Fora Formation

Taxon	**Palaeoecology**	**References**
Valvata	Lakes, slow flowing rivers and streams with dense aquatic vegetation	Brown 1980
Bellamya	Lakes, large slow flowing rivers and streams – tropical	Van Damme 1984
Cleopatra	Stagnant or slowly flowing shallow waters	Brown 1980
Melanoides	Wide variety of brackish and freshwater environments, except papyrus swamps and waters that dry out regularly	Van Damme 1984, Brown 1980
Gabbiella	Large lakes and rivers, associated with fine sediments, and aquatic vegetation	Brown 1980, Van Damme 1984
Bulinus	Stagnant or slowly flowing waters, including waterbodies that dry out seasonally, often associated with aquatic vegetation	Brown 1980
Lanistes	Lakes, rivers and temporary pools	Brown 1980
Chambardia	Deltaic and lacustrine settings	Van Bocxlaer & Van Damme 2009
Iridina	Shallow lacustrine settings	Van Bocxlaer & Van Damme 2009
Pleiodon	Freshwater mussel, lakes, rivers, relatively shallow waters	Van Bocxlaer & Van Damme 2009
Coelatura	Large rivers and lakes, tropical	Van Damme 1984
Pseudobovaria	(extinct) Unionid freshwater mussel	
Pseudodiplodon	(extinct) Freshwater mussel	
Corbicula	Tropical and sub-tropical fresh and brackish waters, variety of substrates, prefers well oxygenated waters and sandy substrates	McMahon 1983
Eupera	Streams, plant roots, aquatic vegetation	Branson 1981

Molluscs collected in August 2006 from the Turkana Basin were examined at the Museum of Natural History in Berlin. This collection included molluscs from the lower Burgi Member of the Koobi Fora Formation including the now extinct genus

Pseudodiplodon (Figure 6.2.3), a specimen of *Lanistes* (Figure 6.2.4), as well as the bivalves *Pseudobovaria* (Figure 6.2.5) and a species identified originally as *Mutela* (Figure 6.2.6), but which may in fact be *Iridina*, although Van Bocxlaer & Van Damme (2009) suggest that the Iridinidae were absent from the lower Burgi Member of the Koobi Fora Formation, suggesting that if this is indeed *Iridina* it may come from the upper Burgi Member.

Figure 6.2.3: *Pseudodiplodon* from the lower Burgi Member of Koobi Fora (scale 10mm)

Figure 6.2.4: *Lanistes* endocast from the lower Burgi Member of Koobi Fora (scale 10mm)

Figure 6.2.5: *Pseudobovaria* from the lower Burgi Member of Koobi Fora (scale 10mm)

Figure 6.2.6: *Iridina* from the Burgi Member of Koobi Fora (scale 10mm)

The molluscan fauna of the upper Burgi Member reflect some of the changes that were occurring in the basin at this time. As Van Bocxlaer et al. (2008) point out, the Turkana Basin for most of its existence through the Plio Pleistocene was dominated by fluvial environments, and molluscs were able to colonise the basin via hydrological connections with other basins and drainage systems. When wet phases occurred more lacustrine conditions dominated, and this resulted in more lentic econiches. Consequently, during these brief lacustrine phases, more morphological disparity was displayed within the molluscan assemblages. *Cleopatra* (Figure 6.2.7), absent in the lower Burgi Member, displays a number of different morphotypes in the upper Burgi Member, and there are also at least two *Melanoides* morphotypes present (Figures 6.2.8).

Figure 6.2.7: *Cleopatra* morphological forms from the upper Burgi Member of the Koobi Fora Formation (scale 10mm)

Figure 6.2.8: *Melanoides* specimens from upper Burgi Member of Koobi Fora (scale 5mm)

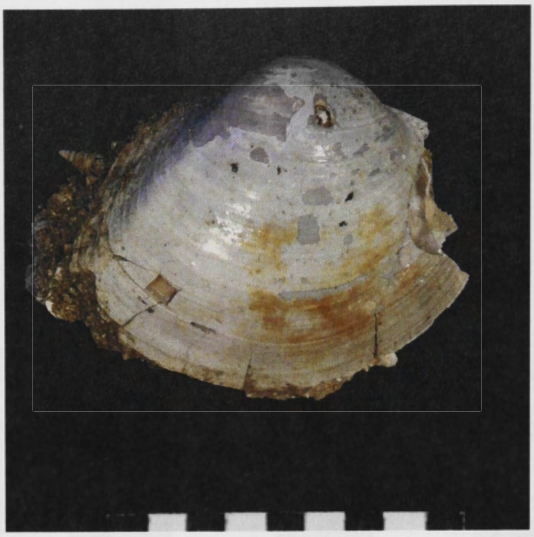


Figure 6.2.9: *Coelatura* cf. *aegyptiaca* from upper Burgi Member, Koobi Fora (scale 5mm)

At least two species of *Coelatura* existed in the Turkana Basin during upper Burgi Member times (Figures 6.2.9 & 6.2.10), as well as *Bellamya* (Figure 6.2.11), *Pleiodon* (Figure 6.2.12) and *Corbicula* (Figure 6.2.13), which apparently took over the niche previously occupied by *Pseudobovaria* (Van Damme 1984).

Figure 6.2.10: *Coelatura* cf. *bakeri* from upper Burgi Member, Koobi Fora (scale 5mm)

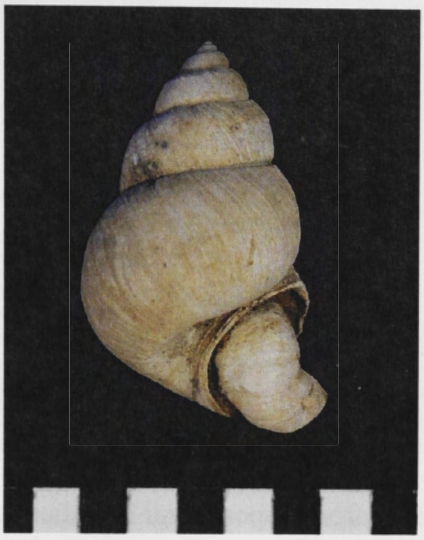


Figure 6.2.11: *Bellamya* specimen (with smaller specimen preserved in aperture) from upper Burgi Member, Koobi Fora (scale 5mm)

Figure 6.2.12: *Pleiodon* from upper Burgi Member, Koobi Fora (scale 10mm)

Figure 6.2.13: *Corbicula* from upper Burgi Member, Koobi Fora (scale 5mm)

The KBS Member has a number of gastropod and bivalve taxa present (Table 6.2.2). Feibel et al. (1991) list four molluscs in the KBS Member including the gastropod *Melanoides tuberculata* and three bivalves; *Aspatharia arcuta (= Chambardia rubens), Mutela nilotica* (=*Iridina omoensis*) and *Corbicula consobrina.* Samples studied at the Natural History Museum of Berlin appear to include *Bellamya*, *Bulinus* and a planorbid gastropod, as well as the bivalves *Coelatura*, *Pseudobovaria*, *Pleiodon*, *Chambardia* and *Etheria.*

Some of the bivalves from the Turkana Basin were of considerable proportions. In the lower Burgi Member, for example, some *Iridina* individuals reached lengths up to 150mm (Figure 6.2.6). The largest *Pleiodon* specimen in the upper Burgi Member measured 112 by 59mm. In the KBS Member there are also large specimens of *Pleiodon* and *Iridina*, as well as a very large specimen of *Chambardia*, measuring 185 by 117mm

(Figure 6.2.14). Some of the *Bellamya* specimens were also relatively large, one measuring 37 by 23mm.

Table 6.2.2: Molluscs from the KBS Member of the Koobi Fora Formation

Taxon	**Palaeoecology**	**References**
Melanoides	Wide variety of brackish and freshwater environments, except papyrus swamps and waters that dry out regularly	Van Damme 1984, Brown 1980
Bellamya	Lakes, large slow flowing rivers and streams – tropical	Van Damme 1984
Bulinus	Stagnant or slowly flowing waters, including waterbodies that dry out seasonally, often associated with aquatic vegetation	Brown 1980
Planorbinae	Usually permanent waterbodies with aquatic vegetation or rocks provide shelter	Brown 1980
Chambardia	Freshwater mussel, lakes and rivers	Van Damme 1984
Iridina	Shallow lacustrine settings	Van Bocxlaer & Van Damme 2009
Pleiodon	Freshwater mussel, lakes, rivers, relatively shallow waters	Van Bocxlaer & Van Damme 2009
Etheria	Flowing water in rivers and large lakes where they cement themselves to hard substrates	Van Bocxlaer & Van Damme 2009
Coelatura	Large rivers and lakes, tropical	Van Damme 1984
Pseudobovaria	Freshwater mussel, lakes and rivers	Van Damme 1984
Corbicula	Tropical and sub-tropical fresh and brackish waters, variety of substrates, prefers well oxygenated waters and sandy substrates	McMahon 1983

Figure 6.2.14: *Chambardia* from Koobi Fora (scale 10mm)

These large sizes indicate that the molluscs had adequate requirements for healthy growth and lived long enough to achieve the relatively large sizes they did. Some unionid bivalves have been estimated to live for up to a century, but to do this these bivalves would require stable ecological conditions. The large sizes of these bivalves reflect mature ages and indicate long periods of ecological stability in the regions inhabited.

6.2.3 Palaeoecology

The mammalian fauna from the Koobi Fora Formation are rich and diverse (Table 6.2.3). In the upper Burgi Member there are mammals indicative of a range of habitats including forests and open habitats. Forests are indicated by the presence of primates such as *Paracolobus* and *Rhinocolobus*, which were most likely arboreal (Fleagle 1988), while the large primate *Theropithecus* is most probably indicative of open habitats.

Table 6.2.3: Non-Artiodactyla mammalian fauna from Koobi Fora (Feibel et al. 1991)

Taxon	Member		Taxon	Member	
	UB	KBS		UB	KBS
PRIMATES			*Hipparion cornelianum*	X	X
Paranthropus boisei	X	X	*Hipparion* sp.	X	X
Homo habilis	X		*Equus koobiforensis*	X	X
Homo ergaster		X	*Equus* cf. *tabeti*		X
Theropithecus oswaldi	X	X	*Ceratotherium simum*	X	X
Cercocebus sp.		X	*Diceros bicornis*	X	X
Parapapio ado	X		**RODENTIA**		
Cercopithecoides kimeui	X	X	*Tatera* sp. A		X
Cercopithecoides williamsi	X		*Arvicanthis* sp.		X
Paracolobus mutiwa	X		*Aethomys* sp.		X
Rhinocolobus turkanaensis	X		*Mastomys* cf. *minor*		X
CARNIVORA			*Mus* sp.		X
Homotherium crenatidans	X	X	*Thallomys quadrilobatus*		X
Dinofelis barlowi	X		*Hystrix* sp.		X
Crocuta crocuta	X		*Thryonomys* sp.		X
Hyaena hyaena	X	X	*Pedetes* sp.		X
Canis cf. *mesomelas*	X	X	**INSECTIVORA**		
PROBOSCIDEA			*Crocidura* cf. *dolichura*		X
Deinotherium bozasi	X	X	*Crocidura* cf. *nana*		X
Loxodonta adaurora	X		**CHIROPTERA**		
Elephas recki	X	X	*Scotophilus* sp.		X
PERISSODACTYLA			*Nycteris* sp.		X
Hipparion hasumense	X		Pteropodidae indet.		X
Hipparion cf. *ethiopicum*	X				

In the KBS Member the colobus monkeys, *Rhinocolobus* and *Paracolobus*, which are present in the upper Burgi Member, are absent, suggesting that the forests that supported these species may no longer have been present. *Cercocebus* would be reliant on forest habitats. *Cercopithecoides kimeui* is also present, and this fossil species is argued to be associated with wooded habitats (Frost et al. 2003). Open, relatively dry habitats in the KBS Member are indicated by the presence of the gerbil *Tatera* and the spring hare *Pedetes*. The cane rat *Thryonomys* inhabits reed beds and long grasses along the edge of lakes and rivers.

The Koobi Fora Formation also has an extensive array of artiodactyls (Table 6.2.4) and these indicate a range of habitats. In the upper Burgi Member there are three *Gazella* species indicating relatively open, arid habitats, and *Oryx* which suggests the climate may have been relatively dry. Members of the tribe Alcelaphini are grass eaters though they today often rely on relatively moist rather than dry grasslands. The variety of *Kobus* species, which are generally water dependent, and the three *Hippopotamus* species are an indication of permanent water. Tree cover is also likely considering the four suid taxa (Bishop 1999) as well as the two species of *Tragelaphus*, which generally prefer closed environments, usually close to water.

In the KBS Member the *Kobus* species are diverse suggesting permanent water. The *Tragelaphus* species from the upper Burgi Member are also present in the KBS Member, as are the suids, suggesting that at least some closed habitats were available locally. Open habitats were present in the KBS Member judging by the occurrence of various *Gazella* species and *Oryx*.

The non-mammalian fauna from the Koobi Fora Formation is also diverse (Table 6.2.5) and points to a large permanent water body in both the upper Burgi and KBS Members. In the upper Burgi Member, for example, there are three species of crocodilian, ten fish taxa and a turtle. The discovery of numerous ostracod species also points to a large body of freshwater.

Table 6.2.4: Artiodactyla fauna from Koobi Fora (Feibel et al. 1991)

Taxon	Member		Taxon	Member	
	UB	KBS		UB	KBS
SUIDAE			Alcelaphini small	X	X
Notochoerus scotti	X	X	*Hippotragus gigas*	X	X
Kolpochoerus heseloni	X	X	*Oryx* sp.	X	X
Metridiochoerus hopwoodi	X	X	? *Kobus* sp.	X	
Metridiochoerus modestus	X	X	*Kobus sigmoidalis*	X	X
HIPPOPOTAMIDAE			*Kobus kob*	X	X
Hexaprotodon karumensis	X	X	*Kobus ancystrocera*	X	X
Hippopotamus gorgops	X	X	*Kobus ellipsiprymnus*		X
Hippopotamus aethiopicus	X	X	*Kobus* aff. *Leche*	X	X
GIRAFFIDAE			*Menelikia lyrocera*	X	X
Sivatherium maurusium	X	X	*Redunca* sp.	X	X
Giraffa jumae	X	X	*Gazella praethomsoni*	X	X
Giraffa stillei	X	X	*Gazella janenschi*	X	X
Giraffa pygmaea	X	X	*Gazella* aff. *Granti*		X
BOVIDAE			*Gazella* spp. indet.	X	X
Megalotragus isaaci	X	X	*Antidorcas recki*	X	X
Damaliscus eppsi	X	X	*Madoqua* sp.		X
Damaliscus cf. *niro*		X	*Cephalophus* sp.		X
Parmularius angusticornis		X	*Raphiceras* sp.	X	X
Parmularius sp.		X	*Tragelaphus nakuae*	X	X
Bovini gen. et sp. indet.	X	X	*Tragelaphus strepsiceros*	X	X
Connochaetes gentryi	X	X	*Pelorovis turkanensis*	X	X
Beatragus cf. *antiquus*	X	X	*Pelorovis oldowayensis*	X	X
Alcelaphini medium	X	X	*Aepyceros melampus*	X	X

Towards the top of the upper Burgi Member the stingray *Dasyatis africana* enters the basin, indicating a connection with the coast, most probably the Indian Ocean via the ancient Turkana River (Feibel 1993). There are more fish taxa associated with the KBS Member than in the upper Burgi Member, two species of fresh water turtle, two crocodilians, numerous ostracods, and the monitor lizard *Varanus*, which is usually associated with water.

Table 6.2.5: Non-mammalian fauna from Koobi Fora (Feibel et al. 1991)

Taxon	Member		Taxon	Member	
	UB	KBS		UB	KBS
REPTILIA			**BRACHIOPTERYGII**		
Geochelone cf. *brachygularias*		X	*Polypterus* sp.	X	X
Trionyx triunguis	X	X	*Hyperopisus* sp.	X	X
Pelusios adansoni		X	**CHONDRICHTHYES**		
Varanus sp.		X	*Dasyatis africana*	X	X
Crocodylus cataphractus	X		**OSTRACODA**		
Crocodylus lloidi	X	X	*Cypris* sp.	X	X
Euthecodon brumpti	X	X	*Hemicypris* sp.	X	X
OSTEICHTHYES			*Megalocypris durbani*	X	
Synodontis sp.	X	X	*Sclerocypris clavularis*	X	X
Lates sp.		X	*Sclerocypris jenkinae*	X	
Gymnarchus niloticus	X	X	*Stenocypris* sp.	X	X
Labeo sp.	X	X	*Plesiocypridopsis newtoni*	X	X
Barbus sp.	X	X	*Potamocypris producta*	X	
Distichodus sp.	X	X	*Ilyocypris gibba*	X	X
Hydrocynus sp.	X	X	*Darwinula stevensoni*	X	X
Sindacharax sp.	X	X	*Cyprideis torosa*	X	X
Tetraodon sp.		X	*Gomphocythere angulata*	X	X
Heterotis sp.		X	*Limnocythere africana*	X	

Recent discoveries within the upper Burgi Member of a stone artefact locality, FwJj20, add important detail to the palaeoecology picture. The site has yielded evidence of animal butchering and occurs in a well-watered environment, probably the floodplain of a deltaic system or major river. Faunal remains from the site indicate freshwater habitats and there is evidence that the hominine residents were consuming water dependant animals such as catfish, crocodilians, turtles, hippopotamids, pigs and bovids, as well as other terrestrial animals (Braun et al. 2010).

The molluscan fauna from Koobi Fora supports the idea that there was a large body of freshwater present in the basin. In the upper Burgi Member *Bellamya*, *Cleopatra* and *Melanoides* are indicative of a large slow moving river or lake in a tropical habitat, with at least some shallow water. The gastropod *Valvata* inhabits slow flowing rivers and streams and prefers areas of dense vegetation (Van Damme 1984).

The bivalves recorded for the upper Burgi Member of the Koobi Fora Formation also point to a large body of permanent water. Small bivalves include *Corbicula*, the presence of which indicates that flowing water occurred locally. Iridinid bivalves from the upper Burgi include *Iridina* and *Pleiodon*. Unionid bivalves from the upper Burgi Member include two species of *Coelatura*, which is relatively common. The large size of many of the iridinid bivalves and the diversity of bivalves within the assemblage is in contrast to some earlier sites, and suggests a large body of permanent water, most probably a lake with river systems including associated streams and marginal wetlands.

In the KBS Member *Melanoides*, *Bellamya* and *Cleopatra* are all also present, suggesting a large slow-flowing river or a lake with at least some shallow sandy habitats and a tropical climate. *Bulinus* is found in lentic habitats and usually associated with open, as opposed to forested, environments, so its presence adds to the argument, based on the mammalian fauna, that the KBS was relatively more open than the upper Burgi Member. Planorbinae specimens similar to *Gyraulus* have also been discovered from KBS. These pulmonate gastropods can tolerate relatively stagnant waters and are often associated with aquatic vegetation (Brown 1980).

Interestingly, from a palaeoanthropological point of view, the KBS Member of the Koobi Fora Formation has yielded stromatolites similar to those found in the Chiwondo Beds of Malawi. These are algal encrusted molluscs, in this case covering small gastropods and bivalves (Figure 6.2.15). One such stromatolite, forming around a small bivalve (Figure 6.2.16), must have been growing for some period of time given the thickness of the built-up algal sedimentation.

Stromatolites usually form in shallow near shore settings. Two of the earliest sites in Africa at which early *Homo* fossils have been found, Koobi Fora and Chiwondo, share conditions favourable to the formation of these unusual structures.

Figure 6.2.15: Stromatolites from KBS Member, Koobi Fora (scale 10mm)

Figure 6.2.16: Stromatolite from KBS Member, Koobi Fora, forming around a small bivalve (scale 10mm)

The bivalves from the KBS Member are indicative of a large body of water, with at least five large freshwater mussel species known. As with the upper Burgi Member, iridinid bivalves are most diverse, and include *Iridina*, *Pleiodon* and *Chambardia*. *Coelatura*, a unionid bivalve, also occurs in the KBS Member deposits. *Corbicula* is present and indicates that flowing water occurred locally. The freshwater oyster, *Etheria*, which forms reefs on top of hard substrates including shell beds, is also present within the KBS Member (Figure 6.2.17). These bivalves require clean, flowing water to survive.

Figure 6.2.17: *Etheria* from KBS Member, Koobi Fora (scale 10mm)

6.2.4 Conclusion

The molluscan fauna from the upper Burgi and KBS Members of the Koobi Fora Formation support the view reached by other data suggesting a large permanent water body existed in the Turkana Basin during times when the shells were deposited. They add detail also to the picture by providing evidence of flowing and well oxygenated waters since genera such as *Corbicula* are present, and also for large connected drainage areas (*Bellamya*), as well as more stagnant waterbodies (*Bulinus*).

Aquatic vegetation and marshy habitats in the lower Burgi Member are indicated by the presence of *Lanistes*, while aquatic vegetation is also suggested in the upper Burgi Member by the presence of *Valvata*, *Gabiella* and *Bulinus*. In the KBS Member aquatic vegetation is indicated by *Bulinus* and the planorbid gastropod. The presence of *Bulinus* also points to relatively open habitats. *Bellamya* was present in both the upper Burgi and KBS Members, signifying tropical conditions. Shallow water habitats are also indicated in the upper Burgi Member by the presence of *Cleopatra*, and in both Members by the freshwater bivalves, which prefer relatively shallow waters.

The molluscan data agree with other data which point to a large fluvial system operating in the Turkana Basin, punctuated with periods when lacustrine conditions prevailed, with adjacent wetlands containing reed beds and other aquatic vegetation. It appears that the KBS Member environment may have been more open than the preceding upper Burgi Member. A lack of specialised lacustrine endemics supports the conclusion that fluvial conditions dominated and that periods in which the basin was occupied by a lake were relatively short-lived.

The hominines from the Turkana Basin around Koobi Fora times could have inhabited the trees, which were more prevalent in Burgi member times (*Homo habilis*), whereas more open habitats, associated with shallow wetlands and gallery forests, could have been more typical for *Paranthropus* and *Homo ergaster*.

6.3 Olduvai Gorge

6.3.1 Introduction

Olduvai Gorge is a fossil site from northern Tanzania (Figure 6.3.1). It is located in the Great Rift Valley, which extends down from Ethiopia (Afar region) through Kenya (Turkana Basin) and south through Tanzania. The site was one of the earliest in eastern Africa to yield hominine fossils and stone artefacts.

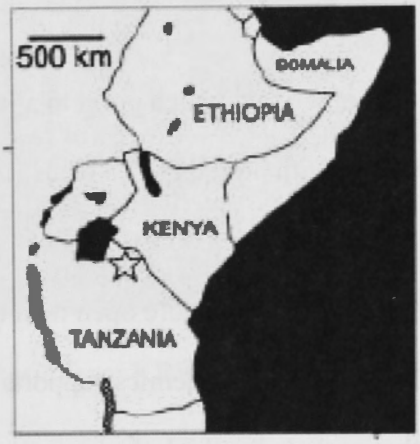


Figure 6.3.1: Map of east Africa showing location of Olduvai Gorge (star), northern Tanzania (Blumenschine et al. 2003)

The Olduvai Gorge deposits are divided into a number of stratigraphic units named Beds (Figure 6.3.2).The fossiliferous units of most interest in terms of palaeoanthropological remains are Beds I, II and IV. Bed I dates between c. 1.87 and 1.75 Ma, with the fossiliferous deposits dated to between c. 1.8 and 1.75 Ma (Walter et al. 1991). Bed II is dated between c. 1.65 Ma and 1.23 Ma, while Bed IV is estimated to date between c. 0.8 and c. 0.6 Ma (Hay 1994).

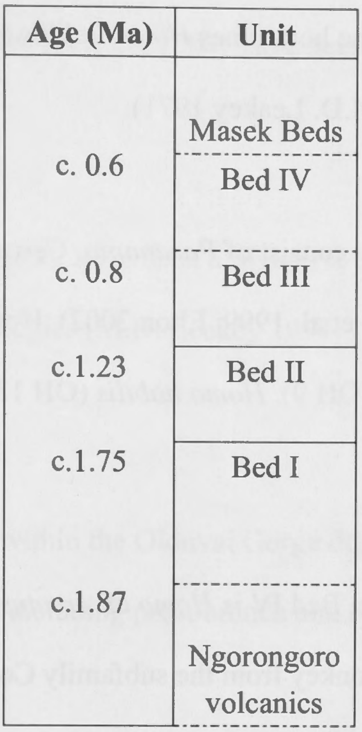


Figure 6.3.2: Simplified Stratigraphic column and dates for Olduvai Gorge

Sediments in Bed I were deposited in lacustrine, lake-margin, alluvial-fan, and alluvial plain deposits (Hay 1976). The sediments of Bed II were deposited in three phases, the lower phase (geologically and faunally similar to Bed I) is made up of fluviatile and lacustrine deposits, the middle phase consists of aeolian sands, sub-aerial soils and weathered clays, while the upper phase begins with river channels filled with torrential gravels and is followed by lacustrine and fluviatile deposits (L. Leakey 1965). Bed IV is made up predominantly of claystones, with the remainder comprising sandstone, siltstone, conglomerate and tuff. The sediments were accumulated along a broad alluvial plain, deposited by meandering streams and rivers, with both fluvial and lacustrine sediments present in the basin (Hay 1994).

Primate fossils have been discovered in all three units. From Bed I the associated primates are the galagid *Galago senegalensis*, a large baboon with affinities to the genus

Papio, a *Colobus* species and the hominines *Homo habilis* (e.g., OH 24) and *Paranthropus boisei* (OH 5) (M.D. Leakey 1971).

From Bed II the primate genera consist of *Parapapio*, *Cercopithecoides*, *Colobus*, and *Theropithecus oswaldi* (Turner et al. 1999, Elton 2002). Hominines present in Bed II deposits are *Homo* cf. *erectus* (OH 9), *Homo habilis* (OH 13) and *Paranthropus boisei* (OH 3).

The only hominine known from Bed IV is *Homo* cf. *erectus* (e.g., OH 12) while other primates from this bed are a monkey from the subfamily Colobinae, *Cercopithecoides kimeui*, a member of the tribe Papionini and the large baboon *Theropithecus oswaldi*.

Artefacts are well known from Olduvai Gorge in Beds I and II, and include assemblages described as representing the Oldowan, Developed Oldowan and early Acheulean industries. All Bed I and Bed II archaeological sites occur near then well watered habitats, with Bed I sites often situated near the lake margin, as indicated by the presence of crocodilians, fish, aquatic birds and evidence for papyrus reed beds, whereas the early Acheulean sites are often correlated with stream and river channels (M.D. Leakey 1976).

In discussing Bed I, Binford (1989) reports that phytoliths from aquatic tuberous plants of the genus *Typha* were recovered from certain stone tools, and that the frequencies of these tools seemed to be correlated with the presence of these plants within the environment. Shreeve (1996) also reported traces of *Typha* on some Neanderthal stone tools, suggesting that at least in later times they may have been used to process these waterside reeds.

Artefacts associated with Bed IV have been assigned to both the Acheulean and Developed Oldowan technologies (M.D. Leakey 1994).

6.3.2 Molluscs

Although molluscs are rare within the Olduvai Gorge deposits, a number of taxonomic groups have been identified including prosobranch and pulmonate gastropods as well as bivalves (Table 6.3.1).

In Beds I and II there is a small bivalve present, similar to *Corbicula*, as well as specimens allied to *Melanoides tuberculata* (L. Leakey 1965). In Bed IV the freshwater mussel *Unio* is the most common mollusc, and a large land snail resembling *Limicolaria* is also present, but neither of these is recorded for Beds I or II. Two species of *Bulinus*, plus *Streptostele*, *Homorus* and a slug (Urocyclidae) are recorded from Bed I, while *Lymnaea natalensis*, *Bulinus tropicus*, *Anisus natalensis*, *Corbicula africana* and *Achatina* have been identified from Bed II deposits (M.D. Leakey 1971, M.D. Leakey 1979).

Table 6.3.1: Molluscs from Olduvai Gorge

Taxon	**Bed**			**Palaeoecology**	**References**
	I	**II**	**IV**		
Melanoides	x	x		Wide variety of brackish and freshwater environments, except papyrus swamps and waters that dry out regularly - tropical	Van Damme 1984; Brown 1980
Bulinus	x	x		Stagnant or slowly flowing waters, including waterbodies that dry out seasonally, often associated with aquatic vegetation – open habitats	Brown 1980
Streptostele	x			Evergreen forest	Verdcourt 1987
Urocyclidae	x			Slug – requires adequate cover to avoid desiccation from the sun	Verdcourt 1987
Homorus	x			Equatorial, evergreen forest	Andrews & Walker 1976
Lymnaea		x		Pulmonate, all kinds of slow moving and stagnant waters, rare in temporary waterbodies	Van Damme 1984; Brown 1980
Anisus		x		Planorbidae – slow flowing and stagnant waters, often associated with aquatic vegetation	Van Damme 1984
Achatina		x		Humid and temperate forest and forest margin	Raut & Barker 2002
Limicolaria			x	Tropical, generally higher rainfall areas; humid forests but can burrow into soil and aestivate in open areas	Verdcourt 1987 El Rayah et al. 1984
Corbicula	x	x		Tropical and sub-tropical fresh and brackish waters, variety of substrates, prefers well oxygenated waters and sandy substrates	McMahon 1983
Unio			x	Unionid – Major permanent river systems, parasitic on fish during larval stage	Van Damme 1984

6.3.3 Palaeoecology

Olduvai Gorge deposits have yielded a wide array of mammalian fauna including a diverse range of rodents (Table 6.3.2).

Table 6.3.2: Rodentia from Olduvai Gorge (M.D. Leakey 1994, Turner et al., 1999)

Taxon	Bed			Taxon	Bed		
	I	II	IV		I	II	IV
Xerus cf. *inauris*	x			*Mastomys* sp.			x
Saccostomus cf. *mearnsi*	x			*Mus petteri*	x	x	
Saccostomus sp.			x	*Oenomys olduvaiensis*	x	x	
Dendromus sp.	x	x		*Pelomys dietrichi*	x		
Steatomys sp.	x		x	*Thallomys quadrilobatus*	x	x	
Dasymus incomputus	x		x	*Thallomys* sp.			x
Gerbillus sp.	x		x	*Zelotomys leakeyi*	x	x	x
Tatera gentryi	x	x		*Otomys petteri*	x	x	
Tatera sp.			x	*Otomys sp.*			x
Muridae indet.			x	*Pedetes* sp.		x	
Arvicanthis primaevus	x	x		*Graphiurus* sp.	x		
Arvicanthis cf. *niloticus*		x	x	*Heterocephalus* sp.	x		x
Aethomys lavocati	x		x	*Heterocephalus jaegeri*	x		
Grammomys sp.	x		x	*Hystrix* sp.	x		x
Mastomys minor	x	x		*Thryonomys* sp.		x	

Other mammalian fauna from Olduvai Gorge include a diverse range of primates and carnivores, a number of perissodactyls, an elephantid, insectivores and lagomorphs (Table 6.3.3).

Table 6.3.3: Non-Artiodactyla & -Rodentia mammalian fauna from Olduvai Gorge Beds I, II and IV (M.D. Leakey 1994, Turner et al., 1999)

Taxon	Bed			Taxon	Bed		
	I	II	IV		I	II	IV
PRIMATES				*Panthera leo*	x	x	x
Paranthropus boisei	x	x		*Panthera pardus*	x	x	
Homo habilis	x	x		*Acinonyx jubatus*		x	
Homo cf. *erectus*		x	x	Hyaenidae			x
Parapapio sp.	?	x		*Crocuta crocuta*	x	x	
Papio sp.	?			*Hyaena hyaena*	x	x	
Cercocebus sp.	?			*Canidae* sp.			x
Papionini			x	*Canis mesomelas*	x		
Cercopithecoides kimeui		x	x	**PERISSODACTYLA**			
Colobus sp.	x	x		*Hipparion lybicum*		x	
Colobinae			x	*Hipparion* cf. *ethiopicum*			x
Theropithecus oswaldi		x	x	*Equus burchelli*		x	
Galago senegalensis	x			*Equus oldowayensis*			x
CARNIVORA				*Ceratotherium simum*		x	x
Atilax sp.		x		*Diceros bicornis*		x	x
Crossarchus sp.	x			**PROBOSCIDEA**			
Herpestes primitivus	x			*Elephas recki*		x	x
Herpestes delibis	x			**INSECTIVORA**			
Mungus minutus	x			*Rhynchocyon pliocaenicus*		x	
Viverridae			x	?*Crocidura* sp.		x	
Pseudocivetta ingens	x	x		**LAGOMORPHA**			
Aonyx sp.			x	Indet.			x
Lutra maculicollis	x	x		*Serengetilagus praecapensis*		x	

Open, relatively arid habitats are indicated in Bed I deposits by the presence of the ground squirrel *Xerus*, and two gerbils *Gerbillus* and *Tatera*. The fact that *Galago senegalensis* is present indicates relatively open habitats with at least some wooded sections. Wooded habitats are indicated by the presence of the monkey *Colobus*, and *Oenomys* is a climbing rodent, so at least some trees or thick vegetation was locally available (Kingdon 1997).

The leopard *Panthera pardus* lives in a wide range of habitats today but usually prefers areas with some cover (Estes 1991). Bed I also has indications of permanent water in the form of the otter *Lutra*.

Bed II deposits also include open, arid adapted taxa in the form of the gerbil *Tatera,* which is often associated with arid habitats, and the springhare *Pedetes,* which prefers sandy grassy plains (Kingdon 1997). *Theropithecus oswaldi* was also likely to have inhabited relatively open habitats. The cheetah *Acinonyx* and the lion *Panthera leo*, as well as the hyaenas *Crocuta* and *Hyaena*, are all indicative of relatively open arid regions (Macdonald 2001). The leopard, *Panthera pardus* on the other hand generally prefers closed or well wooded habitats

The presence of the colobine monkey *Colobus* indicates some forest or wooded regions in Bed II. Papyrus swamps and dense reed thickets are suggested by the marsh mongoose *Atilax* (Kingdon 1997), while the cane rat *Thryonomys* and the grooved tooth rat *Otomys* today inhabit marshy grasslands (Kingdon 1997). *Lutra* emphasises the presence of permanent water. *Oenomys* is a climbing rodent, so at least some trees or thick vegetation was locally available (Kingdon 1997).

Rodents are diverse in Bed IV, with representatives of drier more open habitats such as *Tatera* and *Zelotomys* present, as well as wetland inhabitants *Otomys* and *Dasmys*. The otter *Aonyx* is a clear indication that permanent water was present. Colobine monkeys generally live in wooded to forested habitats today and their presence in Bed IV shows that there were some locally forested or at least wooded regions. *Cercopithecoides* was also likely at least to have been partly arboreal (Macdonald 2001). The leopard *Panthera pardus* lives in a wide range of habitats today but usually prefers areas with some cover (Estes 1991).

The Artiodactyla fauna from Olduvai Gorge is also diverse and includes bovids, which in terms of diversity dominate the assemblage, suids, hippopotamids, giraffids and camelids (Table 6.3.4).

Artiodactyls from Bed I include five suid species, suggesting relatively diverse, closed habitats (Bishop 1999). Closed habitats are also indicated by the presence of two *Tragelaphus* species, who are browsers preferring dense vegetation, thicket or cover. Indicative of water is the hippopotamid from Bed I and the two *Kobus* species. Grasslands were also present at Olduvai Gorge during Bed I times judging by the fact that the grazing bovids of the tribe Alcelaphini were numerous, and relatively dry habitats may also have been locally present since *Gazella* and *Oryx* were present.

In Bed II there was presumably sufficient available water for *Hippopotamus gorgops*. Open, relatively arid habitats may also have existed since *Camelus* was present (Macdonald 2001) and *Gazella* is today well adapted to arid zone regions (Kingdon 1997).

Table 6.3.4: Artiodactyla from Olduvai Gorge Beds I, II and IV (M.D. Leakey 1994, Turner et al. 1999)

Taxon	Bed			Taxon	Bed		
	I	II	IV		I	II	IV
SUIDAE				Alcelaphini *sp.*			x
Kolpochoerus heseloni	x	x	x	*Connochaetes* sp.	x	x	
Kolpochoerus majus	x	x	x	*Damiliscus niro*		x	x
Metridiochoerus andrewsi	x	x		*Damiliscus agelaius*		x	x
Metridiochoerus compactus	x	x	x	*Megalotragus kattwinke*	x	x	x
Metridiochoerus hopwoodi		x	x	*Parmularius altidens*	x		
Metridiochoerus modestus	x	x	x	*Parmularius angusticorn*	x	x	
Phacochoerus antiquus			x	*Parmularius rugosus*		x	x
HIPPOPOTAMIDAE				*Hippotragus gigas*	x	x	
Hippopotamus gorgops		x	x	*Oryx* sp.	x		
Hippopotamus sp.	x			*Kobus sigmoidalis*	x	x	
GIRAFFIDAE				*Kobus kob*		x	
Giraffa jumae		x	x	*Kobus ellipsiprymnus*	x	x	
Giraffa gracilis		x		*Redunca* sp.	x	x	
Giraffa stillei			x	*Gazella* sp.	x	x	
Sivatherium maurusium			x	*Antidorcas recki*	x	x	x
CAMELIDAE				*Antidorcas* sp.		x	x
Camelus sp.		x		Antilopini indet.	x	x	x
BOVIDAE				Neotragini indet.	x		
Thaleroceros radiciformis			x	*Tragelaphus* cf. *scriptus*	x	x	x
Beatragus antiquus	x	x		*Tragelaphus strepsiceros*	x		x
Beatragus sp.	x			*Rabaticeras arambourgi*			x
Alcelaphus sp.	x			*Taurotragus arkelli*		x	x
Sigmoceros sp.		x		*Syncerus acoelotus*	x	x	x
Connochaetes taurinus	x	x	x	*Pelorovis oldowayensis*		x	
Connochaetes africanus		x		*Pelorovis antiquus*			x
Connochaetes gentryi		x		*Aepyceros melampus*	x	x	

Grasslands are signified by the large number (eleven species) of bovids from the tribe Alcelaphini. All species of this tribe are dependent to a greater or lesser degree on water or at least moist grasses (Kingdon 1982), and need to drink daily (Estes 1991). They are unable to colonize truly arid habitats (Kingdon 1997), instead preferring to graze in open woodlands, moist grasslands and the zone in between (Macdonald 2001). *Antidorcas recki* from Bed II inhabited bush or swamp habitats according to ecomorphic analysis of the metapodial functional anatomy (Bishop 1999).

Four species of Reduncini confirm the presence of nearby permanent water at Olduvai Gorge during Bed II deposition and indicate that nearby grasslands and cover in the form of scrub or woodland may have existed (Estes 1991). The presence of *Tragelaphus* and *Taurotragus* suggests dense cover, while the giant buffalo-like *Pelorovis* may have preferred swampy regions. Giraffids are an indication that woodland existed and proboscideans indicate forest, while six suids suggest diverse closed habitats (Bishop 1999).

Equid remains, including both *Equus* and *Hipparion*, are abundant in Bed IV, which suggests open, grassy habitats. Bovids are well represented in Bed IV deposits with the most diverse tribe being the Alcelaphini, which is made up of grassland inhabitants. The buffalo *Syncerus acoelotus* and the giant buffalo-like *Pelorovis antiquus* both point to dense vegetation close to wetland habitats since buffaloes are rarely found far from habitats in which they can wallow (Gentry & Gentry 1978). *Thaleroceros radiciformis*, an ancient reduncine, would most likely have lived at the margin of a permanent water body. Dense cover in the form of either forest, thicket or vegetation is indicated by the presence of two *Tragelaphus* species and *Taurotragus*.

Suids are also diverse in Bed IV, with six species recorded. This diversity most probably reflects a diversity of habitats. Unlike Beds I and II, the suid fauna in Bed IV includes the warthog *Phacochoerus*, which, although it prefers closed, moist habitats, is able to survive in relatively open habitats, thus indicating that drier conditions may have characterised Bed IV deposits. *Hippopotamus* remains are found at nearly every site at which stone tools are found in Bed IV, indicating that permanent water was locally present.

The non-mammalian fauna, excluding molluscs, from Olduvai Gorge are listed in Table 6.3.5. One remarkable aspect of the non-mammalian fauna of Olduvai Gorge is the diversity of avian taxa collected and identified for Beds I and II, especially Bed I, which was once described as the largest assemblage of fossil birds known from anywhere in the world (Brodkorb, quoted in M.D. Leakey 1979).

The avian fauna from Bed I includes seed eating birds including francolins (Phasianidae), quails (Turnicidae) and doves (Columbidae) demonstrating that grasslands were present. Predatory birds and scavengers are rare, but include owls (Strigidae), and less commonly hawks (Accipitridae). Aquatic bird remains are abundant and include swimmers and divers such as grebes (Podicipedidae), cormorants (Phalacrocoracidae), pelicans (Pelecanidae) and ducks (Anatidae). Marine birds include skimmers (Rynchopidae), gulls and terns (Laridae), while wading birds, which are particularly abundant are represented by flamingoes (Phoenicopteridae), herons (Ardeidae), storks (Ciconiidae), rails (Rallidae), jacanas (Jacanidae), plovers (Charadriidae), sandpipers (Scolopacidae) and stilts (Recurvirostridae) (M.D. Leakey 1979).

Table 6.3.5: Non-mammalian vertebrates (M.D. Leakey 1971, 1979, 1994)

Taxon	Bed			Taxon	Bed		
	I	II	IV		I	II	IV
AVES				Sylviidae (warblers)	x		
Indet.			x	Turdidae (thrushes)	x		
Struthio sp.	x	x	x	**REPTILIA**			
Podicipedidae (grebes)	x	x		Chelonia indet.	x	x	x
Phalacrocoracidae (cormorants)	x	x		*Pelusios castaneus*	x		
Pelecanidae (pelicans)	x	x		Agamidae	x		
Phoenicopteridae (flamingoes)	x	x		Chamaeleontidae	x		
Ardeidae (herons, egrets)	x			Scincidae	x		
Ciconiidae (storks)	x			*Python* sp.	x	x	
Balaenicipitidae (stork)	?			Boidae indet.	x		
Anatidae (ducks, geese)	x	x		Colubridae indet.	x	x	
Accipitridae (hawks)	x			*Naja* sp.	x		
Phasianidae (guinea fowl)	x			Elapidae indet.	x		
Turnicidae (quail)	x			*Bitis* sp.	x	x	
Rallidae (rails)	x			*Bitis nasicornis*	x		
Jacanidae (lily trotters)	x			Viperidae indet.	x		
Charadriidae (plovers)	x			*Crocodylus niloticus*	x	x	
Scolopacidae (snipe)	x			*Crocodylus* sp.	x	x	x
Recurvirostridae (avocets, stilts)	x			**AMPHIBIA**			
Laridae (gulls, terns)	x			Indet.			x
Rynchopidae (skimmers)	x			Anura indet.		x	
Columbidae (doves)	x			Pipidae indet.	x		
Cuculidae (cuckoos)	x			*Xenopus* sp.	x		
Psittacidae (parrots)	x			Bufonidae indet.	x		
Strigidae (owls)	x			*Bufo* sp.	x		
Apodidae (swifts)	x			Ranidae indet.	x		
Coliidae (mousebirds)	x			*Rana* sp.	x		
Upupidae (hoopoes)	x			*Ptychadema* sp.	x		
Capitonidae (barbets)	x			**OSTEICHTHYES**			
Picidae (woodpeckers)	x			*Clarias* sp.	x	x	x
Hirundinidae (swallows)	x			Cichlidae indet.	x		
Corvidae (crows)	x			*Tilapia* sp.	x	x	

Bed I also has a diverse range of reptiles including lizards (Agamidae), chameleons (Chamaeleontidae) — which indicate arboreal substrates, and skinks (Scincidae), which can inhabit extremely dry habitats. There are also a range of snakes in Bed I deposits, including the genus *Python*, which is usually found close to water. The mud turtle *Pelusios castaneus* and crocodilian remains indicate permanent water.

A number of amphibians have also been identified in Bed I deposits including *Xenopus*, *Rana* and *Ptychadema*, which are together indicative of permanent water, as well as the toad *Bufo*.

The fish from Bed I include *Tilapia* a freshwater inhabitant of streams, ponds, rivers lakes and estuaries with a preference for aquatic vegetation and detritus, and *Clarias*, a genus of catfish. Together the non-molluscan fauna from Bed I point to a habitat which included both open and relatively closed habitats in the vicinity of a large permanent water body which may have been periodically brackish, and which included marshy areas and ponds.

The avian fauna from Bed II times at Olduvai Gorge include aquatic birds such as grebes (Podicipedidae), cormorants (Phalacrocoracidae), pelicans (Pelecanidae) flamingoes (Phoenicopteridae) and ducks (Anatidae) (M.D. Leakey 1979). These suggest a large permanent water body that may have, at times, or in certain places, been brackish.

Reptiles from Bed II include a number of snakes (*Bitis*, *Python*), plus two varieties of crocodilian and an unidentified member of the superorder Chelonia. Together these point to at least a body of permanent water.

The fish from Bed II mirror those found in Bed I. Catfish are able to tolerate poorly oxygenated waters but are less tolerant of alkaline water (Moyle & Cech 1982), while cichlids are often found in lakes (Moyle & Cech 1982).

Bed IV of Olduvai Gorge has much fewer non-mammalian fauna. The only avian fauna identified from Bed IV is the ostrich *Struthio*, usually associated with relatively open habitats. The reptiles include a member of the superorder Chelonia and a crocodilian *Crocodylus*, indicating permanent water. Also present in Bed IV is an amphibian, though not identified further than class, and catfish remains, sometimes in considerable quantities. The fact that these remains were often associated with stone artefacts and were very fragmentary suggests they may have been consumed by hominins (M.D. Leakey 1994).

Other non-faunal data reveal information regarding the palaeoecology of Olduvai Gorge. Swamp vegetation, for example, is indicated in Bed I by abundant coarse, generally unbranching, vertical root channels and casts, which could have been made by *Typha* or some other kind of reed. Fossil rhizomes of a papyrus-like plant point to marshland or shallow water and there is also evidence of the water plant *Potamageton* (Hay 1981).

Macroplant fossils and phytoliths from Bed II sediments of Olduvai Gorge indicate the presence of sedges, grasses and clumps of palms, while fossil wood most likely represents *Guibourtia coleosperma*, a tree often associated with sandy riverine habitats (Copeland 2007).

The molluscan fauna from Olduvai Gorge adds even more detail to the palaeoecological picture. Bed I mollusc include the land snail *Homorus*, which is today restricted to evergreen forest in equatorial Africa (Andrews & Walker 1976), and a slug from the family Urocyclidae, which is indicative of a moist habitat in which rainfall is relatively high, or a habitat where there are trees and thick vegetation to offer protection from the sun, lining riverine habitats for example (Verdcourt 1987).

Species of the genus *Streptostele* are known to inhabit evergreen forest (Verdcourt 1987). *Bulinus* is a freshwater snail often associated with lentic habitats and aquatic vegetation and prefers non-forested environments (Brown 1980). *Melanoides* is found in a wide range of tropical freshwater habitats, but hardly ever in waterbodies that regularly become dry. *Corbicula*, the only bivalve recorded from Bed I, is most commonly associated with well oxygenated waters such as shallow flowing streams and rivers in tropical and sub-tropical habitats (McMahon 1983). *Corbicula* is found in cemented concentrations in association with hominine fossils in Bed I deposits (Blumenschine et al. 2003).

The molluscs of Bed II include the land snail *Achatina*, which is most commonly associated with tropical forest and forest margin habitats (Raut & Barker 2002). *Achatina* is a popular food source today and its presence in broken form in association with fossil hominines in Bed II, has elicited suggestions that it may have been utilised as a source of protein (M.D. Leakey 1979). Freshwater gastropods that can today tolerate still waters included *Lymnaea natalensis*, *Bulinus tropicus* and *Anisus natalensis*. *Lymnaea natalensis* is usually associated with waterbodies that never dry out. *Bulinus tropicus* is often found in small waterbodies and rarely inhabits larges lakes. *Anisus natalensis* is most probably a synonym of *Ceratophallus natalensis*, which is commonly found in marshes and slowly flowing streams, but is also common in seasonally filled pools (Brown 1980). *Melanoides tuberculata* is found in a wide range of tropical freshwater habitats, but never in waterbodies that regularly become dry. *Corbicula* is intolerant of desiccation and therefore its presence in Bed II indicates that permanent water must have been present. It prefers well oxygenated waters and can tolerate moderate levels of salinity.

Only two mollusc taxa are recorded from Bed IV. The land snail *Limicolaria* is today found in tropical humid forests, but can also survive in open habitats that become seasonally dry. During these dry spells it burrows into the soil and aestivates (El Rayah et al. 1984). The most numerous mollusc from Bed IV is the unionid bivalve *Unio*, which is described as being abundant (L. Leakey 1965). These large bivalves are found in association with stone tools at a number of locations, sometimes fragmented and sometimes intact and articulated (M.D. Leakey 1994). The presence of these large bivalves is evidence of the presence of freshwater, since unionid bivalves are intolerant of alkalinity. They also indicate that the water body was a part of a large stable river system that supported fish capable of acting as hosts to the parasitic larvae of these unionid bivalves.

6.3.4 Conclusion

The molluscan fauna from Bed I points to an environment in which both forests and more open habitats may have prevailed, and where there were both flowing and more stagnant water bodies, some of which were likely associated with aquatic vegetation. Combined with the other faunal data the picture is one of a large water body, probably a lake, with associated rivers and streams and fringed with areas of forest, open reed beds and grasslands.

The molluscs of Bed II complement the conclusions reached through other data. Relatively stagnant marshy habitats with sedges and other aquatic vegetation must have been present because otherwise the pulmonates within Bed II would have had little chance of surviving. Some forested habitats probably also were present (*Achatina*), and possibly more open habitats (*Bulinus*). Flowing waters were also present locally given the presence of *Corbicula*. The overall picture, therefore, of Bed II is of a body of water supporting various types of vegetation, including forest (though less than Bed I), scrubby bushland and swampy grasses. Areas of open grassland are likely to have occurred within the vicinity, with probably moist grassland closer to the water's edge and more arid grasslands further away.

The molluscan fauna from Bed IV offer support to the conclusions based on other faunal data, that there was a large permanent freshwater body within the Olduvai Basin. The climate was probably tropical since *Limicolaria* was present, and the landscape may have been relatively open, though closed habitats are also suggested.

The hominines from Olduvai Gorge in Bed I times (*Homo habilis, Paranthropus boisei*) would have had forest habitats in which to shelter, and while these habitats were also present in later Beds, more open habitats also appear to have increased in later time periods. *Homo* cf. *erectus* in Bed IV would have had a range of potential habitats in which to shelter and forage.

6.4 Humpata, Angola

6.4.1 Introduction

The site of Humpata is situated on the Humpata plateau in the southwest of Angola, southwest Africa (Figure 6.4.1). The Humpata plateau is on average 1750 metres above sea level, and 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).

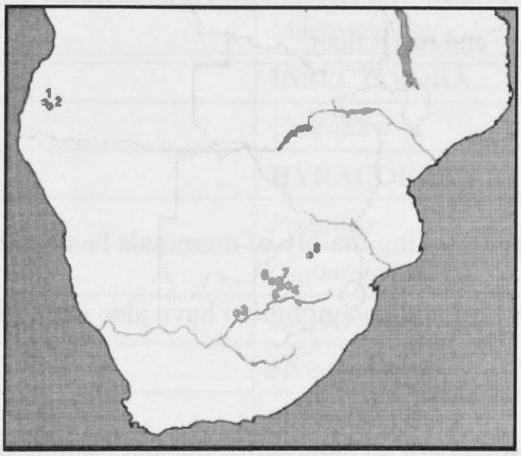


Figure 6.4.1: Map of Africa showing location of Humpata (2, top left) in south west Angola (after Gilbert et al. 2009)

Three cercopithecid primates have been found at Humpata, *Dinopithecus, Parapapio* and *Cercopithecoides.* No hominoid remains have been located from any sites within the Humpata region and no artefacts have been found. The site is included here for comparative reasons.

6.4.2 Molluscs

A number of molluscs are known from Humpata (Table 6.4.1). One is a gastropod belonging to the family Subulinidae, and there are three other genera, *Achatina*, *Edouardia* and *Thapsia*.

Table 6.4.1: Molluscs from Humpata (Pickford et al. 1992)

Taxon	**Palaeoecology**	**References**
Subulinidae	Contains genera such as *Subulona* which occur mainly in forest	Verdcourt 1987
Achatina	Humid tropical and temperate forest and forest margin	Raut & Barker 2002
Edouardia	Trees in savanna and open woodland	Verdcourt 1987
Thapsia	Often associated with forests where it inhabits the understory and forest floor	De Winter 2008

6.4.3 Palaeoecology

A non-molluscan fauna consisting mainly of mammals has been identified at Humpata, though a few reptiles, a bird and an amphibian have also been discovered (Table 6.4.2).

The primates from Humpata are all cercopithecids and include the baboons *Parapapio* and *Dinopithecus* (=*Papio*), and the colobine *Cercopithecoides*. Baboons today are generally able to inhabit open habitats but need either cliffs or trees for shelter. *Cercopithecoides* is a colobine, and it is likely to have had arboreal adaptations, even though there are reasons to believe it may have been predominantly a ground dweller.

The carnivores at Humpata include hyaenids, canids, mustelids and viverrids. Since these have not been identified below the family level, inferring palaeoecological information from them is difficult, although hyaenids and canids are today often associated with relatively open habitats.

Table 6.4.2: Vertebrate fauna from Humpata, Southern Angola (Pickford et al. 1992)

PRIMATES	*Dendromus*
Cercopithecoides	*Steatomys*
Parapapio	*Petromyscus*
Dinopithecus	*Tatera*
CARNIVORA	*Otomys*
Mustelidae	*Cryptomys*
Viveridae	*Graphiurus*
Canidae	*Hystrix*
Hyaenidae	**MACROSCELIDEA**
PERISSODACTYLA	Macroscelidae
Rhinocerotidae	**INSECTIVORA**
Equidae	*Crocidura*
ARTIODACTYLA	**HYRACODEA**
Metridiochoerus	*Procavia*
Bovidae indet.	*Gigantohyrax*
Hippotragini	**LAGOMORPHA**
Connochaetes	*Serengetilagus*
RODENTIA	**CHIROPTERA**
Uranomys	*Rhinolophus*
Acomys	*Miniopterus*
Dasmys	*Nycteris*
Aethomys	**AMPHIBIA**
Thallomys	Amphibia indet.
Zelotomys	**REPTILIA**
Mus	Chelonia indet.
Pelomys	Lacertidae indet.
Malacomys	Ophidea indet.
Praomys	**AVES**
Grammomys	Aves indet.

The hyracoids *Procavia* and *Gigantohyrax* suggest rocky outcrops, caves and fissures, and the hare *Serengetilagus* 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 *Connochaetes* from the tribe Alcelaphini, which inhabits grasslands and open woodlands that are neither too moist nor too dry, with access to water and short herbs (Kingdon 1997).

Humpata deposits have yielded a rhinocerotid, an equid, and a suid *Metridiochoerus*. This could mean any of a range of habitats with the equid possibly indicating open grass or woodlands (Estes 1991), the rhinocerotid indicating woodlands, grasslands or possibly wetlands (Estes 1991), and the suid *Metridiochoerus* perhaps indicating closed habitats (Bishop 1999). The shrew *Crocidura* survives in a range of habitats (Kingdon 1997), while elephant shrews (Macroscelidae) are often found in more arid habitats but require thick undergrowth (Kingdon 1997).

There are three bat species present suggesting caves or trees (Macdonald 2001). The overwhelming majority of identified species belong to the Rodentia, including dry region inhabitants such as the gerbil *Tatera*, and swampy condition inhabitants such as *Malacomys*, *Dasmys* and *Otomys* (Kingdon 1997).

Since the reptiles and birds have not been identified further than class they can not add significantly to the palaeoecological picture. The fact that an amphibian is present, however, does indicate that at least seasonal water must have been present.

The molluscs from Humpata are not too dissimilar to those from Laetoli. They both include the gastropod family Subulinidae, which contains genera such as *Subulona* which occur mainly in forest habitats (Verdcourt 1987), *Achatina*, which is today commonly found in humid and temperate forest and forest margin habitats (Raut & Barker 2002), and *Edouardia*, a tree dweller today in savanna and open woodlands (Verdcourt 1987). Humpata also contained *Thapsia*, which is often found today in the understory and floors of forest habitats (De Winter 2008).

6.4.4 Conclusion

The molluscan fauna from Humpata adds important detail to the palaeoecological picture of the Humpata in pointing to the presence of at least localised areas of forest habitat. There are no molluscs associated with water and the other faunal data from Humpata are also lacking in any evidence of permanent water, though temporary water bodies may have existed.

6.5 Senga 5A

6.5.1 Introduction

Senga 5A is a fossil site from the east bank of the Semliki River in the Western Rift Valley (Figure 6.5.1).

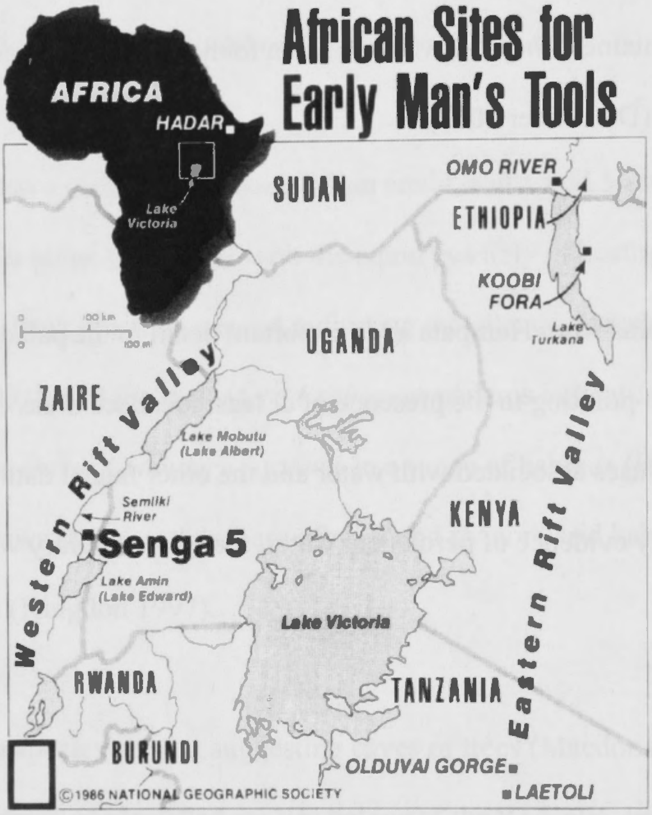


Figure 6.5.1: Map showing location of Senga 5A in relation to Lake Victoria (Harris et al. 1987)

Dating estimates according to faunal correlations suggest an age of between 2.0 and 2.3 Ma for the Lusso Beds in which the stone artefacts have been found (Harris et al. 1987, Figure 6.5.2), though de Heinzelin & Verniers (1996) add a note of caution, suggesting that the artefacts may be much younger, belonging to a terminal Pleistocene-Holocene occupations. The sediments from Senga 5A reflect a low energy, lacustrine deposit environment (Harris et al. 1987).

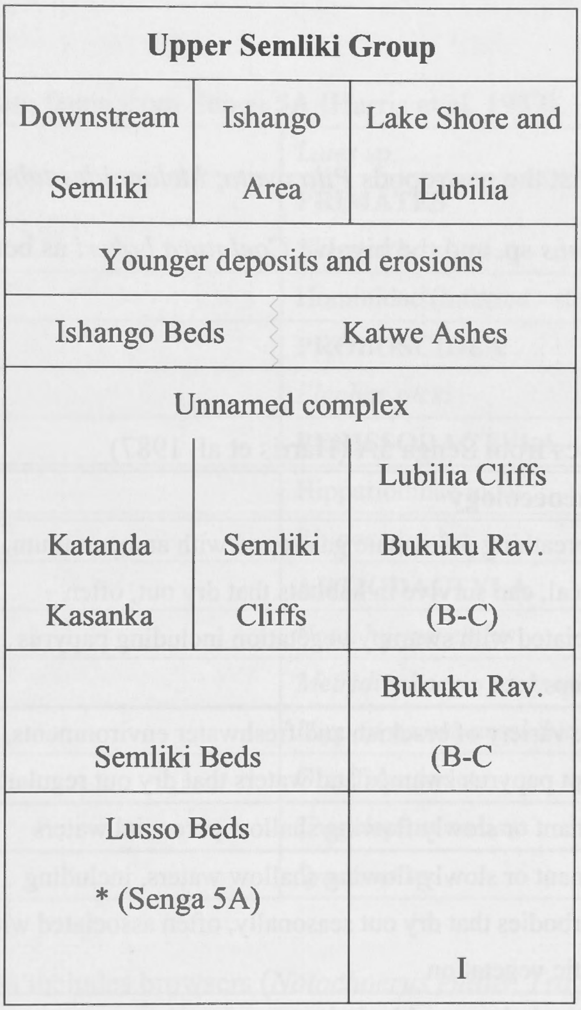


Figure 6.5.2: Stratigraphy section of the Upper Semliki Group (after Harris et al. 1987).

No hominine fossils have been found at Senga 5A, but stone artefacts indicate they were there. The cercopithecid, *Theropithecus*, is also known from Senga 5A (Harris et al. 1987).

The stone artefacts are made predominantly from quartz, which is locally available on the banks of the Semliki River. The assemblage resembles an Oldowan core and flake industry (Harris et al. 1987).

6.5.2 Molluscs

Harris et al. (1987) list the gastropods *Pila ovata, Melanoides tuberculata, Cleopatra bulimoides* and *Bulinus* sp. and the bivalve *Coelatura bakeri* as being present at the archaeological site.

Table 6.5.1: Molluscs from Senga 5A (Harris et al. 1987)

Taxon	**Palaeoecology**	**References**
Pila	Air breathing pulmonate gastropod with an operculum, tropical, can survive in habitats that dry out, often associated with swampy vegetation including papyrus swamps	Brown 1984
Melanoides	Wide variety of brackish and freshwater environments, except papyrus swamps and waters that dry out regularly	Van Damme 1984, Brown 1980
Cleopatra	Stagnant or slowly flowing shallow perennial waters	Brown 1980
Bulinus	Stagnant or slowly flowing shallow waters, including waterbodies that dry out seasonally, often associated with aquatic vegetation	Brown 1980
Coelatura	Relatively large stable drainage systems	Van Damme 1984

6.5.3 Palaeoecology

Vertebrate faunal remains from Senga 5A include mammals, reptiles and fish (Table 6.5.2). The fauna includes an unusually high proportion of aquatic and semi-aquatic forms including a large percentage of fish and smaller numbers of turtles, crocodilians and hippopotamids. The composition of the fish assemblage suggests that the habitat was an inshore setting since three of the taxa are today restricted to inshore settings, two are full or partial molluscivores and the others are macrophytic herbivores and piscivores (Harris et al. 1987).

Table 6.5.2: Vertebrate fauna from Senga 5A (Harris et al. 1987)

REPTILIA	*Lates* sp.
Trionychidae	**PRIMATES**
Pelusios sp.	*Theropithecus* sp.
Crocodylus niloticus	Hominidae (inferred - stone artefacts)
OSTEICHTHYES	**PROBOSCIDEA**
? *Hyperopisus* sp.	*Elephas recki*
Gymnarchus sp.	**PERISSODACTYLA**
Characidae	Hipparioninae indet.
Distichodus sp.	Rhinocerotidae
Hydrocynus sp.	**ARTIODACTYLA**
Sindacharax sp.	*Notochoerus euilus*
Siluriformes indet.	*Metridiochoerus jacksoni*
Bagridae indet.	*Hippopotamus amphibius*
Synodontis sp.	Giraffidae indet.
Cichlidae indet.	*Tragelaphus nakuae*
Lates niloticus	*Syncerus* sp.

The mammalian fauna includes browsers (*Notochoerus euilus*, *Tragelaphus nakuae*) and mixed grazers (*Metridiochoerus jacksoni*), suggesting that some cover was locally available. There must have also been grasslands close to water since *Hippopotamus* was present.

The molluscan fauna is indicative of shallow permanent waters, with marshy areas and at least some abundant aquatic vegetation. *Coelatura*, a unionid bivalve, requires a relatively stable drainage area. *Bulinus* is usually not associated with forested areas so its presence may indicate a relatively open habitat. *Cleopatra bulimoides* is commonly associated with slow flowing or stagnant waters with sandy or muddy substrates and prefers shallow rather than deep waters. *Melanoides* is found in a range of freshwater habitats. *Pila ovata*, an air breathing prosobranch gastropod, is common in temporary water bodies and inhabits papyrus swamps and stony beaches where it deposits its egg clusters amongst rocks and crevices in the ground.

6.5.4 Conclusion

The molluscan fauna from Senga 5A confirms a permanent water body existed, but also adds important information to the overall palaeoecological picture. Aquatic vegetation is indicated by *Pila*, and relatively open habitats associated with slow flowing waters by *Bulinus*. Connection to a large permanent drainage system is indicated by the freshwater mussel *Coelatura*, and shallow water habitats by *Cleopatra*. The fact that *Bellamya* is absent from this assemblage, and that the unionids *Aspatharia* and *Mutela* are also absent, even though all three are known from adjacent sections of the deposits, confirms that the setting may have been a shallow water habitat, and that these deeper water molluscs were absent due to environmental reasons (Harris et al. 1987). A shallow littoral setting including reed beds would fit the molluscan data. The age of the site, and the uncertainty of the hominine responsible for making the stone tools, makes it difficult to place the data into any palaeoanthropological context.

6.6 Erk-el-Ahmar

6.6.1 Introduction

In Chapter 5 and so far in this chapter the sites examined have been African, whereas this is the first site from outside Africa. The site of Erk-el-Ahmar is situated in the Jordan Valley, Israel (Figure 6.6.1), and is one of the earliest sites outside Africa that contains evidence of hominin occupation. Ron & Levi (2001), using high resolution magnetostratigraphy, were able to identify the upper and lower boundaries of the Olduvai subchron within the Erk-el-Ahmar Formation, dating it to between 1.7 and 2 Ma.

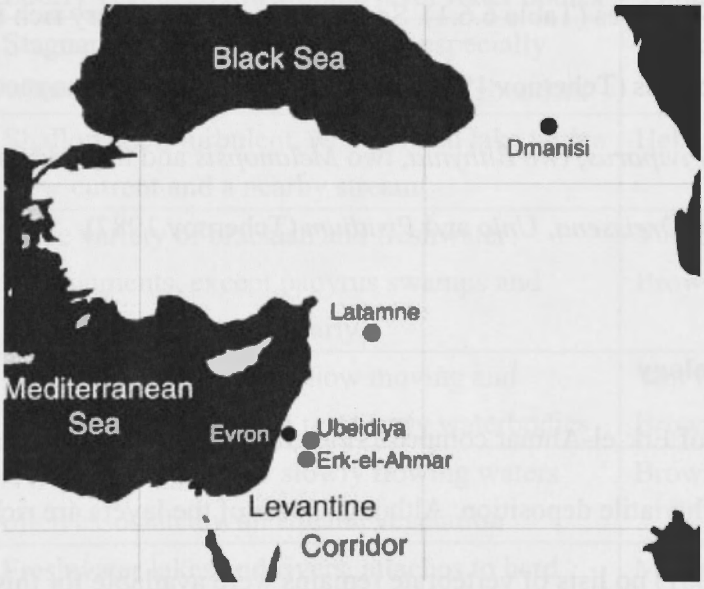


Figure 6.6.1: Map of the Middle East showing location of Erk-el-Ahmar, Ubeidiya and Dmanisi (Ron & Levi 2001).

The sediments of the Erk-el-Ahmar Formation are characterised by lacustrine deposits consisting mainly of brown clays and marls with some intercalations of clayey varves.

Less common are silts and sands probably associated with fluviatile deposits (Tchernov 1987).

Homo is inferred due to the stone artefacts but no other primates are known from Erk-el-Ahmar. The artefacts are typical Oldowan tools including core-choppers and flakes, and are some of the oldest known from the Middle East (Horowitz 1979, Bar-Yosef 1994).

6.6.2 Molluscs

The Erk-el-Ahmar site has revealed a diverse assemblage of molluscs including gastropods and bivalves (Table 6.6.1). Some of the strata are very rich in freshwater mollusc assemblages (Tchernov 1987), with 17 species having been recognised including two species of *Viviparus*, two *Bithynia*, two *Melanopsis* and three *Melanoides*. The bivalves include *Dreissena, Unio* and *Pisidium* (Tchernov 1987).

6.6.3 Palaeoecology

The sediments of Erk-el-Ahmar comprise fine grained clays and marls associated with lacustrine and fluviatile deposition. Although some of the layers are rich in fish remains (Ron & Levi 2001) no lists of vertebrate remains were available for this study, so the molluscan fauna is the only faunal data available.

The molluscs point to a lacustrine system with some aquatic vegetation and some variable water movement. *Lymnaea lagotis* is widespread in rivers and swamps of the coastal plain of the eastern Mediterranean, as well as in small streams, swamps and springs surrounding lakes (Tchernov 1973). *Gyraulus piscinarum* is often associated with swampy and shallow still-water sediments (Tchernov 1973), and the genus *Gyraulus* often inhabits well vegetated wetlands (Brown 1980) but is not usually associated with habitats that regularly dry out (Van Damme 1984).

Table 6.6.1: Molluscs from Erk-el-Ahmar (Tchernov 1987)

Taxon	**Palaeoecology**	**References**
Theodoxus	Variety of water bodies incl. still waters, slow flowing rivers, open more turbulent waterbodies, fresh or brackish, rocky bottoms	Tchernov 1973, Brown 1980, Preston 1915
Viviparus	Rivers, lakes and ponds	Soes et al. 2009
Hydrobia	Brackish and freshwater	Brown 1980
Falsipyrgula	Poorly vegetated low trophic level water bodies	Yildirim 2004
Bithynia	Stagnant or slow flowing water , especially where decaying vegetation or mud is abundant	Preston 1915
Melanopsis	Shallow, non-turbulent, well-aerated lake with a slow current and a nearby stream	Heller & Sivan 2002
Melanoides	Wide variety of brackish and freshwater environments, except papyrus swamps and waters that dry out regularly	Van Damme 1984, Brown 1980
Lymnaea	Pulmonate, all kinds of slow moving and stagnant waters, rare in temporary waterbodies	Van Damme 1984, Brown 1980,
Gyraulus	Generally stagnant or slowly flowing waters often associated with aquatic vegetation	Brown 1980
Dreissena	Freshwater lakes and rivers, attaches to hard substrates, including other mussels, with byssus thread	Morton 1969
Pisidium	Wide range of waterbodies including transient water bodies and trophic lake stages, ponds, swampy woodlands, streams, rivers lakes, organic material substrate	Burky 1983
Unio	Unionid freshwater mussel, lakes and rivers	Van Damme 1984

Theodoxus jordani is today a littoral rock dweller (Tchernov 1973), and is found in slow flowing rivers, streams, lakes and springs. *Viviparus* commonly inhabits the slow flowing parts of rivers but can also inhabit lakes. *Hydrobia* is a small freshwater inhabitant but can tolerant brackish waters (Brown 1980), and species of this genus have been found in springs, oases, lakes and brackish coastal waters (Van Damme 1984). *Bithynia* is found in various freshwater habitats (Van Damme 1984) including stagnant or slow running water, especially where decaying vegetation or mud is abundant (Preston 1915).

Three species of *Melanoides* are known from Erk-el-Ahmar. This genus can tolerate a range of habitats including various salinity levels, temperatures and substrates. The presence of three species suggests a diversity of wetland habitats. The *Melanopsis* fauna suggests that the palaeoenvironment of Erk-el-Ahmar may have consisted of a shallow, well-aerated lake with a slow current and a nearby stream (Heller & Sivan 2002).

The bivalves from Erk-el-Ahmar include the veneroid clams *Dreissena chantrei* and *Pisidium casertanum*. Veneroid clams inhabit a range of habitats including ponds, swampy woodlands, lakes, streams and major rivers. They occur in high densities on substrates with a high organic content (Burky 1983). The now extinct unionid bivalve *Unio subrectangularis* indicates that perennial freshwater must have existed and that the water body was part of a perennial drainage system.

6.6.4 Conclusion

Because no vertebrate fauna have been published for the Erk-el-Ahmar site, the known molluscan fauna provide one of the few opportunities to reconstruct palaeoecological conditions. In sum, the mollusc fauna support the sedimentological data in pointing to a large stable freshwater drainage system including lakes, rivers, swampy regions, shallow habitats, and areas of aquatic vegetation. Some salinity may have occurred at times within the system but freshwater must have been a constant feature, and the drainage area must have included a perennial network of connected rivers.

The hominines may have been attracted to these wetlands and water's edge habitats to drink, forage and possibly to seek refuge. To the extent that forest habitats were available for the hominines of Erk-al Ahmar, the available data give little indication.

6.7 Ubeidiya

6.7.1 Introduction

Also in the Jordan Valley (Figure 6.7.1), but slightly younger than Erk-el-Ahmar is the site of Ubeidiya, which has been biochronologically dated to 1.5 Ma (Belmaker et al. 2002). The Formation is made up primarily of shoreline lake sediments with fluviatile cycles (Belmaker et al. 2002).

Figure 6.7.1: Map of the Middle East showing location of Ubeidiya (Belmaker 2010)

The Ubeidiya fauna includes the cercopithecids *Macaca sylvanus* (Tchernov 1987) and *Theropithecus* (Belmaker 2010), as well as an incisor, molar and several cranial fragments which have been tentatively identified as *Homo ergaster* (Belmaker et al. 2002).

A series of archaeological horizons are also known within lake-shoreline deposits as well as swampy layers and fluviatile conglomerates at Ubeidiya (Bar-Yosef 1987). Within the archaeological assemblages are the remains of hippopotamids, cervids and equids, the bones of which have been fractured and in some cases feature cut marks. The artefacts are mostly flakes including some with retouch, as well as core-choppers and hand axes (Bar-Yosef 1987). They are most similar to the Early Acheulean and Developed Oldowan industries (Tchernov 1987). The artefacts accumulated in marshy areas, meaning it was within this stable wetland context that the hominins were making use of these tools (Mallol 2006). Bar-Yosef & Tchernov (1972:26) report that at Ubeidiya stone tools "are usually found wherever true shoreline deposits are detected, suggesting that the shores of the Ubeidiya Lake were chosen as living sites by human populations".

6.7.2 Molluscs

Ubeidiya has yielded 13 mollusc taxa (Table 6.7.1), including prosobranch (*Theodoxus*, *Viviparus*) and pulmonate (*Lymnaea*, *Gyraulus*) gastropods, and unionid (*Unio*, *Leguminaia*) and veneroid (*Corbicula)* bivalves (Tchernov 1987).

6.7.3 Palaeoecology

A diverse range of mammals have been discovered at Ubeidiya (Table 6.7.2). The mammals reflect Ubeidiya's location as a biogeographical crossroads between the Eurasian and African faunal and floral realms.

Table 6.7.1: Molluscs from Ubeidiya (Tchernov 1987)

Taxon	**Palaeoecology**	**References**
Theodoxus	Variety of water bodies incl. still waters, slow flowing rivers, more open turbulent waterbodies, fresh or brackish, rocky bottoms	Tchernov 1973, Brown 1980, Preston 1915
Viviparus	Freshwater, shallow waters, often among macrophytes	Jonkinen et al. 1982
Bithynia	Stagnant or slow flowing water , especially where decaying vegetation or mud is abundant	Preston 1915
Melanopsis	Shallow, non-turbulent, well-aerated lake with a slow current and a nearby stream	Heller & Sivan 2002
Melanoides	Wide variety of brackish and freshwater environments, except papyrus swamps and waters that dry out regularly	Van Damme 1984, Brown 1980
Lymnaea	Pulmonate, all kinds of slow moving and stagnant waters, rare in temporary waterbodies	Brown 1980, Van Damme 1984
Gyraulus	Generally stagnant or slowly flowing waters often associated with aquatic vegetation	Brown 1980
Planorbarius	Some species inhabit marshes which dry out seasonally	Brown 1980
Acroloxus	Permanent freshwater, often on stalks and leaves of plants, stones covered with algae	Sturm 2007
Unio	Unionid fresh water mussel, lakes and rivers	Van Damme 1984
Leguminaia	Freshwater unionid mussel, shallow muddy substrates	Tchernov 1972
Corbicula	Tropical and sub-tropical fresh and brackish waters, variety of substrates, prefers well oxygenated waters and sandy substrates	McMahon 1983

In terms of palaeoecology, the mammalian fauna point to open landscapes since *Theropithecus* and two species of *Equus* are present, and relatively arid habitats, to judge by the presence of *Oryx*, *Gazella*, *Camelus* and *Gerbillus*.

Table 6.7.2: Mammal fauna from Ubeidiya (Tchernov 1987)

CARNIVORA	*Oryx* sp.
Ursus etruscus	*Gazella* cf. *gazella*
Canis cf. *arnensis*	*Gazellospira torticornis*
Canis sp. (size *falconeri*)	*Bos* sp.
Vulpes sp.	*Pelorovis oldowayensis*
Pannonictis ardea	*Praemegaceros verticornis*
Lutra sp.	Cervidae (indet.)
Vormella cf. *peregusna*	**RODENTIA**
Herpestes sp.	*Hystrix indica*
Crocuta crocuta	*Cricetus cricetus*
Lynx sp.	*Mesocricetus primitivus*
Panthera gombaszoegensis	*Allocricetus bursae*
Felis sp.	*Occitanomys haasi*
Megantereon cf. *cultridens*	*Parapodemus jordanicus*
PROBOSCIDEA	*Apodemus sylvaticus*
Mammuthus meridionalis tamanensis	*Apodemus mystacinus*
PERISSODACTYLA	*Praomys galilensis*
Dicerorhinus etruscus	*Praomys levantinus*
Equus cf. *tabeti*	*Arvicanthis ectos*
Equus sp. (*caballus* type)	*Mus musculus*
PRIMATES	*Gerbillus dasyurus*
Macaca sylvanus	*Parameriones obeidiensis*
Theropithecus sp.	*Allactaga euphratica*
ARTIODACTYLA	*Lagurodon arankae*
Kolpochoerus olduvaiensis	*Arvicola jordanica*
Sus strozzii	*Spalax ehrenbergi*
Hippopotamus gorgops	*Myomimus roachi*
Hippopotamus behemoth	**LAGOMORPHA**
Giraffidae (indet.)	*Hypolagus brachygnathus*
Camelus sp.	

The suids *Kolpochoerus* and *Sus* indicate relatively dense vegetation. Forested habitats are indicated by the rodent genera *Praomys* and *Apodemus*, both of which today prefer humid, well shaded vegetation (Kingdon 1982, Bar-Yosef & Tchernov 1972). Macaques *Macaca* too indicate the presence of forest habitats.

Permanent water is suggested by the presence of the otter *Lutra*, the water vole *Arvicola* and the hippopotamid *Hippopotamus*, while the extinct genus *Pannonictis* is considered to be closely associated with aquatic habitats (Garcia & Howell 2008).

One of the most diverse assemblages of fossil avian fauna known comes from the Ubeidiya Formation (Table 6.7.3). The identified birds include cormorants *Phalacrocorax* which require shallow waters containing abundant fish, including the flat banks of estuaries and lakes and the running waters of lakes, pools or rivers so long as they are protected by dense belts of vegetation (Tchernov 1968). Coots *Fulica* prefer shallow vegetated lakes, and shelducks *Tadorna* and ducks *Anas* are also inhabitants of lakes with margins of dense aquatic vegetation. The water rail *Rallus* makes its home in reed beds while crakes *Porzana* and swamphens *Porphyrio* are also inhabitants of reed beds.

Other birds found at Ubeidiya, such as the seed-eating starlings *Sturnus* and finches *Fringilla, Acanthis* and *Carduelis* indicate the presence of grasslands. Rock pigeons *Columba livia*, indicate that the climate may have been relatively dry and that there were may have been rocky cliffs nearby. Finally, there must have been trees in the region, because many of the birds, including the finches, starlings, blackbirds *Turdus*, shrikes *Lanius* and owls *Athene* require trees for shelter and to nest.

Table 6.7.3: Avian fauna from Ubeidiya (Tchernov 1968)

Phalacrocorax (cormorant)	*Melanocorypha* (lark)
Anas (duck)	*Alauda* (lark)
cf. *Ixobrychus* (heron)	*Motacilla* (wagtail)
Tadorna (shelduck)	*Lanius* (shrike)
Accipiter (hawk)	*Sturnus* (starling)
Falco (falcon)	*Corvus* (crow)
Alectoris (partridge)	*Sylvia* (warbler)
Francolinus (francolin)	cf. *Acrocephalus* (warbler)
Rallus (rail)	*Turdus* (black bird)
Porzana (crake)	*Cercomela* (chat)
Crex (corncrake)	*Petronia* (sparrow)
Fulica (coot)	*Fringilla* (finch)
Porphyrio (swamphen)	*Acanthis* (finch)
Columba (pigeon)	*Carduelis* (finch)
Athene (owl)	*Emberiza* (bunting)
cf. *Asio* (owl)	

From the presence of birds, then, it can be inferred that the Ubeidiya surroundings at times included shallow water in a eutrophic lake at least partly covered by water plants and surrounded by a belt of reeds, as well as a dense area of growth associated with marshy habitats. Further from the water would have been grassy habitats, woodlands and rocky cliffs including crevices and caves (Tchernov 1968).

Other vertebrate fossils include catfish *Clarias*, which suggests shallow, slow moving to stagnant waters and the lizard *Ophisaurus*, which is an indicator of forest or forest edge habitats (Bar-Yosef & Tchernov 1972).

Pollen analysis from Ubeidiya shows that oak trees *Quercus* were well represented in the region, and that the freshwater plant *Myriophyllum* probably inhabited the rivers.

The molluscan fauna from Ubeidiya is informative from the point of view that it shows different depositional environments over time. In certain layers, for example, the majority of *Melanopsis* feature costated shells, which were probably advantageous in turbulent waters since the costae strengthen the shells and offer protection against wave action (Bar-Yosef & Tchernov 1972).

In the layers where costated *Melanopsis* occur, thin shelled gastropods such as *Lymnaea* and *Gyraulus* are less common. This may indicate deposition in relatively turbulent waters. Alternatively, in the layers where the majority of *Melanopsis* individuals are smooth shelled, there are also a number of thin shelled species present, which probably indicates relatively stagnant, swampy deposits.

The shells of *Theodoxus*, too, varied between being smooth and possessing conspicuous keels (always two). The smooth varieties were associated with still water bodies such as pools, shallow streams and swamps, while the keeled individuals were indicative of larger, more open, turbulent waters (Tchernov 1973). During the Pliocene the Jordan Valley was an extension of the Mediterranean Sea and Grossu (1984) argues that *Theodoxus* was once part of the marine fauna of the ancient Tethys (now Mediterranean), and subsequently adapted to freshwater.

The molluscan evidence from Ubeidiya therefore indicates that the environmental conditions shifted back and forth from shallow high energy shore environments in which littoral rock-dwellers such as *Melanopsis* and *Theodoxus* were common, to lower energy, shallow, swampy habitats in which mud-dwelling molluscs such as *Valvata* and *Melanoides*, and species that are regularly associated with aquatic vegetation such as *Lymnaea* and *Gyraulus*, were more common (Bar-Yosef & Tchernov 1972).

At Ubeidiya there are four species of bivalve including three unionid species in two genera, *Unio* and *Leguminaia*. This diversity of freshwater mussels attests to the large area that must have been covered by the particular drainage system that the Ubeidiya wetlands were part of. Suitable fish hosts must have been available for the larvae of these unionid species to attach to in their parasitic larval stage, and suitable perennial freshwater rivers, or streams must have also been available to provide the adults of these species with the requirements they needed to disperse and survive. *Corbicula fluminalis* is indicative of relatively lotic habitats.

The freshwater mussel *Leguminaia* has been found in distinctive quantities in association with artefacts, such as a gigantic flint chopper, that are some of the oldest known at the site (Bar-Yosef & Tchernov 1972: 14-15).

6.7.4 Conclusion

The molluscan fauna confirm the conclusions drawn from other data suggesting a large permanent water body existed in the area, including areas of high energy as well as more stagnant areas of shallow marshy wetlands that most probably supported dense bands of aquatic vegetation. The molluscan fauna confirm the existence of various freshwater habitats and also record changes in the hydrological system over time. The climate must have been at least sub-tropical given the presence of *Corbicula* and *Melanoides*, and a connected network of perennial rivers must have also been present given the presence of the unionid bivalves and *Viviparus*.

The shallow reed beds may have provided foraging opportunities for the hominin populations of Ubeidiya. Trees, more open habitats, and nearby cliffs with caves were also part of the hominin landscape. The overall morphology of the Ubeidiya hominins is unknown due to a lack of fossil evidence, but much better early hominin fossil remains are known from Dmanisi.

6.8 Dmanisi

6.8.1 Introduction

The site of Dmanisi, in Georgia (Figure 6.8.1), is one of the earliest hominin fossil sites outside Africa. Faunal associations, dating of basalts and palaeomagnetic correlations suggest the Dmanisi site has an age of c.1.75 Ma (Vekua et al. 2002). The Dmanisi fauna was buried rapidly with minimal transport; articulated skeletal parts are common. An overlying calcareous horizon helped protect the bones from diagenetic damage and the compaction that normally occurs to fossilised specimens (Vekua et al. 2002).

Figure 6.8.1: Map showing location of the Dmanisi site, Georgia (Vekua et al. 2002)

Carnivores are well represented in the assemblage, both in terms of diversity and overall proportions, and tooth marks and carnivore breakage patterns appear on some bones. Hyaena coprolites are present, but Vekua et al. (2002) caution against labeling the assemblage a carnivore lair.

The only primate known from Dmanisi is a hominin placed in the genus *Homo*. Fossils include cranial (Gabunia et al. 2001, Lordkipanidze et al. 2006) and post-cranial

(Lordkipanidze et al. 2007) remains, which have been interpreted as linking the populations to the early *Homo* species from Africa such as *Homo habilis* and *Homo ergaster* (Vekua et al. 2002).

Artefacts made of local raw materials (river gravels) are known, and described as 'primitive'; belonging to a Mode 1 type industry similar to the Oldowan of East Africa (Vekua et al. 2002). The vast majority (77%) of artefacts are flakes (Gabunia et al. 2001). Tool-marked bones are known from Dmanisi (Lordkipanidze et al. 2006).

6.8.2 Molluscs

A number of gastropods have been discovered at Dmanisi, but no bivalves (Table 6.8.1). The molluscs were referred to in the text of Gabunia et al. (2000), but whether these are all the molluscs found at Dmanisi is unclear and attempts to contact the relevant researchers have been unsuccessful. The gastropods are all pulmonates.

Table 6.8.1: Molluscs from Dmanisi

Taxon	**Palaeoecology**	**References**
Helicopsis	Some species inhabit grasslands and can tolerate dry habitats	Saghy & Hornung 2001
Pseudochondrula	High altitudes and relatively dry country, sheltering under rocks; calcareous territories, relict forests	Gumus 2010
Helix	Generally cool, moist habitats, limestone soils, not usually found in forests; some species can survive dry periods by aestivating	Morton 1979
Jaminia	Limestone soils, range of habitats, can tolerate dry conditions; often under rocks; lichen grazers	Heller 1984

6.8.3 Palaeoecology

A diverse range of vertebrate fauna has been found at Dmanisi (Table 6.8.2). The assemblage contains a mix of taxa suggesting both forest and steppe environments (Gabunia et al. 2001). Steppe conditions are indicated by the ostrich *Struthio* and the pika *Ochotona*.

Table 6.8.2: Vertebrate fauna from Dmanisi (Gabunia et al. 2000)

SORICOMORPHA	*Equus stenonis*
Sorex sp.	*Dicerorhinus etruscus etruscus*
LAGOMORPHA	**ARTIODACTYLA**
Ochotona cf. *lagreli* *Hypolagus brachyagnatus*	*Gazella* cf. *borbonica* *Soergelia* sp.
RODENTIA	*Dmanisibos georgicus*
Kowalskia sp.	*Cervus perrieri*
Cricetus sp.	*Eucladocerus* aff. *Senezensis*
Mimomys reidi	Cervidae cf. *Arvernoceros*
Mimomys cf. *pliocaenicus*	*Dama nestii*
Gerbillus sp.	Giraffidae cf. Paleotraginae
Marmota sp.	**PRIMATES**
CARNIVORA	*Homo* sp.
Canis etruscus	**REPTILIA**
Ursus etruscus	*Erix* sp.
Martes sp.	*Natrix* sp.
Megantereon megantereon	*Coluber najadum*
Homotherium crenatidens	*Coluber robertmertensi*
Panthera gombaszoegensis	*Elaphe* aff. *Dione*
Pachycrocuta perrieri	*Pelias* sp.
PROBOSCIDEA	*Daboia* cf. *raddei*
Archidiskodon meridionalis	**AVES**
PERISSODACTYLA	*Struthio dmanisensis*

Relatively dry habitats are suggested by the occurrence of the snake *Coluber najadum*, the gerbil *Gerbillus* and the ancient elephant *Archidiskodon*, which was apparently adapted to steppe and riparian biotopes (Noskova 2001). On the other hand forested habitats are indicated by the fact that Cervids are abundant at Dmanisi, making up more than 80% of the artiodactyl assemblage (Gabunia et al. 2000). The shrew *Sorex* and the caprine *Soergelia* as well as *Dmanisibos* are all likely to represent forest or forest edge species.

The site of Dmanisi is situated on a promontory between two rivers. The early Pleistocene deposits are directly associated with a lake that formed when a lava stream blocked one of the rivers (Gabunia et al. 2000). The climate is reconstructed as warm and semi-dry, and this part of Georgia during the Plio-Pleistocene was characterised by many rivers and lakes and a rich faunal and floral component (Gabunia et al. 2000).

Arboreal forest taxa as well as shrubs and grasses were present according to pollen remains. A high percentage of seeds have been found, including from the hackberry (*Celtis*), leading Gabunia et al. (2000) to hypothesise that fruit from these trees may have been eaten by the hominin inhabitants.

The molluscs referred to in Gabunia et al.'s (2000) site reports of Dmanisi are all land snails (pulmonates). One of the identified genera is *Helicopsis*, which contains species today such as *Helicopsis striata* which are known to inhabit grasslands and can tolerate dry habitats (Saghy & Hornung 2001). This species prefers generally warmer climates (Krolopp & Sumegi 1995). *Helix* aff. *pomatia* is apparently similar to the edible or

Roman snail. These snails prefer mild temperatures and suitable vegetation for shelter and food, and are often found in association with limestone based soils but rarely in thick forest. *Jaminia* can tolerate dry conditions, is often associated with limestone soils and is known from a wide range of habitats. Species of *Pseudochondrula* prefer high altitudes and relatively dry country, often sheltering under rocks, though they are associated with calcareous territory and relict forests in Turkey (Gumus 2010).

6.8.4 Conclusion

The terrestrial gastropods support the conclusions reached based on other data that a steppe environment existed at Dmanisi. This habitat must have included suitable vegetation and/or rocks to provide cover for the gastropod inhabitants. The local area likely included limestone based soils. The temperature appears to have been mild to warm and the local climate may have been dry.

The hominins from Dmanisi were apparently well adapted to climbing and were also upright striding bipeds. The Dmanisi landscape was relatively open but some trees were also present. Although the faunal data do not provide evidence for it, other data point to the presence of a river or pond, and nearby hills.

6.9 Pabbi Hills

6.9.1 Introduction

Pabbi Hills is a fossil site from northern Pakistan (Figure 6.9.1). Although the dating of the site remains contested, there are claims that some of the fauna is of Plio-Pleistocene age. The sites examined here belong to the Pinjor Faunal Stage of the Upper Siwaliks (Dennell 2004). The Pabbi Hills deposits consist of a cyclical series of fluvial deposits made up of sands, silts and clays, with each cycle capped by a layer of sandstone (Dennell et al. 2006). Some fossil show signs of having been accumulated by carnivores (Dennell 2004).

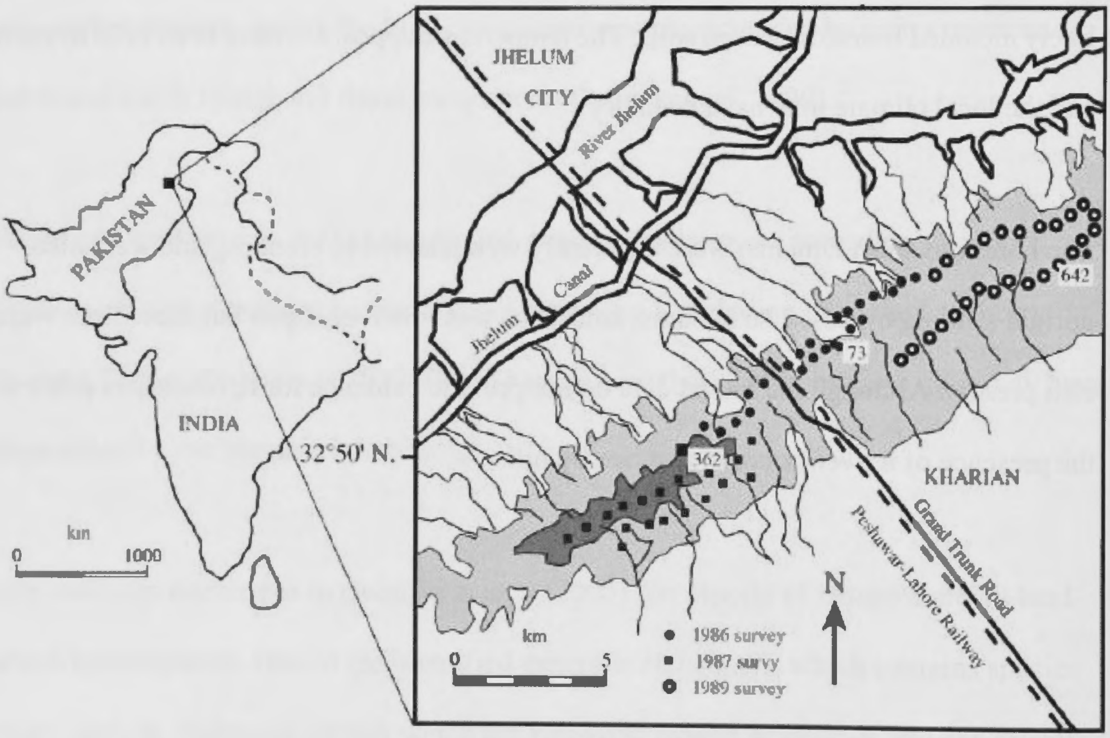


Figure 6.9.1: Map showing location of Pabbi Hills, Pakistan, including excavated fossil localities (Dennell 2008)

Primate fossils at Pabbi hills are rare. A small mandibular fragment, possibly belonging to a macaque, has been discovered in the Upper Siwalik deposits, and other specimens have characteristics aligning them to the Cercopithecidae (Dennell 2004).

Simple stone tools have been found on surfaces that are believed to have eroded from late Pliocene – Early Pleistocene deposits, and these tools point to the presence of a hominin species, likely the genus *Homo* (Hurcombe 2004).

6.9.2 Molluscs

A number of molluscs have been discovered in the Pabbi Hills deposits including the gastropod *Bellamya* and three unionid bivalves (Table 6.9.1).

Table 6.9.1: Molluscs from Pabbi Hills (Dennell et al. 2006).

Taxon	**Palaeoecology**	**References**
Bellamya	Lakes, large slow flowing rivers and streams – tropical	Van Damme 1984
Indonaia	Large slow moving rivers with clean, shallow water, typically less than 5 meters	Dennell et al. 2006
Lamellidens	Tropical freshwater mussel, abundantly distributed throughout Indian freshwater habitats	Mishra et al. 2008
Parreysia	Unionid freshwater mussel, common in rivers	Van Damme 1984

6.9.3 Palaeoecology

Dennell et al. (2006) record a number of vertebrate fossils from the Pabbi Hills (Table 6.9.2). The fauna give the impression of relatively open landscapes since *Equus*, *Gazella* and *Struthio* today prefer these habitats. Closed or forested habitats are also indicated by the cervids, while the suids indicate well vegetated, closed habitats.

Permanent water is reflected in the fact that hippopotamids and their relatives, the amphibious anthracotheriids, have been discovered at the site. *Crocodylus* and *Gavialis* were also part of the Pabbi Hills ecosystem and these suggest tropical woodlands with wide river systems and associated riverine shore areas for *Gavialis*, and hot swamp areas including riverine forest habitats, streams, ponds, lakes and the slower parts of tropical rivers for *Crocodylus* (Patnaik & Schleich 1993).

Table 6.9.2: Vertebrates from Pabbi Hills (Dennell et al. 2006)

ARTIODACTYLA	*Stegodon*
Hemibos triqueticornis	**CARNIVORA**
Damalops palaeindicus	*Crocuta crocuta*
Medium sized alcelaphine	*Pachychrocuta brevirostris*
Medium sized bovid	*Hyaenictis/Lycyaena*
Very large bovid	*Panthera uncial*
Gazella sp.	*Megantereon cultridens*
cf. *Cervus*	Large *Felis*, not leopard
cf. *Dama*	*Canis cautleyi*
Sivatherium giganteum	Canid, small
Suid, large	Ursid
Suid, small	Herpestid
Hippopotamids/*Hexaprotodon*	**REPTILIA**
Anthracotheriidae	*Crocodylus*
PERISSODACTYLA	*Gavialis*
Rhinoceros sivalensis	Cheloniidae
Equus sivalensis	**AVES**
PROBOSCIDEA	Struthio
Elephas hysudriscus	

Soil carbonate analyses suggest a large flood plain that was dominated by grasslands with some tree cover probably along the river margins (Dennell 2004).

The most common molluscs found at Pabbi Hills in the period from 2.2 to 1.7 Ma are the unionid bivalves *Lamellidens* and *Parreysia* (Dennell et al. 2006). These are indicative of a large drainage area with shallow slow moving rivers. The gastropod *Bellamya* is similarly adapted to slow moving rivers and requires hydrological connections for dispersal.

6.9.4 Conclusion

The combined molluscan fauna from Pabbi Hills indicate the presence of a large, permanent, slow moving river, with clean, shallow water. This confirms the findings based on sedimentology and the crocodilian remains. *Bellamya* is today restricted to freshwater tropical habitats, so its presence at Pabbi Hills indicates tropical freshwater habitats.

6.10 Mojokerto (Perning)

6.10.1 Introduction

Along with Dmanisi, one of the earliest instances of *Homo* fossils discovered outside Africa comes from the site of Perning, near Mojokerto, Java (Figure 6.10.1)

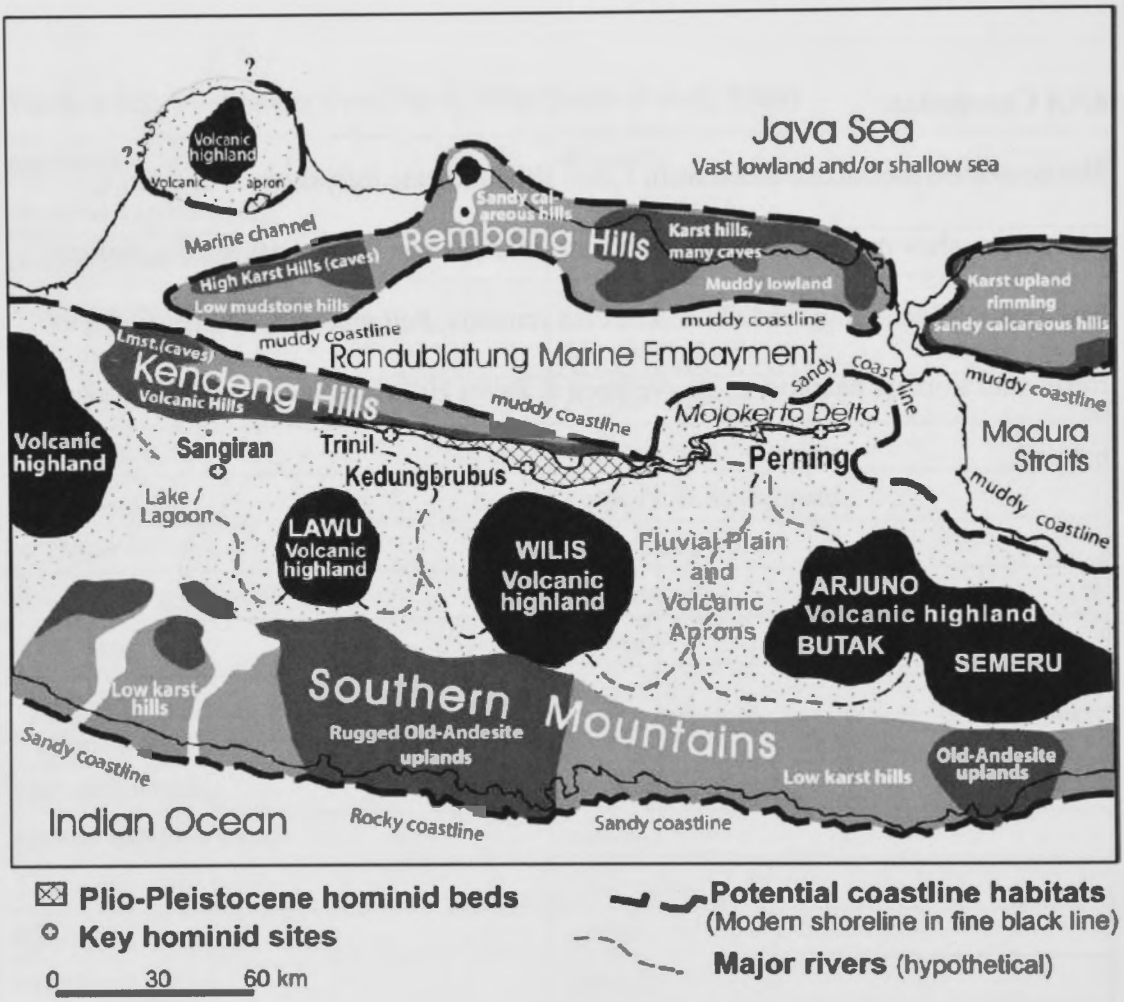


Figure 6.10.1: Palaeogeographic map showing possible setting in relation to coast, given changes in sea levels, of Perning fossil site, near Mojokerto, Java (Huffman & Zaim 2003)

Perning is located in the Sangiran (previously Pucangan) Formation of Java, which lies above the marine Puren Formation and below the Bapang Formation (Figure 6.10.2). The site has been dated to 1.81 Ma (Swisher et al. 1994), and although this date has been questioned (e.g. de Vos & Sondaar 1994), recent fieldwork and archival research appears to confirm its reliability (Huffman 2001).

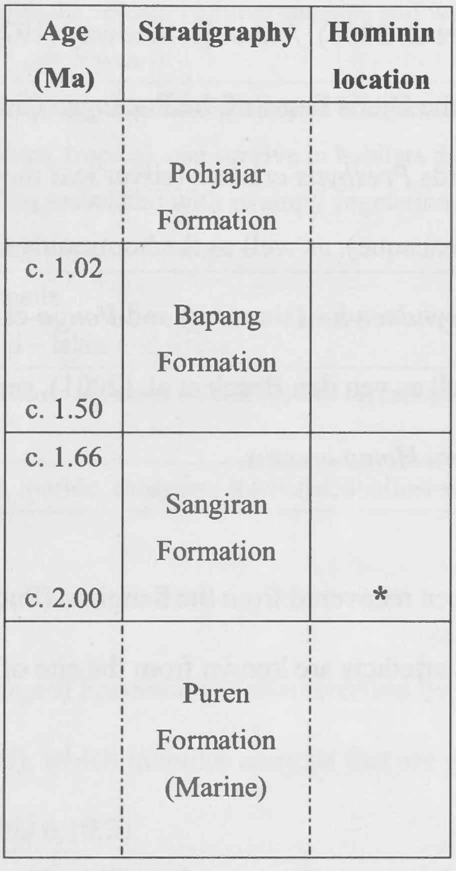


Figure 6.10.2: Simplified stratigraphic diagram of eastern Java

The Sangiran Formation is made up of a basal part composed of volcanic breccia containing marine and fresh water molluscs, and an upper part, known as the 'black clays', which includes siltstone and mudstone associated with shallow marine, brackish water and marsh environments (Ninkovich & Burckle 1978, Bettis et al. 2004). The so called hominin bed from Mojokerto contains conglomeratic sandstone formed as a sand

and gravel bar in a swift moving, shallow-water river channel in a deltaic setting near the coast (Huffman & Żaim 2003). The condition of the skull and the sedimentological setting suggests *in situ* preservation, with the individual probably dying in the delta rather than being transported any distance by river action (Huffman et al. 2006).

The juvenile hominin skull from the Mojokerto Beds is generally assigned to the species *Homo erectus* (Huffman et al. 2006). Although Medway (1972) lists a number of other primates as belonging to the Djetis fauna of the Pucangan (Sangiran) Formation, including the cercopithecids *Presbytis cristata* (silver leaf monkey) and *Macaca fascicularis* (long tailed macaque), as well as the hominoids *Hylobates* cf. *moloch* (gibbon), *Symphalangus syndactylus* (siamang) and *Pongo* cf. *pygmaeus* (orang utan), Larick et al. (2000), as well as van den Bergh et al. (2001), see the Ci Saat fauna as being free of primates, apart from *Homo erectus*.

No lithic artefacts have been recovered from the Sangiran (Pucangan) Formation (Choi & Driwantoro 2007) and no artefacts are known from the site of Perning.

6.10.2 Molluscs

The hominin bed of Mojokerto contains a number of bivalve and gastropod molluscs (Table 6.10.1). The most common mollusc is the small gastropod *Brotia*. Other gastropods include *Melanoides* and an unidentified stylommatophoran land snail. The bivalves include the freshwater unionid *Elongaria orientalis* and fragments of a large clam, possibly *Polymesoda* cf. *coaxans*. The marine oyster *Crassostrea* is also known from the hominin deposits. Fossils collected from the nearby Perning district, likely to have been part of the same delta formation, include the apple snail *Pila* (Huffman & Zaim 2003).

Table 6.10.1: Molluscs from Perning (Huffman & Zaim 2003)

Taxon	**Palaeoecology**	**References**
Brotia	Usually restricted to flowing water	Dudgeon 1999
Melanoides	Wide variety of brackish and freshwater environments, except papyrus swamps and waters that dry out regularly	Van Damme 1984, Brown 1980
Pila	Air breathing pulmonate gastropod with an operculum, tropical, can survive in habitats that dry out, often associated with swampy vegetation including papyrus swamps	Brown 1984
Stylommatophora	Land snails	
Elongaria	Unionid – lakes and rivers	Van Damme 1984
Polymesoda	*Polymesoda coaxans* is a mangrove forest species	Brockwell & Akerman 2007
Crassostrea	Oyster, marine, estuaries, intertidal, shallow waters	Nehring 2006

6.10.3 Palaeoecology

The upper Sangiran (Pucangan) Formation is characterised by an endemic island fauna (Ci Saat) (Bettis et al. 2004), which includes animals that are generally strong swimmers (Joordens et al. 2009) (Table 6.10.2).

The vertebrate fauna from the Mojokerto hominin bed (Table 6.10.2) give an indication of the types of habitats that existed at the time of deposition. Well forested habitats were present because cervids such as *Axis* are today generally forest adapted and *Hexaprotodon* is typically an inhabitant of rivers and swamps in dense forest. The tiger *Panthera tigris* is also an inhabitant of forest habitats including mangrove forests.

Table 6.10.2: Vertebrates from relocated Mojokerto skull bed (Huffman et al. 2006)

CARNIVORA	*Duboisia santeng*
Panthera tigris	? *Bibos palaeosondaicus*
PROBOSCIDEA	? *Bubalus palaeokerabau*
? *Stegodon trigonocephalus*	? *Epileptobos groeneveldtii*
? *Elephas hysudrindicus*	**OSTEICHTHYES**
ARTIODACTYLA	Siluridae indet.
Sus sp.	**REPTILIA**
Hexaprotodon sivalensis	*Crocodylus* sp.
Axis lydekkeri	*Gavialis* sp.
Rusa sp.	*Trionyx* sp.

A large water body was also present judging from the presence of *Crocodylus*, some species of which are adapted to salt water, and *Gavialis* which is generally a riverine species, preferring calmer areas of deep fast moving rivers. The soft-shell turtle *Trionyx* is today an inhabitant of slow moving freshwater bodies such as large rivers, creeks, ponds and lakes, but some species can also tolerate slightly salty water. Also found at Perning are the remains of the freshwater catfish Siluridae, indicating that shallow, slow moving waters were locally present.

Palaeobotanical data indicate the presence of fruit bearing palms such as *Nypa fruticans* and *Borassus*, trees associated with mangroves, aquatic herbaceous vegetation, climbing ferns associated with swamps and a scattering of trees and bamboo thickets associated with grasslands (Huffman & Zaim 2003).

The molluscs from Perning include the gastropods *Brotia* and *Melanoides*, both of which inhabit a wide range of fresh water environments, though *Brotia* is particularly associated with flowing water (Dudgeon 1999), especially the clear waters of small mountain streams (Kohler & Glaubrecht 2006). *Melanoides* can tolerate brackish waters. These gastropods generally live at or near the surface, for example on plants or on firm ground, or else dwell in mud. *Pila* lives in shallow and slow flowing freshwater environments often in association with aquatic vegetation.

The large clam *Polymesoda* today occurs in abundance on mudflats in estuaries and deltas and is known from channel-sand deposits elsewhere in Java (Huffman & Zaim 2003). It can tolerate relatively brackish water as well as fresh water and *Polymesoda coaxans* is a mangrove forest dweller (Brockwell & Akerman 2007). *Elongaria orientalis* is a fresh water unionid bivalve that inhabits rivers and lakes. *Crassostrea*, a marine oyster, attaches itself to almost any hard surface in sheltered habitats such as estuaries, although it is also known to live in sand and mud. They are usually found in intertidal and shallow subtidal zones, to a depth usually of about 3 metres (Nehring 2006).

6.10.4 Conclusion

The mollusc faunal assemblage adds important detail to the palaeoecological picture of the Perning site. The coast must have been within the vicinity as well as mangroves, with rivers of both high and low energy also present locally, plus swampy freshwater habitats with sufficient aquatic vegetation to support the swamp snail *Pila*. The habitat was most likely tropical to sub-tropical because *Melanoides* and *Pila* are both inhabitants of these climates. These palaeoecological impressions fit well with other data that point to a tropical coastal deltaic setting for the Mojokerto site. The hominins at Mojokerto would have had a range of waterside habitats as well open and closed habitats in which to forage and seek shelter.

6.11 Trinil

6.11.1

The fossil site of Trinil, Java, is situated on the Solo River approximately 100kms west of the Perning site near Mojokerto (Figure 6.11.1).

Figure 6.11.1: Map of east Java showing location of Trinil (from Joordens et al. 2009)

The main fossiliferous layer of Trinil (Trinil HK) comes from the Lower part of the Bapang Formation, which overlies the Sangiran Formation (Figure 6.11.2). Once thought to have an age of about 1 Ma (de Vos & Sondaar 1994), recent dating suggests the site may be closer in age to 1.5Ma (Larick et al. 2001).

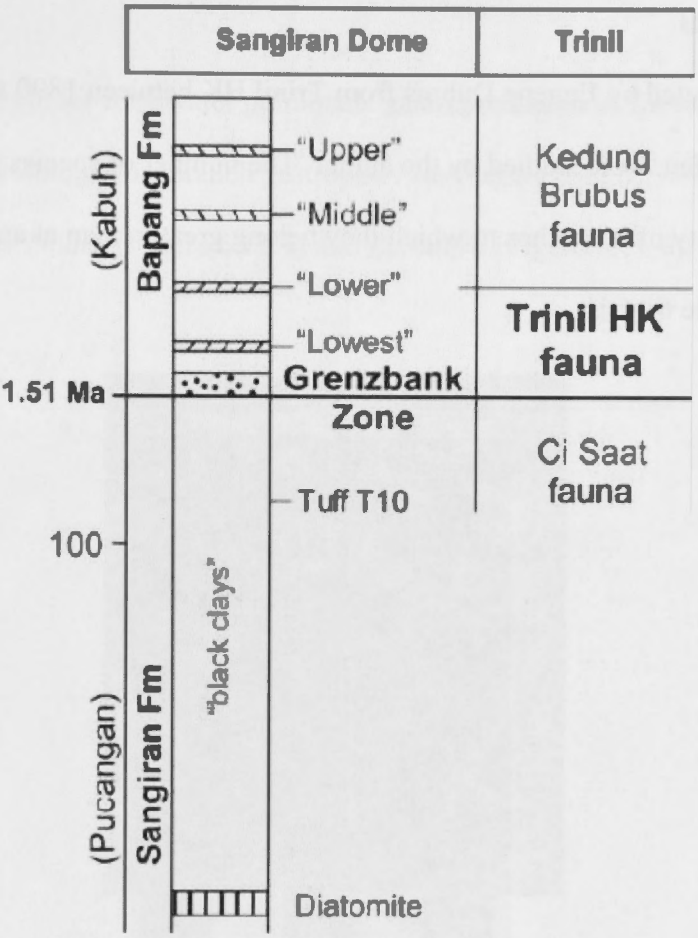


Figure 6.11.2: Simplified stratigraphic diagram showing position of Trinil HK, which has yielded *Homo erectus* fossils, in relation to the Grenzbank Zone of the Sangiran Dome (from Joordens et al. 2009, adapted from Indriati & Anton 2008)

The Bapang Formation represents an aggraded fluvial system built up over a number of energetic cycles consisting of fine to very coarse tuffaceous sandstones containing lenses of pumiceous conglomerate that grade up to silts and silty clays (Ninkovich & Burckle 1978, Larick et al. 2001, Bettis et al. 2004). *Homo erectus* is known from the lower part of the Bapang Formation (Trinil HK), as is the macaque *Macaca fascicularis* (van den Bergh et al. 2001) and the silvered leaf monkey *Trachypithecus cristatus* (Joordens et al. 2009). Lithic artefacts have not been discovered at Trinil (Bartstra 1982).

6.11.2 Molluscs

Molluscs collected by Eugene Dubois from Trinil HK between 1890 and 1900, held at Naturalis, Leiden, were studied by the author. The number of species present is higher, and the diversity of econiches to which they belong greater, than at any other site so far analysed (Table 6.11.1).

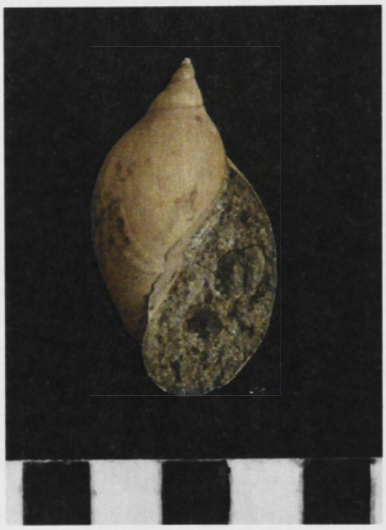


Figure 6.11.3: *Lymnaea* from Trinil (scale 5mm)

Figure 6.11.4: *Thiara* specimens from Trinil (scale 5mm)

The assemblage includes freshwater pulmonate gastropods such as *Lymnaea* (Figure 6.11.3), the air breathing prosobranch gastropod *Pila* (Figure 6.11.5), and freshwater gastropods such as *Thiara* (Figure 6.11.4) and *Bellamya* (Figure 6.11.6).

Figure 6.11.5: *Pila conica* from Trinil (scale 5mm)

Figure 6.11.6: *Bellamya javanica* from Trinil (scale 5mm)

Table 6.11.1: Molluscs from Trinil HK (Joordens et al. 2009)

Taxon	**Palaeoecology** (Dillon 2000; Robba et al. 2002, 2003)
Pila	(*conica*) Vegetation zone of stagnant water, ponds, swamps
Bellamya	(*javanica*) Bottom-or plant dweller, lives in ponds and swamps
Stenothyra	Brackish water mudflats
Digoniostoma	Bottom or plant dweller, lives in ponds and swamps
Cerithium	Shallow marine
Brotia	(*testudinaria*) Eurytopic: in running as well as stagnant freshwater
Melanoides	Ponds, rivers, lakes, estuaries, can tolerate brackish water
Tarebia	Lakes, rivers, shallow fast-flowing freshwater streams, ponds and swamps, occasionally in slightly brackish water
Thiara	Freshwater, occasionally brackish
Melongena	Estuaries, salt marshes, mangroves, shallow marine biotopes
Quirella	(marginal) marine, parasite
Cingulina	(marginal) marine, parasite
Didontoglossa	Sandy mud bottoms, 10-50m depth
Gyraulus	Vegetation zone of stagnant water, ponds, swamps
Lymnaea	Vegetation zone of stagnant water, ponds, swamps
Ameria	Vegetation zone of stagnant water, ponds, swamps
Jupiteria	Marine soft bottom
Anadara	Tidal flat and muddy bottoms seaward fringe of mangroves
Mytilidae	Marine or marginal marine, substrate dependent
Eamesiella	Marine to brackish chemoautotrophe
Cycladicama	Marine, sand-mud bottom, 10-50m depth
Tellimya	Marine, parasite
Arcopagia	(*pudica*) Muddy bottom infralittoral zone and in front of mangroves (*yemenis*) Marine soft bottom
Gari	Marine soft bottom
Theora	Marine soft bottom
Elongaria	Lakes and rivers
Rectidens	Lakes and rivers
Pseudodon	Forest streams and sandy, shallow areas in lakes and rivers
Corbicula	Streams, quiet fresh to occasionally brackish waters
Geloina	Estuaries, mud flats, mangroves
Dentalium	Scaphopoda - marine tusk shell

Figure 6.11.7: *Pseudodon vondembuschianus trinilensis* from Trinil (scale 10mm)

Figure 6.11.8: *Elongaria orientalis* from Trinil (scale 5mm)

Bivalves are represented by freshwater unionids including *Pseudodon* (Figure 6.11.7) and *Elongaria* (Figure 6.11.8), and by at least two species of *Corbicula* (Figure 6.11.9). In addition, a number of marine molluscs are present at Trinil including the gastropods *Cerithium* and *Melongena*, as well as the bivalves *Gari* and *Eamesiella* (Figure 6.11.10).

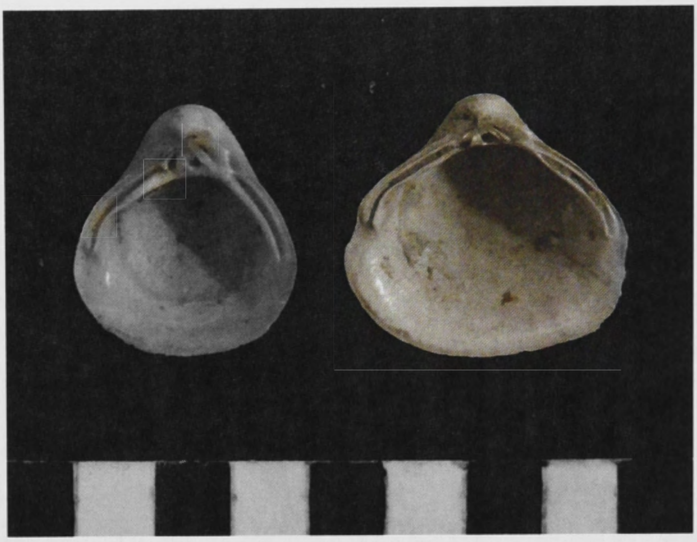


Figure 6.11.9: Two varieties of *Corbicula* from Trinil (scale 5mm)

Figure 6.11.10: *Eamesiella* from Trinil (scale 5mm)

Trinil also is the only site analysed that includes a non-gastropod or non-bivalve mollusc in the form of the scaphopod *Dentalium* (Joordens et al. 2009).

6.11.2 Palaeoecology

Vertebrate fossils from Trinil include mammals, birds, reptiles and fish (Table 6.11.2).

Table 6.11.2: Vertebrate fauna from Trinil (Joordens et al. 2009)

CARNIVORA	**REPTILIA**
Panthera tigris	*Crocodylus siamensis*
Prionailurus bengalensis	*Gavialis bengawanicus*
Cuon (=Mececyon) trinilensis	cf. *Batagur* sp.
Lutrogale sp.	cf. *Trionyx* sp.
PERISSODACTYLA	cf. *Hardella isoclina*
Rhinoceros sondaicus	*Varanus* sp.
PROBOSCIDEA	**AVES**
Stegodon trigonocephalus	*Leptoptilos* cf. *dubius*
ARTIODACTLYA	*Ephippiorhynchus* cf. *asiaticus*
Bubalus palaeokerabau	*Branta* cf. *ruficollis*
Bibos palaeosondaicus	*Tadorna tadornoides*
Duboisia santeng	*Pavo muticus*
Muntiacus muntjak	**OSTEICHTHYES**
Axis lydekkeri	*Anabas microcephalus*
Cervus sp.	*Channa* cf. *striata*
Sus brachygnathus	*Clarias batrachus*
RODENTIA	*Clarias leiacanthus*
Hystrix (=Acanthion) brachyuran	*Hemibagrus nemurus*
Rattus trinilensis	**CHONDRICHTHYES**
PRIMATES	*Glyphis gangeticus*
Macaca fascicularis	*Pristis* sp.
Trachypithecus cristatus	*Himantura* cf. *chaophraya*
Homo erectus	*Carcharius taurus*

The range of habitats indicated by the mammals from Trinil include grasslands, bushland, woodland, riverine forest, swamp and mangrove. Clearly there were forested areas since the cervids *Axis* and *Cervus*, the suid *Sus*, and *Rhinoceros* all today have a preference for forest habitats. The tiger *Panthera tigris* and the leopard cat *Prionailurus bengalensis*, are also both commonly associated with forest habitats today. Also present at Trinil were the crab-eating macaque *Macaca fascicularis* and the silvered leaf monkey *Trachypithecus* cf. *cristatus*, which are both indicative of forest habitats, especially *Trachypithecus* which is almost completely arboreal.

The mammalian fauna includes the otter *Lutrogale*, which points to freshwater wetlands, forested rivers, lakes or forested swamps.

The reptilian fauna includes two genera of crocodilian, *Crocodylus* and *Gavialis*, three turtle genera (*Hardella*, *Trionyx* and *Batagur*) as well as the monitor lizard *Varanus*, all of which have a close association with water, including swamps, lakes, rivers, mangroves, and in the case of *Crocodylus*, estuaries (Joordens et al. 2009).

The avian fauna from Trinil include four wetland genera, the storks, *Ephippiorhynchus* and *Leptoptilus*, geese *Branta* and shelducks *Tadorna.* The other avian representative is the green peafowl *Pavo muticus* which is found in grassland, scrubland and forests never far from water (Joordens et al. 2009).

A variety of fish species are known from Trinil including species able to survive in stagnant and poorly oxygenated waters by being able and to breathe air, such as the catfish *Clarias* and the snakehead *Channa*. These fish are also able to survive and move outside water, making them well suited to waterbodies that undergo periodic desiccation.

Another fish from Trinil with similar abilities is the climbing perch *Anabas microcephalus*, which is often associated with areas of dense vegetation.

The Trinil fauna includes evidence of a number of cartilaginous fish Chondrichthyes, some of which grow to quite large size. The Ganges shark *Glyphis gangeticus* lives in muddy, turbid rivers, lakes and estuaries and reaches two metres in length, while the sand tiger shark *Carcharius taurus* is found in shallow bays as well as deep (190m) waters along the continental shelf, but also inhabits estuaries and will enter river mouths. It can reach lengths of three metres. The giant freshwater stringray *Himantura* can grow up to five metres and inhabits the sandy bottoms of large rivers and estuaries, while the sawfish *Pristis*, which can grow up to six metres, today inhabits rivers, lakes, estuaries and shallow coastal waters (Joordens et al. 2009).

Figure 6.11.11: *Melanoides* from Trinil (scale 5mm)

The molluscs of Trinil include freshwater, estuarine and marine forms. The gastropods *Tarebia*, *Thiara* and *Melanoides* (Figure 6.11.11) are freshwater inhabitants, though each can also tolerate brackish to slightly brackish water. They are known from a range of habitats from lakes, rivers and shallow fast-flowing streams to ponds, swamps and estuaries. *Bellamya* is a tropical freshwater inhabitant which prefers the bottom of slow moving rivers, ponds and swamps. Interestingly, many opercula of the tropical genus *Pila* were found in the fossiliferous beds of West Turkana in which the *Homo ergaster* 'Turkana Boy' fossil (WT 15000), was found (Walker 1993), and opercula from this genus are also known from the Trinil beds (Figure 6.11.12). *Pila conica* is most commonly associated with the vegetation zone of stagnant water bodies such as ponds and swamps.

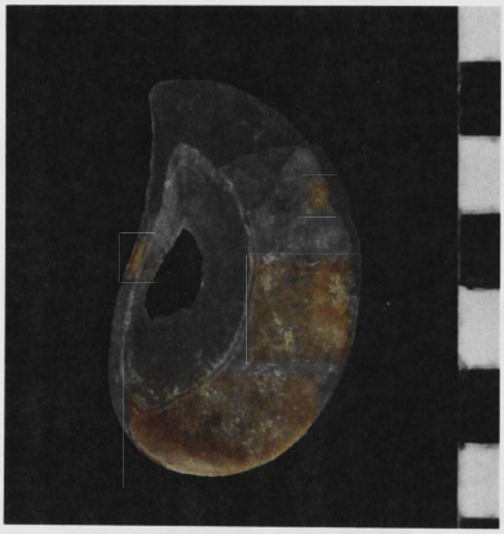


Figure 6.11.12: Operculum of the species *Pila conica* from Trinil (scale 5mm)

The pulmonate gastropods *Gyraulus*, *Lymnaea* and *Ameria* (Figure 6.11.13) are all indicative of dense vegetation in shallow lentic waters. None of these genera are usually associated with water bodies that regularly dry out, although because they are air breathers they are capable of tolerating various periods of dryness providing they have adequate cover in the form of vegetation.

Figure 6.11.13: *Ameria* specimens from Trinil (Scale 5mm)

The bivalve *Corbicula* is occasionally able to tolerate brackish water, but it is most commonly found in freshwater habitats that are well oxygenated such as streams, rivers and the shallow parts of lakes. *Elongaria orientalis* is found in lakes and rivers and like all unionids is parasitic on fish during the larval stage of its life cycle. The most common large bivalve in the Trinil assemblage is *Pseudodon vondembuschianus trinilensis*.

The *Pseudodon* bivalves from Trinil are all of a typically large size (c.100mm x 60mm, see Figure 6.11.14), with apparently no juveniles or sub-adult individuals included in the assemblage. This is significant since it suggests some type of selective agent for large size. The shell wall is very thick and the interior displays prominent adductor scars and a well defined pallial line, but no pallial sinus (Figure 6.11.14), indicating that this species was probably not a deep burrower, but instead resided close to the surface of the substrate on which it lived (Frank Wesselingh, pers. comm. May 2007). Damage to a number of shells appears to conform to a particular pattern, and there are markings on some shells which may be anthropogenic (Figure 9.8.1, Appendix 1).

Figure 6.11.14: *Pseudodon* from Trinil showing pallial line; note the lack of a pallial sinus (scale 10mm)

A number of marine gastropods have also been found at Trinil including *Cerithium*, *Quirella* and *Cingulina*. The crown conch *Melongena* today inhabits shallow marine environments such as estuaries, lagoons and mangroves. The morphology of the *Thiara* specimen, with a shell more sculptured than most specimens encountered in this analysis (Figure 6.11.15), is suggestive of marine rather than freshwater dwelling.

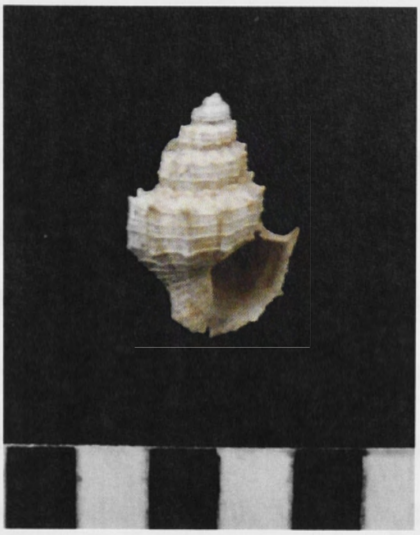


Figure 6.11.15: *Thiara* specimen from Trinil; note the elaborate sculpture (scale 5mm)

Marine bivalves have also been found at Trinil, including *Jupiteria*, *Gari* and *Theora*. All of these are inhabitants of soft marine sediments, usually from shallow intertidal environments. Together these bivalves are a strong indication that marine habitats, while not a predominant influence on the composition of the assemblage, were nevertheless close to the Trinil site (Joordens et al. 2009). Mangroves were also nearby judging by the presence of the bivalves *Geloina, Arcopagia* and *Anadara*, all of which are commonly associated with mangrove habitats.

The Trinil molluscan fauna also includes the genus *Dentalium*, a scaphopod or tusk shell. These marine molluscs inhabit the soft bottoms of offshore marine habitats and their presence at Trinil is another indication that the site could not have been too far from the ancient coast.

6.11.4 Conclusion

The molluscan fauna from Trinil is able to add significant detail to the palaeoecological picture of the site based on other data. A combination of freshwater and brackish to marine forms suggests a wetland habitat on a coastal plain, while mangrove species and freshwater swamp specialists point to a variety of vegetative zones within the vicinity. A large river meandering through a tropical coastal plain, with fast and slow flowing sections as well as swamps and sheltered ponds along the associated flood plains, with at least some forested habitats, would fit with the available molluscan data.

The hominins from Trinil had access to a mosaic of waterside habitats including river, swamp and coast, with mangrove and other forest habitats also present. The lack of arboreal adaptations and massive bones of *Homo erectus* make it unlikely that they regularly climbed.

6.12 Nihewan

6.12.1 Introduction

The Nihewan Basin contains a number of important sites in relation to hominin occupation of mainland Asia. The basin is situated in northern China about 100kms west of Beijing (Figure 6.12.1). The Majuangou sediments from the Nihewan Basin have provided some of the earliest evidence for occupation by hominins of northeast Asia.

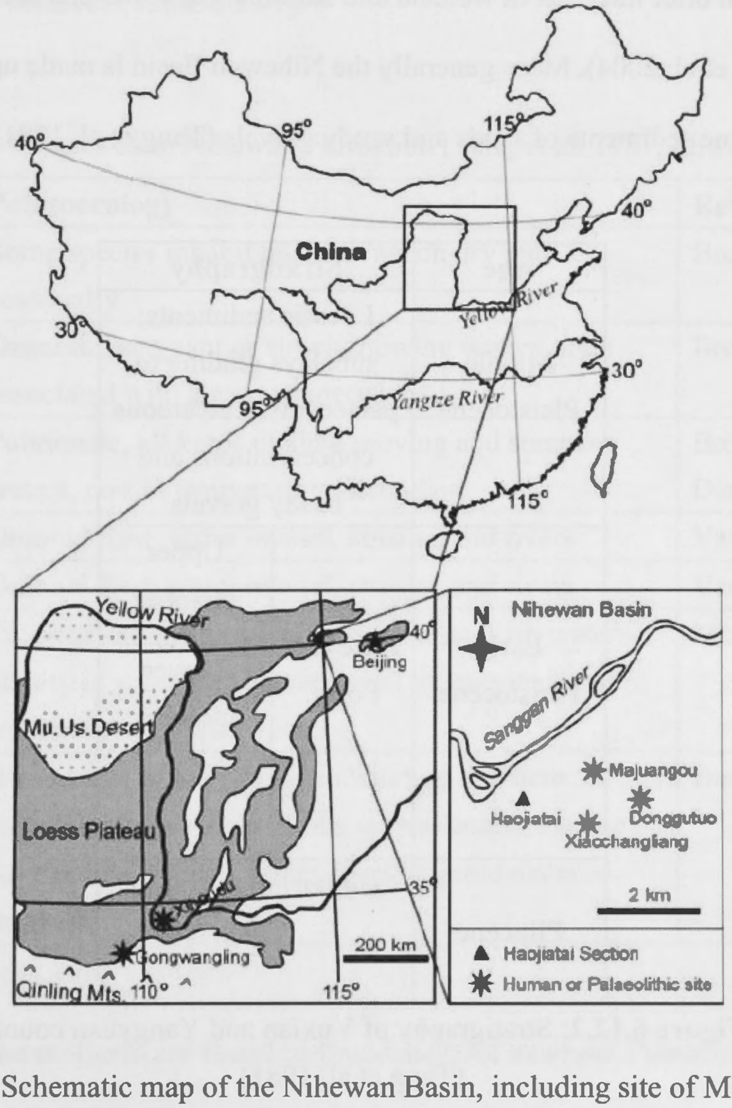


Figure 6.12.1: Schematic map of the Nihewan Basin, including site of Majuangou (Zhu et al. 2004)

The stratigraphy of the Nihewan Basin is complicated. Tang et al. (1981) divide the Nihewan Formation into two members and position it above the Pliocene '*Hipparion* red clays' and below the Loessic sediments of Middle Pleistocene age (Figure 6.12.2). The Majuangou section has four layers within the Nihewan Formation (from youngest to oldest; Bashan, MJG-I, MJG-II and MJG-III), dating from 1.32 to 1.66 Ma (Zhu et al. 2004). MJG III, the site at which the oldest artefacts dated to 1.66 Ma are known, is also referred to as Goudi (Gao et al. 2005). Majuangou is made up predominantly of lacustrine sediments with brief intervals of wetland and lake-margin sediments consisting of clays and silts (Zhu et al. 2004). More generally the Nihewan Basin is made up of massive fluvio-lacustrine sediments of sands and sandy gravels (Tang et al. 1981).

Age	**Stratigraphy**	
Middle Pleistocene	Loessic sediments: subclays grading to palaeosols. Calcareous concentrations and sandy gravels	
Early Pleistocene	Nihewan Form.	Upper member
		Lower member
Pliocene	"*Hipparion* red clays"	

Figure 6.12.2: Stratigraphy of Yuxian and Yangyuan counties (Tang et al. 1981)

No primates have been recorded from the Nihewan Formation, though artefacts have been found indicating that hominins were present. Each of the layers at Majuangou contains stone artefacts, while bones with tool percussion marks indicate that some animal exploitation occurred (Zhu et al. 2004).

6.12.2 Molluscs

A number of molluscs are known from the Nihewan Basin including pulmonate gastropods and bivalves (Table 6.12.1).

Table 6.12.1: Molluscs from Nihewan Formation (Tang et al. 1981, Zhu et al. 2004).

Taxon	**Palaeoecology**	**References**
Planorbis	Some species inhabit marshes which dry out seasonally	Brown 1980
Gyraulus	Generally stagnant or slowly flowing waters often associated with aquatic vegetation	Brown 1980
Lymnaea	Pulmonate, all kinds of slow moving and stagnant waters, rare in temporary waterbodies	Brown 1980, Van Damme 1984
Lamprotula	Unionid fresh water mussel, streams and rivers	Van Damme 1984
Cuneopsis	Unionid fresh water mussel, streams and rivers	Van Damme 1984
Corbicula	Tropical and sub-tropical fresh and brackish waters, variety of substrates, prefers well oxygenated waters and sandy substrates	McMahon 1983
Pisidium	Wide range of waterbodies including transient waterbodies and trophic lake stages, ponds, swampy woodlands, streams, rivers lakes, organic material substrate	Burky 1983

In some cases the molluscs are found in abundance; for example *Planorbis youngi* and *Gyraulus chihliensis* are numerous in the artefact bearing layer of MJG-III (Zhu et al.

2004). *Lamprotula, Cuneopsis, Corbicula, Pisidium* and *Limnea* (=*Lymnaea*?) are also known from the Nihewan Formation (Tang et al. 1981).

6.12.3 Palaeoecology

The vertebrate fauna from Nihewan include numerous mammals and a few fish (Table 6.12.2). The small mammals include taxa that are today adapted to relatively dry, open landscapes such as the pika *Ochotonoides* and the jerboa *Allactaga*. The artiodactyls *Equus*, *Gazella* and *Camelus* are all also indicative of open, relatively dry habitats, while *Coelodonta* was probably a steppe inhabitant. Cervids, on the other hand, point to more closed habitats and these are prominent within the assemblage of Nihewan, with as many as five species present. Other large mammals that are likely to have been associated with closed or well vegetated habitats are the suid *Sus*, and the rhinocerotid *Rhinoceros*. The Chalicotheriidae probably indicate forest, woodland, or open woodland habitats (Sarac & Sen 2005).

The presence of the otter *Lutra licenti* suggests a permanent water body. The fish species are also indicative of water with the stickleback *Pungitius* pointing to aquatic vegetation within a freshwater setting, and the Cyprinidae also suggesting freshwater with aquatic vegetation.

At Nihewan the remains of leaves and the fruits of aquatic plants such as the water chestnut *Trapa* indicate a low energy lake shore or marsh environment rich in organic materials (Zhu et al. 2004).

Table 6.12.2: Vertebrate fauna from Nihewan (Tang et al. 1981)

LAGOMORPHA	**PERISSODACTYLA**
Ochotonoides complicidens	*Hipparion* (*Proboscidipparion*) *sinense*
INSECTIVORA	*Equus sanmeniensis*
Erinaceus cf. *dealbatus*	*Rhinoceros* cf. *sinensis*
RODENTIA	*Coelodonta antiquitatis*
Allactaga cf. *annulatus*	*Elasmotherium* sp.
Myospalax tingi	*Cirotherium* sp.
Arvicolidae indet.	Chalicotheriidae indet.
CARNIVORA	**ARTIODACTYLA**
Canis (*Nyctereutes*) *sinensis*	*Sus* cf. *lydekkeri*
Canis chihliensis	*Camelus* (*Paracamelus*) *gigas*
Vulpes sp.	*Cervulus* cf. *sinensis*
Ursus cf. *etruscus*	*Cervus* (*Elaphurus*) *bifurcatus*
Mustela pachygnatha	*Cervus* (*Eucladoceros*) *boulie*
Meles cf. *leucurus*	*Cervus* (*Rusa*) *elegans*
Lutra licenti	*Cervus* (*Rusa*) sp.
Hyaena brevirostris	*Gazella* cf. *subgutturosa*
Hyaena sp.	Antilopinae indet.
Megantereon nihowanensis	*Spiroceros wongi*
Felis sp.	*Ovis shantungensis*
Felis (*Lynx*) sp.	Ovibovinae indet
Cynailurus cf. *pleistocaenicus*	*Bison palaeosinensis*
PROBOSCIDEA	**OSTEICHTHYES**
Palaeoloxodon namadicus	Cyprinidae
	Pungitius

The molluscan fauna includes gastropods that are usually associated with dense aquatic vegetation in relatively stagnant waters. These include *Planorbis youngi*, *Gyraulus chihliensis* and *Lymnaea*. The bivalves are consistent with a large body of perennial water which must have included well oxygenated habitats. The unionid bivalves *Lamprotula* and *Cuneopsis* indicate that there must have been fish to act as hosts for the parasitic larvae, and suitable areas to allow for dispersal; probably large slow moving rivers or a lake and associated distributaries with sandy or muddy substrates. The pisidiid clam *Pisidium* is often abundant in trophic habitats and is associated with shallow, well oxygenated habitats.

6.12.4 Conclusion

The molluscan assemblage of the Nihewan Basin confirm the presence of a large body of permanent water, either a river or lake, with lotic and lentic habitats and with areas of relatively dense aquatic vegetation. The molluscs include unionid bivalves which suggest a large, relatively stable freshwater drainage system. Sub-tropical habitats are suggested by the presence of *Corbicula*, though many of the other molluscs are capable of surviving in more temperate climates.

No fossil hominins from Nihewan have been discovered, so the anatomy is unknown. More open habitats suggest that tree dwelling may not have been a regular behavioural trait, though some tree cover does seem to have been present. Waterside habitats including areas with abundant aquatic vegetation, as well as open steppe habitats were available for hunting, scavenging and foraging.

6.13 Conclusion

Chapter 6 examined the molluscs from Plio-Pleistocene sites. The range of sites in this chapter differed to those in Chapter 5 primarily because they included sites from outside Africa, and they also included sites representing the genus *Homo*. The aim of the chapter was to examine the molluscs to see whether they provided any information which could add detail to the palaeoecological picture of the sites in question, and in every case they did. In most sites other fauna apart from the molluscs was available to help draw conclusions, but at Erk-el-Ahmar there was no other faunal data, meaning the molluscs provided most of what was known about the palaeoecology.

The composition of the molluscan assemblages in Chapter 6 differed to that of the assemblages in Chapter 5 in that *Corbicula* and veneroid bivalves in general were more common, while iridinid bivalves were less well represented. These differences can be accredited to the fact that Chapter 6 included sites from outside Africa, and also because the African sites in Chapter 6 were more recent than the sites in Chapter 5. The family Iridinidae is an African endemic, and therefore not expected to occur in Eurasia, while *Corbicula* has an Asian origin, and only dispersed to Africa relatively recently in the mid Pliocene (Van Damme 1984). The sites from Chapter 6 also included assemblages that contained marine molluscs, which were unknown in Chapter 5, including the only non-gastropod or non-bivalve mollusc from Trinil, a species of Scaphopoda.

In Chapter 7 the molluscs from palaeoanthropological sites from the middle Pleistocene of Africa, Europe and Asia will be examined and this will conclude the individual site analysis section of the study.

7 Middle Pleistocene molluscs and palaeoecology

In the previous chapter molluscs from sites of Plio-Pleistocene age were examined. These included sites from Africa, the Middle East, the "gates of Europe" in Georgia (Dean & Delson 1995), Pakistan, Java and China. The sites included many of the first appearances of *Homo* within a particular region, and many of these were c. 2.0 to 1.6 Ma.

In this chapter molluscs from sites that are younger than those in the previous chapter are analysed. These represent the continued presence of *Homo* in Africa, Asia and Europe from c. 1.0 Ma to 0.6 Ma. The exception is the site of Omo Kibish, which, at c. 0.19 Ma, is the youngest site in the study, but which is significant from a palaeoanthropological point of view because it represents the earliest fossil occurrence of *Homo sapiens*. While some of the sites in this chapter contain artefacts only, others feature fossil remains of hominin species from the genus *Homo*.

The aim of this chapter and the treatment of the sites are similar to those of the previous two chapters, with an introduction in each section focusing on stratigraphical and taphonomical aspects of the site, the presence of primates and artefacts, and then details of the molluscs and an overview of the palaeoecology based on other data such as other faunal evidence. Each section concludes with a summary of what molluscs reveal about the palaeoecology of each site from a palaeoanthropological context.

7.1 Daka

7.1.1 Introduction

Although, from the early Pleistocene, hominins are found outside Africa, there are also a number of sites from Africa that continue to show evidence of the presence of hominins throughout the Pleistocene. One such site is that of the Dakanihylo ('Daka') Member of the Bouri Formation from the Afar Rift of Ethiopia (Figure 7.1.1).

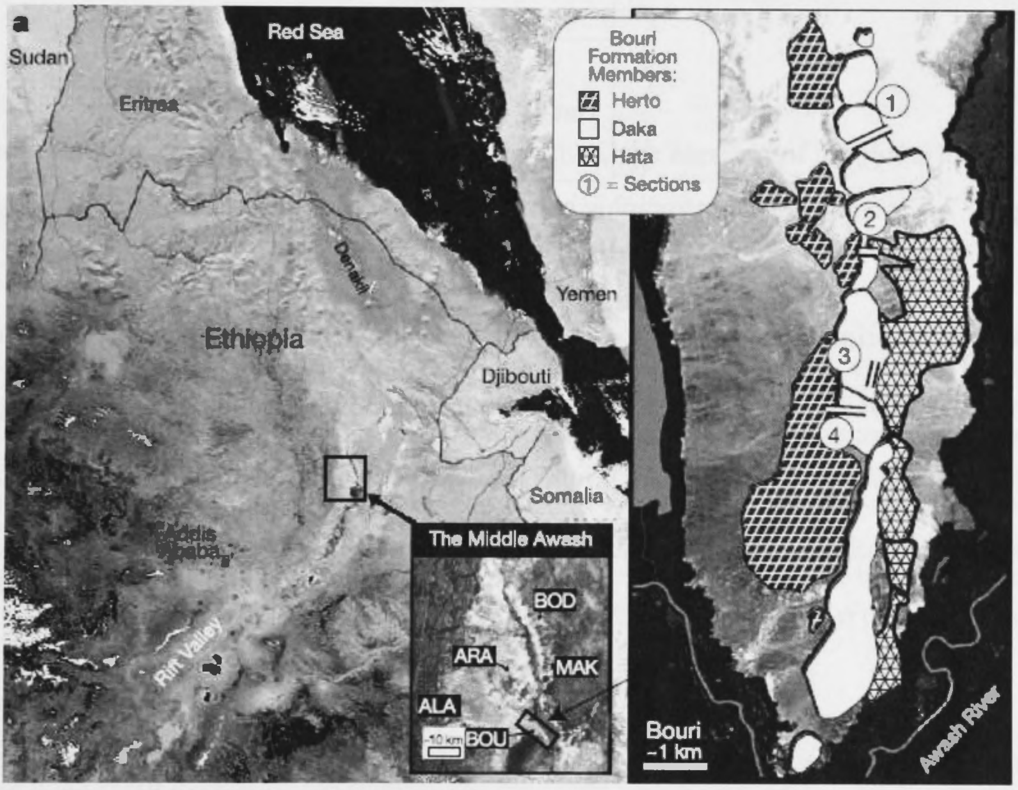


Figure 7.1.1: Map showing location of The Middle Awash, Ethiopia, and exposures of the Bouri Formation (Asfaw et al. 2002)

The Daka Member of the Bouri Formation lies stratigraphically above the Pliocene Hatayae ('Hata') Member, and below the Herto Member (Figure 7.1.2). It is dated to c.

1.0 Ma (Asfaw et al. 2002). The Daka Member is made up primarily of alluvial deposits associated with lakeside beaches or shallow water deposits in distributary channels (Asfaw et al. 2002).

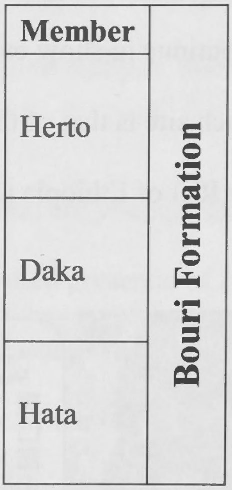


Figure 7.1.2: Simplified stratigraphic column showing Members of the Bouri Formation

A number of primate species are known from the Daka Member and these include a fossil calvarium (BOU-VP-2/66), three femora and a proximal tibia which have been assigned to the species *Homo erectus*. In addition, two cercopithecids are known from the Daka Member: a colobine *Cercopithecoides alemayehuii*, and a cercopithecine *Theropithecus oswaldi leakeyi* (Gilbert & Asfaw 2008).

Early Acheulean stone tools are abundant in the deposits and there is evidence that equid, bovid and hippopotamid bones were subject to modification (Asfaw et al. 2002).

7.1.2 Molluscs

Gastropods and bivalves have both been discovered within the Daka Member (WoldeGabriel et al. 2008, Table 7.1.1), but no identification beyond class have been made and no samples are known to have been collected and available for study.

Table 7.1.1: Molluscs from Daka

Taxon	**Palaeoecology**
Gastropoda	Wide range of habitats from marine, freshwater to terrestrial
Bivalvia	Aquatic, including marine and freshwater

7.1.3 Palaeoecology

Numerous vertebrate fauna have been found in the Daka Member of the Bouri Formation (Table 7.1.2).

Alcelaphine bovids are both diverse and abundant at Daka compared to a number of older African sites, indicating that open grassland habitats had become prominent (Asfaw et al. 2002). The presence of *Connochaetes*, *Damaliscus* and *Parmularius*, for example, all point to open habitats with enough moist grass to support these grazing bovids. Drier landscapes are also possible since *Gazella* and *Oryx* are both present.

More wooded or even forested regions are indicated by the presence of three species of *Tragelaphus*, which require suitable cover and are usually associated with dense vegetation. The two cercopithecids are also likely to have preferred wooded habitats, with *Cercopithecoides* probably spending more time in the trees than *Theropithecus*.

Table 7.1.2: Vertebrate fossils from the Daka Member (Gilbert & Asfaw 2008, Asfaw et al. 2002)

PRIMATES	*Connochaetes* cf. *taurinus*
Cercopithecoides alemayehuii	*Damaliscus* sp.
Theropithecus oswaldi leakeyi	*Megalotragus kattwinkeli*
Homo cf. *erectus*	*Nitidarcus asfawi*
RODENTIA	*Numidocapra crassicornis*
Arvicanthis	*Parmularius angusticornis*
CARNIVORA	*Gazella* sp.
Crocuta crocuta yangula	cf. *Antidorcas* sp.
Panthera cf. *leo*	*Pelorovis antiquus*
Panthera cf. *pardus*	*Pelorovis oldowayensis*
PROBOSCIDEA	*Syncerus* sp.
Elephas recki recki	*Bouria anngettyae*
PERISSODACTYLA	*Hippotragus* cf. *gigas*
Equus sp.	*Oryx gazella*
Eurygnathohippus cf. *cornelianus*	*Kobus* aff. *ancestrocera*
Ceratotherium simum	*Kobus* cf. *ellipsiprymnus*
Diceros sp.	*Kobus* cf. *kob*
ARTIODACTYLA	*Tragelaphus* cf. *imberbis*
Kolpochoerus majus	*Tragelaphus* cf. *scriptus*
Kolpochoerus olduvaiensis	*Tragelaphus* cf. *strepsiceros*
Metridiochoerus compactus	**OSTEICHTHYES**
Metridiochoerus cf. *hopwoodi*	Siluriformes
Metridiochoerus modestus	**AVES**
Phacochoerus sp.	aff. Ciconiiformes
Hippopotamus cf. *gorgops*	**REPTILIA**
Giraffa sp.	Chelonia
Sivatherium sp.	Crocodylia
Aepyceros cf. *melampus*	

The fact that the hippopotamid *Hippopotamus* is found at Daka means that a large body of permanent water must have been present, and this is indicated also by the presence of three *Kobus* species, which are today generally closely associated with permanent water.

The only small mammal reported from the Daka Member is the rodent *Arvicanthis*, which is common in grasslands and savannas. Asfaw et al. (2002) reported the presence of a *Thryonomys*-like genus at Daka but no mention of this was made in the report of Gilbert & Asfaw (2008).

The fauna from Daka is limited mainly to mammals. This is at least partly due to the fact that other vertebrates were not systematically collected. Crocodilian fossils, for example, were not collected (Gilbert & Asfaw 2008), and presumably neither were those of Chelonia. It is known that these were present because Asfaw et al. (2002) include them in the site's faunal report. The order Chelonia includes turtles and tortoises and from a palaeoecological perspective is not very informative. The fact that crocodilians were present, however, indicates that the environment contained sufficient permanent water.

Fish fossils also were generally not collected (Gilbert & Asfaw 2008), except for a complete cranium of a member of the Siluriformes, recovered because of its excellent preservation. The presence of the catfish order certainly indicates water was present, and probably shallow freshwater habitats, but without more detailed identification more specific interpretations are difficult.

Whether Aves fossils were systematically collected is unclear, but only one specimen has been described. This belongs to a bird possibly from the order Ciconiiformes, which contains large wading birds such as herons, egrets and storks (Gilbert & Stidham 2008). The presence of such a bird at Daka indicates that there were shallow wetlands at Daka.

Other palaeoecological data from the Daka Member include the taphonomic processes that have affected some of the fossil remains. The *Homo* calvarium BOU-VP-2/66, for example, is penetrated in many places by fossilised root casts that probably belong to the papyrus plant *Cyperus papyrus* (Asfaw et al. 2008). This tropical and subtropical sedge forms stands in swamps and shallow lakes and along the banks of streams.

The Daka Member contains both gastropods and bivalves (WoldeGabriel et al. 2008). The section from which the *Homo* calvarium was recovered, for example, consisted of ‘bivalve rich basal shelly sandstone’ (WoldeGabriel et al. 2008: 25). No mention of the molluscs is made in the faunal or palaeoecological sections of Gilbert & Asfaw (2008), however, and no identifications or descriptions of the gastropods or bivalves appear in the literature.

7.1.4 Conclusion

Because the molluscs at Daka have not been identified other than as gastropods and bivalves, it is difficult to draw firm palaeoecological conclusions based on the molluscs. It can be said that because bivalves were present there must have been water present, but the size of the water body, its connection to other hydrographic systems, whether it flowed slowly, swiftly or not at all, various depths, substrate and presence or not of aquatic or other vegetation, is difficult to ascertain.

The gastropods similarly are difficult to interpret due to lack of identification, though we can guess that at least some of the gastropods were associated with a lake since “the occurrence of thick silty clays capped by mixed bivalve- and gastropod-rich layers suggests that the dynamics of the depositional environment changed from fluvial to lacustrine” (WoldeGabriel et al. 2008: 22).

More detailed studies of the molluscs from the Daka Member would no doubt provide further palaeoecological information.

7.2 Olorgesailie

7.2.1 Age and stratigraphy

The Olorgesailie Formation from southern Kenya (Figure 7.2.1) is similar in age range to the Daka Member of the Bouri Formation.

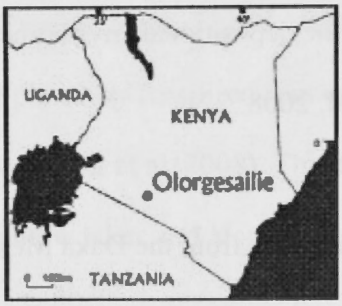


Figure 7.2.1: Map of Kenya showing location of the Olorgesailie site (Potts et al. 1999)

The Formation consists of 14 members which progress from bottom (1) to top (14). Most archaeological remains have been found in Members 1, 7, 10 and 11 (Deino & Potts 1990). The lower portion of the formation (Members 1-10) contains archaeological occurrences and a hominin fossil was found near the boundary of Members 5 and 6/7 (Potts et al. 2004) (Figure 7.2.2). Single-crystal ^{40}Ar/^{39}Ar dating from the lower part of Member 5 yielded an age of c. 0.974 Ma, whereas the top of Member 8 was dated to c. 0.747 Ma (Deino & Potts 1990). Based on sedimentary evidence and estimations of accumulation rates, Potts et al. (2004) consider the hominin fossil to have an age between c. 0.970 and c. 0.900 Ma.

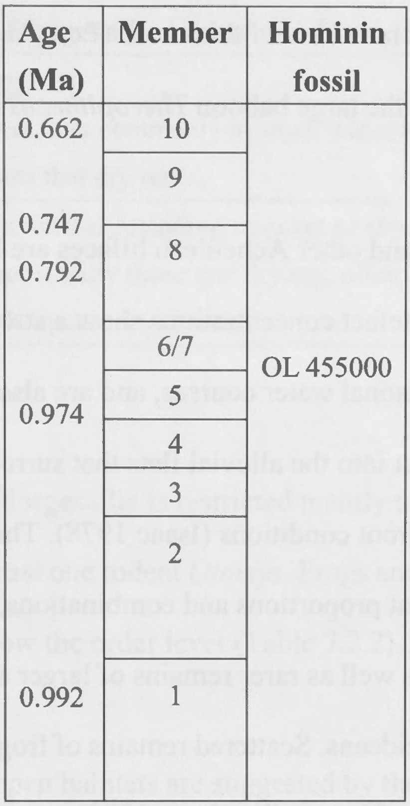


Figure 7.2.2: Simplified stratigraphic column of the lower portion of the Olorgesailie Formation (after Potts et al. 2004)

The Olorgesailie Basin was fed by rivers that had flowed appreciable distances over low gradients, to judge by the sedimentary evidence, which shows that coarser material had already been dumped by the time it reached the basin, leaving only silt, clay and biogenic sediments to be deposited. Occasional influxes of sands and fine gravels from volcanic activity also occurred. According to the sedimentary sequences the basin contained a lake fluctuating between deep and shallow, with flood plains and associated stream channels (Isaac 1978).

Primate fauna from Olorgesailie include the above-mentioned hominin and a cercopithecid. A partial cranium discovered in 2003 (KNM-OL 45500) was assigned to *Homo erectus*, although it has a number of characteristics, including relatively small size, distinguishing it from other members of this taxon (Potts et al. 2004). The other primate known from Olorgesailie is the large baboon *Theropithecus oswaldi mariae* (Isaac 1978).

Numerous stone handaxes and other Acheulean bifaces are known from throughout the Olorgesailie Formation. Artefact concentrations show a strong tendency to be located along the sandy beds of seasonal water courses, and are also known to occur on or near rocky ledges that project out into the alluvial flats that surrounded the lake, or on flood plains or in beach or delta front conditions (Isaac 1978). The species associated with artefacts include, in different proportions and combinations, mainly medium sized bovids, equids and suids, as well as rarer remains of larger animals such as giraffids, hippopotamids and proboscideans. Scattered remains of frog, catfish and rodents occur at almost all fossil locations at Olorgesailie (Isaac 1978).

7.2.2 Molluscs

Two gastropod genera have been found within the Olorgesailie Formation (Table 7.2.1), but these have not been studied in any great detail. Isaac (1978) reports the presence of *Bithynia neumanni*, but concedes this may be *Gabbia subbadiella.* Brown (1980) refers to *Gabbia* as *Gabbiella.* Isaac also records *Biomphalaria* as being present within the Olorgesailie Formation, although Van Damme (personal communication) points out that this genus otherwise first appears in the fossil record as recently as 0.25 Ma.

Table 7.2.1: Molluscs from Olorgesailie Formation (Isaac 1978)

Taxon	Palaeoecology	References
Bithynia	Lakes and rivers, less commonly in small water bodies, rarely in habitats that dry out	Brown 1980
Biomphalaria	Variety of waterbodies including stagnant or slow flowing, but not usually those that dry out, often associated with aquatic vegetation	Van Damme 1984

7.2.3 Palaeoecology

The vertebrate fauna from Olorgesailie is restricted mainly to large mammals, although there is also evidence of at least one rodent *Otomys*. Frogs and catfish are also known, but have not been identified below the order level (Table 7.2.2).

In terms of palaeoecology, open habitats are suggested by the presence of the giant baboon *Theropithecus oswaldi* and two equid species, while grasslands are indicated by the presence of the grazing bovids *Connochaetes* and *Aepyceros* and the grazing rhinocerotid *Ceratotherium simum*.

Dense vegetation also appears to have been locally available since *Tragelaphus* is present, and wooded habitats are indicated by the presence of *Taurotragus* and two *Giraffa* species.

A large permanent water body must have been present since *Hippopotamus gorgops* formed part of the local fauna, and *Kobus* indicates permanent water. The rodent *Otomys* today inhabits the grasses that grow next to swamps, lakes and rivers.

Table 7.2.2: Vertebrate fauna from Olorgesailie Formation (Isaac 1978, Potts et al. 2004, Geraads et al. 2004).

PERISSODACTYLA	*Redunca* sp.
Ceratotherium simum	*Connochaetes* sp.
Hipparion albertense	*Megalotragus* cf. *kattwinkeli*
Equus aff. *grevyi*	*Aepyceros* sp.
Equus oldowayensis	*Antidorcas*?
ARTIODACTYLA	**PRIMATES**
Hippopotamus gorgops	*Theropithecus oswaldi*
Metridiochoerus hopwoodi	*Homo* cf. *erectus*
Metridiochoerus compactus	**PROBOSCIDEA**
Kolpochoerus majus	*Elephas recki recki*
Giraffa cf. *camelopardalis*	**RODENTIA**
Giraffa gracilis ?	*Otomys* sp.
Tragelaphus sp.	**AMPHIBIA**
Taurotragus sp.	Anura
Pelorovis antiquus ?	**OSTEICHTHYES**
Kobus sp.	Siluriformes

Amphibian bones have been found throughout the formation, including from the sandy silt adhered to the frontal bone of the *Homo* fossil OL-45500 (Potts et al. 2004), which suggests the hominin may have came to rest in swampy habitats.

Catfish were also present throughout the beds of the Formation (Isaac 1978), indicating relatively shallow, possibly poorly oxygenated waters.

According to Isaac (1978) there are no indications that Lake Olorgesailie was ever strongly saline or highly alkaline, and since this suggests the continued existence of freshwater in the basin throughout deposition, there must have been some outlet, either a perennial or intermittent surface overflow or else a subterranean leak. The diatomaceous silts point to shallow lake or swamp conditions with abundant reed beds and emergent vegetation (Isaac 1978).

Sikes et al. (1999), studying palaeosol stable isotopes, found evidence for grasslands and wooded grasslands, which is in agreement with previous studies that found evidence for reeds growing along the shores of the lake.

Although molluscan remains from Olorgesailie are rare (Isaac 1977), they do reveal important information regarding the palaeoecology. The family Bithyniidae, represented at Olorgesailie either by *Bithynia* or *Gabbiella*, includes rather cosmopolitan species which inhabit a variety of freshwater habitats, though not usually those that dry out. Some *Gabbiella* species are found in association with *Vallisneria* plants growing in shallow waters (Brown 1980). *Biomphalaria* is a freshwater inhabitant of generally slow flowing or stagnant waters, and it too is rarely associated with waters that regularly become dry. The family Planorbinae, to which *Biomphalaria* belongs, includes numerous species which are often associated with dense aquatic vegetation growing in relatively shallow, lentic waters.

7.2.4 Conclusion

The molluscan fauna confirm a number of aspects of the palaeoecology that other data point to, such as a permanent body of freshwater and the presence of some type of aquatic vegetation. Given the uncertainty of the identification of *Biomphalaria* it is difficult to be too specific about the possible implications of its presence at Olorgesailie, but the data overall point to relatively open habitats, possibly seasonally dry, with areas of denser vegetation and some cover associated with the permanent drainage system.

The small size of the *Homo* species from Olorgesaillie (Potts et al. 2004), suggests it may have retained some arboreal capabilities, but without postcranial remains it is difficult to be certain.

7.3 Buia

7.3.1 Introduction

Another site similar in age to those of Daka and Olorgesailie is Buia, Eritrea (Figure 7.3.1).

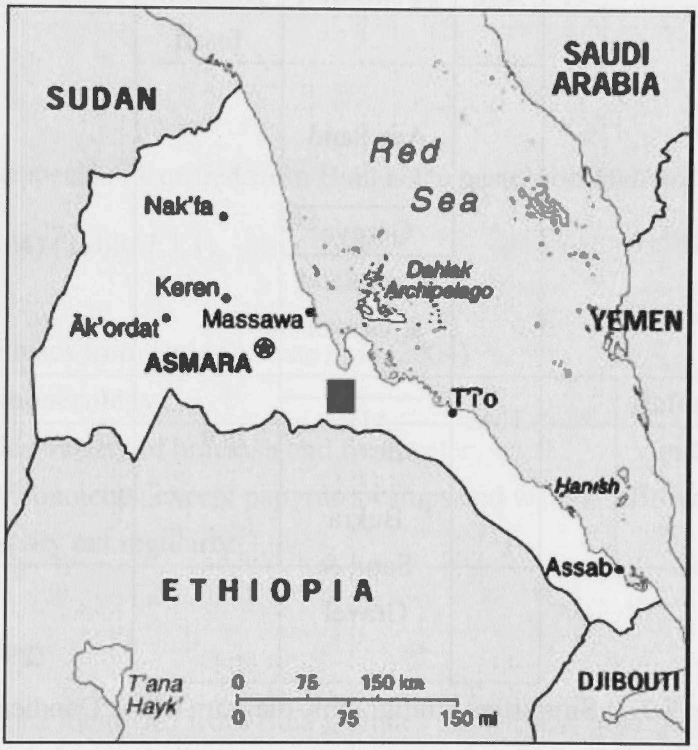


Figure 7.3.1: Map of Eritrea with Buia study area shown as shaded square (Albianelli & Napoleone 2004)

The site of Buia comes from the Alat Formation, part of the Dandiero Group of the Danakil Depression (Figure 7.3.2). The Alat Formation is dated to c. 1.0 Ma. In the Buia-Dandiero region the Dandiero Group ranges in age from the Early to Middle Pleistocene and is made up of six formations, from oldest to youngest: the fluvial Bukra

Sand and Gravel, the deltaic and lacustrine Alat Formation, the fluvial Wara Sand and Gravel, the lacustrine Goreya Formation and the fluvial-deltaic Aro Sand Formation. This succession lies unconformably over Neoproterozoic basement and is overlain by the Addai Fanglomerate. The sequence above the Neoproterozoic basement is known as the Maebele Synthem, and is overlain by the Boulder beds (Abbate et al. 2004).

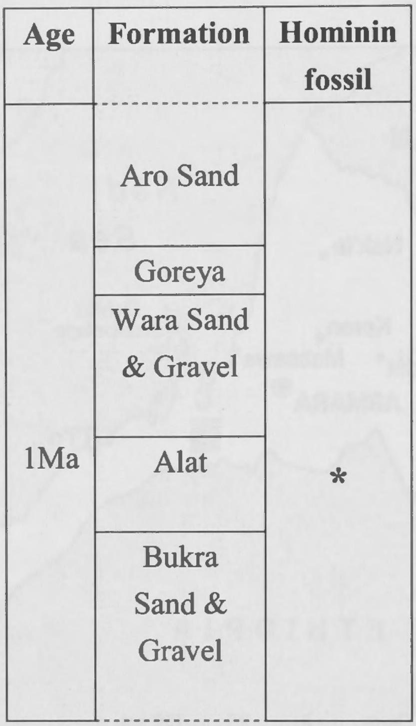


Figure 7.3.2: Simplified stratigraphic diagram of the Dandiero Group

Sediments of the Alat Formation consist primarily of lacustrine silts, sands and clays deposited in association with a deltaic system (Abbate et al. 2004).

The primate fauna from Buia includes a hominin and a cercopithecid. A cranium (UA-31), two teeth and three pelvic fragments from the Uadi Aalad site in the Alat Formation have been described as *Homo* '*erectus* like', while the only other primate recorded is *Theropithecus* cf. *oswaldi* (Martinez-Navarro et al. 2004).

More than 200 sites containing lithic artefacts have been discovered at Buia. The tools belong to the Acheulean tradition and the assemblages are characterised by differing frequencies of choppers, hand axes, cleavers and flakes (Martini et al. 2004). Traces of butchering have also been discovered on a number of specimens including most frequently the bones of *Hippopotamus gorgops*, as well as bovids (including *Kobus* cf. *ellipsiprymnus*) and the distal femur of a crocodilian (Fiore et al. 2004).

7.3.2 Molluscs

The only mollusc species identified from Buia is the gastropod *Melanoides tuberculata* (Abbate et al. 2004) (Table 7.3.1).

Table 7.3.1: Molluscs from Buia (Abbate et al. 2004)

Taxon	**Palaeoecology**	**References**
Melanoides	Wide variety of brackish and freshwater environments, except papyrus swamps and waters that dry out regularly	Van Damme 1984, Brown 1980

7.3.3 Palaeoecology

The vertebrate fauna identified from Buia includes the remains of large mammals and reptiles (Table 7.3.2). Fish are also known from Buia (Abbate et al. 2004) but these have not been identified.

The most abundant large mammal remains from Buia are the hippopotamid *Hippopotamus gorgops*, and the waterbuck-like bovid *Kobus*. These animals are both water-dependent, and along with the suid *Kolpochoerus* and the sitatunga-like *Tragelaphus*, they point to a large body of permanent water within the vicinity.

The fact that three suids are present suggests some areas of dense vegetation, and the extinct buffalo-like *Pelorovis* probably also preferred areas with some cover. *Tragelaphus* is today often associated with closed or well vegetated habitats (and *Tragelaphus spekii*, the sitatunga, to which the Buia fossil is affiliated, swamps, into which it can submerge) and *Hexaprotodon* prefers well forested regions associated with water.

Wooded habitats are indicated by the giraffid *Giraffa*. *Theropithecus* and *Hippopotamus* point to the local availability of open habitats and *Gazella* indicates that open, possibly arid, habitats may have been present. The rhinocerotid *Ceratotherium* is a grazer and its presence points to open grasslands.

Table 7.3.2: Vertebrate fauna from Buia (Martinez-Navarro et al. 2004, Abbate et al. 2004)

PRIMATES	*Metridiochoerus* aff. *modestus*
Homo '*erectus*-like'	*Giraffa* cf. *jumae*
Theropithecus cf. *oswaldi*	*Tragelaphus* cf. *spekii*
CARNIVORA	*Pelorovis oldowayensis*
Crocuta cf. *crocuta*	*Kobus* cf. *ellipsiprymnus*
PROBOSCIDEA	*Hippotragus gigas*
Elephas recki	*Gazella* sp.
PERISSODACTYLA	Caprini indet.
Ceratotherium cf. *simum*	**REPTILIA**
Equus cf. *grevyi*	*Crocodylus niloticus*
ARTIODACTYLA	*Pelusios* cf. *sinuatus*
Hippopotamus gorgops	*Varanus niloticus*
Hexaprotodon sp.	*Python* ex gr. *Sebae*
Kolpochoerus olduvaiensis	**OSTEICHTHYES**
Kolpochoerus majus	Gen. & sp. indet.

The reptilian fauna includes the Nile crocodile *Crocodylus niloticus*, which today is found in lakes, rivers, marshes, coastal lagoons and estuaries, the mud turtle *Pelusios*, which prefers shallow, slow moving bodies of water with muddy bottoms, the Nile monitor *Varanus niloticus*, which is usually closely associated with water, and the water python *Python*, which is most abundant near low altitude rivers, lakes and swamps (Delfino et al. 2004). The fish at Buia are described as being freshwater varieties, but no identifications have been made.

An ostracod *Cypria* is also known from the Alat Formation (Abbate et al. 2004). This is a freshwater genus.

7.3.4 Conclusion

The only mollusc species known from Buia is *Melanoides tuberculata*, which has been found in abundance in some beds. This freshwater gastropod can tolerate a wide range of habitats including moderate levels of salinity, and is usually associated with permanent water. It is often the last mollusc species to survive in freshwater bodies that become increasingly saline. The shell floats when the animal has died, which is one reason why *Melanoides* specimens are often found in large numbers within the sediments left by ancient water bodies. Perhaps this could explain their abundance in some beds at Buia. Lacustrine conditions are likely given the depositional environment of these gastropods.

The hominin from Buia would have had a mosaic of habitats, including open grasslands, and waterside landscapes sometimes thick with vegetation in which to forage and seek shelter. Not enough of the postcranial bones of the Buia hominin have been discovered to know for certain what its anatomy was like.

7.4 Soa Basin

7.4.1 Introduction

Slightly younger than the African sites of Daka, Buia and Olorgesailie, the site of Mata Menge from the Soa Basin in Flores represents the earliest occurrence of hominins east of Wallace's Line (Figure 7.4.1).

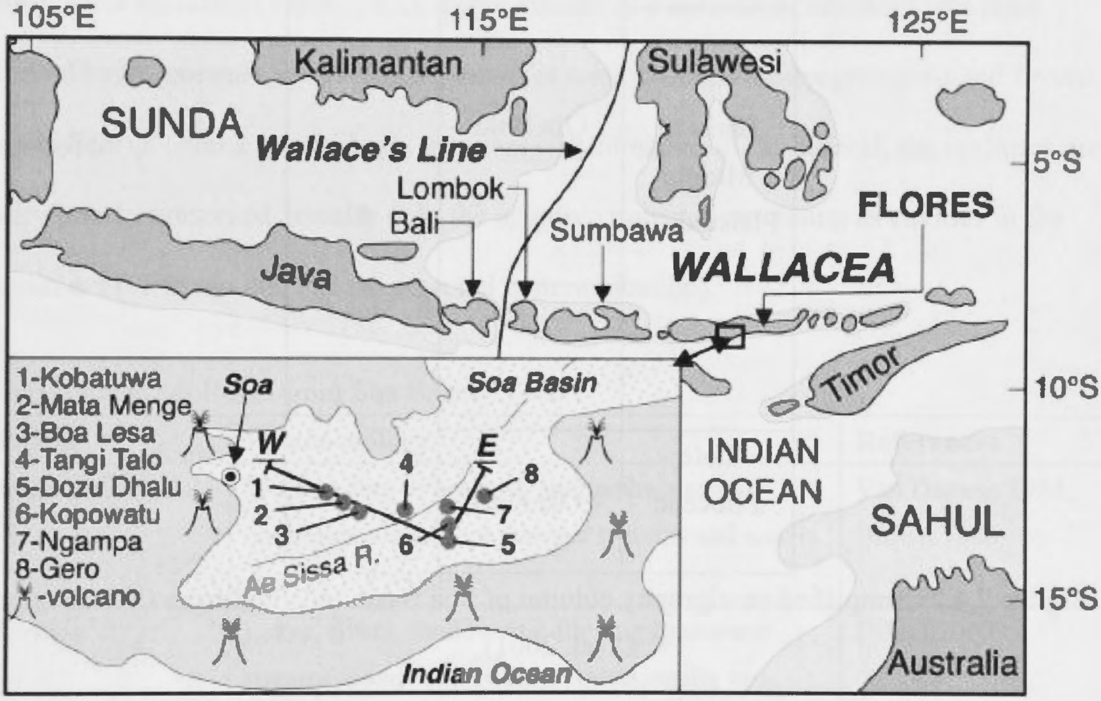


Figure 7.4.1: Map showing island of Flores and key sites, including Mata Menge, within the Soa Basin (O'Sullivan et al. 2001)

Mata Menge is part of the Ola Bula Formation and has been dated to between 800 and 880 ka using fission track dating methods (Morwood et al. 1998). The Ola Bula Formation is a 120m thick series of tuffaceous sandstones and siltstones which overlies the Ola Kile Formation (Morwood et al. 1999, Figure 7.4.2).

Epoch	Formation	Artefacts
Holocene	Recent volcanics	
Late Pleistocene	Ola Bula	
Early to Middle Pleistocene		*
Late Pliocene	Ola Kile	

Figure 7.4.2: Simplified stratigraphy column of Soa Basin (adapted from O'Sullivan et al. 2001)

No primate remains have been found in the Soa Basin deposits of Flores, though the presence of stone tools within the Ola Bula Formation at Mata Menge is evidence that hominins had reached the island by at least 800 ka (Morwood et al. 1998). In fact recent discoveries of stone tools at the Wolo Sege site near Mata Menge in the Soa Basin extend that date back to about 1.0 Ma (Brumm et al. 2010)

The stone artefacts are simple, based on the removal of small to medium sized flakes from cobbles and flake blanks. They are similar to the tools found in association with *Homo floresiensis* from terminal Pleistocene deposits at Liang Bua cave, 50km west of the Soa Basin (Brumm et al. 2006).

7.4.2 Molluscs

The site of Mata Menge, from which stone tools have been recovered, has also yielded freshwater molluscs (Table 7.4.1). These consist of a number of cerithoideans from fluvial conglomerates, including *Melanoides tuberculata*, *Tarebia granifera* and *Brotia* '*testudinaria*' (Frank Wesselingh, personal communication). In general, the molluscs are very poorly preserved, usually only the negative imprints remaining as cavities in the sediment (Gert van den Bergh, personal communication).

Table 7.4.1: Molluscs from Soa Basin

Taxon	**Palaeoecology**	**References**
Melanoides	Wide variety of brackish and freshwater environments, except papyrus swamps and waters that dry out regularly	Van Damme 1984, Brown 1980
Tarebia	Lakes, rivers, shallow fast-flowing freshwater streams, ponds and swamps, occasionally in slightly brackish water	Dillon 2000
Brotia	(*testudinaria*) Eurytopic: in running as well as stagnant freshwater, between sea level and 1500m	Dillon 2000
Basommatophora	Freshwater air breathing gastropods	

7.4.3 Palaeoecology

Of all sites examined in this thesis, the fauna from Soa Basin is the most limited in terms of vertebrate diversity. The fauna, if *Homo* is excluded, includes only two mammals: A large *Stegodon* and a giant rat *Hooijeromys nusatenggara.* A crocodilian is also present and bird remains have also been recovered but not identified. Each of these species is either a strong swimmer (*Stegodon*, crocodilian) or is known to be capable of colonising islands by floating on debris (rat), or by flying and/or swimming (bird). The impoverished nature of the fauna reflects the fact that Flores was an island throughout the time that the Soa Basin deposits were forming. Also discovered at Mata Menge were small fish, freshwater diatoms and ostracods, algae, plants and aquatic vegetation (Morwood et al. 1998, O'Sullivan et al. 2001, Brumm et al. 2006).

Table 7.4.2: Vertebrate fauna from Mata Menge, Soa Basin (Brumm et al. 2006)

PROBOSCIDEA
Stegodon florensis
PRIMATES
Homo (inferred from artefacts)
RODENTIA
Hooijeromys nusatenggara
REPTILIA
Crocodylia
AVES
OSTEICHTHYES

Sedimentological evidence combined with the faunal data suggests that the Soa Basin contained a large lake or series of lakes for long periods during the early Pleistocene, though periodically a river outlet formed to drain the basin, resulting in savanna grasslands with a dissecting fluvial system (Morwood et al. 1998, Brumm et al. 2006). The occasional occurrence of foraminifera in the basin indicates periodic small scale marine transgressions (O'Sullivan 2001).

Molluscs from Mata Menge were collected by Gert van den Berge and examined by Frank Wesselingh, who identified the freshwater gastropods as *Brotia testudinaria*, *Tarebia granifera* and *Melanoides tuberculata*.

These molluscs are all eurytopic freshwater dwellers with *Brotia* inhabiting lotic as well as more stagnant waterbodies and *Tarebia* associated with lakes, rivers, ponds, swamps and fast-flowing shallow freshwater streams. *Tarebia* can tolerate slightly brackish waters. *Melanoides tuberculata* occurs in a range of freshwater habitats but is not generally associated with temporary waterbodies. It can tolerate moderate levels of salinity.

7.4.4 Conclusion

The mollusc species from Mata Menge confirm the view based on other data that the basin contained a freshwater hydrological system that fluctuated between fluvial and lacustrine conditions. The system must have been long enough lived for each of these taxa to become established.

Since fossil remains of the hominins from Soa Basin have not been discovered, their morphology is unknown. *Homo floresiensis*, a possible descendant of this earlier hominin population, had very small stature, long arms, *Pan*-like wrist bones, curved phalanges and very long feet, suggesting it may have spent time climbing in trees.

7.5 Bodo

7.5.1 Introduction

The Ethiopian hominin site of Bodo, like Daka, is situated in the Middle Awash region of the Rift Valley in Ethiopia (Figure 7.5.1). It is, however, younger than Daka, Buia, Olorgesailie and the Soa Basin.

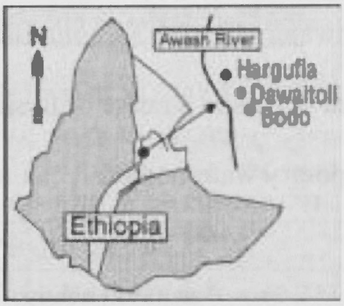


Figure 7.5.1: Map of Ethiopia showing location of Bodo (from Clark et al. 1994)

The age of the Bodo hominin unit, based on faunal, archaeological and laser fusion determinations, is placed at c. 0.6 Ma (Clark et al. 1994). The hominin remains were found in the Upper Bodo Sand Unit (UBSU), part of the Bodo Member of the Wehaietu Formation (Kalb et al. 1982, Kalb 1993, Figure 7.5.2). The sediments consist of fluviatile deposits composed of conglomerates, sands and silts (Kalb et al. 1980).

The hominin cranium appears to have been preserved in a face down position, with the back part of the specimen exposed to weathering before the front, and subsequently broken up, with the fragments dispersed or lost (Rightmire 1996). Skulls of other large vertebrates found *in situ* were unfragmented; indicating that exposure from erosion was primarily responsible for the fragmentation seen in the hominin cranium (Kalb et al. 1980).

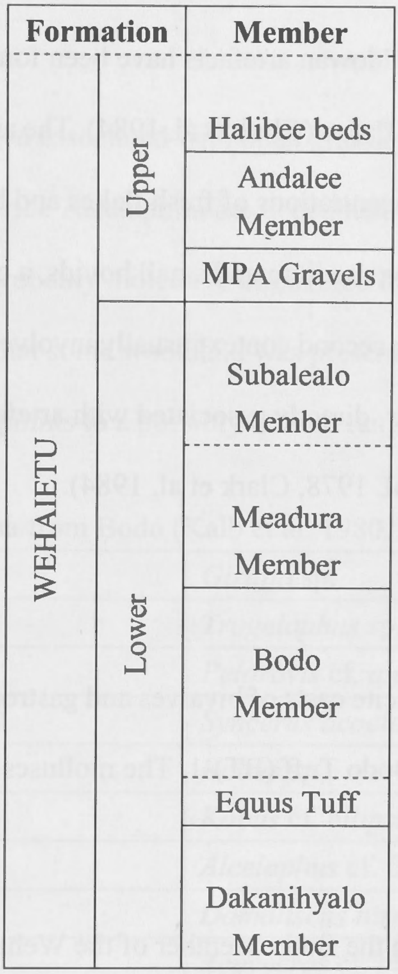


Figure 7.5.2: Simplified stratigraphy of the Wehaietu Formation (after Kalb 1993)

The hominin remains from Bodo include a cranium, a parietal and a distal humerus fragment. In combination these specimens are said to show affinities to both *Homo erectus* and *Homo sapiens*, leading some researchers to refer to them as "archaic" *Homo sapiens* (Clark et al. 1994). Rightmire (1996) grouped the Bodo specimens with similar Middle Pleistocene specimens from Africa and Europe under the taxon *Homo heidelbergensis,* while according to Geraads et al. (2004) they are *Homo erectus*.

The other primates identified from the Bodo Member of the Wehaietu Formation are *Papio* and *Theropithecus oswaldi* (Kalb et al. 1980).

Acheulean and developed Oldowan artefacts have been found including hand axes, cleavers, core/choppers and flakes (Clark et al. 1984). The artefacts occur in two contexts. The first involves small concentrations of fresh flakes and broken bone 'representing possible food waste' of large, medium and small bovids, a canid, crocodilians and catfish (Clark et al. 1984: 427). The second context usually involves the remains of a single large animal, often *Hippopotamus*, directly associated with artefacts and inferred to be a butchering site (Conroy et al. 1978, Clark et al. 1984).

7.5.2 Molluscs

Kalb et al. (1980) report calcite casts of bivalves and gastropods from a tuff at the base of the Bodo Member named Bodo Tuff (BT)-1. The molluscs remain unidentified (Table 7.5.1).

Table 7.5.1: Molluscs from the Bodo Member of the Wehaietu Formation

Taxon	**Palaeoecology**
Gastropoda	Wide range of habitats from marine, freshwater to terrestrial
Bivalvia	Aquatic, marine to fresh water

7.5.3 Palaeoecology

A range of vertebrate fauna have been recovered from Bodo, mainly mammals but also reptiles and fish (Table 7.5.2). The mammals include a number of taxa that are indicative of water. The genus *Kobus*, for example, is a bovid well adapted to wetland environments, whereas *Hippopotamus* requires permanent water in which to submerge during daylight hours. The presence of the rodent *Thryonomys* indicates that reed beds grew along the margin of a perennial water body. The suid *Kolpochoerus* indicates permanent water.

Theropithecus oswaldi is often associated with open grassland habitats near water, while equids and bovids from the tribe Alcelaphini are dependent to some degree on open grasslands. *Tragelaphus* is probably indicative of covered habitats, and giraffids require trees to browse, suggesting that some woodland was present locally, though the absence of clearly arboreal primates points to a possibly limited range of tree cover.

Table 7.5.2: Vertebrate fauna from Bodo (Kalb et al. 1980, Geraads et al. 2004)

PRIMATES	*Giraffa* sp.
Papio sp.	*Tragelaphus* sp.
Theropithecus oswaldi	*Pelorovis* cf. *antiquus*
Homo cf. *erectus*	*Syncerus acoelotus*
RODENTIA	*Kobus* sp.
Thryonomys sp.	*Kobus* cf. *ellipsiprymnus*
PROBOSCIDEA	*Alcelaphus* cf. *buselaphus*
Elephas recki	*Damaliscus niro*
PERISSODACTYLA	*Aepyceros* cf. *melampus*
Equus sp.	**REPTILIA**
ARTIODACTYLA	Chelonia
Hippopotamus sp.	*Crocodylus* sp.
Kolpochoerus majus	**OSTEICHTHYES**

The non-mammalian vertebrate fauna are restricted to reptiles and fish. While the fish are not identified, Clark et al. (1984) refer to catfish found in association with artefacts in the Wehaietu Formation. These fish are well adapted to shallow waterways and can tolerate relatively poorly oxygenated waters.

A crocodilian *Crocodylus* is also known from the Bodo Member and these are also indicative of permanent water.

The faunal remains from Bodo are indicative of a large permanent water body, taking the form either of a lake or a river, with reed beds, open grassland and some local tree cover all likely. Root casts and algal fragments are known from the Bodo Member of the Wehaietu Formation, and algal stromatolites in areas adjacent to the Bodo localities indicate a sizable reservoir (Kalb et al. 1980).

7.5.4 Conclusion

Molluscs from the Bodo Member include both gastropods and bivalves but since no identification of these has been made, the amount of information that can be added to the palaeoecological picture of the Member is restricted. The fact that bivalves were present indicates a perennial water body, supporting conclusions drawn from other data, but more informed inferences must await more detailed identification of both the bivalve and gastropod specimens.

7.6 Pakefield

7.6.1 Introduction

The earliest evidence of *Homo* occupation in northern Europe comes from the site of Pakefield, Suffolk, United Kingdom. The site at the time of preservation would have been close to the coast of the North Sea (Figure 7.6.1).

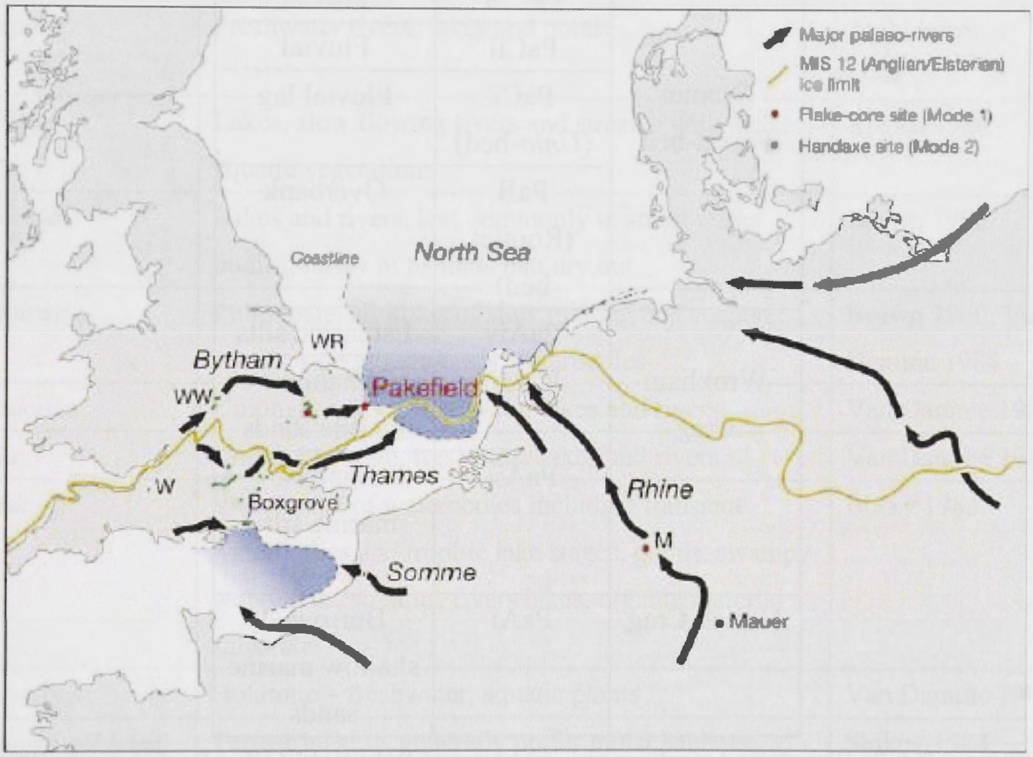


Figure 7.6.1: Map showing location of Pakefield, United Kingdom (Parfitt et al. 2005)

The Pakefield site comes from the Cromer Forest-bed Formation (CF-bF), which formed in an interglacial period and overlies marine sediments (figure 7.6.2). The CF-bF in turn is overlain by a sequence of marine sands and glaciofluvial sediments. The archaeological deposits are dated, on the basis of biostratigraphy, palaeomagnetism and amino acid geochronology, to the early part of the Brunhes Chron, about 700 ka. The CF-bF is made up of overbank sediments, lag gravels and laminated silts. Although most of the artefacts from Pakefield were found in the CF-bF, the oldest artefact was found below this in the Wroxham Formation (PaAiv), in the upper layer of the estuarine silts (Parfitt et al. 2005).

Formation	**Lithofacies**	**Interpretation**
Wroxham Crag	PaD	Shallow marine sands
Cromer Forest-bed	PaCiii	Fluvial
	PaCii	Fluvial
	PaCi (*Unio*-bed)	Fluvial lag
	PaB (Rootlet bed)	Overbank
Wroxham Crag	PaAiv	Estuarine silts
	PaAiii	Shallow marine sands
	PaAii	Shallow marine silty sands
Norich Crag	PaAi	Burrowed shallow marine sands

Figure 7.6.2: Simplified stratigraphic column of Pakefield (after Parfitt et al. 2005)

No primates have been found in the CF-bF but the discovery of artefacts implies that *Homo* was present. The artefacts include cores, choppers and hammer struck flakes, made from black flint probably collected from the adjacent river channel. Because the assemblages lack formal tools they are consistent with a Mode 1 Technology (Parfitt et al. 2005).

7.6.2 Molluscs

A diverse range of molluscs has been found in the Cromer Forest-bed Formation including freshwater and terrestrial gastropods and a variety of bivalves (Table 7.6.1). A number of genera have more than one species represented including *Valvata* (two), *Unio* (at least three), *Sphaerium* (at least four) and *Pisidium* (at least seven).

Table 7.6.1: Molluscs from Cromer Forest-bed Formation, Pakefield (Parfitt et al. 2005)

Taxon	**Palaeoecology**	**References**
Viviparus	Freshwater rivers, lakes and ponds	Jonkinen et al. 1982
Valvata	Lakes, slow flowing rivers and streams with dense aquatic vegetation	Brown 1980
Bithynia	Lakes and rivers, less commonly in small water bodies, rarely in habitats that dry out	Brown 1980
Lymnaea	Pulmonate, all kinds of slow moving and stagnant waters, rare in temporary waterbodies	Brown 1980, Van Damme 1984
Anodonta	Unionid bivalve, freshwater lakes and rivers	Van Damme 1984
Unio	Unionid bivalve, freshwater lakes and rivers	Van Damme 1984
Pisidium	Wide range of waterbodies including transient waterbodies and trophic lake stages, ponds, swampy woodlands, streams, rivers lakes, organic material substrate	Burky 1983
Sphaerium	Holarctic – freshwater, aquatic plants	Van Damme 1984
Deroceras/*Limax*	Terrestrial slug, generally prefer moist habitats, along the banks of water bodies, flood plain meadows	Shikov 1984
Trichia	Terrestrial snail, meadows, often found under leaves, rocks and pieces of wood. Found in secondary forest and pine forest	Shikov 1984

In addition, the marine mollusc *Neptunea contraria* was found in the estuary silts (PaAiv) of the Wroxham Crag Formation, which contain the oldest known artefacts from Pakefield.

7.6.3 Palaeoecology

The vertebrate fauna from Pakefield includes fish, amphibians, and a range of mammals (Table 7.6.2). The mammalian fauna includes species adapted to open and closed habitats as well as those adapted to an aquatic lifestyle.

Relatively open habitats are suggested by the presence of a hamster *Cricetus*, which is today often associated with steppe like habitats, two species of *Equus*, and the extinct rhinoceros *Stephanorhinus*, which is also thought to have inhabited steppe like habitats.

Relatively dense vegetation in the form of forests or dense shrub land is suggested by the presence of a squirrel *Sciurus*, an extinct forest vole *Pliomys*, and the bank vole *Clethrionomys glareolus*, which prefers woodland and dense vegetation. Also indicative of forest biotopes are the fallow deer *Dama*, the roe deer *Capreolus capreolus* and the boar *Sus scrofa* (van Kolfschoten 1992).

Aquatic environments at Pakefield are indicated by the presence of a water shrew, *Neomys*, the water vole *Mimomys savini* (van Kolfschoten 1992), the beaver *Castor fiber* and an extinct giant beaver *Trogontherium cuvieri*. The wolf *Canis lupus* is an inhabitant of various temperate habitats, from forest to mountain and even desert.

The oldest artefacts from Pakefield come from the estuarine silts of the Wroxham Crag Formation, and the mammalian fauna from here include marine mammals such as dolphin and walrus (Parfitt et al. 2005).

Table 7.6.2: Vertebrate fauna from Pakefield (Parfitt et al. 2005)

OSTEICHTHYES	*Castor* cf. *fiber*
Esox lucius (northern pike)	*Trogontherium cuvieri*
Tinca tinca (tench)	*Clethrionomys glareolus*
Scardinius erythrophthalmus (rudd)	*Pliomys episcopalis*
Rutilus rutilus (roach)	*Mimomys* aff. *pusillus*
Cyprinidae indet.	*Mimomys savini*
Anguilla anguilla (eel)	*Microtus agrestis* (or *arvalis*)
Pungitius pungitius (stickleback)	*Apodemus* cf. *sylvaticus*
Perca fluviatilis (European perch)	**CARNIVORA**
AMPHIBIA	*Canis* cf. *lupus* (small)
Rana sp.	Cf. *Crocuta* (coprolites)
Anuran indet.	**PERISSODACTYLA**
INSECTIVORA	*Equus* sp. (large)
Macroneomys brachygnathus	*Equus* cf. *altidens*
Neomys sp.	*Stephanorhinus hundsheimensis*
Sorex (*Drepanosorex*) *savini*	**ARTIODACTYLA**
Sorex sp.	*Sus scrofa*
Talpa minor	*Megaloceros verticornis*
CHIROPTERA	*Megaloceros savini*
Myotis sp.	*Megaloceros dawkinsi*
PRIMATES	*Megaloceros* cf. *dawkinsi*
Homo sp. (artefacts)	*Dama* sp.
RODENTIA	*Cervus elaphus*
Sciurus sp.	*Capreolus capreolus*
Cricetus sp.	*Bison* cf. *schoetensacki*

A diverse range of fish are also associated with the Pakefield deposits and these offer a number of specific palaeoecological insights.

The ninespine stickleback *Pungitius pungitius* is a bottom feeder on crustaceans and aquatic insects and prefers cool, quiet, shallow, vegetated areas of ponds, lakes, estuaries and streams. The northern pike *Esox lucius* and the European perch *Perca fluviatilis* are top carnivores, the presence of which within an assemblage indicates a balanced and stable freshwater community (Florea Luiza 2008). The rudd *Scardinius erythrophthalmus* and the roach *Rutilus rutilus* inhabit freshwater habitats where they feed on submerged aquatic vegetation (Petr 2000). The tench *Tinca tinca* is a freshwater and brackish benthic feeder which prefers the slow moving, well vegetated waters of lakes, rivers and marshes (Whitton 1982). The European eel *Anguilla anguilla* is catadromous (inhabiting freshwater rivers and returning to the ocean to spawn). The larvae of this species feed on ocean plankton and then move into estuaries before migrating up stream along rivers where they grow into adults.

The vertebrate fauna includes at least two amphibians including a frog *Rana*, indicating a pond or some other relatively still water body.

The CF-bF is also rich in palaeobotanical remains and includes species such as the water chestnut *Trapa natans*, which is also found in the Nihewan Basin and usually grows in shallow, slow-moving waters in warm temperate habitats, and *Salvinia natans* which is similarly adapted to still waters. *Corema album* is today known from maritime dunes and sands along the Atlantic. *Typha* grows along the edges of water courses, as does *Carex*, which is also known from the site of Ceprano (Chapter 7.7). *Groenlandia densa* is a totally submerged pondweed which grows in base rich lakes. Pollen analysis also indicates that the local terrestrial habitat was dominated by broad-leafed woodland that included the hornbeam *Carpinus*.

The molluscan fauna from Pakefield provide additional palaeoecological information. *Lymnaea* and *Valvata* are freshwater gastropods that are often associated with well vegetated shallow wetlands. *Bithynia* is found in a range of perennial freshwater habitats from ponds to lakes and rivers, and *Viviparus* prefers soft substrates in slow moving streams and rivers.

Pakefield has a relatively high number of bivalve species including at least three unionid mussels and ten veneroid clams. The Beds from which the *Homo* artefacts are found are known as the *Unio* Beds, which is testament to the prominence of these bivalves in terms of abundance. At least three species of *Unio* are present, including *Unio pictorum*, and the genus *Anadonta*. Today *Anadonta* and two species of *Unio* including *Unio pictorum* are found in the Danube River, in particular in shallow waters less than 2m. These bivalves require large connected freshwater drainage areas for dispersal and suitable fish species to act as hosts for their parasitic larval stage.

At least seven species of *Pisidium* and three species of *Sphaerium* have also been discovered at Pakefield. This diversity of clams suggests there were adequate resources to support a variety of filter feeding bivalves. Although pisidiids are often associated with transient bodies of water because of their ability to disperse efficiently (Burky 1983) and are found in habitats ranging from ponds and swampy woodlands to permanent ponds, they are also known from lakes, streams and major rivers. Pisidiid clams are good indicators of trophic lake stages, with a number of species occurring in greatest numbers in association with the highest levels of organic material in the substrate (Burky 1983).

In the earliest deposits in which stone tools have been found at Pakefield, in the estuarine silts of the Wroxham Crag Formation (PaAiv), the marine gastropod *Neptunea contraria* is known. This genus of whelk is usually found in the soft substrates of shallow marine environments.

7.6.4 Conclusion

The combination of data from Pakefield is consistent with a large perennial river on a coastal plain, with associated grasslands, swamps, shrubs, trees, reed-beds and aquatic vegetation. The molluscs reinforce the conclusion that aquatic vegetation was present, and also indicate that both flowing water and more stagnant wetlands appear to have been present, and there was probably a range of substrates including mud, sand and rocks. Trophic levels in some sections of the waterways appear to have been high. No tropical or even sub-tropical restricted molluscs have been discovered at Pakefield, which suggests that the climate at this site may have been milder than at other sites at which *Homo* remains had up until this time been found.

The hominins from Pakefield had a range of habitats available in which to forage and seek shelter, including waterside habitats, open steppe, and woodland. The Boxgrove hominins, younger than the Pakefield population, were heavy boned individuals, making arborealism at least for these populations unlikely.

7.7 Ceprano

7.7.1 Introduction

Sediments in the Ceprano Basin have yielded important palaeoanthropological finds. The site of Campo Grande, for example, from the Ceprano Basin, which is one of a suite of basins that form the middle Sacco-Lili river valley south of Rome in Italy (Ascenzi et al. 1996), has yielded some of the earliest hominin fossils known from southern Europe (Figure 7.7.1).

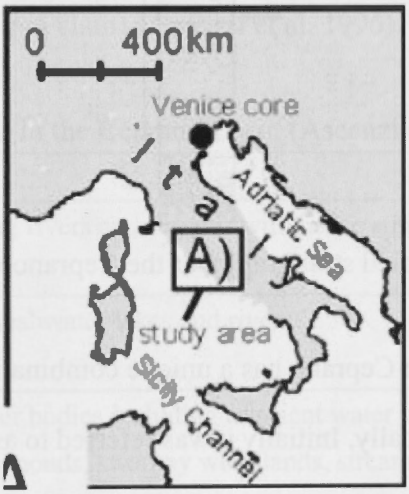


Figure 7.7.1: Map of Italy showing location of Ceprano study area (Muttoni et al. 2009)

Sediments from the Ceprano basin preserve a human calvarium which was once estimated to be between 800 and 900 ka (Manzi et al. 2001, Figure 7.7.2), although more recent dating places the date closer to c. 450 ka (Muttoni et al. 2009). The series of layers in the Ceprano basin include gravels, sands, silts and clays associated with fluvial, marsh, lacustrine and alluvial fan deposition (Ascenzi et al. 1996, Muttoni et al. 2009).

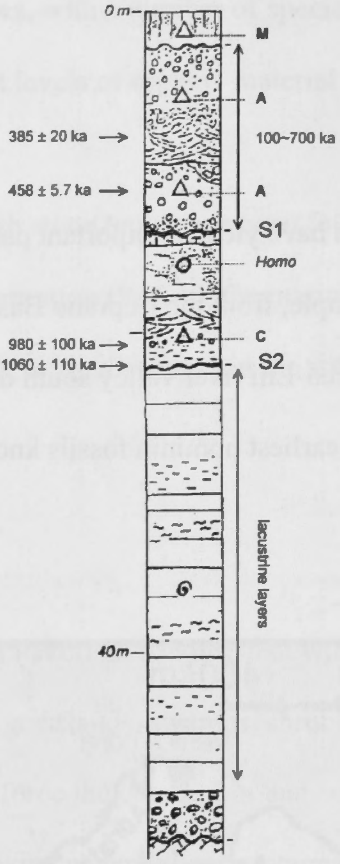


Figure 7.7.2: Simplified stratigraphy of the Ceprano site (Manzi et al. 2001)

The human calvarium from Ceprano has a unique combination of features making it difficult to place taxonomically. Initially it was referred to as late *Homo erectus* (Ascenzi et al. 1996), but later studies suggested that *Homo antecessor* may be a more appropriate taxon (Manzi et al. 2001), and some authors have suggested placing it in its own species, *Homo cepranensis* (Mallegni et al. 2003). No other primates are known from the Ceprano Basin.

Stone and bone tools are known throughout the upper section of the Ceprano Basin. Archaic Mousterian tools are known from the upper layers, while Upper Acheulean artefacts are known from further down in the section, and further down still, older

Acheulean artefacts have been found in the same layers as bone tools and fauna, and finally in the lower cross-bedded fluvial sands, pebble and quartzite chopper artefacts are known (Ascenzi et al. 1996).

7.7.2 Molluscs

The Ceprano Basin sediments contain a number of freshwater molluscs (Table 7.7.1). In layers that also contain Acheulean artefacts and bone tools, *Unio* (*Auricolaria*) *sinuata* specimens of very large size have been found, while *Unio* fragments are also known from lower down in the section. In addition, some layers contain *Valvata* and *Pisidium amnicum* (greater European pea clam) (Ascenzi et al. 1996).

Table 7.7.1: Molluscs found in the Ceprano Basin (Ascenzi et al. 1996)

Taxon	Palaeoecology	References
Valvata	Lakes, slow flowing rivers and streams with dense aquatic vegetation	Brown 1980
Unio	Unionid bivalve, freshwater lakes and rivers	Van Damme 1984
Pisidium	Wide range of water bodies including transient water bodies and trophic lake stages, ponds, swampy woodlands, streams, rivers lakes, organic material substrate	Burky 1983

7.7.3 Palaeoecology

The vertebrate faunal remains from the Ceprano Basin include mammals and a reptile (Table 7.7.2). The mammalian fauna includes a beaver *Castor*, which is essentially a riverine specialist whose habit of building dams creates ponds which a number of other animals take advantage of. The presence of a hippopotamid *Hippopotamus* is consistent with a perennial body of water, a relatively warm climate and open grasslands.

Fallow deer genus *Dama* today prefer mixed woodland, while *Elephas* (*Palaeoloxodon*) *antiquus* was a woodland inhabitant judging by its browsing features.

The European pond turtle *Emys orbicularis* is indicative of slow flowing waters.

Table 7.7.2: Vertebrate remains from Ceprano basin (Ascenzi et al. 1996)

PRIMATES	*Dama* (cf. *dama*) *clactoniana*
Homo cepranensis	**PROBOSCIDEA**
RODENTIA	*Elephas* (*Palaeoloxodon*) *antiquus*
Castor sp.	**PERISSODACTYLA**
ARTIODACTYLA	*Stephanorhinus hemitoechus*
Hippopotamus sp.	**REPTILIA**
Megaloceros verticornis	*Emys orbicularis*

Sedges of the genus *Carex* are known to have occurred within the basin (Ascenzi et al. 1996), and these are often associated with the margins of marshy shallow water habitats. This genus is also known from Pakefield.

The molluscan fauna of the Ceprano Basin offers a number of palaeoecological insights. Species of *Valvata* are known to live in lakes, slowly flowing rivers and streams with dense aquatic vegetation (Brown 1980), whereas the bivalve *Pisidium* is often associated with running water. The presence of unionid bivalves of a very large size means this must have been a large hydrological system connected to other waterways.

Unionid bivalves are associated with stone tools in a number of layers in the Ceprano basin (Ascenzi et al. 1996).

7.7.4 Conclusion

In combination, the molluscan fauna confirms conclusions drawn from other data, which point to a large body of water, possibly alternating from lake to river, with sections fringed by sedges. Aquatic vegetation in relatively swampy wetland habitats perhaps associated with riverine floodplains or lake margins were probably also present, and the molluscan fauna also indicates flowing as well as more stagnant waterbodies, and a large connected hydrological drainage area.

The Ceprano hominin featured very thick cranial bones and a relatively large brain (c. 1185 cc), so it is unlikely to have been a climber. It could have foraged in waterside habitats and woodlands.

7.8 Yuanmou

7.8.1 Introduction

One of the earliest fossil *Homo* sites in China is the site of Yuanmou. The Yuanmou Basin is situated in Yunnan Province, in southwest China about 110km northwest of Kunming (Figure 7.8.1), and has yielded many mammalian and other fossils including hominins and stone artefacts.

Figure 7.8.1: Map showing location of Yunnan Province, China. Yuanmou is located about 110kms northwest of Kunming (Urabe et al. 2001)

The age of the Yuanmou hominin fossils has long been contested, with palaeomagnetic dating of the Yuanmou hominin-bearing deposits giving various dates. Early estimates placed the fossil beds of Yuanmou at close to 1.7 Ma (Cheng et al. 1977, Li et al. 1977), but later dates suggested a much later date of c. 0.7 Ma (Hyodo et al. 2002). More recently, a date of c. 1.7 Ma has again been put forward (Zhu et al. 2008). The hominin-bearing bed comes from the Yuanmou Formation (earlier known as Member 4) which consists of fluvial and deluvial deposits composed of sandy gravel, silty clay and clay (Wu & Poirier 1995). The Yuanmou Formation is divided into two sections; the lower Dainawu Member and the upper Niujianbao Member (Urabe et al. 2001, Figure 7.8.2).

Age	**Formation**		**Sedimentary environment**
Pleistocene	**Yuanmou Form.**	Niujianbao Member	Braided channel of alluvial fan (mid fan)
		Dainawu Member	Gravely braided river (ephemeral) system on Alluvial plain
	Gantang Form.	Daipojing Member	
Pliocene		Yangliuchun Member	Braided river system on Alluvial plain

Figure 7.8.2: Simplified stratigraphy of Yuanmou Formation (after Urabe et al. 2001)

The only primate remains discovered from the Yuanmou Formation are incisors assigned to the species *Homo* cf. *erectus* (Wu & Poirier 1995). The presence of *Homo* has also been confirmed by the discovery of stone tools consisting of cores, flakes and points made of quartzite and sandstone (Wu & Poirier 1995).

7.8.2 Molluscs

The Yuanmou Formation molluscan fauna contains a number of gastropods and a bivalve (Table 7.8.1). All these taxa except *Cathaica* are also found in the lower Gantang Formation, plus *Semisulcospira elegans*, *Margarya* and *Unio* (Li et al. 1977).

Table 7.8.1: Molluscs from Yuanmou Formation (Zhu et al. 2008)

Taxon	**Palaeoecology**	**References**
Radix	Freshwater pulmonate – shallower waters of lakes, ponds, marshes, rivers and streams, often in association with aquatic vegetation in lentic waters, rocks in lotic conditions	Russell-Hunter 1978
Viviparus	Freshwater rivers, lakes and ponds	Jonkinen et al. 1982
Cathaica	Some *Cathaica* species are found today living on lichenous stones along the slopes of hills	Wu et al. 2003
Gyraulus	Generally stagnant or slowly flowing waters often associated with aquatic vegetation	Brown 1980
Gastropoda	Snails and slugs – from marine to freshwater and terrestrial	Anderson 1998
Corbicula	Tropical and sub-tropical fresh and brackish waters, variety of substrates, prefers well oxygenated waters and sandy substrates	McMahon 1983

7.8.3 Palaeoecology

The vertebrate fauna from the Yuanmou Formation contains mainly mammals, with one reptile and one fish taxon also recorded (Table 7.8.2). The mammalian fauna includes inhabitants of both open and closed habitats.

In contrast to the earlier Gantang Formation, the Yuanmou Formation is characterised by the appearance of numerous grazers, reflecting a reduction in the dense forest habitats that were interspersed with grassy plains in the lower section, and an expansion of sparsely wooded grassy planes in the Yuanmou Formation (Qian & Zhou 1991). For example the bovid *Gazella* is a grazer usually associated with open grassland habitats. Also indicative of open habitats is the extinct horse *Equus yunnanensis*, which was most likely a grazer on open tracts of grassland (Elewa 2008). The vole *Microtus* is also an inhabitant of grasslands.

The civet *Viverricula*, although an agile climber, is mainly terrestrial. Extant species of this genus are found in semi-evergreen and deciduous forests, mixed deciduous forest, bamboo forest, scrubby areas, grassland and riverine habitats (Duckworth et al. 2008).

Wooded or forested habitats must have also been present since there are a number of cervids present, including the genera *Axis* and *Rusa*, both of which typically incorporate areas of forest or woodland within their range. Wild boars *Sus* also are generally restricted to forest or woodland habitats (Macdonald 2001).

The water vole *Arvicola*, today builds burrows in the banks of ponds, slow moving rivers and streams and is also known to build nests in reed beds. The preferred habitat for *Arvicola* is highly layered bankside vegetation with tall grasses and stands of flowers fringed with thick stands of rushes, sedges or reeds (Macdonald 2001). A number of the faunal elements from Yuanmou are reliant on fresh sources of nearby drinking water, such as the suid *Sus* and wild cattle *Bos*.

Table 7.8.2: Vertebrate fauna from Yuanmou (Qian & Zhou 1991, Li et al. 1977)

PRIMATES	*Rhinoceros sinensis*
Homo erectus	*Rhinoceros* sp.
LAGOMORPHA	**ARTIODACTYLA**
Leporidae	*Sus* sp.
RODENTIA	*Bos* sp.
Rhizomys sp.	*Eostyloceros longchuanensis*
Microtus sp.	*Metacervulus capreolinus*
Arvicola sp.	*Paracervulus attenuates*
Hystrix subcristata	*Muntiacus lacustris*
CARNIVORA	*Cervoceros ultimus*
Viverricula (cf. *malaccensis*) *fossilis*	*Axis* sp.
Hyaena licenti	*Axis shansius*
Megantereon nihowanensis	*Axis* cf. *rugosus*
Panthera cf. *tigris*	*Rusa yunnanensis*
Panthera cf. *pardus*	*Rusa* sp.
Felidae	*Procapreolus stenosis*
PROBOSCIDEA	*Bibos* sp.
Stegodon elephantoides	*Gazella* sp.
Stegodon sp.	**OSTEICHTHYES**
PERISSODACTYLA	*Cyriuus caspio* (*Cyprinus carpio*?)
Equus yunnanensis	**REPTILIA**
Nestoritherium sp.	*Testudo* sp.

The vertebrate fauna from Yuanmou also includes the remains of fish. Li et al. (1977) list the species *Cyriuus caspio*. Whether this taxon is a misprint for *Cyprinus carpio* is uncertain. If so, then it would suggest a large body of relatively slow moving water and soft, vegetative sediments and a temperate climate.

The only reptile from Yuanmou is a tortoise *Testudo*. This genus contains species with a wide range of habitat preferences.

Ostracods have also been collected from the Yuanmou Formation, including the genera *Neocypridopsis*, *Ilyocypris*, *Candona* and *Candoniella*, which together reflect a shallow lake or pond setting (Qian & Zhou 1991).

The fossil molluscs from Yuanmou indicate freshwater fluvio-lacustrine deposition in a sub-tropical environment, with running water indicated by *Corbicula* and relatively stagnant waters suggested by *Radix*. Areas of relatively abundant aquatic vegetation in lentic wetland habitats are inferred by *Gyraulus* and *Radix* (Qian & Zhou 1991). Although *Corbicula* is capable of tolerating moderate salinity levels (McMahon 1983), the molluscan fauna is indicative of a freshwater habitat. Some *Cathaica* species are found today living on lichenous stones along the slopes of hills (Wu et al. 2003), so these types of habitat may have been present.

In the earlier Gantang Formation the marsh snail *Semisulcospira* existed, as did the unionid bivalve *Unio*. These point to swampy habitats (*Semisulcospira*) and a perennial freshwater river containing fish species able to act as hosts for the parasitic larval stage of the freshwater mussel (*Unio*).

Conclusion 7.8.4

The molluscs confirm the presence of a large body of water, possibly a slow-flowing river with associated flood plains, which supports the view reached based on other faunal data. The climate may have been sub-tropical since *Corbicula* is restricted to this and tropical zones. The molluscs also indicate both relatively swift (*Corbicula*) and slow flowing freshwater habitats (*Gyraulus*) with shallow areas (*Radix),* and areas of abundant aquatic vegetation (*Radix*, *Gyraulus*). The water body was connected to a larger permanently flowing drainage system because this is the habitat *Viviparus* is restricted to.

No morphological evidence for hominins, apart from teeth, are known from Yuanmou. The habitats at Yuanmou included open habitats, come forest regions, and waterside habitats sometimes with aquatic vegetation. Hills may have been close by.

7.9 Omo Kibish

7.9.1 Introduction

Sites examined in this chapter so far have included the earliest archaeological occurrences within a region (Soa Basin, Pakefield) or sites associated with archaic *Homo* fossils such as *Homo* cf. *erectus* (Olorgesailie, Yuanmou, Daka). To conclude this chapter one of the earliest known *Homo sapiens* fossil site is examined. Omo Kibish is a fossil site from southern Ethiopia (Figure 7.9.1).

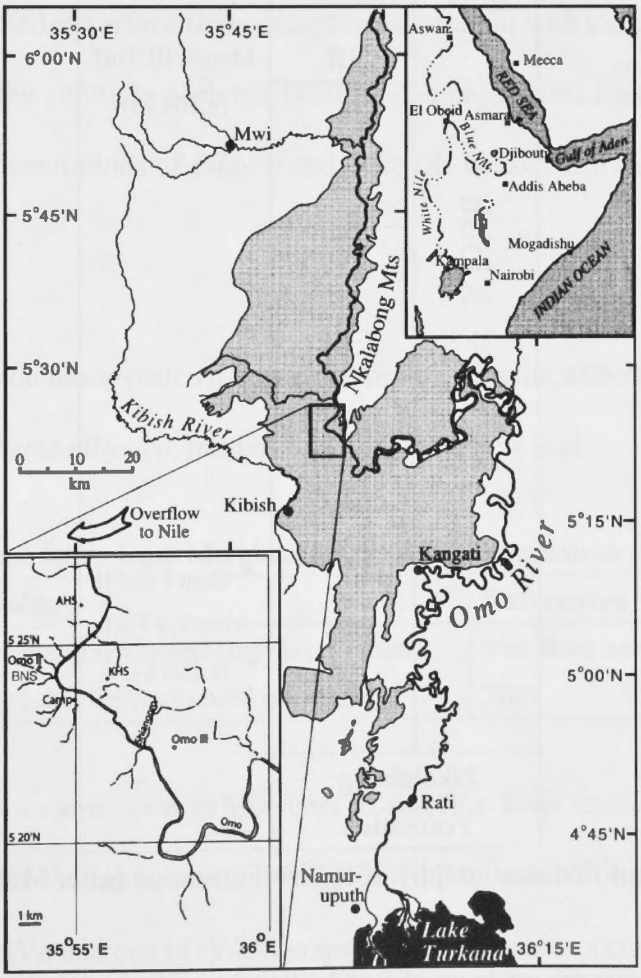


Figure 7.9.1: Map showing location of Omo Kibish, southern Ethiopia (Shea 2008)

Two hominin crania, Omo I and II, were discovered in Member I of the Kibish Formation (Figure 7.9.2), just below a tuff dated to c.196 ka, making them the oldest anatomically modern humans yet described (McDougall et al. 2005).

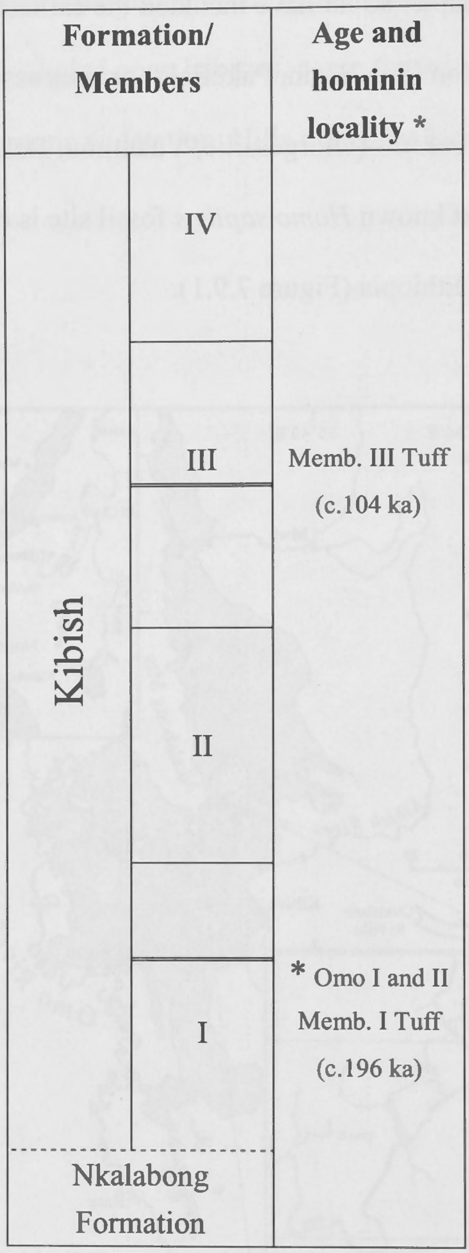


Figure 7.9.2: Simplified stratigraphy of Kibish Formation (after McDougall et al. 2005)

The Kibish sediments are made up of flood silts, channel and deltaic deposits of the Omo River, as well as lacustrine and littoral deposits of Lake Turkana (Howell 1968).

Members I, II, and III consist of delta plain, delta fringe and pro-deltaic sedimentation, while Members IV*a* and IV*b* are littoral deposits (Butzer 1969).

Primate material in the Kibish Formation is scarce. R. Leakey (1969) reported the presence of two specimens which appear to represent a large species of *Colobus*, but the stratigraphic provenance of these fossils is unclear and so it is uncertain whether they were part of the Member I faunal assemblage (Assefa et al. 2008). Two human crania, Omo I and II, from Member I are said to represent *Homo sapiens*.

Stone tools are limited to surface finds except in association with the Omo I skeleton in Member I (R. Leakey 1969). In Member IV*a* harpoon heads were found, usually associated with concentrations of *Etheria* and *Unio* (R. Leakey 1969).

7.9.2 Molluscs

The Kibish Formation has revealed a number of mollusc fossils, although from Member I only one taxon, *Etheria elliptica*, has been recorded (Table 7.9.1).

Table 7.9.1: Mollusc fauna from Member I of the Kibish Formation

Taxon	Palaeoecology	References
Etheria	Flowing water in rivers and large lakes where they cement themselves to hard substrates	Van Bocxlaer & Van Damme 2009

Etheria elliptica banks also occur in Members III and IV*a*. *Unio* shells occur in Members III, IV*a* and IV*b*, *Melanoides* occurs in Members III, IV*a* and IV*b*, two species of *Corbicula* occur in IV*a* and one in IV*b*, two species of *Cleopatra* occur in IV*a*, and one in

IV*b*, while *Viviparus* occurs in Member IV*b* (Butzer et al. 1969) as does *Bithynia* (Butzer & Thurber 1969).

7.9.3 Palaeoecology

A diverse vertebrate faunal sample has been collected from Member I of the Kibish Formation and includes mammals, birds and fish (Table 7.9.2).

The mammalian fauna consist of mainly terrestrial taxa which indicate a mosaic environment of open and closed habitats in the vicinity of a permanent water body. Grasslands were locally available as indicated by the numerous grazers such as the bovids *Alcelaphus*, *Oryx* and *Gazella*, and three species of *Equus*.

Closed habitats, possibly of a riverine nature, are suggested by the duiker *Cephalophus* which today prefers dense cover. Other mammals usually associated with well covered habitats include the bushbuck *Tragelaphus scriptus*, while the giraffid *Giraffa* and the greater kudu *Tragelaphus strepsiceros* are both browsers which rely on woodland habitats for food and/or cover.

The hippopotamid *Hippopotamus amphibius* indicates the presence of relatively open grasslands close to a permanent water body. Two other artiodactyls that require permanent water are the waterbuck *Kobus ellipsiprymnus* and the reedbuck *Redunca redunca*.

Table 7.9.2: Vertebrate fauna from Member I of the Kibish Formation (Assefa et al. 2008, Louchart 2008, Trapani 2008)

ARTIODACTYLA	**PERISSODACTYLA**
Alcelaphini indet.	*Equus* sp.
Alcelaphus sp.	*Equus* cf. *grevyi*
Cephalophini indet.	*Equus* cf. *burchellii*
Cephalophus cf. *weynsi*	**PRIMATES**
Madoqua sp.	*Homo sapiens*
Madoqua cf. *kirkii*	**RODENTIA**
cf. *Kobus*	*Thryonomys swinderianus*
Kobus cf. *ellipsiprymnus*	*Hystrix cristata*
Kobus ellipsiprymnus	*Heterocephalus*
Redunca sp.	**AVES**
Redunca redunca	*Pelicanus* cf. *onocrotalus*
Antilopini indet.	*Pelicanus* aff. *rufescens*
Gazella sp.	*Anhinga melanogaster* (darter)
Oryx cf. *gazelle*	*Ardea* sp. (heron)
Tragelaphini indet.	Numidinae indet. (guinea fowl)
Tragelaphus strepsiceros	**OSTEICHTHYES**
Tragelaphus cf. *scriptus*	*Gymnarchus niloticus*
Tragelaphus scriptus	*Barbus* sp.
Bovini indet.	*Clarias* sp.
Syncerus caffer	*Bagrus* sp.
Hippopotamus amphibius	*Synodontis* sp.
Phacochoerus africanus	*Lates* sp.
Giraffa camelopardalis	*Tetraodon* sp.

Small mammals are rare in the Kibish Formation, although three rodents are known from Member I. One of these, the porcupine *Hystrix*, is today found in a range of environments and therefore is not a good indicator of palaeoecologies, but the naked mole rat *Heterocephalus* is usually associated with arid habitats, and the cane rat *Thryonomys* *swinderianus* inhabits long grasses in marshy habitats along the edges of rivers and lake banks.

The avian fauna includes two species of pelican *Pelicanus*, a heron *Ardea* and a darter *Anhinga melanogaster*. Pelicans inhabit coastal and inland waters where they feed primarily on fish, herons are waders in wetland habitats and feed on fish, frogs, invertebrates and snakes, and darters are foot propelled divers which usually hunt fish, and more occasionally hunt large invertebrates. The presence of these birds indicates a local body of freshwater in the form of a lake or large river supporting resources of fish (Louchart 2008). Guinea fowls Numidinae are ecologically wide ranging, but their presence in Member I of the Kibish Formation indicates there must have been some trees locally present (Louchart 2008).

The Kibish Formation has a relatively diverse range of fish fauna. Member I contains seven genera (Table 7.9.2). *Gymnarchus niloticus* is a nocturnal hunter with poor vision and inhabits swamps and vegetated river edges. It builds its nests in dense aquatic vegetation. A number of catfish fossils have been found in Member I deposits including *Clarias*, *Bagrus* and *Synodontis*. *Clarias* can tolerate poorly oxygenated waters and are often associated with swampy habitats. *Lates*, on the other hand, are unable to tolerate poorly oxygenated waters and generally inhabit open, well oxygenated waters. The puffer fish *Tetraodon* inhabits shallow waters and eats invertebrates. The fish fauna from Member I of the Kibish Formation are indicative of shallow water environments, with fairly well oxygenated waters likely combined with fringe and channel environments in and around a delta setting (Trapani 2008).

7.9.4 Conclusion

The only mollusc recorded from Member I of the Kibish Formation is the freshwater oyster *Etheria*. This bivalve forms reefs on hard substrates in areas of high water flow such as rivers or the shores of large lakes in tropical habitats. Their presence indicates that a perennial flow of clean water and relatively shallow habitats were present at the time of deposition. This information confirms some of the conclusions reached based on other data, while adding important additional information also.

The early *Homo sapiens* populations of Omo Kibish would have had access to a mosaic habitat including open grasslands, areas or forest and permanent water in the form of a large drainage system associated with waterside habitats including shallow vegetated wetlands.

7.10 Summary

In the previous three chapters sites linked to hominin evolution have been examined from a palaeoecological perspective with a focus on the molluscan remains associated with each site. Sites examined include hominine sites from the Miocene and Pliocene of Africa, Plio-Pleistocene sites from Africa, the Middle East, Europe and Asia which contain early *Homo* fossils or artefacts indicating the presence of early hominins, and Middle Pleistocene sites with early archaeological records or fossils of archaic *Homo* species. Finally, the site of Omo Kibish, where the earliest evidence for *Homo sapiens* has been discovered, was examined.

The results of these site examinations will be analysed further in the next two chapters.

8 Review of results

In Chapters 5, 6 and 7 sites from the Miocene, Pliocene and Pleistocene were examined from a palaeoecological context. The molluscs from each site were analysed with a focus on what they revealed about the palaeoecology of each site. Each site was also examined using other data, mainly non-molluscan fossil faunal data, to build a picture of the palaeoecology.

In this chapter the results from Chapters 5, 6 and 7 are analysed so that the mollusc make up of each site can be compared and contrasted. The aim of this chapter is to examine the data from a palaeoecological perspective. The mollusc taxa are therefore divided into four ecological groups:

- Terrestrial
- Amphibious
- Aquatic (fresh water)
- Aquatic (marine)

The sites of Daka and Bodo are not included in the following sections because the gastropods in these sites have not been identified, making it impossible to determine their ecology.

8.1 Overview

The number of sites containing molluscs from the four broad ecological categories, terrestrial, amphibious, freshwater (here termed aquatic) and marine is shown in Figure 8.1.1.

The terrestrial molluscs (gastropods that live, feed and reproduce independent of water) are known from just over a third of the study's sites. Amphibious molluscs (air-breathing gastropods that spend time both in and out of the water), are known from almost two thirds of sites. Aquatic (freshwater) molluscs (freshwater bivalves and gastropods that live more or less permanently in water) are known from about 86% of sites, while marine molluscs are found in only about 6% of sites.

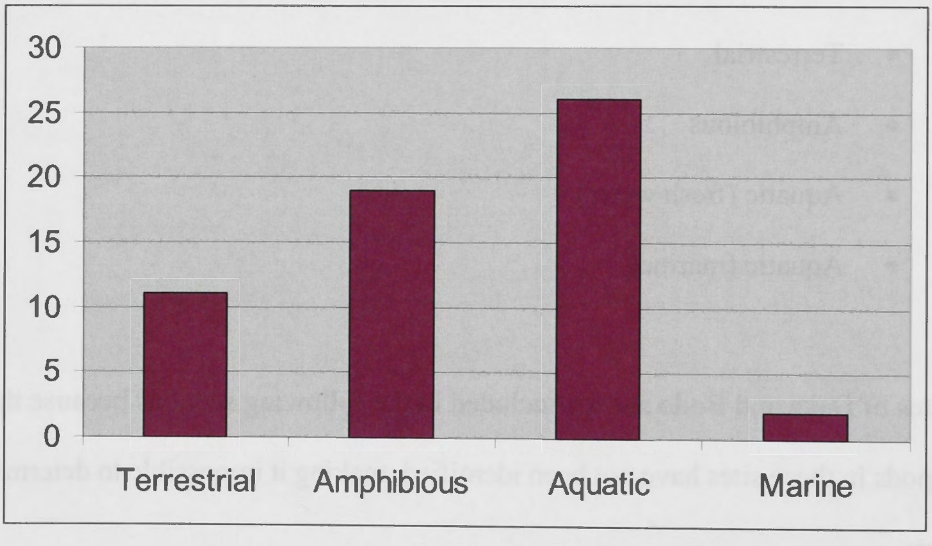


Figure 8.1.1: Number of Sites (n=30) with particular groups of mollusc present according to ecology.

These results no doubt are affected by taphonomic processes. Many of the sites surveyed were formed through hydrological processes and sedimentation associated with lakes and rivers, so it is not unexpected that freshwater molluscs would be found at a high percentage of sites. On the other hand, coastal sites are rare within the time-frame surveyed, and it is therefore not surprising that marine molluscs are not found at a high percentage of sites.

8.2 Terrestrial

Terrestrial snails are found in just over a third of the sites studied (Figure 8.2.1). The majority of terrestrial snail taxa found in the study come from just four sites: Fort Ternan, Laetoli, Humpata and Dmanisi, and for each of these sites terrestrial gastropods are the only molluscs known. Terrestrial snails have also been found in the Chiwondo Beds of Malawi, Olduvai Gorge Beds I, II and IV, Yuanmou and Pakefield. The majority of sites contain no terrestrial molluscs.

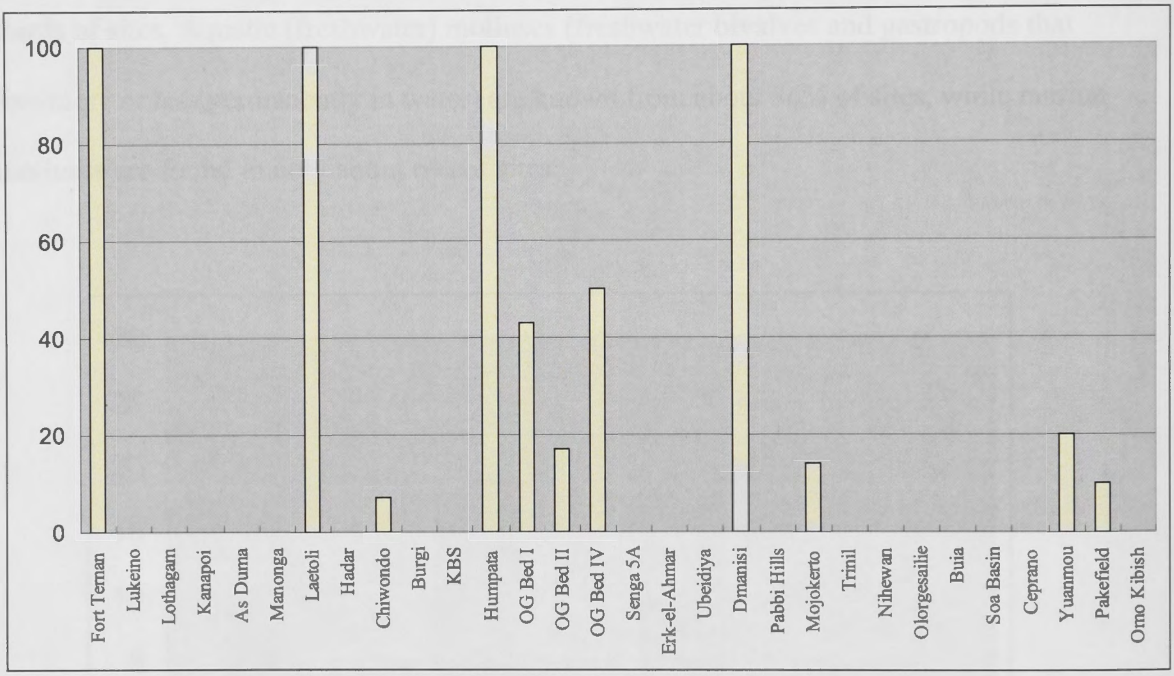


Figure 8.2.1: Percentage of mollusc taxa from each site identified as terrestrial gastropods (for number of taxa per site see Appendix 2)

The most common terrestrial snail in the study is *Achatina*, found at Laetoli, the Chiwondo Beds of Malawi, Humpata and Olduvai Gorge Bed II. Other genera of the family Achatinidae are *Burtoa*, found at Fort Ternan and Laetoli, and *Limicolaria*, found at Laetoli and Olduvai Gorge Bed IV. Since this is a tropical family these sites were most probably tropical too. Forest or forest edge habitats are likely for the sites at which *Achatina* and *Burtoa* are known, whereas *Limicolaria* is capable of inhabiting more open, arid habitats.

The genus *Edouardia* is known from Laetoli and Humpata, suggesting these sites share some similarities, and *Homorus* is known from Fort Ternan and Olduvai Gorge Bed I. These genera are primarily forest dwelling.

Streptostele is known from Laetoli and Olduvai Gorge Bed I, but no other terrestrial gastropod genus is found at more than one site. The most common terrestrial gastropod families are the Achatinidae, Subulinidae and Enidae.

The sites of Pakefield and Yuanmou have terrestrial gastropods within their assemblages not known from any other site. The terrestrial gastropods from the site of Dmanisi, which unlike Pakefield and Yuanmou only contains terrestrial gastropods, are not known from any other site.

8.3 Amphibious

A number of snail species inhabit wetlands and water bodies that temporarily dry up, and others spend time in permanent waters where they crawl above the surface and breathe air, such as by climbing on emergent vegetation. These gastropods belong to a number of different taxonomic groups, including the Ampullariidae, which, because they posses both gills and lungs, can spend time in and out of water. Most amphibious snails are pulmonates, possessing lungs instead of gills.

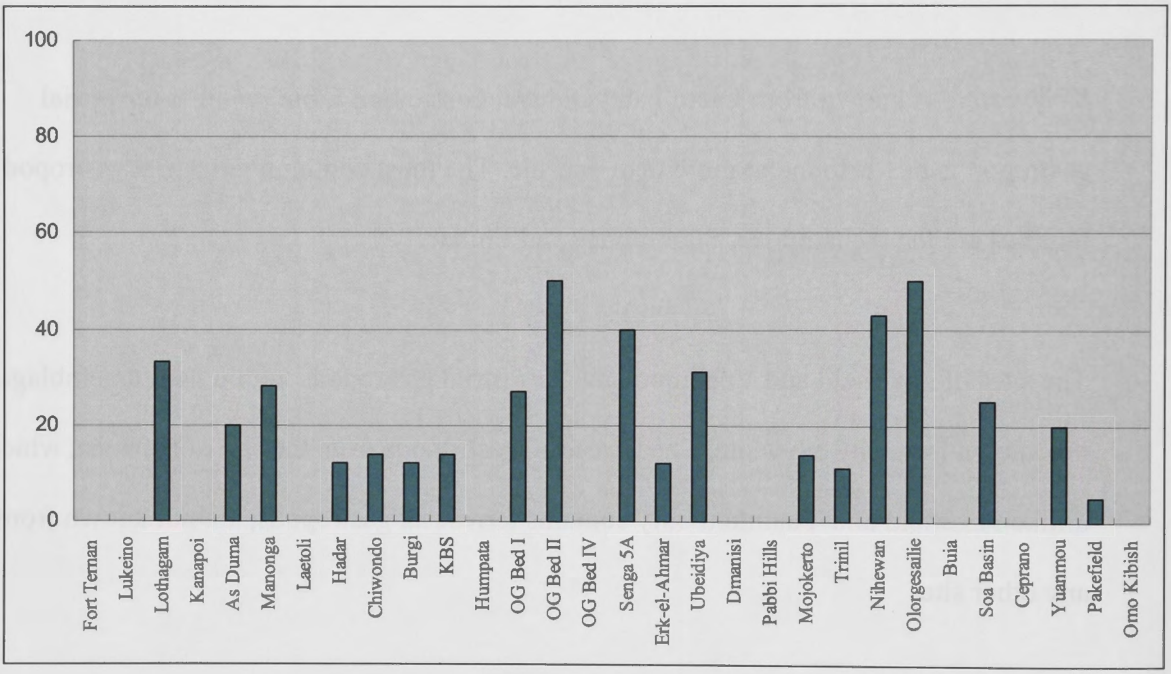


Table 8.3.1: Percentage of mollusc taxa from each site identified as amphibious gastropods (for number of taxa per site see Appendix 2)

Amphibious snails occur at about 63% of sites analysed (Figure 8.3.1). Unlike terrestrial gastropods, amphibious gastropods do not make up 100% of the molluscan fauna of any site. Generally, amphibious taxa make up between 10 and 30% of the molluscan fauna in the sites at which they occur. The highest representation at a site is 50%, but these are sites (Olorgesailie and Olduvai Gorge) where n=2. Amphibious gastropods are found at a greater percentage of sites than terrestrial gastropods.

Pila ovata is known from Manonga Valley and Senga 5A and *Pila conica* is known from Lothagam, Manonga Valley, the lower Burgi Member of the Koobi Fora Formation and the Chiwondo Beds of Malawi. Another species from Lothagam identified as *Ampullaria* most probably belongs to *Pila wernei*. Mojokerto and Trinil also have yielded *Pila* remains.

Most gastropods belonging to the clade Basommatophora are essentially air-breathing freshwater species. A number of sites at which hominine fossils or artefacts have been found also have gastropods from this group present. From a taphonomic viewpoint it is important to note that these pulmonate gastropods are often small and have relatively fragile shells, so preservation in the fossil record is not always assured, particularly for older sites. The two main families of Basommatophora associated with hominine sites in this study are the Planorbidae and the Lymnaeidae.

The Planorbidae include the two sub-families Planorbinae and Bulininae. The Planorbinae generally have discoid shells and are associated with aquatic vegetation in lentic pools and swamps. *Gyraulus* is known from Nihewan, Trinil, Yuanmou, Erk-el-Ahmar, and is very widespread in the Ubeidiya Beds (Tchernov 1973). A *Gyraulus*-like gastropod has also been discovered at As Duma and a planorbin gastropod is known from the late Pleistocene Busidima Formation deposits.

Planorbis is known from Nihewan and Ubeidiya. *Anisus* (=*Ceratophallus*) *natalensis* has been found at Olduvai Gorge Bed II and specimens belonging to the subfamily Planorbinae are known from Olorgesailie and the KBS Member of the Koobi Fora Formation.

The subfamily Bulininae consists of small to medium sized gastropods including the genus *Bulinus*. This genus is able to aestivate and therefore able to inhabit seasonal pools and streams and is perhaps the most characteristic gastropod of African freshwater habitats. It has been found in Bed I and Bed II of Olduvai Gorge, the upper Burgi and KBS Members of the Koobi Fora Formation, Hadar, The Chiwondo Beds of Malawi and Senga 5A. Members of this group are more likely to be found in ephemeral waterbodies, and waterbodies isolated from larger drainage areas, including flood plains. Significantly, 'pulmonate' gastropods can disperse from one water body to another without a connection, via transportation by birds, insects or other animals.

The freshwater limpet *Acroloxus lucustris* is known only from the site of Ubeidiya within this study.

Lymnaea natalensis is known from Olduvai Gorge Bed II. *Lymnaea* can apparently tolerate enormous ranges in temperature. *Lymnaea lagotis* is associated with the marshy layers of the Ubeidiya and Erk-el-Ahmar archaeological sites (Tchernov 1973). *Lymnaea* gastropods have also been found at Trinil, Nihewan and Pakefield. The genus *Radix* has been found at the Pakefield archaeological site. *Ameria duboisi* is known from Trinil.

An unidentified Basommatophora gastropod is also known from the Soa Basin deposits of Flores.

The amphibious snails in the study point to water bodies of either a permanent or temporary nature, with some genera pointing to more permanent (*Pila*) and some to more temporary (*Bulinus*) water bodies. In between there is a range but the most common feature seems to be aquatic vegetation, or at least vegetation in moist sands. It can be inferred that the sites that share amphibious snails also share in common areas of relatively shallow, still waters with abundant aquatic vegetation.

8.4 Aquatic

Aquatic molluscs are the best represented sub-group within the study (Figure 8.4.1). They occur at about 86% of sites, and at many of these they are the best represented group in terms of the number of taxa present. At six sites, for example, they are the only mollusc group known, and at a further nine they represent more than 70% of the molluscan taxa. Unlike terrestrial and amphibious molluscs, which are restricted to the Gastropoda, aquatic molluscs include the Gastropoda and Bivalvia.

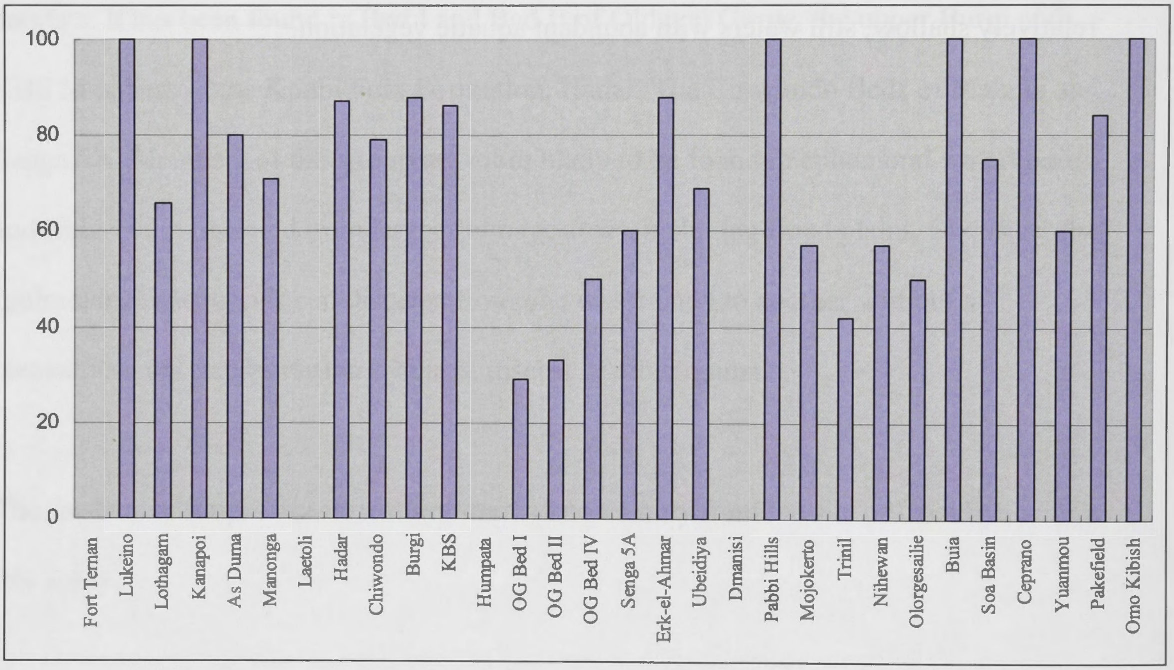


Figure 8.4.1: Percentage of molluscan taxa for each site identified as aquatic (freshwater) (for number of taxa per site see Appendix 2)

Only four of the sites examined had no aquatic mollusc taxa present: Fort Ternan, Laetoli, Humpata and Dmanisi.

8.4.1: Gastropods: Aquatic freshwater

Most of the prosobranch freshwater gastropods associated with the sites in this survey belong to the clade Caenogastropoda, most to the group Sorbeoconcha and others to the Architaenioglossa. The clades Heterobranchia and Cycloneritimorpha are both represented in the study.

Theodoxus jordani belongs to the family Neritidae, the sole representative of the Cycloneritimorpha in this study. It is found at Erk-el-Ahmar and Ubeidiya. Many neritids are marine, but *Theodoxus* inhabits freshwater.

The Architaenioglossa contain three families; the amphibious Ampullariidae, dealt with in the previous section, the Maizanidae, which contains the terrestrial genus *Maizania*, found at Fort Ternan, and the Viviparidae.

The Viviparidae are one of the best represented families in the survey (Figure 8.4.2), with two genera, *Viviparus* and *Bellamya*, occurring in just under half (46%) of all sites examined. *Bellamya* is known from As Duma, the upper Burgi and KBS Members of the Koobi Fora Formation, Hadar, Manonga Valley, the Chiwondo Beds of Malawi, Pabbi Hills, Kanapoi, Trinil, Lothagam and Dikika. These sites have in common therefore a tropical climate, and the presence of a permanent water body connected to a relatively large drainage system. *Viviparus* is broadly similar in terms of morphology and palaeoecology to *Bellamya*, although it is found in temperate as well as tropical habitats, and is known from Erk-el-Ahmar, Ubeidiya, Yuanmou and Pakefield.

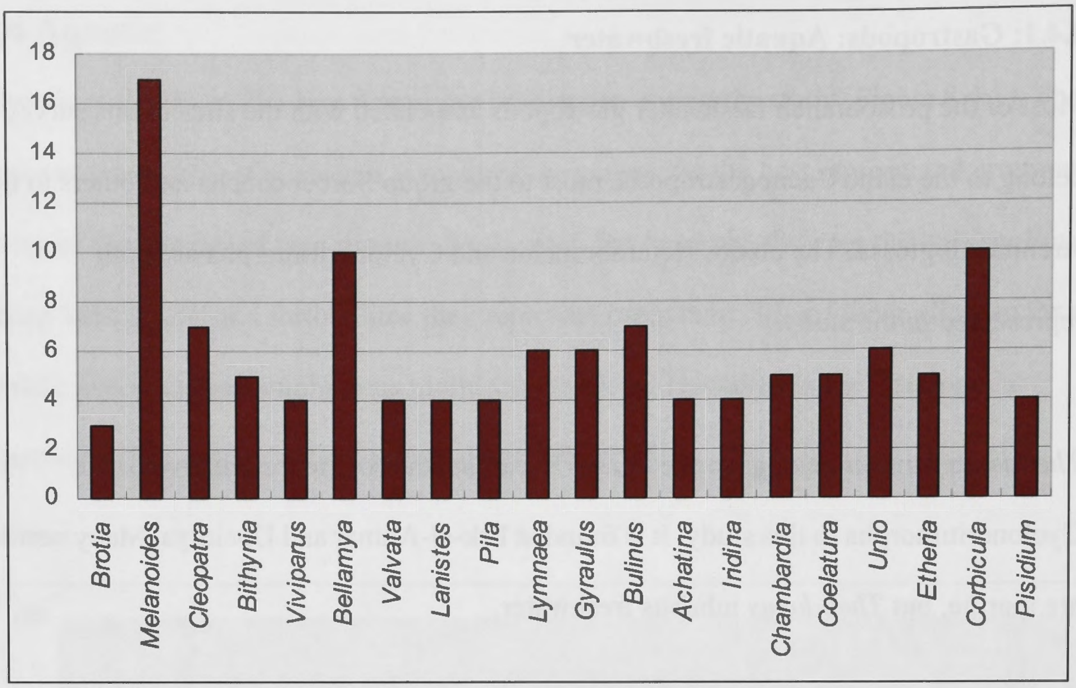


Figure 8.4.2: Number of sites at which genera found at three or more sites occur

The number of sites *Bellamya* and *Viviparus* have been discovered at is relatively high. These sites range from late Miocene (Lothagam, Kanapoi and As Duma), to mid-Pleistocene (Pakefield), and include African (Chiwondo), European (Pakefield), Middle Eastern (Ubeidiya) and East Asian (Yuanmou) sites. All these sites appear to share in common some type of permanent water body such as a lake, slow flowing river or permanent stream.

The Sorbeoconcha contain a number of freshwater families associated with various hominine fossil and archaeological sites. The family Hydrobiidae is represented by two species, *Falsipyrgula barroisi* and *Hydrobia longiscata*, at Erk-el-Ahmar in the Jordan Valley. Two genera from the family Pachychilidae occur at sites within the survey. *Brotia* has been discovered from middle Pleistocene deposits of the Soa Basin, Flores, as well as from early Pleistocene deposits at Trinil and Mojokerto, Java. *Potadoma* occurs at Kanapoi, indicating that at least gallery forest was present at this early hominine site.

Of all the molluscan families in the survey the Thiaridae is the most widespread in terms of the numbers of sites at which it occurs (Figure 8.4.3). Within this family of tropical snails, the genus *Melanoides* occurs at more sites than any other genus (Figure 8.4.2).

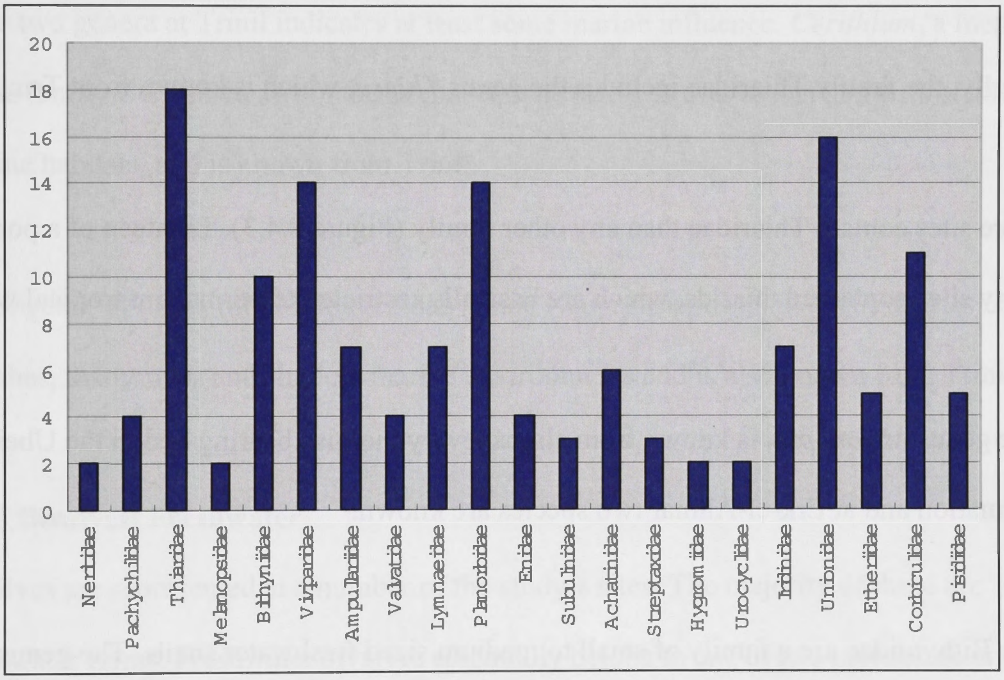


Figure 8.4.3: Number of sites at which families found at more than one site occur

Melanoides is known from 60% of the sites surveyed: Lukeino, Kanapoi, Lothagam, As Duma, Hadar, Manonga Valley, the upper Burgi and KBS Members of Koobi Fora, Chiwondo, Senga 5A, Erk-el-Ahmar, Ubeidiya, Mojokerto, Trinil, Buia, Olduvai Gorge Beds I and II, the Soa Basin, and the Hadar and Busidima Formations at Dikika.

Another member of the Thiaridae is *Tarebia granifera*, which is found at Trinil and the Soa Basin.

Cleopatra is restricted to African sites and in this study is known from sites ranging in age from Miocene to early Pleistocene, including Kanapoi, Hadar, Senga 5A, the upper Burgi and KBS Members of Koobi Fora, Manonga Valley, As Duma and Chiwondo. *Cleopatra* has also been identified from the Dikika deposits (see Chapter 4).

Finally, the family Thiaridae includes the genus *Thiara*, which is known from Trinil.

More sites contain Thiaridae than any other family (Figure 8.4.3). Eighteen of a possible thirty sites contained thiarids, which are basically restricted to permanent tropical water.

The genus *Melanopsis* is known from almost every mollusc bearing bed in the Ubeidiya Formation and at Erk-el-Ahmar two species are known.

The Bithyniidae are a family of small to medium sized freshwater snails. The genus *Bithynia* is found in Ubeidiya, Erk-el-Ahmar, Olorgesailie, Trinil, Pakefield and Mojokerto.

Gabbiella has been found in the Chiwondo Beds of Lake Malawi and Manonga Valley. The Lower Heterobranchia, of the clade Heterobranchia, includes the Valvatidae, a family of freshwater gastropods which has been found in the upper Burgi Member of the Koobi Fora Formation, Pakefield, the Chiwondo Beds of Lake Malawi and Ceprano.

8.4.2 Gastropods: Marine

Although the vast majority of gastropods in the examined sites are terrestrial or freshwater, there are also a few marine examples at the site of Trinil.

Also from the Lower Heterobranchia group of the clade Heterobranchia, the family Pyramidellidae contains the genera *Quirella* and *Cingulina*. These gastropods inhabit sands and muds in shallow marine environments (Joordens et al. 2009). The presence of these two genera at Trinil indicates at least some marine influence. *Cerithium*, a member of the family Cerithiidae, from the Sorbeoconcha clade, is also associated with shallow marine habitats, and is known from Trinil.

Melongena, of the family Melongenidae (clade Neogastropoda), inhabits estuaries, salt marshes, mangroves and shallow marine environments and is also known from Trinil.

8.4.3 Bivalves: Freshwater

Bivalves are represented at a number of the study's sites. The majority of these are freshwater forms. Freshwater bivalves essentially belong to one of two taxonomic orders; the Veneroida, an order which includes freshwater and marine genera, and the Unionoida or freshwater pearly mussels, or naiads, which contain only freshwater varieties.

- **Veneroida**

The order Veneroida contains a number of families common to sites within the study. The Corbiculidae are tropical and subtropical fresh and brackish water bivalves that are today widespread throughout the world (Banarescu 1990). Corbiculids are dispersed passively by currents, and by attachment to fish can be transported upstream and by birds to unconnected water bodies (Van Damme 1984).

Corbicula species have been discovered at Hadar, in the Upper Burgi and KBS Members of Koobi Fora, at Ubeidiya, the Chiwondo Beds of Malawi, Olduvai Gorge Beds I and II, Nihewan, Yuanmou and Trinil. These sites probably share together at least some habitat characteristics such as running water, either in the form of a stream or river or large shallow lake with well-oxygenated margins, relatively shallow waters and possibly moderately saline waters.

The species *Polymesoda coaxans* is a lotic freshwater inhabitant of mud in intertidal, estuarine mangrove environments (Bernard et al. 1993). Molluscs with affinities to this species have been found at Mojokerto and Trinil, where the genus *Geloina*, considered by some a synonym of *Polymesoda*, has been identified.

Members of the family Pisidiidae (fingernail, pill or pea clams) are often associated with transient bodies of water, due partly to their ability to disperse efficiently between watersheds (Burky 1983), so that they can be found in habitats ranging from temporary ponds and swampy woodlands to permanent ponds, lakes, streams and major rivers. Because of this they are one of the most widely dispersed and abundant families of freshwater bivalve known. The genus *Pisidium* has been found at Erk-el-Ahmar, Ceprano, Nihewan and Pakefield, where more than six different species are known to have existed. *Sphaerium*, a freshwater genus containing temporary water body inhabitants, is also known from Pakefield. The pisidiid clam *Eupera* was found in the upper Burgi member of the Koobi Fora Formation.

One member of the Dreissenidae family, *Dreissena chantrei* has been discovered at Erk-el-Ahmar. This genus probably comes originally from the Caspian-Aral region and can tolerate fresh and brackish waters (Banarescu 1990).

- **Unionoida**

The Unionoida are represented in this study by three families. The Iridinidae are an endemic African family and include the genera *Aspatharia,* which is known from Kanapoi; *Chambardia*, known from Manonga Valley, Hadar, Dikika and the KBS and Burgi Members of Koobi Fora; *Iridina*, found at Kanapoi, the KBS and upper Burgi Members of Koobi Fora and Lukeino; and *Pleiodon* known from the KBS and upper Burgi Members of Koobi Fora. The Iridinidae are essentially a tropical family. Sites at which they are found therefore are inferred to be tropical regions with relatively large, permanent and long lived drainage systems.

The Unionidae are one of the most diverse and widespread families of freshwater bivalves and they are well represented in this survey (Figure 8.4.3). Found in permanent water bodies such as lakes, rivers and streams, they are not found in high mountain lakes because these lack nutrition and suitable fish hosts (Smith 2001).

Coelatura has been found at Senga 5A, the upper Burgi and KBS Members of the Koobi Fora Formation, Chiwondo and Lothagam, *Unio* is known from Hadar, Erk-el-Ahmar, Ubeidiya, Ceprano, Olduvai Gorge Bed IV and Pakefield where at least three species have been discovered.

Elongaria orientalis has been discovered at Trinil and Mojokerto. At Ubeidiya the unionid *Leguminaia* is part of the mollusc fauna, while at Pabbi Hills three unionid genera *Indonaia*, *Parreysia* and *Lamellidens* are known. At Nihewan the unionid bivalves *Lamprotula* and *Cuneopsis* are present, and at Trinil *Rectidens sumatrensis*, an inhabitant of lakes and rivers, has been discovered.

Etheria elliptica is known from sites in this study from the early Pliocene to the late Pleistocene including Kanapoi, Lothagam, the KBS Member of the Koobi Fora Formation, Chiwondo and Omo Kibish. Since the Etheriidae are a tropical family, it can be inferred that the sites at which it is found were tropical at the time of deposition.

8.4.4 Bivalves: Marine

Although the majority of sites contain freshwater clams or mussels, a small number also have marine species, especially the Javan site of Trinil. These include a number of genera that today inhabit soft marine sediments, usually from shallow intertidal environments such as *Theora*, *Gari* and *Tellimya*. Together these bivalves are a strong indication that marine habitats were proximal to the Trinil site.

At Mojokerto the marine oyster *Crassostrea* is also known. This indicates that the coast was within the vicinity of the Mojokerto site.

8.4.5 Scaphopoda

Trinil also yielded the only non-bivalve or -gastropod mollusc in the study, a tusk shell *Dentalium*, which belongs to the class Scaphopoda. These marine molluscs live on soft sandy or muddy substrates where they burrow in with their foot. *Dentalium* occurs in marine waters world wide, except the polar regions from depths of 6-1830 metres. In India it occurs in coastal and littoral waters (Bhamrah & Juneja 2001).

The presence of a scaphopod at Trinil points to some connection with the coast. Shells of these molluscs have been prized by humans as ornaments and for trade and exchange for thousands of years (e.g., Clarke & Clarke 1980, Bar-Yosef Mayer 2005).

8.5 Conclusion

This chapter reviewed the results from Chapters 5 to 7, grouping the molluscs into broad ecological categories and comparing the sites to determine which molluscs were common to more than one site. In Chapter 9 the results of this study will be analysed further to determine in more detail what they reveal about the palaeoecology of the various sites, which will be grouped into categories based on their hominine status. This will allow comparisons between site groups, to see for example if a particular mollusc taxon or group of taxa are more prevalent at one group than another.

9 Analysis and synthesis

In Chapter 8, the results from Chapters 5 to 7 were reviewed with each taxonomic group placed into an ecological context. In this chapter the results are examined further to see what they reveal about the palaeoecology of the sites examined. Visual analysis via tables and graphs are used to answer questions concerning the ecological characteristics of ancient hominine sites.

One of the limitations of this study is the relatively small sample size, particularly the number of non-hominine sites. For reasons of practicality the number of sites in the study was restricted to about thirty, but since every effort was made to include relevant hominine sites fitting the specified criteria, the sites are skewed in favour hominine compared to non-hominine sites. These latter were included for comparison, but because the sample of non-hominine sites is small, gaining meaningful statistical results is difficult.

Non-hominine sites in the following analysis are compared to various hominine groups; including 'erectine grade' and non-'erectine grade' hominine, and *Homo* and non-*Homo* hominine sites. It is possible when analysing the molluscan data from a palaeoecological perspective to ask a number of questions. Here the analysis will concentrate on the terrestrial, amphibious and aquatic molluscs, including questions such as is it possible to determine a) whether water was present at a site, and b) if so, whether it was permanent or ephemeral? Other questions addressed are how open or closed was the site, what type of vegetation existed, what was the climate like, was there still or flowing water, and what was the depth?

9.1 Theoretical issues

As noted in Chapter 1, discussing hominine evolution can be problematic because of the many disagreements researchers have regarding the taxonomy and phylogeny of the Homininae.

In this analysis the term ‘erectine grade’ is used to specify populations of big-brained, big bodied hominins who emerged, at least according to the fossil record, some time in the early Pleistocene, and who dispersed widely between Africa, Asia and Europe. These populations share in common characteristics such as a long, low braincase and several other features which distinguish them from australopithecines and *Homo sapiens*. ‘Erectine grade’ hominins are generally considered not to have had arboreal adaptations (Klein 1999).

The informal term ‘erectine grade’ was coined by Groves (2009) to group the ‘archaic’ *Homo* fossils sometimes referred to as *Homo erectus* (*sensu lato*), *Homo* cf. *erectus*, or ‘archaic’ *Homo*. While some researchers place all or most Pleistocene *Homo* species in a single species (*Homo erectus*), others suggest this is a mistake. Groves, for example, demonstrated that early Pleistocene *Homo* fossils from the Turkana Basin, formerly allocated to the species *Homo erectus*, did not fit the established criteria for this species, and therefore established *Homo ergaster* Groves & Mazak 1976.

Fossil species considered ‘erectine grade’ are those that share to differing degrees and in different combinations, a suite of features including relatively thick cranial bones with a long, low skull cap, prominent brow ridges, prominent nuchal crests, sagittal keel, limited basicrania flexion resulting in a peculiar poise of the head (Maier & Nkini 1985), femoral bones featuring platymeria, generalised postcranial pachyostosis, narrowest femoral point distal to the midpoint, long and more horizontal femoral necks (than modern humans) and wide pelvic bones, i.e., flared ilia (e.g., Kennedy 1985, Groves 1989).

This grade includes *Homo erectus* (*sensu stricto*) from Java (Trinil, Sangiran), *Homo pekinensis* from China (Zhoukodian), *Homo ergaster* from the Turkana Basin (ER and KNM WT fossils) and other fossils from east Africa such as OH 9 and other remains from Olduvai Gorge, OL 45500 from Olorgesailie, fossils from Daka, Bouri, Bodo, the Dmanisi hominins, fossils assigned to *Homo heidelbergensis* (e.g., Boxgrove), plus later fossils from Europe and Asia such as those from Ceprano and Dali.

Since it is assumed that the stone artefacts found at early and middle Pleistocene sites outside Africa come from *Homo erectus*-like species, these sites are attributed to 'erectine grade' hominins for this study, but the possibility remains that the makers of these stone tools were morphologically different from 'erectine grade' hominines.

Non-'erectine grade' hominine sites include those that contain *Australopithecus* or other early hominines such as *Orrorin*, as well as *Homo rudolfensis* and *Homo habilis* (Table 9.1.1). These taxa as a 'grade' appear to have certain adaptations of the arm in common which apparently allowed them to climb efficiently (Wood & Collard 1999). Their often small stature is not unexpected in this context since being taller would mean being heavier, which would be a disadvantage for a climbing animal.

Table 9.1.1: Sites grouped according to hominine status and epoch. Omo Kibish not included because it is considered *Homo sapiens*, not 'erectine grade'

Epoch	**Non-hominine**	**Non-'erectine grade' hominine, includes *habilis* and *rudolfensis***	**'erectine grade'**	
Miocene- early Pliocene	Fort Ternan Manonga Valley	Lukeino Lothagam Kanapoi As Duma Laetoli Hadar		
Plio-Pleistocene	Humpata	Upper Burgi Olduvai Gorge I Chiwondo Beds	**Africa** Olduvai Gorge II KBS Senga 5A	**Eurasia** Dmanisi Pabbi Hills Erk-el- Ahmar Ubeidiya Mojokerto Trinil Nihewan
Middle Pleistocene			**Africa** Olduvai Gorge IV Daka Bodo Buia Olorgesailie	**Eurasia** Yuanmou Soa Basin Pakefield Ceprano

These non-'erectine grade' hominines possess bipedal adaptations, but do not appear well adapted to open grasslands, because they almost certainly would have lacked adequate speed. In fact recent studies suggest that bipedalism may have begun as a climbing adaptation (Thorpe et al. 2007), and Wrangham et al. (2009) have argued that terrestrial bipedalism may have developed from shallow wetland wading for aquatic underground storage units, as opposed to arid grasslands. If human bipedalism was associated with arboreal apes that occasionally waded, we would expect the palaeoecologies of the sites at which they lived to reflect this, in having areas of forest and shallow wetlands.

Table 9.1.1 reflects the dispersal of the 'erectine grade' hominine group. While hominines were restricted to Africa from the Miocene and for most of the Pliocene, from the earliest Pleistocene hominins had spread from east Africa to Georgia, Java and China, and by a million years ago had crossed Wallace's Line (Soa Basin).

Since 'erectine grade' hominines have no obvious arboreal adaptations, it seems plausible that they dispersed after having left the trees. The alternative would require parallel adaptation in different regions.

9.2 Models of hominine evolution

The hypothesis that 'erectine grade' hominins evolved in African savannas as specialist hunters and moved out of Africa by following savanna grasslands forms the basis for a number human evolutionary models (Stanley 1992, Bramble & Lieberman 2004, MacDonald 2006, Lieberman et al. 2007). Alternative models argue that 'erectine grade' hominins may have originated outside Africa (Dennell & Roebroeks 2005), and, as discussed above, that wet as well as arid savannas were influential for hominine evolution (Wrangham 2005). It has also been argued that *Homo* may have emerged as a coastal specialist (Sauer 1962).

Coastal savannas may have offered an alternative niche for early hominins, allowing them to disperse more widely than if restricted to isolated forest fragments (other hominoids), or savanna grasslands (baboons). If they did adapt to coastlines, we would expect some very distinct changes in their anatomy and physiology (Hardy 1960).

Hominin populations following savanna coasts would have come across rivers which led to inland savannas via freshwater drainage systems. Dispersal of hominine populations between savanna eco-blocks via rivers and lakes has been postulated by Avery (2003) and Kingdon (2003). The role of coasts in the dispersal of hominins and the lack of evidence due to now submerged landscapes are discussed by Bailey et al. (2007).

The following analyses and discussion will be in light of the palaeoanthropological models outlined above.

9.3 Palaeoecological tests

Chapters 5 to 7 showed that it is possible to make inferences about the palaeoecological characteristics of a site based on the molluscan fauna. The mollusc data help corroborate what other data have revealed, and occasionally the mollusc data add some specific detail to the overall palaeoecological picture. In this chapter the molluscan faunas from the various sites are compared. First the molluscs are divided into families and grouped according to the sites at which they occur, then the molluscs are divided into taxonomic groups and compared in terms of the proportion of the molluscan fauna they make up in each of the different groups of sites. 'Erectine grade' sites here include most, but not all, *Homo* sites.

Since the numbers of sites and molluscs differ from group to group, percentages are used in many of the analyses. Graphs show the data arranged so that each group of sites can be compared.

- **Families**

Mollusc families can be informative from a palaeoecological point of view because most have a set of specific ecological requirements. Whether the ecological requirements of a specific mollusc taxon can be inferred from its relationship with modern mollusc families is uncertain. In this thesis it is assumed that modern characteristics apply generally to their fossil counterparts. It is assumed here, for example, that bivalves are an indication of permanent water.

In this section the following question is posed: Do the families differ significantly from one group of sites to another, in terms of the percentages of terrestrial, amphibious and aquatic mollusc taxa found at each site?

A number of mollusc families were found at the sites analysed, many occurring at a single site only. Here, so that the data is more manageable, families found at more than one site are analysed. The various groups of sites are compared in terms of the percentage of terrestrial, amphibious and aquatic taxa that make up the mollusc fauna (Figure 9.3.1).

The Thiaridae, today fresh and brackish water inhabitants of tropical and subtropical regions, make up a high proportion of the non-'erectine grade' hominine group, comprising 20% of the total known taxa. This family is also found at non-hominine and 'erectine grade' hominine of sites, where it makes up 11 and 12% of the taxa respectively. The Viviparidae makes up 13% of the non-'erectine grade' hominine site's molluscan fauna, while the Ampullariidae makes up 11% of the molluscan fauna at non-hominine sites. These sites also contain relatively high percentages of the families Enidae, Subulinidae and Hygromiidae (11%), all terrestrial pulmonates.

The non 'erectine grade' hominine sites yielded high proportions of riverine (Viviparidae, Iridinidae) and swamp (Thiaridae) taxa, non-hominine sites had high proportions of swamp (Thiaridae, Ampullariidae), and forest (Enidae, Subulinidae, Achatinidae) taxa, and 'erectine grade' sites had high proportions of swamp (Thiaridae) and river (Viviparidae, Unionidae) taxa, but very low proportions comparatively of forest dwelling taxa (Subulinidae, Achatinidae).

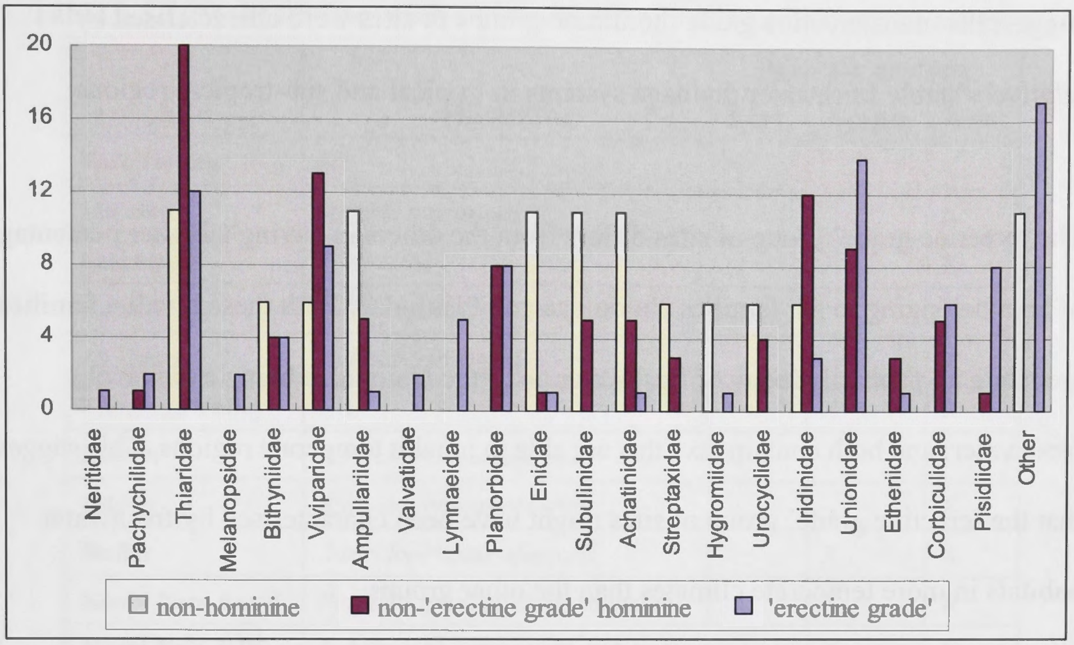


Figure 9.3.1: Percentage of families as a total of the molluscan fauna for each group of sites (non-hominine: n=18, non-'erectine grade': n=76, 'erectine grade': n=151)

The non-'erectine grade' hominine group of sites contained no mollusc taxa belonging to families that were not represented at least at two sites, whereas the non-hominine and 'erectine grade' group of sites were both well represented by taxa that occurred at only one site (11 and 17% respectively – 'Other' column: Figure 9.4.1). For the non-hominine group of sites the families occurring only at one site were terrestrial gastropods, whereas for the 'erectine grade' group of sites many were marine bivalves and snails, especially numerous taxa from Trinil.

The non-'erectine grade' hominine sites have a molluscan fauna made up of a relatively high proportion of the families Thiaridae, Viviparidae and Iridinidae. Today, apart from being mostly freshwater inhabitants of large stable drainage areas, these families are characterised by their distribution in tropical and sub-tropical habitats, which might suggest that non-‘erectine grade’ hominine groups of sites were characterised by relatively stable freshwater drainage systems in tropical and sub-tropical regions.

The ‘erectine grade’ group of sites differs from the others in having a higher percentage of taxa belonging to the families Unionidae and Pisidiidae. Both these bivalve families are made up primarily today of freshwater taxa (the Unionidae being exclusively freshwater) and both contain taxa that are able to inhabit temperate regions. This suggests that the ‘erectine grade’ group of sites might have been characterised by freshwater habitats in more temperate climates than the other groups.

- **Ecology**

The molluscs in this section are divided into the basic ecological units of terrestrial, amphibious and aquatic (Table 9.3.1). In this section each mollusc taxon is separated into one of three ecological categories (Table 9.3.1). Terrestrial molluscs can live independently of permanent water, amphibious molluscs require water but can tolerate ephemeral sources, and aquatic molluscs require permanent water.

Most sites contain aquatic or amphibious molluscs, the exceptions being Fort Ternan, Humpata, Laetoli and Dmanisi. There are no faunal indicators for permanent water; no bivalves, fish, crocodilians or hippopotamids, at either Laetoli or Humpata. Other data suggest the presence of at least ephemeral water at Laetoli, and to a lesser extent Humpata.

Table 9.3.1: Molluscs from each site representing particular ecological categories

Site	Hominine	Mollusc ecology		
		Terr.	Amph.	Aqu.
Fort Ternan	Nil	X		
Lukeino	*Orrorin tugenensis*			X
Lothagam	?Hominine		X	X
Kanapoi	*Australopithecus anamensis*			X
As Duma	*Ardipithecus ramidus*			X
Manonga Valley	Nil		X	X
Laetoli	*Australopithecus afarensis*	X		
Dikika	*Australopithecus afarensis*			X
Hadar	*Australopithecus afarensis*		X	X
Koobi Fora Burgi	*Paranthropus boisei, Homo habilis*		X	X
Koobi Fora KBS	*P. boisei, H. ergaster, H. habilis*		X	X
Humpata	Nil	X		
Chiwondo	*P. boisei, H. rudolfensis*	X	X	X
Olduvai Gorge I	*P. boisei, H. habilis*	X	X	X
Olduvai Gorge II	*P. boisei, H. habilis, H. erectus*	X	X	X
Olduvai Gorge IV	*H. erectus*	X		X
Senga 5A	*Homo* (artefacts)		X	X
Erq-el Ahmar	*Homo* (artefacts)		X	X
Ubeidiya	*Homo* (artefacts)		X	X
Dmanisi	*H. georgicus*	X		
Pabbi Hills	*Homo* (artefacts)			X
Mojokerto	*H. erectus*	X	X	X
Trinil	*H. erectus*		X	X
Nihewan	*Homo* (artefacts)		X	X
Daka	*H.* cf. *erectus*			X
Olorgesailie	*H.* cf. *erectus*			X
Buia	*H.* cf. *erectus*			X
Soa Basin	*Homo* (artefacts)			X
Bodo	*H.* cf. *erectus*			X
Ceprano	*H.* cf. *erectus*			X
Yuanmou	*H.* cf. *erectus*	X	X	X
Pakefield	*Homo* (artefacts)	X	X	X

At Fort Ternan there was clearly water present, as indicated by *Kenyapotamus*, Potamidae and *Crocodylus* (Andrews & Walker 1976). At Dmanisi the non-molluscan fauna lacks evidence for permanent water, but other indicators suggests the site accumulated in association with a lake, which was formed when a lava flow blocked a river, or rivers (Gabunia et al. 2000).

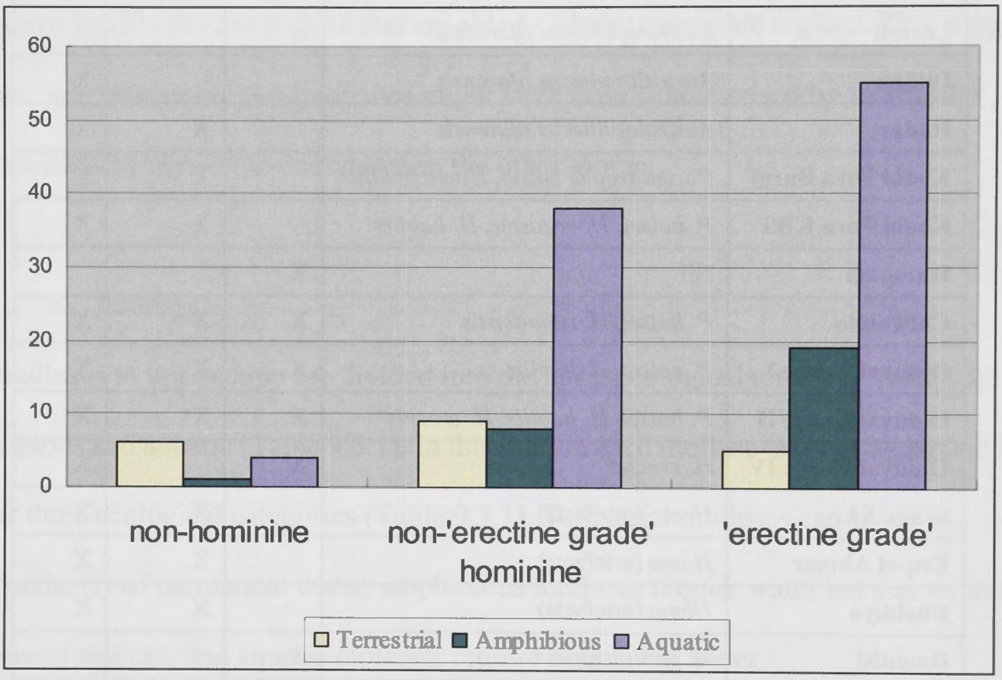


Figure 9.3.2: The number of taxa according to ecology at different groups of sites

The aquatic molluscan fauna can be further divided into freshwater and marine taxa. Figure 9.4.2 shows the number of mollusc taxa according to ecology per group of sites. The non-hominine sites obviously contain far fewer families than the other two groups of sites, which reflects the comparatively small number of sites (e.g., non-hominine n=3, ‘erectine grade’ n=19). The other observation is the high proportions of aquatic mollusc taxa in each of the hominine groups of sites, compared to the non-hominine sites.

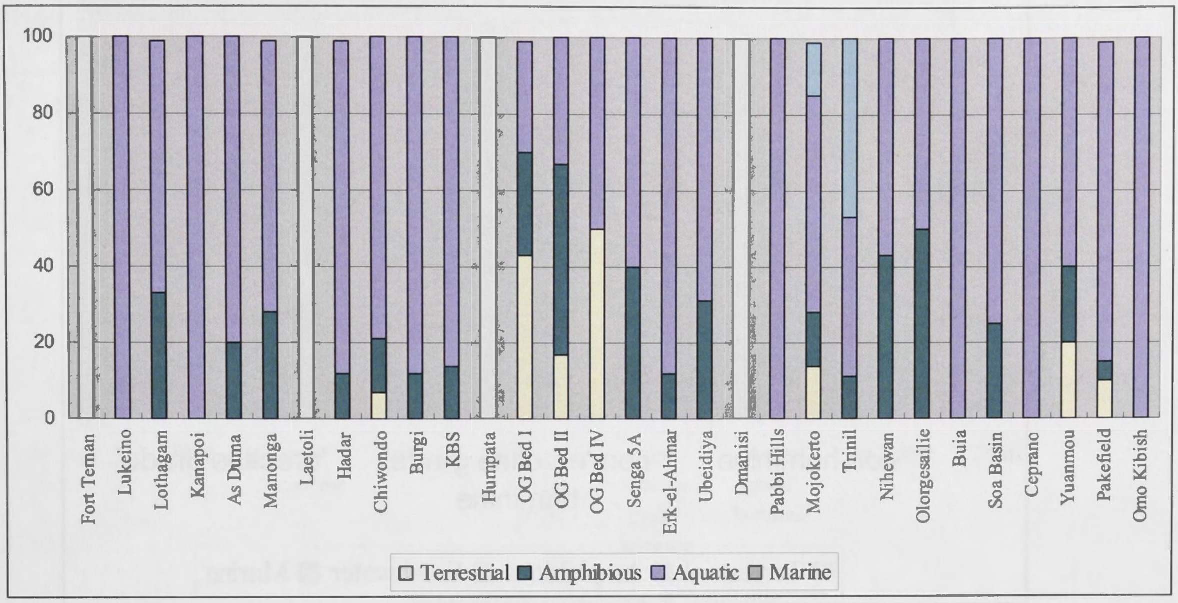


Figure 9.3.3: The proportion of taxa of different ecological groups at each site, as a percentage (for n see Appendix 2)

When the mollusc taxa are divided according to their ecological status, and aquatic molluscs are divided into freshwater and marine (Figure 9.3.3), freshwater molluscs are the most prevalent. Freshwater molluscs occur at 26 of the 30 sites, amphibious molluscs occur at 19, marine molluscs at two, and terrestrial snails at 11. When they do occur, terrestrial snails frequently dominate the site assemblage, in four of the 11 sites, for example, they make up 100% of the assemblage.

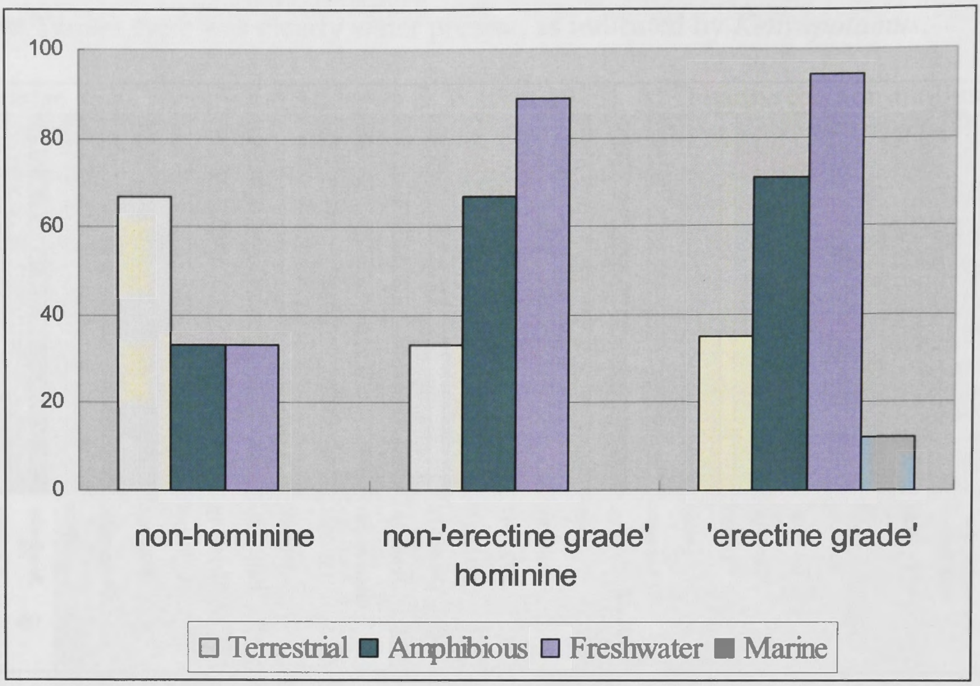


Figure 9.3.4: The percentage of sites which have yielded molluscs of a particular ecology (non hominine: n=3, non-'erectine grade' hominine: n=10, 'erectine grade': n=19)

Terrestrial mollusc taxa are found at a higher proportion of non-hominine sites than they are at the two hominine groups of sites. Aquatic and amphibious taxa, on the other hand, occur at more hominine sites proportionally compared to non-hominine sites (Figure 9.3.4). The two hominine groups of sites are visually much more similar to each other than either is to the non-hominine group. The difference is that marine taxa are known from a relatively small percentage of 'erectine grade' sites.

9.4 Statistical analysis

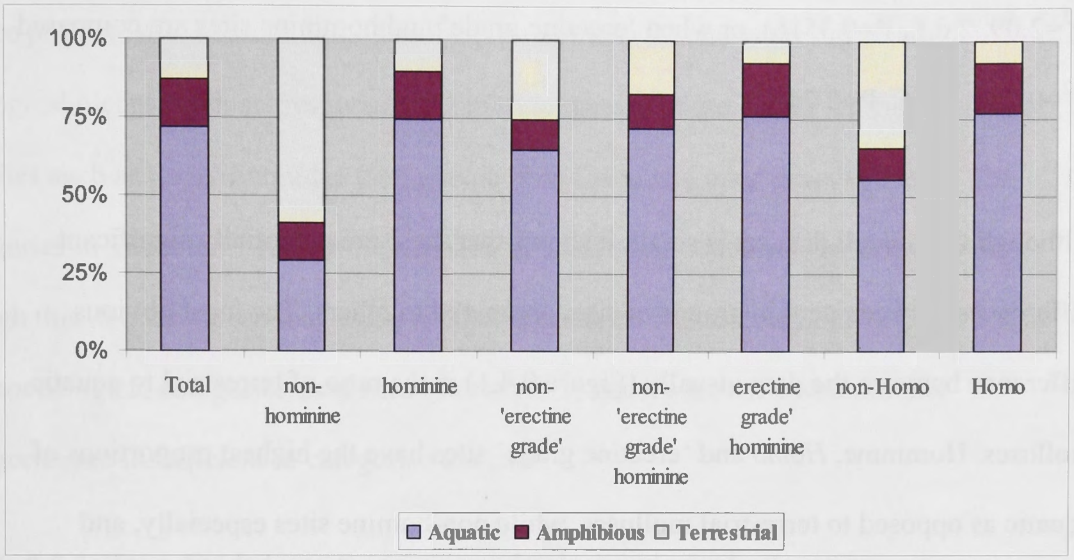


Figure 9.4.1: The proportion of mollusc taxa according to ecology at various groups of sites (total n= 247, non hominine n=17, hominine n=230, non-‘erectine grade’ n=97, non-‘erectine grade’ hominine n=80, ‘erectine grade’ n=150, non-*Homo* n=58, *Homo* n=189)

When the molluscs are divided into ecological categories and the groups are compared, a few groups look to be different from the others (Figure 9.4.1). Chi Square tests show that when compared directly, non-hominine sites are significantly different from hominine sites (χ^2=54.787, 2 d.f., P<0.001), *Homo* and non-*Homo* sites are significantly different (χ^2=22.532, 2 d.f., P<0.001), as are ‘erectine grade’ and non-‘erectine grade’ sites when they are directly compared (χ^2=12.964, 2 d.f., P=0.06). Also significantly different are ‘erectine grade’ and non-‘erectine grade’ hominine sites (χ^2=5.618, 2 d.f., P=0.06) and non-hominine sites compared to the group overall (χ^2=47.358, 2 d.f., P<0.001).

No such significance is evident when the sites as a whole are compared with the hominine goup of sites (χ^2=0.453, 2 d.f., P=0.7973), or with the 'erectine grade' group of sites (χ^2=2.09, 2 d.f., P=0.3516), or when 'erectine grade' and hominine sites are compared (χ^2=0.588, 2 d.f., P=0.7452).

Although the overall data set is small, it shows that there are potentially significant differences between certain groups of sites compared to others. The most obvious difference between the data visually (Figure 9.4.1) is the ratio of terrestrial to aquatic molluscs. Hominine, *Homo* and 'erectine grade' sites have the highest proportions of aquatic as opposed to terrestrial molluscs, while non-homine sites especially, and non-'erectine grade' and non-*Homo* sites to a lesser degree have rerlatively smaller percentages of aquatic molluscs, with a larger terrestrial component.

Much more data is needed and more comprehensive statistical analysis to see whether this reflects a common trend for these groups of sites, or whether the results are more an artefact of the site selection process.

9.5 Palaeoecological analysis

Inferring specific palaeoecological characteristics based on identification to family level can be problematic, because some families contain taxa that have very different ecological niches, such as freshwater and marine species of the family Corbiculidae, or families such as the Achatinidae that contain both forest and open grassland taxa. The categories in Table 9.5.1 reflect the habitat a taxon is most commonly associated with, though this does not mean that taxon is never associated with other habitats. In the list of palaeoecological categories used here (Table 9.5.1) genera are used when family categories are insufficient to categorise the taxa.

Table 9.5.1: Taxa divided into taxonomic and palaeoecological categories

Terrestrial/arid/ open	Forest	Amphibious	Freshwater gastropod	Freshwater bivalve	Marine gastropod	Marine bivalve
Jaminia	*Potadoma*	Ampullariidae	Neritidae	Unionoida	*Cerithium*	Nuculanidae
Pseudochondrula	*Maizania*	Lymnaeidae	Hydrobiidae	*Corbicula*	*Melongena*	Ostreoida
Limicolaria	Subulinidae	Planorbidae	Pachychilidae	Pisidiidae	Pyramidellidae	*Geloina*
Cathaica	*Edouardia*		Thiaridae	*Dreissena*	*Didontoglossa*	*Polymesoda*
Hygromiidae	*Cerastua*		Melanopsidae			*Theora*
Helicidae	*Achatina*		*Semisulcospira*			*Gari*
Deroceras	*Burtoa*		Bithyniidae			*Tellimya*
Heliocarionidae	Streptaxidae		*Stenothyra*			*Cycladicima*
	Thapsia		Viviparidae			*Arcopagia*
	Urocyclidae		Valvatidae			*Eamesiella*
			Acroloxidae			Arcidae
						Mytilidae

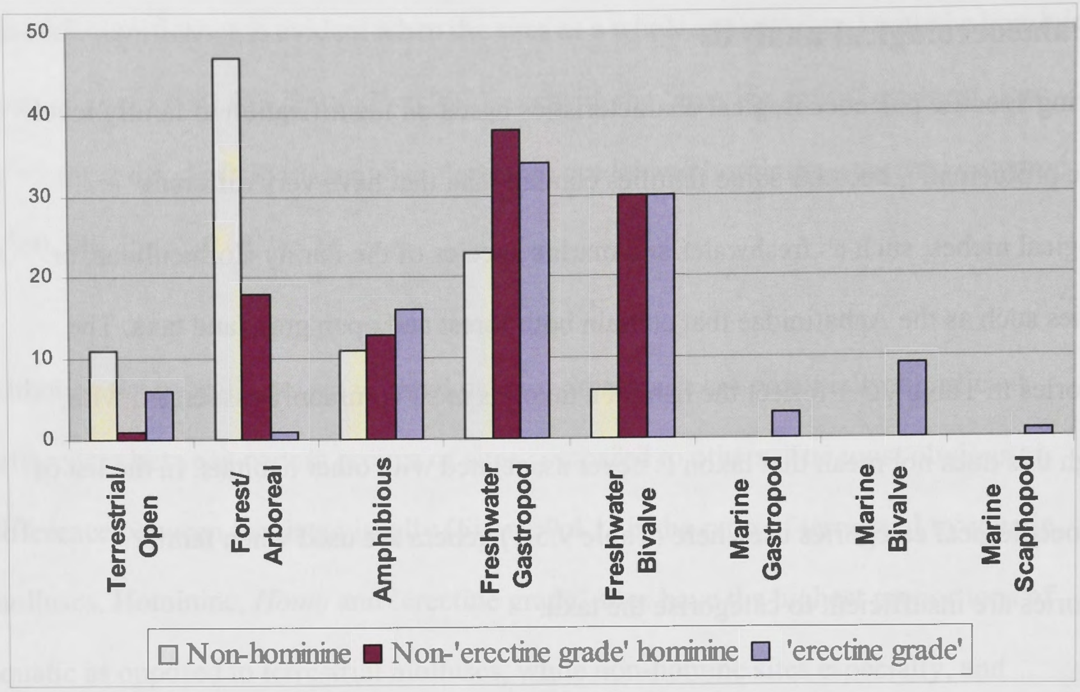


Figure 9.5.1: Percentage of mollusc taxa, according to ecology, for each group of sites (non hominine: n=3, non-'erectine grade' hominine: n=10, 'erectine grade': n=19)

The results show some obvious differences when the various groups of sites are compared (Figure 9.5.1). The non-hominine sites, for example, contain a significantly higher percentage of land snails (pulmonates), compared to the hominine groups, especially pulmonates today associated with forests. The non-'erectine grade' hominine sites contain higher levels of forest dwelling gastropods compared to 'erectine grade' sites, which tends to agree with the conclusions based on other data (see e.g., Vrba 1985), that the origins of *Homo* may have coincided with an opening up of the landscape. 'Erectine grade' sites have a higher percentage of open habitat snails compared to non-'erectine-grade' hominine sites, though both are lower then non-hominine group of sites.

The two hominine groups of sites are similar in that they have both yielded high percentages of freshwater gastropods and bivalves. They differ, however, in that the 'erectine grade' group of sites contains marine molluscs.

These data could support the idea that 'erectine grade' hominines were associated with an opening up of habitats, and this may have ccurred in habitats near water, including permanent water along rivers and coasts. To further explore the idea of permanent water presence the bivalves are examined in more detail.

- **Bivalves**

Bivalve families today have specific distribution and habitat requirements, though these can sometimes be complex, varied and can overlap. Here the bivalves are examined to highlight data related to the permanency of water. It is assumed that the presence of a bivalve is evidence of permanent water.

The only bivalves known from non-hominine sites are Iridinidae (Figure 9.5.2), whereas the two hominine groups have both yielded at least five bivalve families each. The two hominine sites are alike in that they are overall well represented by bivalves, but they differ in terms of the families found at each group.

Non-'erectine grade' hominine sites have yielded Iridinidae, Unionidae, Corbiculidae and Etheriidae in relatively high proportions. 'Erectine grade' sites yielded high proportions of Unionidae, Pisidiidae and Corbiculidae, while they have relatively smaller proportions of Iridinidae and Etheriidae, especially compared to non-'erectine grade' sites, which also contain relatively high percentages of marine bivalve families.

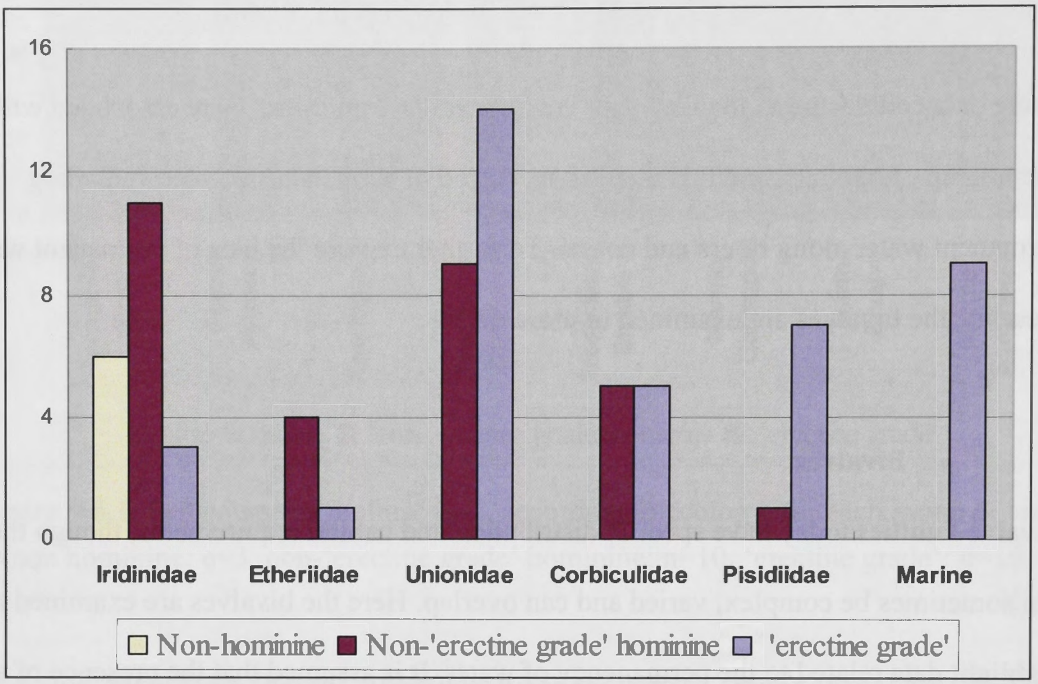


Figure 9.5.2: Bivalve families as a percentage of the total mollusc fauna, for each group of sites (non-hominine n=17, non-'erectine grade' hominine n=79, 'erectine grade' n=148)

The Iridinidae are an endemic African family restricted to topical habitats. 'Erectine grade' sites have the highest proportion of unionid taxa, which comprise 14% of the total taxa found at these sites. These freshwater mussels appear to have had a north American/Eurasian distribution originally, including more temperate adapted taxa than are known for the Iridinidae. The data support the conclusions based on other data that 'erectine grade' hominines, rather than hominines generally, were the first to disperse out of the Africa, and out of the tropics.

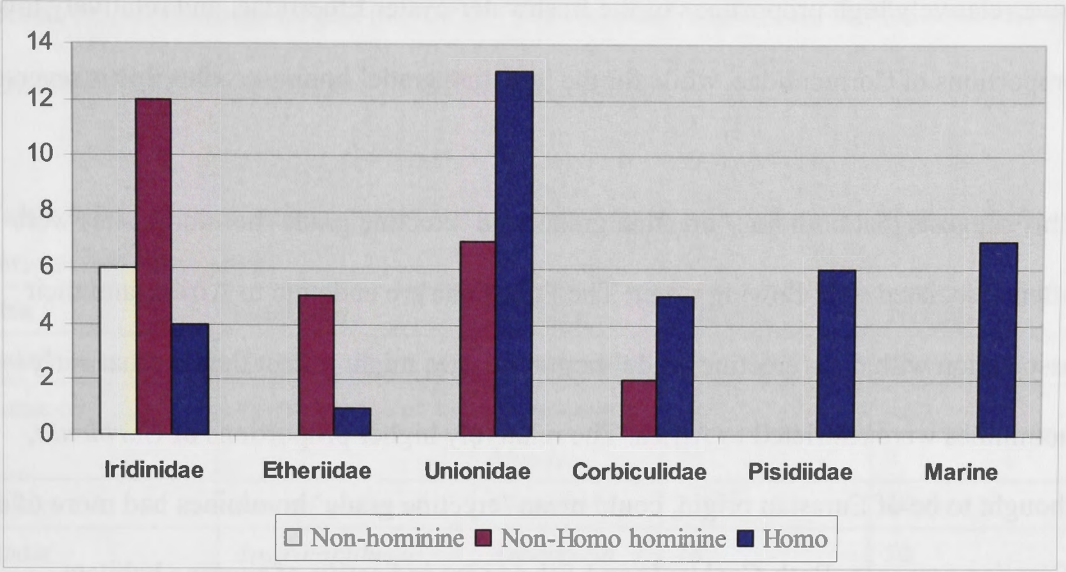


Figure 9.5.3: Percentage of bivalve families as a total component of assemblage (Non-hominine N=17, Non-*Homo* hominine N=41, *Homo* N=186)

When sites that contain the genus *Homo* are grouped instead of 'erectine grade' sites (i.e., including *Homo habilis* and *rudolfensis*), there is very little overall difference (Figure 9.5.3). The only real departure from Figure 9.5.2 is that the *Homo* sites, unlike 'erectine grade' sites, contain the only Pisidiidae taxa, and have a higher percentage of corbiculids as a percentage of total taxa than 'erectine grade' sites as well as non-*Homo* hominine and non-hominine sites. The genus *Corbicula* first appears in the African fossil record during the Pliocene (Van Damme 1984). It is at the beginning of the Pleistocene that 'erectine grade' sites begin to become visible in the fossil record.

- **Water velocity**

Corbiculidae and Etheriidae are generally associated with flowing rivers or at least moving waters. They are found at 'erectine grade' and non-'erectine grade' hominine sites, but are not known from non-hominine sites. Non-'erectine grade' hominine sites have relatively high proportions of the freshwater oyster Etheriidae, and relatively lower proportions of Corbiculidae, while for the 'erectine grade' hominine sites this is reversed.

This suggests that both non-'erectine grade' and 'erectine grade' hominine sites were often associated with flowing water. The Etheriidae are endemic to Africa, and their association with non-'erectine grade' hominine sites might reflect the fact that early hominines were restricted to Africa. The relatively higher proportions of *Corbicula*, thought to be of Eurasian origin, could mean 'erectine grade' hominines had more of a Eurasian presence. Both *Corbicula* and *Etheria* are indicative of riverine habitats.

- **Water depth**

Certain molluscs are characteristic of water depth, such as freshwater mussels. These bivalves live in the sediment of relatively shallow rivers and lakes, where they burrow into the sediment, and use a siphon to feed on small particles filtered from the moving water. Freshwater bivalves favor shallow habitats and are found in relatively high proportions at non-'erectine grade' and 'erectine grade' hominine sites. Shallow water habitats are therefore likely to have been a characteristic of hominine sites.

- **Size**

Each group of sites contains freshwater mussels from the order Unionoida. Measurements of the largest individuals examined for this study, excluding *Etheria*, reveal that the larger sized individuals came from *Homo* sites, whereas the uniformly smaller specimens were from non-*Homo* hominine sites (Table 9.5.1). Only one measurement, from the largest individual, was recorded, and because of the small sample size statistical ‘meaningfulness’ is difficult to interpret.

Table 9.5.1: Maximum measurements (mm) for largest non-Etheriidae Unionoida in various hominine sites

Site	Hominine	Bivalve	Length	Height
Lukeino	*Orrorin*	*Cameronia*	71	29
Kanapoi	*Australopithecus*	*Aspatharia*	70	42
		Mutela	76	?
Dikika	*Australopithecus*	*Chambardia*	71	44
Hadar	*Australopithecus*	*Aspatharia*	78	50
Chiwondo Beds	*Homo*	*Aspatharia*	106	65
Koobi Fora Burgi	*Homo*	*Mutela*	150	55
		Pleiodon	112	59
Koobi Fora KBS	*Homo*	*Chambardia*	185	117
Trinil	*Homo*	*Pseudodon*	115	70

The smaller specimens come from the four earliest sites (Figure 9.5.4). These sites have in common their association with hominine fossils (e.g., *Australopithecus*), and the larger measurements are found in later sites associated with *Homo* including at some *Paranthropus* sites (Chiwondo and Koobi Fora). *Homo* here includes *Homo erectus*, *Homo ergaster* and other species such as *Homo habilis* and *Homo rudolfensis*. *Etheria*, which can grow to a massive size, is known from Lukeino and Lothagam, as well Koobi Fora, but these were not always available to study so are not included here. Since sampling methods are unknown for many of these sites some caution is required in interpreting these results.

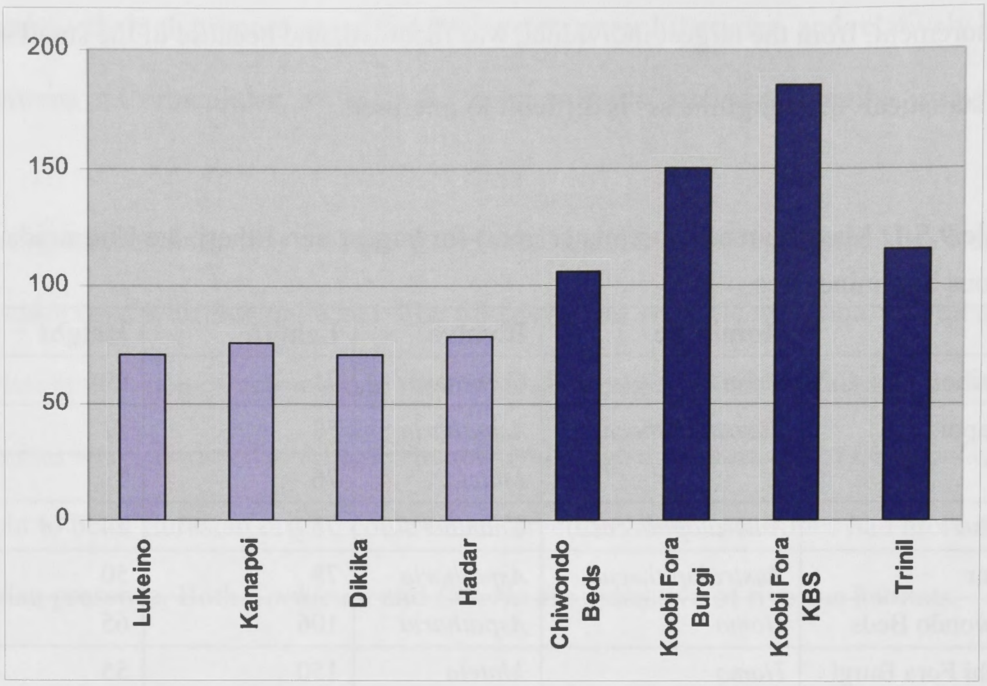


Figure 9.5.4: Length of the largest non-Etheriidae bivalve specimen from each assemblage. Dark blue sites indicate the genus *Homo*

Whether there is a correlation between *Homo* sites and large sized bivalves is difficult to tell based on this data alone, since the sample size is too small to place any great weight on the results. Even if there were a correlation, though, it is not immediately clear what the implications would be in terms of palaeoecology. The most reliable conclusion is probably that because large size in bivalves is correlated with longevity, these sites share conditions that allow freshwater mussels to live to a relatively long age. Possibly, the largest mussels could give clues as to the suitability (for a mussel) of the waterway, and therefore as a consequence its duration.

9.6 Permanent water

According to this relatively small data set, mollusc assemblages appear to typically contain aquatic taxa. Since many of the sites were laid down in lakes or deltas, this is not too surprising. But not all sites are laid down in deltas or lakes. Fort Ternan, Laetoli, Humpata and Dmanisi all contain primates and molluscs, but none of the mollusc are indicative of aquatic habitats.

Dmanisi is the only *Homo* (and 'erectine grade') site that has yielded no aquatic molluscs. The Dmanisi fauna suggests open steppe habitats though some tree cover also occurred locally, possibly associated with nearby mountain ranges. This site accumulated in direct association with a lake, which was formed when a lava stream blocked a river (Gabunia et al. 2000).

Hominine sites contain relatively high percentages of bivalves when compared to non-hominine sites. The distribution of bivalve families differs when non-'erectine grade' and 'erectine grade' hominine sites are compared. The 'erectine grade' hominine sites contain relatively higher percentages of the families Unionidae and Pisidiidae, whereas non-'erectine grade' hominine sites contain more bivalves from the family Iridinidae. This difference might be accounted for by the geographical range of *Homo*, and 'erectine grade' populations, which overlapped with these bivalve families in Asia, Europe and Africa. The Iridinidae, and the non-'erectine grade' hominines, were possibly both endemic to Africa.

When *Homo* and non-*Homo* hominine sites are compared, the *Homo* sites have a higher percentage of Corbiculidae and Pisidiidae. The 'erectine grade' group of sites is the only one that contains marine molluscs.

Since a high percentage of 'erectine grade' and *Homo* sites contain permanent water dwelling molluscs such as bivalves, *Melanoides* and *Bellamya*, is it possible that permanent water was a characteristic of 'erectine grade' and *Homo* sites?

9.7 Mollusc data in light of other data

The molluscan data seem to indicate that permanent water was a characteristic feature of hominine, 'erectine grade' and *Homo* sites. Molluscs reliant on permanent water are found at almost all hominine sites. Sites with no malacological evidence for permanent water include the non-hominine site of Humpata, and the non-'erectine grade' site of Laetoli. Apart from Dmanisi, 'erectine grade' and *Homo* sites are never found in areas where there was not also permanent water, according to the molluscan data.

Other studies have concluded, based on studies of large mammals, that *Homo* generally and *Homo erectus* specifically emerged as a result of adaptations to increasingly arid habitats (Stanley 1992, Reed 1997). This idea is supported by the molluscan data which show that 'erectine grade' sites contain lower percentages of forest dwelling molluscs than non-'erectine grade' sites. These data confirm findings by Vrba (1999) that grazing bovids increased around the time that *Homo* emerged.

Studying antelopes and micro-mammals, Stanley (1992) concluded that *Homo* was the first hominine to adapt to open, arid environments. While the idea of open habitats is supported by the data analysed here, the idea of arid habitats away from water is not. Instead, the molluscan data point to habitats that included at least some local permanent water source. The combined data might support the idea of a permanent water body in an otherwise relatively arid landscape.

9.7.1 Absence of permanent water

After studying the large mammal fauna associated with various hominine sites in Africa, Reed (1997: 289) concluded that *Homo* was the first hominine "to exist in areas of fairly open, arid grassland." Reed analysed data from 25 Plio-Pleistocene hominine and non-hominine sites from south and east Africa to reconstruct the habitats of three fossil hominine genera: *Australopithecus*, *Paranthropus*, and *Homo*. For each site the macro-mammalian fauna was subject to functional morphological and ecological structural analysis. Each taxon was placed in an ecological category, of which there were seven:

- Arboreality
- Aquatic
- Frugivory
- Terrestriality
- Meat/bone
- Fresh grass
- Grass.

After compiling the results in tables and comparing them to modern faunal communities, Reed concluded that (my emphasis):

1) *Australopithecus* inhabited "fairly wooded, *well watered regions*"
2) *Paranthropus* inhabited "similar environs and also in more open regions, but always in habitats that *include wetlands*"
3) *Homo* was "the first hominid to exist in areas of fairly *open, arid grasslands*".

4) *Homo erectus* was "the first hominid adapted to life on the *open 'savanna*'" (Reed 1997: 289).

That the earliest 'erectine grade' fossils were associated with arid, open grassland environments has been supported by other studies (e.g., deMenocal 2004).

Reed's data come from a number of sites and are used to show the number of mammalian taxa belonging to various ecological niches (Table 9.7.1). Edaphic here refers to mammals that feed on specific grasses that grow in water-logged soils such as swamps and wetlands (Reed 1997). Both aquatic and edaphic grassland adapted mammals are therefore classed here as indicators of at least wetlands.

The percentages of aquatic and edaphic grassland adapted mammals occurring as a proportion are as high for 'erectine grade' sites as for any other group (Figure 9.7.1). But because of other data, Reed concluded that later *Homo* species were associated with assemblages 'that indicate extremely arid and open landscapes" (1997: 318). Although 'erectine grade' sites yielded high percentages of aquatic and wetland mammals (Figure 9.7.1), there was one compelling reason to assume 'late *Homo*' was adapted to arid, open landscapes: Sterkfontein 5.

Table 9.7.1: Percentage of large mammal taxa from each site that is aquatic or edaphic (data from Reed 1987). Figures for *Homo erectus* sites in bold (n= number of taxa).

Site	Date	n	Aquatic	Edaphic	Total	Hominine
Laetoli 1	3.6	25	0	0	0	*A. afarensis*
Laetoli 7	3.6	28	0	0	0	*A. afarensis*
Sidi Hakoma	3.34-3.2	44	6.81%	12.5%	19.31	*A. afarensis*
Tulu Bor	3.36-2.68	38	7.89%	15.78%	23.67	*A afarensis*
Usno	3.36-3.0	32	6.25%	6.25%	12.5	*Australopithecus* sp.
M'sgat 3	3.2-3	55	1.82%	3.64%	5.46	*A. africanus*
M'sgat 4	3	31	0	3.23%	3.23	*A. africanus*
Denen Dora	3.2-3.18	43	6.98%	9.3%	16.28	*A. afarensis*
Shungura B	2.95	44	4.44%	11.11%	15.55	*Australopithecus* sp.
Shungura C	2.85	54	5.56%	11.11%	16.67	*P. aethiopicus* *Australopithecus* sp.
Burgi Member	2.68-1.88	53	9.43%	13.21%	22.64	*Paranthropus* sp. *Homo* sp.
S'fontein 4	2.6-2.4	30	0	3.33%	3.33	*A. africanus*
Shungura D	2.52	31	6.45%	12.9%	19.35	*P. aethiopicus* *Australopithecus* sp.
WT 17000	2.5	39	5.12%	23.08%	28.2	*P. aethiopicus*
Shungura E	2.4	33	6.06%	9.09%	15.15	*P. aethiopicus* *P. boisei*
Shungura F	2.36	44	6.82%	6.82%	13.64	*P. aethiopicus*
Shungura G	2.3	52	5.78%	13.46%	19.24	*P. boisei, H. habilis*
Kromdraai B	2.0-1.5	15	0	0	0	*P. robustus*
KBS Member	1.88-1.6	67	**7.46%**	**14.93%**	**22.39**	***H.* cf. *erectus*,** *P. boisei*
Swartkrans 1	1.8	36	5.56%	2.78%	8.34	*P. robustus, Homo* sp.
Swartkrans 2	1.6	34	5.88%	0	5.88	*P. robustus, Homo* sp.
Swartkrans 3	1.4	48	6.25%	4.17%	10.42	*P. robustus*
Natoo Member	1.51	30	**10%**	**16.67%**	**26.67**	***H.* cf. *erectus***
Kromdraai A	1.5-1.0	41	0	2.44%	2.44	No hominines
Okote Member	1.6-1.39	38	**10.53%**	**18.42%**	**28.95**	*P. boisei*, ***H.* cf. *erectus***
S'fontein 5	1.0	16	0	0	0	*Homo* sp.
M'sgat 5	1.0	13	15.38%	15.38%	30.76	No hominines

Sterkfontein is a set of limestone caves from South Africa and has a rather complicated stratigraphic history (Kuman & Clarke 2000 and see Chapter 10.1.2.). Member 5 is associated with stone tools and hominine fossil remains, although the hominine fossil Stw 53 is now thought to come from a separate infill (Kuman & Clarke 2000). The fossil had been placed within the *Homo habilis* hypodigm (Curnoe & Tobias 2006), but recently was assigned to a new species *Homo gautengensis* (Curnoe 2010).

Critically, Reed's study included Sterkfontein 5 as a late *Homo* site of about 1.0 Ma. Late *Homo*, therefore, in Reed's study, was characterised by one of the driest sites in the survey according to the large mammal fauna (Table 9.7.1). According to Curnoe (2010), however, Sterkfontein 5 was not an 'erectine grade' site, and he has been quoted as suggesting the fossil species from this site may have been only about three foot tall and spent considerable time in the trees (Viegas 2010).

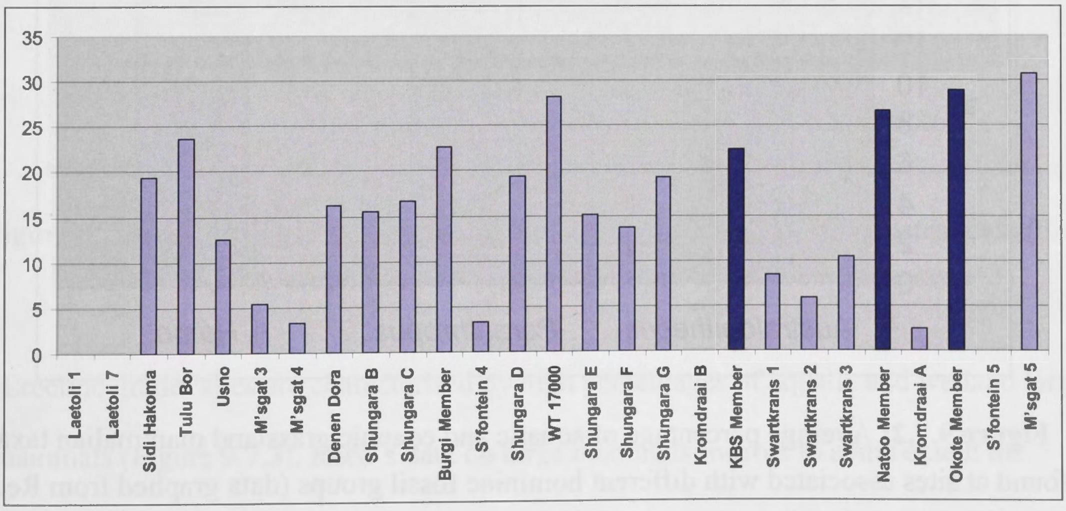


Figure 9.7.1: Percentages for aquatic and wetland grass feeders combined, dark blue columns represent the three 'erectine grade' sites (Data from Reed 1997)

Not much is known about the infill containing the Stw 53 fossil, but Member 5 represents a drier environment than the earlier Member 4, judging by the presence of numerous grassland species such as *Equus* and *Pedetes*, and some usually but not invariably grassland-associated such as *Panthera leo*, although morphological analysis of fossil remains also suggests some tree cover (Kuman & Clarke 2000).

Locally moist conditions are indicated at Sterkfontein 5 by sediment analysis, which reveals high clay and silt content, and the presence of frogs and the monitor lizard *Varanus* cf. *niloticus* (Brain 1981, Kuman & Clarke 2000) could indicate ephemeral water. Member 5 is unlikely to be as young as one million years old with the infill containing Stw 53 probably between 2.6 and 2 Ma (Kuman & Clarke 2000).

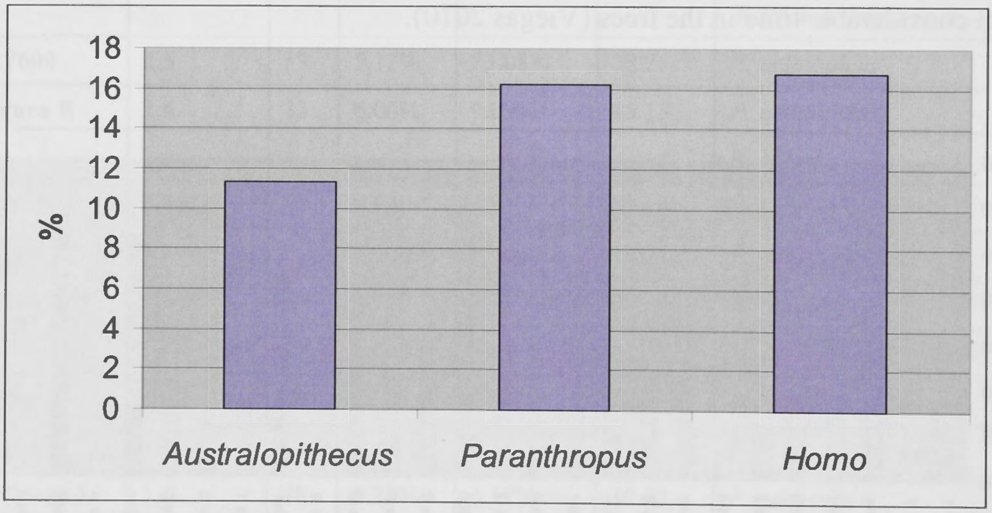


Figure 9.7.2: Average percentage of aquatic and edaphic grassland mammalian taxa found at sites associated with different hominine fossil groups (data graphed from Reed 1997) (*Australopithecus* N=12, *Paranthropus* N=13, *Homo* N=8)

If Sterkfontein Member 5 is not included as an 'erectine grade' site, then the conclusion that 'erectine grade' hominine sites were adapted to arid, open habitats becomes baseless. 'Erectine grade' hominines according to the data, in fact, were associated just as well-watered habitats as *Australopithecus* and *Paranthropus* (Figure 9.7.2).

Each group of fossil sites yielded mammalian taxa indicative of water and wetlands. But sites associated with *Paranthropus* and *Homo* had higher percentages than *Australopithecus* (Figure 9.7.2).

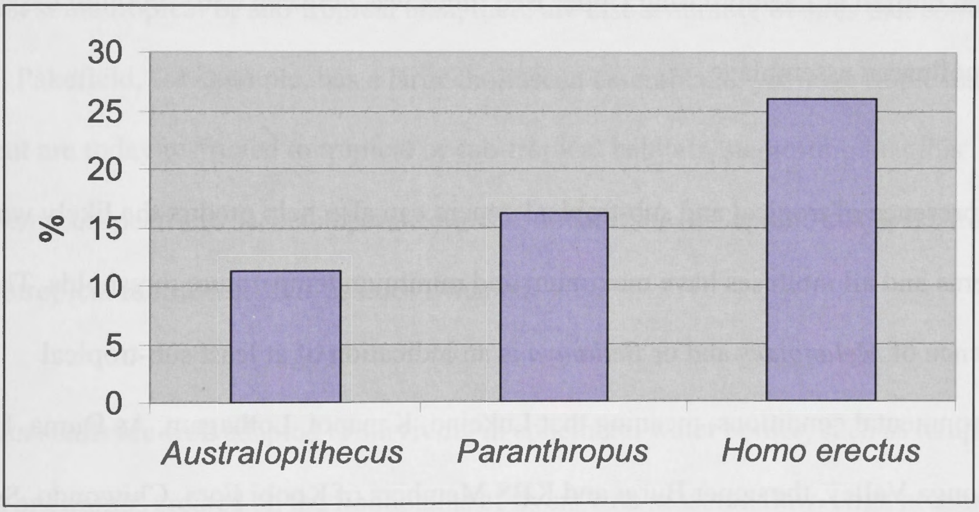


Figure 9.7.3: As per Fig. 9.7.2, except *Homo erectus* sites replace *Homo* sites (data from Reed 1997) (*Australopithecus* n=12, *Paranthropus* n=13, *Homo erectus* n=3)

'Erectine grade' sites are characterised by high percentages of aquatic and wetland large mammals (Figure 9.7.3). Reed's data on large mammals mirrors to some extent the results of the present study on molluscs.

9.8 Building a palaeoecology picture of hominine sites using molluscs

In order to survive and reproduce, animals need to find enough food, water, a mate and shelter, including refuge from predators. Ecology can be divided into a number of sub-groups, and some of these are discussed here in light of the results, and from a palaeoanthropological context.

9.8.1 Temperature and rainfall

Molluscs can be very good indicators of certain aspects of the weather such as rainfall, temperature, seasonality and humidity. Verdcourt (1987), for example, estimated that the annual rainfall at Laetoli during Upper Bed times was between 650–1000mm based on the molluscan assemblage.

The presence of tropical and sub-tropical genera can also help predict the likely weather patterns and all molluscs have maximum and minimum temperature thresholds. The presence of *Melanoides* and or *Bellamya* is an indication of at least sub-tropical environmental conditions, meaning that Lukeino, Kanapoi, Lothagam, As Duma, Hadar, Manonga Valley, the upper Burgi and KBS Members of Koobi Fora, Chiwondo, Senga 5A, Erk-el-Ahmar, Ubeidiya, Pabbi Hills, Mojokerto, Trinil, Buia, Olduvai Gorge Beds I and II the Soa Basin and Dikika during the Hadar and Busidima Formations were at least sub-tropical. These sites include many that have yielded early hominines and hominins, which could indicate that hominines were adapted to these tropical regions, and that early hominins were also.

The freshwater bivalve families Etheriidae and Iridinidae are also restricted to tropical waters (Strayer 2008), so sites at which these mussels are known would have had tropical climates, and the same can be said for sites at which the amphibious gastropod family Ampullariidae, the Thiaridae and *Corbicula* are found.

The freshwater bivalve *Corbicula* is known from a number of sites, and is restricted to tropical and sub-tropical water bodies.

While a number of sites, indeed the majority, have molluscan assemblages which include at least some tropical or sub-tropical taxa, there are also a number of sites that contain none. Pakefield, for example, has a large molluscan assemblage, yet none of the taxa present are today restricted to tropical or sub-tropical habitats, suggesting that this northern European site had a temperate climate, and the site of Ceprano also lacks tropical or subtropical molluscan taxa, as does Dmanisi.

Certain snails are well adapted to surviving in ephemeral water bodies, such as temporary pools or swamps created on the floodplains of rivers with seasonal flow. High proportions of these gastropods could indicate, therefore, seasonal rainfall patterns, leading to seasonal flooding creating ephemeral pools and creeks adjacent to lakes and rivers. The molluscan assemblage from the Busidima Formation at Dikika, differed from the earlier Hadar Formation mollusc assemblage (see Chapter 4) in that it included a number of pulmonate gastropods adapted to living in oxygen-poor water bodies as well as water bodies that temporarily dry out. Combined with the presence of *Melanoides tuberculata*, the molluscan assemblage from the Busidima Formation at Dikika indicates a perennial river subject to seasonal flooding, leading to ephemeral pools and swamps along relatively open floodplains (Wynn et al. 2008).

9.8.2 Other animals

Molluscs themselves of course are ‘other animals’ and therefore knowledge of the molluscan data adds to the overall palaeoecological picture. This study has shown that molluscs are not uncommon at palaeoanthropological sites.

Because unionoid bivalves require suitable fish hosts for survival, it can be assumed that where they occur, suitable fish hosts also occur, but it can also be assumed that predators of mollusc would have been drawn to where they lived. Many vertebrates and quite a few invertebrates eat molluscs, and so the sites where aquatic snails and bivalves lived could have attracted crabs, fish, birds, reptiles, and mammals to feed on them.

Some molluscs, such as *Bulinus* and *Biomphalaria*, act as intermediate hosts for the human parasite *Schistosoma*, a major agent for the disease schistosomiasis; though whether this parasite afflicted ancient humans is unknown.

9.8.3 Place to live

For any organism a place to live includes a place to find food, and a place to rest and shelter, and for a primate this includes being safe from numerous potential predators. Primates live mainly in trees. Of the extant hominoids, the gibbons and orangutans have either re-evolved or simply continued to live arboreal lifestyles, while gorillas and chimpanzees live just as much on the ground as they do in the trees, though are still very agile climbers. Some male mountain gorillas hardly climb at all.

Gibbons sleep in trees but unlike great apes do not build nests. Orangutans and chimpanzees build nests in trees, while gorillas build nests in both the trees and on the ground, and there have been reports of chimpanzees building ground nests also (Koops et al. 2006).

The molluscs in this study indicate that forest habitats existed at Fort Ternan, Laetoli and Humpata, and therefore all of these sites had potential shelter for a typical hominoid or cercopithecid. The hominoids from Fort Ternan and the hominine from Laetoli, inhabited regions where trees could have provided potential shelter from, for example, hyaenas, dogs, big cats, and crocodiles especially at Fort Ternan.

Trees are less obvious according to the molluscan fauna in the 'erectine grade' sites. This could indicate that 'erectine grade' sites were more open. From an anatomical point of view 'erectine grade' hominins appear unlikely tree dwellers; they had, after all, massive and therefore heavy bones (Kennedy 1985). One possible place where 'erectine grade' populations were able to seek temporary shelter is in dry reed beds where they could have built temporary nests. Reed beds differ from place to place, but they commonly grow in areas where water and land meet in open habitats. Even if they didn't shelter in reed beds, hominins are likely to have exploited the abundant available food resources associated with them, including frogs, birds' eggs, turtles and the roots of some of the reeds themselves.

Binford noted that at Olduvai Gorge stone artefacts appear to be correlated with *Typha* reed beds. In the Turkana Basin the famous fossil KNM-WT 15000 (Turkana Boy) was associated with shallow, swampy reed beds in which the most abundant faunal element was the swamp snail *Pila*. This snail is also known from Trinil, and reed beds are a part of the habitat at Erq-el-Ahmar, Ubeidiya and Nihewan according to the molluscan data.

At Daka the *Homo erectus* calvaria BOU-VP-2/66 shows evidence of having been penetrated by the roots of the papyrus plant *Cyperus papyrus* (Asfaw et al. 2008). At Olorgesailie, a site of similar age to Daka, diatomaceous silts point to the presence of reed beds and emergent vegetation, and the molluscan fauna, a planorbid gastropod similar to *Biomphalaria* and the freshwater snail *Bithynia*, confirm that habitats including shallow waters and aquatic vegetation were present. Whether 'erectine grade' hominins could have sheltered in reed beds is unknown, but reed beds certainly appear to have been present at a number of 'erectine grade' sites.

Caves are another potential place of shelter, but none of the molluscs in the sites examined in this study are cave dwellers, although *Cathaica*, from Yuanmou, has been found on lichen covered rocks on the slopes of hills, which might indicate that caves or rock shelters were available locally. The Humpata sites are associated with caves, but here there are no hominines.

Open habitats appear to have been present at Dmanisi, according to the molluscan fauna, but these steppes may not have offered much in the way of shelter for the resident hominins, who may have retained some climbing component judging by their relatively short stature and ape-like upper limbs (Lordkipanidze et al. 2007). The mammalian fauna points to at least some forest habitat at Dmanisi, and therefore potential shelter for a climbing hominin.

Another potential living place is on a sheltered beach. At Mojokerto, according to the molluscan data, there appear to be mudflats, beaches and mangrove forests. Whether the hominin residents of this deltaic setting were able to make use of these areas as living sites at times during the year is unknown, but if modern human behaviour is a guide, then at least some of these econiches would have provided areas to feed and seek shelter, at least at certain times of the year, and for an arboreal hominine, there would have been trees available, including palms and mangroves.

Offshore islands are another possible living place, but Flores is the only island site in the study. Here, the molluscan fauna is indicative of a freshwater river system with intermittent lacustrine stages. Early arrivals to newly created islands, if they are capable of exploiting the available resources, will have relatively few competitors for resources in the beginning, and a limited number of predators compared to the mainland, making them potentially rich and relatively easy areas to establish a niche in.

9.8.4 Food

Undoubtedly molluscs add to the overall ecological picture of a site in terms of the available food, particularly from a palaeoanthropological perspective, since many molluscs are used as food today by humans. There is no compelling reason to expect hominines not to have gathered and eaten molluscs. Bears, otters, walruses and other primates are capable of exploiting the meat of molluscs, so why not hominines and hominins?

Perhaps the reason that mollusc consumption is not discussed is because there is no evidence in the form of shell middens going back millions of years. Should this absence of evidence be taken as evidence of absence, however?

There is some circumstantial evidence of mollusc consumption in the Pleistocene fossil record, including possible consumption of *Achatina*-like land snails at Olduvai Gorge Bed II (M.D. Leakey 1979). These snails can grow to very large size and would have provided good nutrition and they are an important food resource for many African and Asian populations today (Raut & Barker 2002, Hardouin 1995).

At Dmanisi the terrestrial gastropod *Helix* is known, and though there is no evidence of hominin consumption, it has to be considered a potential food resource. *Helix* and other land snails found in prehistoric shell mounds throughout the Circum-Mediterranean in the late Pleistocene and early Holocene are almost certainly the remains of meals (Lubell 2004a), and land snails are known to have been gathered for consumption from a number of other prehistoric sites such as those on the Batanes Islands, northern Philippines (Szabó et al. 2003).

The family Ampullariidae, including the genera *Pila* and *Lanistes* occur at various hominine sites including Trinil, Chiwondo, Lothagam and the Turkana Basin. Human populations are today known to eat *Pila* (Cowie 2002, Patil & Talmale 2005). According to Van Damme (1984) they are used for ritualistic purposes in some present day African communities, and are an important source of food in India (Ahmed & Raut 2005).

Brotia was eaten in quantity at the Leang Burung Pleistocene site in Sulawesi (Glover 1981), and evidence from the nearby Holocene site of Ula Leang suggests it was the main shellfish eaten there between 3000-7000 years ago (Glover 1978). This freshwater snail continues to be eaten by local villagers in Sulawesi today (Glover 1981). *Brotia* was also found at Gua Gunung Runtah in association with the Perak Man burial (Majid 2005).

At Niah Cave the inhabitants in the late Pleistocene were collecting estuarine and freshwater molluscs to eat, and collecting rarely occurring marine and freshwater species probably for use as grave goods (Manser 2007). Freshwater snails were also collected for consumption at the late Pleistocene site of Batadomba-Lena in Sri Lanka (Szabó 2007). Other gastropods that might have been used for food include the freshwater gastropods *Viviparus*, *Bellamya* and *Melanoides* (Bequaert 1943, Cowie 2002, Patil & Talmale 2005, Joordens et al. 2009).

A number of amphibious and aquatic gastropods live on aquatic vegetation, and this is another potential food resource for hominines. Water plants such as the water chestnut *Trapa*, papyrus *Cyperus* and cattails *Typha*, provide substrates and protection from water currents and predators as well as nutrition either directly (some gastropods feed on these macrophytes) or indirectly (some gastropods feed on the *Aufwuchs* and detritus that coat these plants). When the family Planorbidae and other aquatic vegetation-loving gastropods, such as the Ampullariidae, are present at a site, it seems a safe enough assumption most of the time to think that aquatic plants or vegetation would also be present (Ndifon & Ukoli 1989), providing a potential food resource for hominines.

Bivalves are an important food resource for human populations (Suryanarayanan & Alexander 1972, Van Damme 1984, Erlandson 1988, Ahmed & Raut 2005) and there is evidence of freshwater mussel consumption in the archaeological record going back thousands of years (Deacon 1976, Ossa et al. 1995). Whether the presence of an edible bivalve at a hominine site implies that that particular variety of bivalve was consumed is not easy to determine. Joordens et al. (2009), from a primate behavioural perspective, argue that if edible aquatic food resources were available then the null hypothesis should be that they were gathered and consumed. This hypothesis may or may not be correct; what are needed are clearer indications of bivalve consumption going back further in the archaeological and fossil record and more overall data.

It has been argued that molluscs were consumed earlier, for example in China, at Gehe, about 600ka, hominins are argued to have gathered and consumed thick-shelled unionid bivalves (Jia 1980), and the collection and consumption of unionid bivalves at Dali is hinted at since numerous shells are found in the layer containing the skull (Yin et al. 2002, Keates 2003). Evidence of the consumption of freshwater bivalves has been reported from the Bilzingsleben Middle Pleistocene *Homo erectus* site (Mania & Vlcek 1981).

The appearance of the freshwater unionid mussel *Leguminaia* in distinctive quantities at Ubeidiya coincides with the earliest known artefacts from that site (Bar-Yosef & Tchernov 1972: 14-15), and the unionid bivalve *Unio* is abundant in Bed IV deposits at

Olduvai Gorge (Leakey 1965) where it is found in association with stone tools at a number of locations, sometimes fragmented and sometimes intact and articulated (Leakey 1994).

Unionoid mussels are known from early hominin sites such as the Turkana Basin (Feibel et al. 1991), Ubeidiya (Tchernov 1973), Pabbi Hills (Dennell 2004), Ting-ts'un (Aigner 1981), Nihewan (Tang et al. 1981), Ceprano (Ascenzi et al. 1996) and Pakefield (Parfitt et al. 2005). The Mid-Pleistocene archaeological site of Campitello Quarry, central Italy, yielded the earliest known evidence for hafted lithic tools, found in association with an elephant skeleton, rodent remains and *Unio* bivalves (Mazza et al. 2006).

At Terra Amata c. 300ka there are indications that hominin inhabitants were consuming oysters, mussels and limpets (Poirier 1987). Oysters, other bivalves, and marine snails such as winkles, whelks and limpets were undoubtedly a major food of prehistoric man (Yonge 1960). At the Pleistocene whale butchering site of Dungo V at Baia Farta (Benguela, Angola) there are numerous molluscs, including oysters and other marine invertebrates preserved in the same level (Gutierrez et al. 2001). Freshwater and marine molluscs would presumably have been available to the hominin inhabitants of Mojokerto, Trinil and Pakefield.

Not only are freshwater bivalves suitable as a direct food resource, but their presence indicates the existence of certain fish that are needed to act as hosts for the parasitic larval stage of the unionoid life cycle. These fish (genera acting as hosts include carp and catfish) would themselves have been a potential food resource for hominines and hominins, particularly catfish, some of which can inhabit shallow waters and therefore are at times able to be caught by hand.

Studies of cut-marks on bones at the early Pleistocene site of Sangiran suggest the hominins there were using thick shelled clams as tools (Choi & Driwantoro 2007). The *Pseudodon* bivalves from Trinil, being of relatively large size, would have provided a valuable potential food resource for any animal with the ability to gather, open, and extract the meat. *Homo erectus*, present at Trinil when *Pseudodon* "must have been very common" (Van Benthem Jutting 1937: 156), may have exploited this particular food.

Finding evidence in the fossil record of hominin predation of bivalves is complicated by the fact that if hominin populations did not gather large quantities of shells to take to a central place for processing and consumption, then shell middens in the form of mounds are unlikely to have been created. Other clues such as breakage patterns and size selection may reveal clues as to whether a shell was predated upon, but in these cases other predators and causes must first be discounted, and this is not always easy (Appendix 1).

One other way to determine whether or not a shell may have been used by humans is to find markings that could only have been made by humans. At Trinil, an examination of the *Pseudodon* shells found a number of specimens that had marks that looked like possible cut marks. One valve in particular was found to have markings that appear to be the result of human modification (Figure 9.8.1). Preliminary tests indicate that the markings may be as old as the shell itself, but further testing is required to confirm more detail about the markings of the shell.

Figure 9.8.1 removed pending forthcoming publication

Figure 9.8.1: *Pseudodon* bivalve specimen from Trinil (top) with close-up of possible anthropogenic markings (scale 10mm)

For *Homo sapiens* there is no doubt how important littoral shellfish consumption has been. Prehistoric shell middens are known from locations all around the world (Parmalee & Klippel 1974, Meehan 1982, Stiner 1994, Erlandson 2001). In Member IV of the Omo Kibish Formation, the earliest *Homo sapiens* fossil site known, harpoon heads were found associated with concentrations of *Etheria* and *Unio* (R. Leakey 1969). The earliest appearance of *Homo sapiens* in Australia, at Lake Mungo, Willandra Lakes, is associated with unionoid middens.

Shallow water habitats may have been suitable niches for hominine food gathering activities. Having an orthograde posture, it has been suggested that hominines may have waded in shallow waters to collect underground storage organs, i.e., the corms, tubers and/or rhizomes of aquatic and semi-aquatic or emergent macrophytes such as water-lilies *Nymphaea* and cattails *Typha* (Wrangham et al. 2009).

Since these potentially important food resources grow in shallow waters, evidence of shallow water environments could give an indication that these sorts of plant resources were available. Freshwater gastropods such as *Cleopatra* are indicative of shallow waters, so their presence at sites such as Kanapoi, As Duma, the Chiwondo Beds of Malawi and the Turkana Basin, points to the possible existence of suitable habitats for shallow water foraging.

Amphibious pulmonate gastropods are also most commonly found in shallow water habitats that could have provided important food resources to hominines, and therefore the occurrence of *Bulinus*, *Gyraulus* or *Lymnaea* indicates shallow waters, as does the occurrence of freshwater bivalves *Corbicula* and most species of the Unionoida.

Molluscs therefore provide important ecological data in terms of hominine sites both directly, since they themselves are a potential food resource, and indirectly, since they point to the presence of other potential food resources such as certain types of fish, plants and shallow water organisms.

9.8.5 Summary

Molluscs are able to provide detailed information regarding the palaeoecology of a site, both directly and indirectly. The data presented here suggest that open landscapes were a feature of 'erectine grade' sites as opposed to 'non-erectine' grade sites, and that permanent water was a common characteristic of hominine sites, and 'erectine grade' sites especially.

Taphonomic processes are an important consideration in any analysis using fossil data, and in this study one criticism could be that the sites are bias in that they all contain molluscs. Is it possible that if hominin sites with no molluscs were examined, the evidence for permanent water would diminish? To answer this, the next chapter reviews sites not included in this study because they didn't contain molluscs. This is followed by the concluding chapter, which will discuss the data in light of models of hominin dispersal and evolution.

10 Hominine sites not included in the study

Although the data set in this study (n=32) is relatively large compared to other studies comparing fossil faunas from hominine sites, there are a number of important hominine sites that are not included. This is because they either; a) do not have identified molluscs associated with them; b) are controversial in terms of whether or not they actually are hominine sites; or c) were published too recently to be included.

Because only sites that contain molluscs are included in the main data set, the study risks presenting a skewed view of the overall palaeoecology of hominine sites. That is, it might be suggested that inclusion of sites that do not contain molluscs would present a different view of the overall nature and ecology of hominine sites. This chapter therefore focuses primarily on those sites that have not been included in this study because they do not contain molluscs, so that the discussion and conclusions in the final chapters can be placed in an appropriate context.

Sites that are considered controversial are also examined in this chapter so that they can also be considered in the final analysis, as well as one site that was not included because it was published too recently. The analysis in Chapter 9 showed that 'erectine grade' sites were associated with open habitats more than non-'erectine grade' sites, and that both hominine and 'erectine grade' hominine sites are commonly associated with molluscs suggesting permanent water. In this chapter the palaeoecological focus is on the presence or not of closed and open habitats, and evidence for permanent.

10.1 Sites without molluscs

10.1.1 Toros-Menalla

Toros-Menalla is situated in the central African country of Chad (Figure 10.1.1) and is significant since it has yielded one of the earliest known hominine fossil species, *Sahelanthropus tchadensis*. Toros-Menalla is a considerable distance from the African Rift Valley, where virtually all early hominine fossil remains had been found previously. The site is dated at between 6 and 7 Ma, which is close to or before the human-chimpanzee split. Anatomical evidence (the position of the foramen magnum) suggests that the hominine had an orthograde posture (often interpreted as evidence for bipedalism).

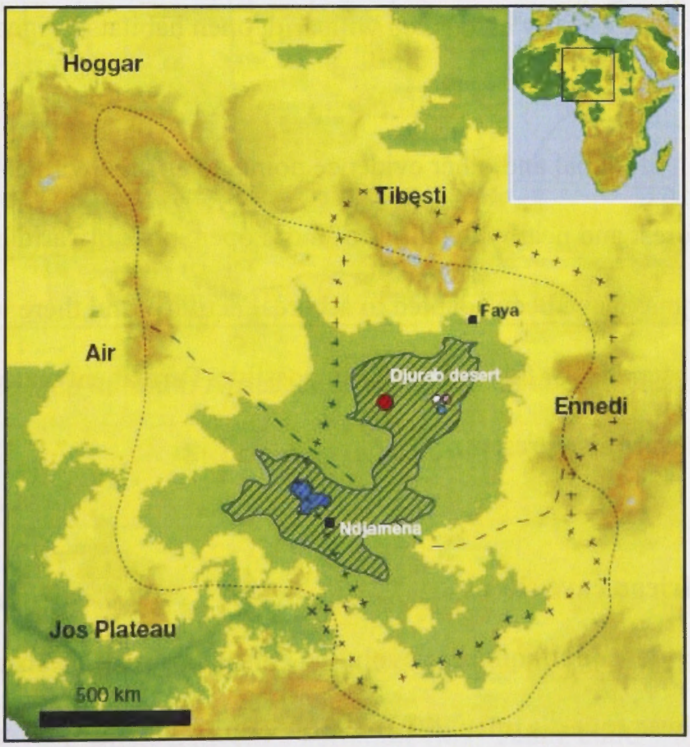


Figure 10.1.1: Map showing location of Toros-Menalla (red circle), Chad (Vignaud et al. 2002)

Although no molluscs have been reported from Toros-Menalla, there are good indications that a large permanent water body was locally present. Remains of at least ten fish taxa including Siluridae, Perciformes and *Polypterus* have been discovered, as well as three crocodilian genera: *Crocodylus*, *Euthecodon* and *Gavialidae*. An otter of the sub-family Lutrinae, a hippopotamid *Hexaprotodon*, and turtles, Trionychidae and Testudinae, have also been discovered.

Forested regions are also indicated by the presence of monkeys (Colobinae), browsing mammals (*Sivatherium*), and liana-like papilionoid plants, which are characteristic of forested habitats.

Open areas are indicated by the presence of rodents such as *Xerus* and bovids including Antilopini, which are usually associated with arid, open habitats (Vignaud et al. 2002).

The combination of faunal and other evidence points to an area with an extensive water body, areas of forest and nearby localities of more open, possibly arid habitats. *Sahelanthropus* may have been adapted to arboreal activity, and there was sufficient forest at Toros–Menalla for this to have been possible. Permanent waterside habitats and open grasslands were also present.

10.1.2 South African cave sites

South African evidence for hominine evolution comes primarily from cave sites. The stratigraphy in these caves is often difficult to determine, and the preservation of fossils varies according to a number of factors. Some Plio-Pleistocene sites from South Africa have yielded good examples of vertebrate fossil remains but very few molluscs. This might have something to do with the manner in which the fossils came to be deposited in the caves. For example, the microvertebrate faunal remains from some caves appear to be the result of owl predation, and at least some of the large mammals from certain South African caves were likely the remains of felid predation (Brain 1981, 1985). Neither of these predators is likely to introduce molluscs into a cave.

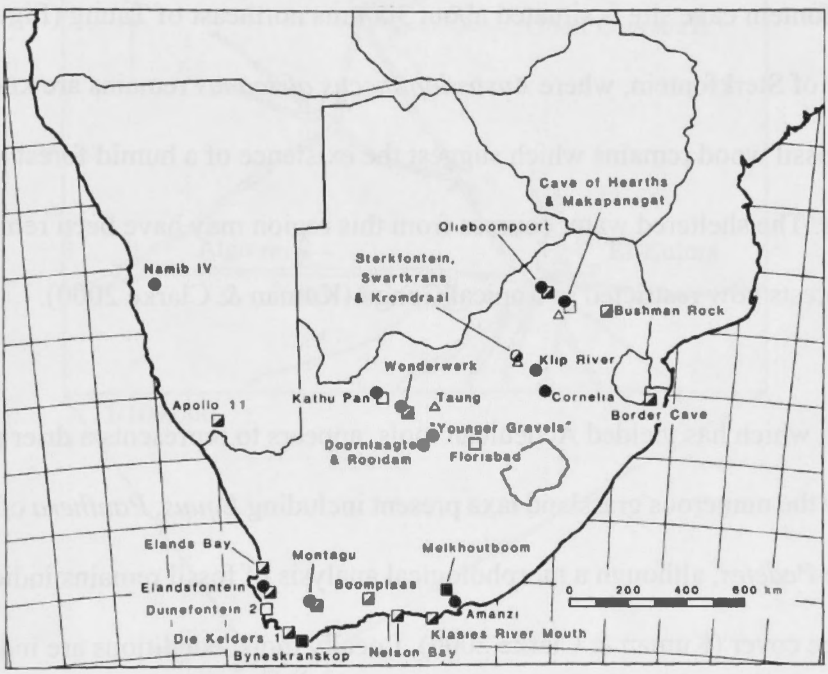


Figure 10.1.2: Map of South Africa showing important sites, including Taung and Sterkfontein (Klein 1983).

- **Taung**

One of the earliest African hominine sites known was that of Taung in central South Africa (Figure 10.1.2), where a juvenile hominine (the 'Taung child') with signs of an orthograde posture was discovered. Although early reports from Taung assumed that the region at the time of deposition was similar to the margin of the Kalahari Desert of today — that is open and relatively arid savanna habitat (Dart 1925) — more recent investigations have revealed that at the time that *Australopithecus africanus* lived, the environment was relatively wet (Partridge 1985), and crabs associated with the deposits indicate water was locally present (Brain 1981).

- **Sterkfontein**

The Sterkfontein cave site is situated about 300kms northeast of Taung (Figure 10.1.2). Member 4 of Sterkfontein, where *Australopithecus africanus* remains are known, contains fossil wood remains which suggest the existence of a humid forest supporting liäna vines. The sheltered water courses from this region may have been remnants of the tropical forests now restricted to tropical Congo (Kuman & Clarke 2000).

Member 5, which has yielded Acheulean tools, appears to represents a drier period judging by the numerous grassland taxa present including *Equus*, *Panthera* cf. *leo* and the springhare *Pedetes*, although a morphological analysis of fossil remains indicates some level of tree cover (Kuman & Clarke 2000). Locally moist conditions are indicated by sediment which reveals high clay and silt content, while the presence of frogs and the monitor lizard *Varanus* cf. *niloticus* provide further evidence of moist conditions near the cave (Brain 1981, Kuman & Clarke 2000).

10.1.3 Ain Hanech

Lithic artefacts belonging to an Oldowan Mode 1 technology have been discovered at the 1.8 Ma North African site of Ain Hanech, Algeria (Sahnouni et al. 2002, Figure 10.1.3).

The faunal remains from Ain Hanech, especially bovids such as *Gazella pomeli*, indicate an open savanna with arid habitats. The sedimentary deposits themselves are associated with an alluvial flood plain that was dissected by a meandering river channel that subsequently formed an oxbow lake (Sahnouni 1998). The presence of hippopotamid remains is consistent with permanent water.

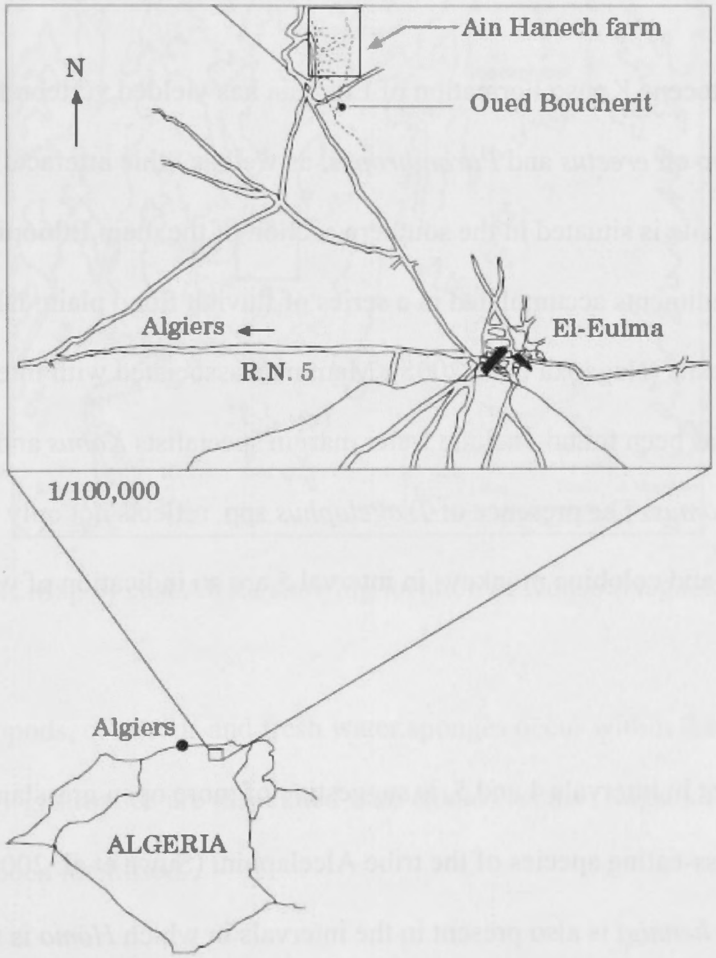


Figure 10.1.3: Location of Ain Hanech, Algeria (Sahnouni & de Heinzelin 1998)

Although no mollusc remains have been found in the layers containing artefacts, gastropod remains have been found within the Beni Fouda basin, including remains of the land snail *Helix*, and in later deposits, freshwater gastropods including *Planorbis, Bithynia* and *Hydrobia* (Sahnouni 1998). How these relate in terms of chronology to the Ain Hanech archaeological site remains unclear. The southern spur of the Ain Hanech Formation contains a bed of pure grey silt which contains well preserved gastropod and ostracod shells, but this is older than the layer containing archaeological remains.

10.1.4 Konso

The Plio-Pleistocene Konso Formation of Ethiopia has yielded vertebrate fossils including *Homo* cf. *erectus* and *Paranthropus,* as well as lithic artefacts of an Acheulean character. The site is situated in the southern section of the main Ethiopian Rift (Figure 10.1.4). The sediments accumulated in a series of fluvial, flood plain, lake-margin and lacustrine deposits (Nagaoka et al. 2005). Mammals associated with intervals 4 and 5, in which *Homo* has been found, include water margin specialists *Kobus* and *Redunca*, along with *Hippopotamus*. The presence of *Tragelaphus* spp. reflects not only water but closed environments, and colobine monkeys in interval 5 are an indication of well wooded habitats.

Gazella, present in intervals 4 and 5, is suggestive of more open grassland habitats as are the diverse grass-eating species of the tribe Alcelaphini (Suwa et al. 2003). *Ancylotherium hennigi* is also present in the intervals in which *Homo* is found. *Ancylotherium* is associated with deposits yielding hominines from Lukeino and Laetoli, but has not often been associated with *Homo* discoveries. It is a browser and often associated with forest habitats (Young 1981).

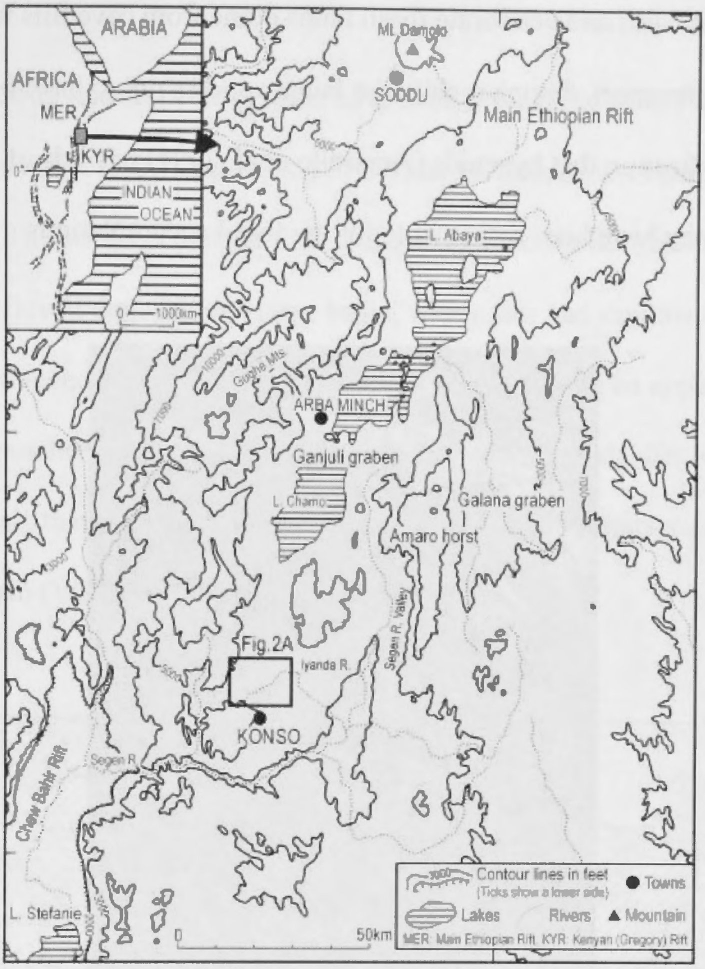


Figure 10.1.4: Map of east Africa showing location of Konso (Nagaoka et al. 2005)

Bivalves, gastropods, ostracods and fresh water sponges occur within the Konso Formation. Only gastropods are associated with *Homo erectus* (Nagaoka et al. 2005) but these have not been identified.

10.1.5 Pirro Nord

Pirro Nord is an Italian fossil site (Figure 10.1.5). Lithic artefacts, including cores and flakes, have been discovered at Pirro Nord, indicating that the genus *Homo* was present between 1.3 and 1.7 Ma (Arzarello et al. 2007). No molluscs have been reported from the site. The lithic remains and vertebrate fossil fauna come from cave fills which show a few signs of fluvial transport, though mostly the fauna appears not to have been transported, and there are indication that hyaenids (Arzarello et al. 2007) or birds of prey (Delfino & Bailon 2000), may have been responsible for the fossil accumulations.

Figure 10.1.5: Location of the Pirro Nord site, Italy (Arzarello et al. 2007)

The local habitat appears to have been open with an arid climate. The presence of Charadriiformes (marine, shore and wading birds) and Anatidae (ducks), as well as amphibians, turtles and occasional fish (Delfino & Bailon 2000), indicates that a good source of water was present locally. Possibly these local waters were temporary, with a permanent water source nearby, since most fish are unable to survive in temporary waters, and the pond turtle *Emys* and frog *Rana* generally require permanent water.

10.1.6 Gadeb

Developed Oldowan and Acheulean tools have been discovered from Pleistocene deposits dated to between 0.7 and 1.5 Ma at the site of Gadeb, east central Ethiopia (Figure 10.1.6). The artefacts include flakes, chopping tools, bifaces and cleavers, and are associated with fluvial deposits in a large basin, with pools and shallow channels associated with a receding lake. Broken animal bones, including an apparent *Hippopotamus* butchery site, and the location of artefacts suggests that hominins were exploiting animals that either lived in, or came to drink in the waters associated with the centre of the basin (Williams et al. 1979).

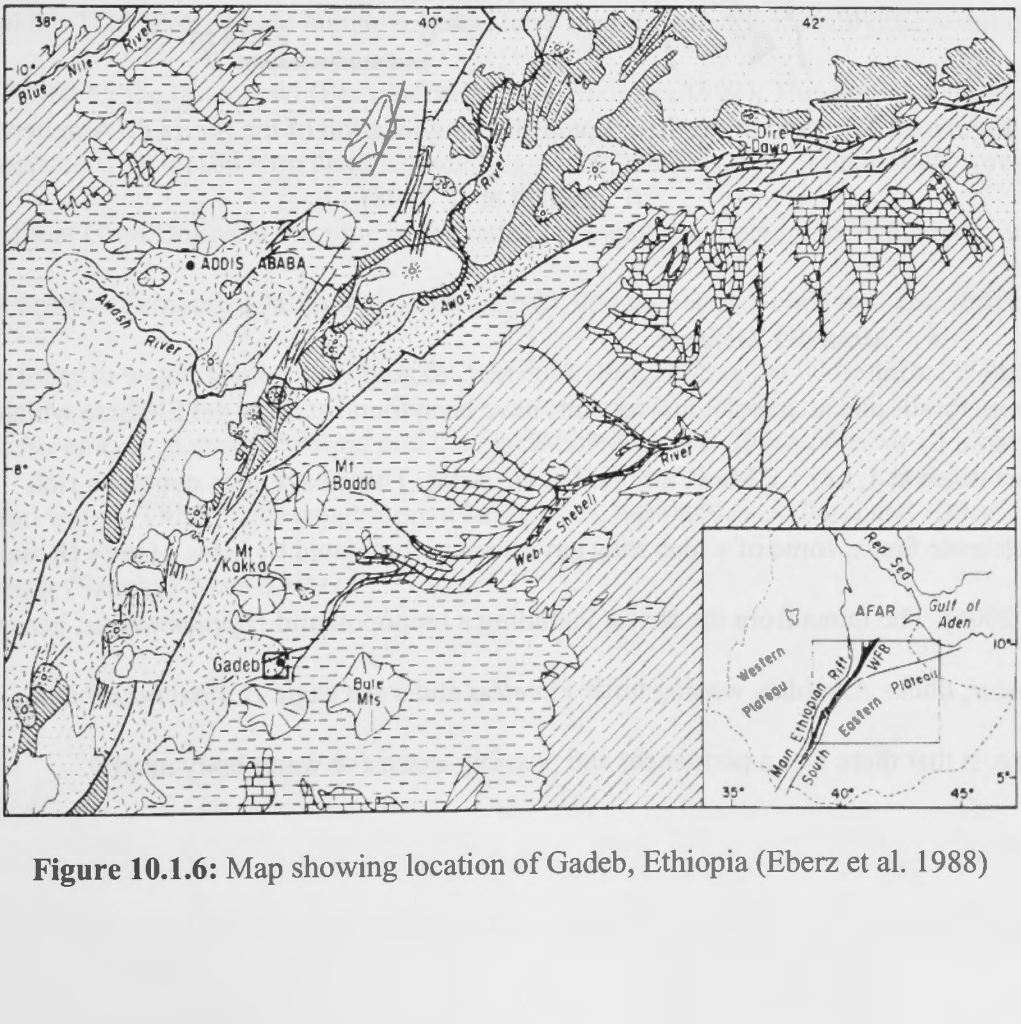


Figure 10.1.6: Map showing location of Gadeb, Ethiopia (Eberz et al. 1988)

10.1.7 Sierra de Atapuerca

The Sierra de Atapuerca (Atapuerca Mountains) in Spain (Figure 10.1.7) contain a number of cave sites that have produced evidence of early to middle Pleistocene hominins in southern Europe. Two of the sites are Sima del Elefante and Gran Dolina.

Figure 10.1.7: Map of northern Spain showing location of the Sierra de Atapuerca (Carbonell et al. 2008)

- **Sima del Elefante**

Homo fossils and archaeological remains have been found at Sima del Elefante which has been dated at 1.1 to 1.2 Ma (Carbonell et al. 2008). These cave sites contain a rich vertebrate fauna, some of which may have been accumulated by birds of prey (Rosas et al. 2006). The fauna from the caves, including a hippopotamid *Hippopotamus*, beaver *Castor*, ducks Anatidae, wading birds *Vanellus* and a sea eagle *Haliaeetus albicilla*, suggest that there was a permanent and possibly extensive water body nearby.

There is evidence for the presence of trees including *Acer* and the deciduous *Quercus* (Rosas et al. 2006). The preponderance of horses later in the sequence indicates a more open landscape and possibly a cooler drier climate (Rosas et al. 2006). Snails have been found, including in association with archaeological remains (Rosas et al. 2006), but no identifications have been reported.

- **Gran Dolina**

Another site from Atapuerca where human remains have been discovered is Gran Dolina, dated to between 780 and 857 ka (Falgueres et al. 1999). At least some of the fossil remains from this site were probably accumulated by predatory birds; the small mammals from the TD6 layer, where human remains have been found, are probably the result of predation by the tawny owl (Fernandez-Jalvo & Andrews 1992). This predator is usually associated with closed woodland habitats suggesting that this type of habitat was present locally at Gran Dolina at the time of the human occupation. Beavers indicate that water was nearby (Fernandez-Jalvo & Andrews 1992), and the reptiles and birds also reflect proximity to water. Ducks, including the teal duck *Anas crecca*, the white-throated dipper *Cinclus cinclus*, a crake *Porzana* and the black-tailed godwit *Limosa limosa* all inhabit inland waters. Other birds suggest open landscapes, bushland, woodland and rocky habitats (Sanchez-Marco 1999).

10.2 Sites of controversy

The previous section examined sites which had no mollusc remains or no identified mollusc remains. In this section sites which are considered controversial will be discussed. There are a number of sites which are claimed by some to contain evidence of hominine evolution, but which others deny have anything to do with hominines. In case any of these sites are actually hominine sites, their palaeoecological characteristics are summarised here, but since they remain controversial no further judgment on them will be made.

10.2.1 Sahabi

The Mio-Pliocene site of Sahabi, located in the Sirt Basin Libya, northern Africa (Figure 10.2.1), was once hailed as a possible early hominine location (Boaz 1980). The fossil remains from the site are fragmentary, however, and because of this, taxonomic assignments have not always been straightforward. For example, one fossil bone was claimed to be a hominine clavicle, but this same fossil bone was identified by other researchers as the rib of a dolphin (White et al. 1983).

The site, dated to c. 5.2 Ma (Bernor & Scott 2003), if it did contain a hominine as has been maintained (Boaz 1987), would be a potentially important site for the origins of the hominine clade, because it lies reasonably close to the time when the last common ancestral population of humans and chimpanzees existed.

The site was probably near the coast, and other remains suggest lagoon, fluvial and deltaic conditions associated with shallow marine environments. Wooded and open areas are indicated by the faunal remains (Bernor & Scott 2003). The molluscs are all of marine origin, and include bivalves such as oysters cf. *Crassostrea* and gastropods such as *Strombus* (Boaz et al. 1979). Chelonians, sirenians and cetaceans are all indicative of marine conditions.

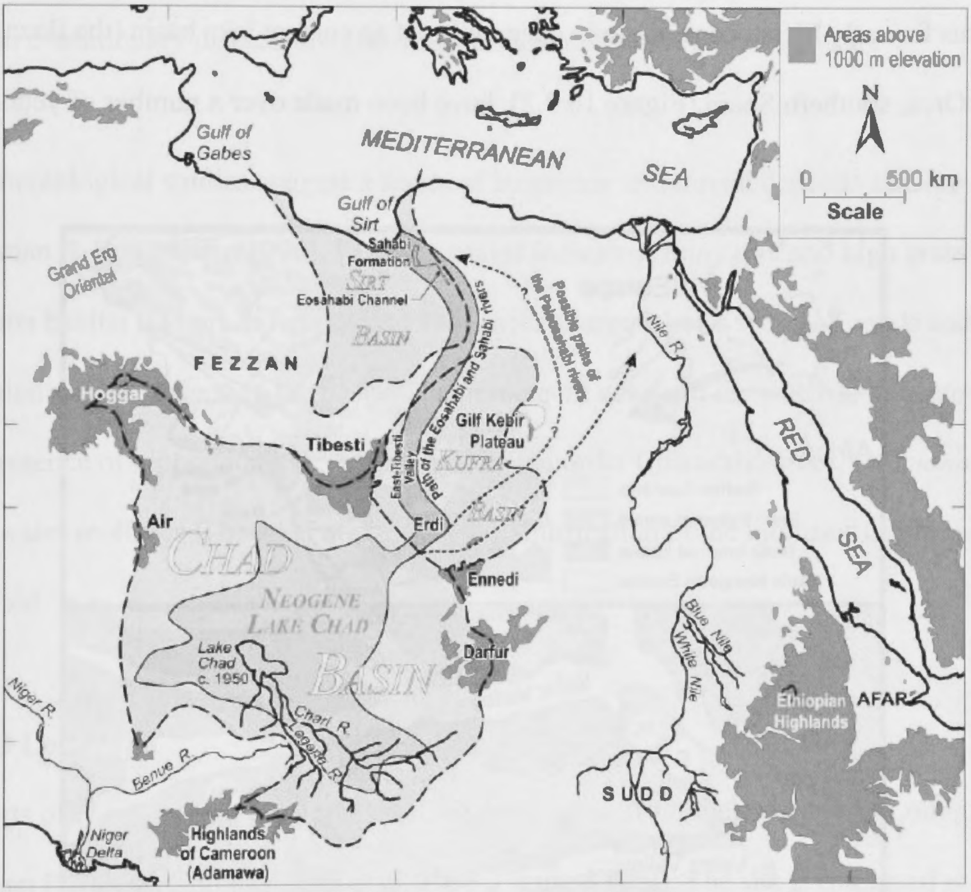


Figure 10.2.1: Map of northern Africa showing location of the Sahabi Formation, near the Gulf of Sirt (Griffen 2006)

The site was probably close to the sea with a lagoon, or large river, fringed with woodland and relatively open habitat further from the water. Interestingly, the Sahabi site is part of the Sirt Basin of Libya, and this was connected in the late Miocene by an aquatic corridor to Toros-Menalla, central Chad, where *Sahelanthropus* was discovered, allowing the semi aquatic *Libycosaurus* (Boisserie et al. 2005) to disperse there from the north African coast (Lihoreau 2006).

10.2.2 Orce

Claims for early Pleistocene hominin occupation of an ancient lake basin (the Baza basin) near Orce, southern Spain (Figure 10.2.2), have been made over a number of years.

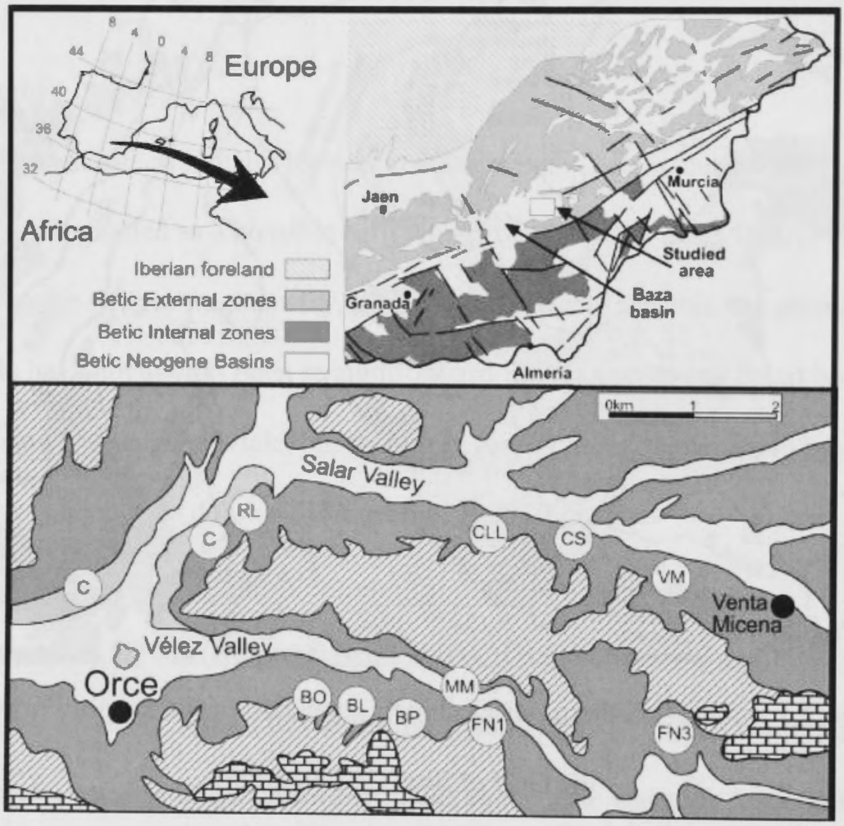


Figure 10.2.2: Map showing location of the Baza basin and Orce, southern Spain (Scott et al. 2007)

At sites including Fuentenueva 3 (FN3) and Barranco Leon (BL) stone artefacts of an Oldowan and Developed Oldowan tradition have been discovered, and at Venta Micena (VM) fossils claimed to be hominin, including molars, cranial fragments, and humeral remains, have been found (Zihlman & Lowenstein 1996). Criticisms of some of the identifications, however, have been made, and accordingly these sites are often left out of human evolutionary discussions (Moya-Sola & Kohler 1997).

Sedimentological studies suggest a series of lacustrine and fluvial deposits at Orce (Zihlman & Lowenstein 1996). Faunal remains indicate a spiny tree and high grass savanna habitat (Gibert & Palmqvist 1995), with a large lake or series of ponds and an occasional river traversing the basin. The permanent nature of the water is indicated by the presence of hippopotamids, frogs, birds of the order Charadriiformes, *Desmana* and freshwater molluscs (Gibert et al. 2004). No identification of the molluscs has been reported.

10.2.3 Longgupo

Reports of *Homo* fossils and lithic artefacts have come from the cave site of Longgupo, Sichuan Province, China (Huang et al. 1995, Figure 10.2.3). The site is estimated to be of late Pliocene- early Pleistocene age, possibly 1.96-1.78 Ma. The fossils include teeth and a mandibular fragment argued to belong to *Homo*, and these have been described as having similarities to *Homo erectus*, *Homo habilis* and *Homo ergaster*. The stone tools include a chopping tool and an extremely pitted hammer.

The hominine status of the fossils has been questioned on the grounds that the mandibular fragment is indistinguishable from the extinct fossil ape *Lufengpithecus*, and the incisor may be a modern intrusion into the deposits (Wu 2000, Etler et al. 2001, Ciochon 2009).

Figure 10.2.3: Map of China showing location of important sites, Longgupo No. 8 (Huang & Hu 1997)

No molluscs have been reported from the site but a number of mammalian species are known including *Gigantopithecus blacki* and a pygmy giant panda *Ailuropoda microta*. The habitat at the time of the deposits included evergreen forested regions since squirrel species were numerous, and palynological studies indicate a warm and wet environment with an increase in evergreens and a decrease in grass (Wu & Poirier 1995). The fauna included a tapir *Tapirus sanyuanensis*, which probably required a closed, wet habitat. A river probably flowed close to the cave and may have contributed, along with carnivores, to the accumulations within the cave (Huang et al. 1995).

10.3 Recently published sites

10.3.1 Aramis

The site of Aramis, which has yielded fossil remains of the hominine species *Ardipithecus ramidus,* comes from the Lower Aramis Member of the Sagantole Formation, which is part of the Afar Rift, Middle Awash, Ethiopia (Figure 10.3.1). The site contains identified gastropods, but was not included in the main data set of this thesis because it was published after the selected sites had been finalised. The mollusc and palaeoecological data of the site are instead included here so that they can be considered in the final discussion.

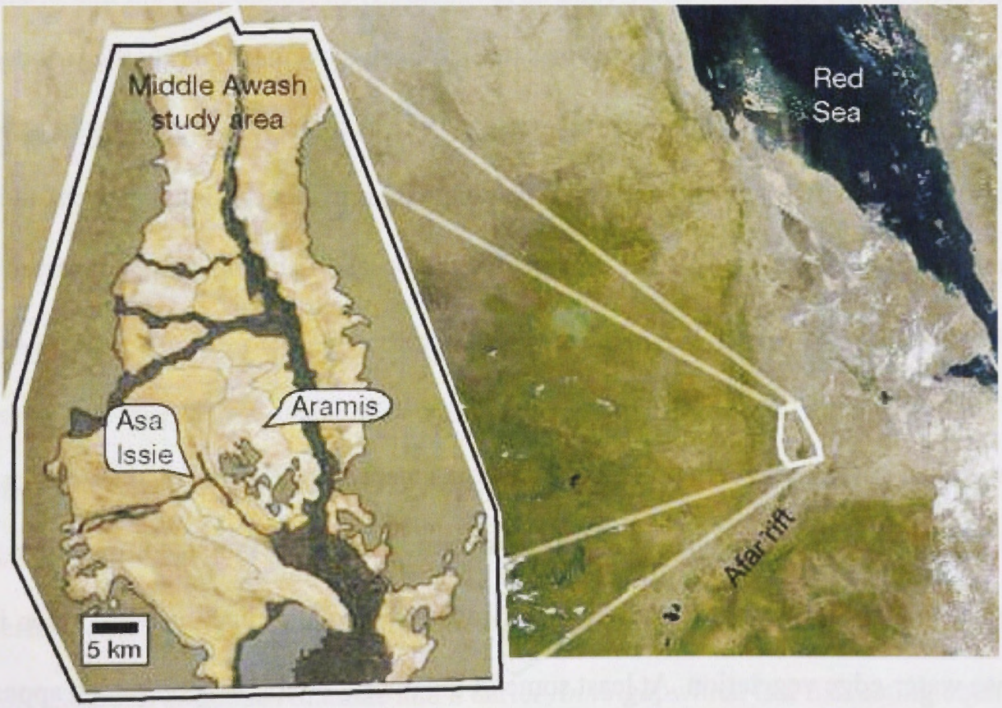


Figure 10.3.1: Map of Northeast Africa showing Middle Awash study area and site of Aramis (White et al. 2006)

Aramis has yielded evidence suggesting that well-wooded habitats existed within the locality at the time of deposition. Evidence for tree cover comes from the comparative abundance of woodland-dwelling bovids belonging to the tribe Tragelaphini, as well as cercopithecids adapted to an arboreal lifestyle (White et al. 2009a). Dental mesowear and microwear, as well as stable isotopes also support the conclusion of heavy woodland, and enamel isotope values of *Ardipithecus* suggest its diet included forest and woodland foods (White et al. 2009b). The postcranial skeletal anatomy of *Ardipithecus* also suggests it was adapted to arboreal activity (White et al. 2009b).

Cerling et al (2010) argue, based on the carbon isotopic composition of palaeosols and mammalian tooth enamel, as well as relative abundance of micro-mammals and phytoliths, that the habitat of Aramis was tree- or bush-savanna, and that the wooded and forest elements can be explained by the presence of a riparian corridor. This is rejected by White et al. (2010), however, who assert that there is no evidence for a major channel, nor the aquatic fauna expected for the type of riverine or lake-margin setting suggested by a riparian corridor.

Since most of the large vertebrate faunal remains were carnivore ravaged (White et al. 2009a), it is possible that there is some taphonomic bias in the faunal composition. Cerling et al. (2010) contend that this could indicate specialised ambush predation in dense water-edge vegetation. At least some of the microvertebrate assemblage appears to be derived from owl pellets (Louchart et al. 2009).

Open savanna or grassy woodland taxa at Aramis are indicated by grazing bovids of the tribe Alcelaphini, dry adapted or open habitat species such as the mice *Acomys*, *Saidomys* and *Arvicanthis*, the ground squirrel *Xerus*, hare *Lepus*, hedgehog *Atelerix*, gerbil *Tatera* and the bats *Rhinolophus*, *Cardioderma* and *Coleura* (Louchart et al. 2009). The bustard Otididae and quail *Coturnix* are also present, although exceedingly rare, but indicate nevertheless that open habitats must have been present (Louchart et al. 2009).

Apart form the cercopithecids and tragelaphines, other forest or woodland inhabitants at Aramis include the shrews *Crocidura*, *Myosorex* and *Suncus*, the mice *Dendromus*, *Praomys* and *Mus*, the dwarf mongoose *Helogale*, the porcupine *Atherurus*, the rodent *Oenomys* and the bat *Taphozous* (Louchart et al. 2009). The peafowl *Pavo* is one of the more common birds at Aramis, indicating forested habitats, while parrots such as lovebirds *Agapornis*, are also well represented, and these inhabit forest to grasslands environments (Louchart et al. 2009)

Although rare, aquatic mammals occur at Aramis, and these include a hippopotamid, and at least three otter taxa, *Enhydriodon* and two genera with similarities to *Lutra* and *Torolutra* respectively (White et al. 2009a).

Waterfowl are also rare at Aramis, but include a genus similar to the iris or spoonbill *Platalea,* a duck or goose Anatidae and a darter *Anhinga,* which is a fish eating aquatic bird that inhabits warm shallow waters (Louchart et al. 2009). These birds indicate that a water body was present somewhere at Aramis.

Also indicative of a permanent water body nearby are the fish remains including the catfish *Clarias*, the cyprinid *Barbus* and cichlids Cichlidae, which are all shallow water inhabitants capable of living in oxygen poor waters (WoldeGabriel et al. 2009).

The reptiles at Aramis include the mud turtle *Pelusios*, the flapshell turtle Cyclanorbinae, African helmeted turtle *Pelomedusa*, and the giant terrestrial turtle *Geochelone*. The Nile crocodile was also present (WoldeGabriel et al. 2009) and in combination with the turtles and fish gives a good indication that aquatic environments were locally present.

Evidence for the local flora at Aramis includes endocarps of the hackberry fruit *Celtis*, wood of the fig tree *Ficoxylon* and pollen from palm trees (WoldeGabriel et al. 2009).

The molluscan fauna from Aramis includes the terrestrial snails *Maizania* from the *M. hildebrandti* group, *Limicolaria*, and *Chlamydarion* cf. *hians*. The most common gastropod at Aramis is *Maizania*, which is an equatorial forest inhabitant, restricted today to evergreen forest (Andrews & Walker 1976, Verdcourt 1984). This genus is known from the Miocene site of Fort Ternan. *Limicolaria* occurs in a range of habitats from forest to more open habitats and is known from Laetoli and Olduvai Gorge Bed IV, while *Chlamydarion hians* inhabits woodland to forest environments (Pickford 1984). The gastropods from Aramis therefore support the view that at least some woodland to forested habitats were locally present.

Ardipithecus probably lived in trees, which were not uncommon at Aramis, though whether these were part of a riparian corridor is unknown. Overall the faunal data suggest a locally present permanent water source.

11 Molluscs as palaeoecology indicators, and hominin origins and dispersal

This study's aim was to see whether the molluscan data could provide any additional information regarding the palaeoecology of fossil and archaeological sites. The results suggest they can. But in the context of hominin origins and dispersal, are the molluscs of any great value? What relevance are the molluscs as ecological indicators in a palaeoanthropological context?

This study, based on inferences from individual taxa, reveals that sites were often, though not in all cases, diverse, in the sense that they often contained more than one amphibious and aquatic snail and at least one species of bivalve. This level of diversity reflects excellent water quality and an abundance of varied macrophytes (Begum & Khan 2002).

Not only do molluscs help describe the physical characteristics of a site's palaeoecology, they also add information regarding certain predator-prey relationships. For a number of organisms, such as certain fish, birds and mammals, molluscs are an important food resource. The presence of molluscs at a site therefore satisfies one of the pre-requisites of a habitable niche for at least some species, because it provides a specific potential food resource. Some primates, such as macaques and capuchin monkeys, very occasionally, exploit molluscs, but this practice is not a common one for most primates.

Modern humans regularly exploit molluscs and have so for a considerable time (certainly hundreds of thousands of years), but when exactly molluscs came to be regularly consumed by humans is not known. The sites examined in this study provide no undeniable evidence that hominines were exploiting molluscs, but at many sites the potential at least is there, since edible molluscs were present. Circumstantial evidence at some sites gives further reason to believe there may have been an actual association between certain molluscs and hominins (section 9.8.2, Appendix 1).

11.1 Hominin dispersal

The genus *Homo*, and 'erectine grade' populations in particular, have dispersed more widely and quickly than any other extant primate genus over the past few million years, with only the old world monkey *Macaca*, restricted mainly to Eurasia, rivaling this migration. Hominins occupied Africa, Eurasia and Wallacea by a million years ago, and eventually they reached Sahul, the Americas and the Pacific islands. Can molluscs provide any clue as to the palaeoecology of this dispersal?

Ecological studies are necessarily limited by the categorisation of various biomes. Rather than a single ecotype, many organisms survive in mixed bio-types. Elephants, for example, can tolerate and indeed are found in dense habitats as well as open landscapes. They need permanent water, but are able to survive in almost desert-like landscapes. Suids are well adapted to and often found in forests, but some species today are also able to survive in open habitats. For molluscs the same problems exist, but often some general assumptions can be made.

11.1.1 Basin endemism

When the molluscan data from this study are considered, it is clear that hominine sites generally, and 'erectine grade' sites in particular, have relatively high percentages of molluscs generally restricted to drainage system such as Viviparidae and the Unionoida, and this association has been noted elsewhere (Van Damme 1984, Nagel 2000). Non-hominine sites, according to this study, do not have the same high percentage of sites containing these drainage system molluscs.

Surface water on land occurs in rivers, lakes, pools and permanent swamps. Many of these form part of a larger drainage system, or hydrological basin. Because these basins are usually separate from each other, it is possible to view them as separate ecological communities (Anderson 1981). If hominins were tied to the permanent waters of specific drainage systems, they might begin to evolve independently from hominins in other drainage areas. In terms of hominin dispersal, if any hominin site was shown to have no evidence for permanent water, it woud weaken the basin andimism idea.

Since by the early Pleistocene the genus *Homo* had spread between Africa, Europe and East Asia, it has been hypothesised that a savanna corridor must have existed between these areas to allow *Homo* to disperse (Dennell & Roebroeks 2005). A difficulty for the across land (between basin) dispersal idea is that 'erectine grade' populations were probably poorly adapted to long distance terrestrial locomotion, on account of having an extremely heavy skeleton, among other unsuitable features (Kennedy 1985, Klein 1999).

The phylogenetic and taxonomic image of *Homo* during the Pleistocene reflects a complicated mix of clades and lineages, with various species sharing a mosaic-like combination of traits, making it difficult to place them all in a specific phylogenetic scheme (Argue 2003). This diversification seems at odds with traditional savanna models (dispersal overland between hydrological systems), because in these cases one would expect the populations to have remained genetically connected. A model advocating that human ancestors lived in in open savanna grasslands but were tied to permanent waters of specific drainage basins, fits with evidence for the diversification in the Homininae generally, and the *Homo* genus in particular. This model would involve hominin populations inhabiting waterside habitats, and following coasts and also rivers to inland drainage systems, where they evolved in semi isolation. Basin endemism has been hypothesised for the hippopotamids in Africa, (Boisserie 2004, Boisserie & Haile-Selassie 2009).

In fact hippopotamids and crocodilians are often found in association with archaic *Homo*. The association of hippopotamid remains with stone artefacts at a number of sites including Daka, the Turkana Basin, Olduvai Gorge and Buia led Boisserie & Gilbert (2008) to conclude that hippopotamid palaeobiology may have been correlated with the ecology and behaviour of early *Homo*.

It has already been hypothesised that early hominine evolution may have been associated with an expansion by early hominines from coastal forest enclaves to separate inland basin complexes along the east African coast (Kingdon 2003). It is conceivable that early populations of the genus *Homo* may have moved from the coast up rivers to colonise inland drainage areas that included, according to the molluscan data, swamps, ponds and adjacent open grassy wetlands associated with the lakes and rivers of basins at Olduvai Gorge, Lake Turkana, Lake Malawi, the Awash Valley, the Jordan Valley, Nihewan Basin, as well as the near coastal rivers of Trinil and Pakefield. Mojokerto is essentially a coastal delta, and the Soa Basin on the island of Flores, reached only by a marine crossing, contained a lake or river. Pabbi Hills was on a river, and Bodo, Buia and Daka all seem to have been connected to permanent drainage areas, while Ceprano and Yuanmou combine fluvial and lacustrine sediments. Dmanisi, with no aquatic molluscan data, is situated on a promontory at the confluence of two rivers and is thought to have had a local permanent water source at the time that the hominins were present.

11.1.2 Coastal dispersal

Since the basin endemic model is based on the coastal dispersal model, the data from this thesis are examined in light of the latter. The molluscan data show that the only sites containing marine molluscs are the 'erectine grade' sites, Mojokerto and Trinil, while the earliest artefacts at Pakefield were associated with estuarine sediments. No non-'erectine grade' site contained marine molluscs. This does not contradict the coastal dispersal to basin drainage systems hypothesis.

It was hypothesised fifty years ago that the genus *Homo* may have had its origins along the coast (Hardy 1960, Sauer 1962). Since the last common ancestor of humans and chimpanzees were likely to have been arboreal, it is possible that if coastal dwelling did occur, it began in an arboreal context. Trees offer apes protection from most terrestrial and aquatic predators, provide a place to sleep and rest, and provide food, including vitamin C containing fruits. Initially, early hominines may have been restricted to forests that lined coasts (Kingdon 2003), then later to trees in more open coastal habitats, such as coconut palms on sandy beaches. If hominins were capable of surviving in areas where only a few palm trees grew, they could have dispersed around otherwise poorly vegetated coasts with little surface water, because palm trees can provide shelter and refuge, while the fruits from palms such as coconuts provide energy, nutrition and freshwater (Harries 1979). These hominins would have been able to disperse around coasts, diversifying by becoming isolated on offshore islands (Flores), and adapting to various eco-zones such as deltas (Mojokerto), estuaries (Pakefield) or inland rivers and lake basins (Turkana Basin).

When following rivers inland, *Homo* populations, if they were arboreal, could have adapted to the gallery forests and other tree-lined waterways of inland habitats, and expanded via forest blocks. If they were not arboreal, then they were presumably adapted to foraging along water's edges (coasts), and could have continued to forage along water's edge habitats in inland savanna habitats. One available food in both habitats (coasts and inland waters) are hard shelled foods such as nuts, fruits, crabs and molluscs, for which tools are useful for opening.

Other evidence corroborates this coastal dispersal model. The large brains of 'erectine grade' hominins could be explained at least partly by the inclusion in their diet of substantial Omega 3 fatty acids, such as Docosahexaenoic acid (DHA), which is an important and substantial element in vertebrate brains (Broadhurst et al. 2002). DHA originates in the food chain in algae and plankton. Primary consumers of these foods therefore contain good natural supplies of DHA. It is argued that waterside foods, by having good sources of these brain building lipids, may have provided the genus *Homo* with a distinct advantage in terms of the potential for brain expansion (Cunnane & Crawford 2003).

While coastal habitats are an important source of foods rich in Omega 3 fatty acids, so too are inland waterside habitats, because freshwater plankton and algae are similarly high in Omega 3 fatty acids, and freshwater mussels have proven to be good sources of these nutrients (Ersoy & Sereflisan 2010). The expansion of the human brain relative to the chimpanzee brain might thus be partly explained if waterside habitats were a focus of hominin foraging strategies.

Evidence of coastal habitation is less likely to be found in the Pleistocene fossil record compared with inland sites because sea levels in the Pleistocene were much lower (sometimes by hundreds of metres) than today, and coastal regions are not always favourable places for fossilisation to occur due to wave and wind erosion. Even so, sites such as Trinil, Mojokerto, Soa Basin and Pakefield in this study provide evidence that coastal habitats were amongst those inhabited by archaic *Homo* populations, and there are numerous other examples of coastal dwelling for *Homo* populations such as the Lower Palaeolithic sites of Dungo V à Baia Farta, Angola (Gutierrez et al. 2001), Terra Amata (Poirier 1987) and particularly in the more recent fossil and archaeological record (Bruggemann et al. 2004, Marean et al. 2007, Stringer et al. 2008).

11.1.3 Open habitats

There are indications that open habitats may have been important in the evolution of the hominins. Hypotheses of human evolution have long been set in arid, open habitats (Dart 1925, Simons 1989). Recently the open savanna has been employed as a backdrop to the endurance running model of *Homo* origins, in which human ancestors interpret signs of mammalian death in the form of vultures, and run to scavenge the carcasses of dead mammals before dogs or hyaenids arrive (Bramble & Lieberman 2004), or run slowly but steadily after an antelope or other cursorial mammal which, because of the continuing need to flee its pursuers, eventually collapses due to exhaustion, providing an easy kill (Lieberman et al. 2007).

The main problem with the endurance running model is that it relies on a form of locomotion that humans are comparatively poor at (Bramble & Lieberman 2004), and the data suggest humans living in the African savanna two million years ago were even more poorly adapted, either because they were still committed to climbing (*Australopithecus*, *Homo habilis*), or else they were much too heavy ('erectine grade').

Human do have good endurance, it is true, and modern humans can run, but these two facts do not together prove that human ancestors two million years were adapted to running, or that the origins of running and the origins of endurance are necessarily linked. Endurance abilities may in fact be much older than running.

But there are other problems with the persistence hunting model of human evolution. For example, there are no guarantees that a large mammal would flee when approached by a hominin two million years ago. Most antelopes have horns, hooves, considerable size and great power. Early hominins may in fact have been more at risk from large grazing mammals than the other way around, but would have had the considerable disadvantage of being much slower. Also, if an antelope did run away, humans even today are far too slow to keep up, and it would literally be out of sight in a matter of seconds, and certainly within minutes. Yet the model insists our ancestors were capable of keeping them galloping for 15 minutes at a time, or sprinting for minutes at a time. With heavier bones, shorter legs, wider pelvic bones and longer and more horizontal femoral necks than modern humans, it is difficult to imagine 'erectine grade' hominins being very effective long distance pursuers. It is more likely that human ancestors butchered animals they found dead around the waterways where their remains have been found.

Because open habitats have long been seen as potentially explaining the transition from tree dwelling to terrestrialism, researchers have often focused on whether the landscapes of early hominines were open or closed. At the time that 'erectine grade' populations began to emerge, there is evidence of more open habitats according to certain data (Stanley 1992, Vrba 1999). Grass eating bovids and other grazing animals are consistent with open grassland habitats. This evidence for open habitats, with the associated possibility of a degree of seasonality, has reinforced the idea that human evolution may have conincided with an opening up of previously closed habitats (Reed 1996, Wynn 2000).

The molluscan data analysed in this study support the idea that 'erectine grade' hominine sites were more open than closed, whereas non-hominine and non-'erectine grade' hominine sites, according to the molluscan data, had better evidence for forested habitats.

The fact that open habitats may have been more prevalent than closed habitats for 'erectine grade' hominine sites suggests a possible connection. Possibly, open habitats lining wetlands were favourable habitats for early hominines (Wrangham et al. 2009). One characteristic of open wetlands is that they contain reed beds. Foraging in shallow reed beds as well as open waterside habitats could possibly explain the shift from arborealism to terrestrialism. The most complete skeleton of an 'erectine grade' individual is that of KNM-WT 15000, the 'Turkana Boy', who was found amongst the opercula of the large swamp snail '*Pila*' which is often associated with the vegetation belts lining waterways.

11.2 Conclusion

Molluscs are able to provide information regarding the ecology of a site, either corroborating other data, or providing new insights. Molluscs are especially good at providing information about whether water was present at a site, and this is important from a palaeoanthropological context because some models of human evolution specify the presence of wetland habitats (e.g., Wrangham 2005, Wrangham et al. 2009).

The molluscan fauna analysed in this study show that sites generally have high proportions of aquatic as opposed to terrestrial molluscs, but non-hominine sites are significantly different in this regard, as are non-'erectine grade' sites compared to 'erectine grade' sites, and non-*Homo* sites compared to *Homo* sites. Practically all *Homo* and 'erectine grade' sites have yielded molluscs dependent on permanent water. The only exception is the site of Dmanisi, where permanent water is indicated by other data.

Non-'erectine grade' hominine sites are often but not always, associated with evidence of permanent water, for example at Laetoli the molluscs consist only of terrestrial gastropods, and there are no other data that point to permanent water.

Two of the three non-hominine sites, Fort Ternan and Humpata, contain molluscs but no permanent water taxa. Other data from Fort Ternan indicate that permanent water was present there, but at Humpata there are no indications of permanent water. 'Erectine grade' sites were the only sites that included marine molluscs.

‘Erectine grade’ sites have the lowest proportion of forest dwelling molluscan taxa, and slightly higher proportions of open habitat taxa than non-erectine grade hominine sites (though not non-hominine sites). This could reflect the fact that ‘erectine grade’ hominines were better adapted to open habitats than non-‘erectine grade’ hominines, as is indicated by other data (Reed 1997).

The molluscs most commonly associated with ‘erectine grade’ sites are taxa indicative of large drainage systems, especially *Melanoides*, the Viviparidae and the Unionoida. Possibly, hominins inhabited the open savanna grasslands that lined the rivers, lakes and swamps in which the above molluscs lived. More sites and more analysis are needed to provide more data to further test this and other hypotheses.

In terms of food, the freshwater mussels, which have been found at many hominin sites, would have been an attractive food resource; being relatively easy to gather, easy to open (with tools), easy to eat (without large teeth or powerful chewing muscles), and containing important nutrients (Ersoy & Sereflisan 2010). Circumstantial evidence suggests that an association between hominins and certain molluscs at some sites may have existed.

At Trinil, the type locality for *Homo erectus*, there is a uniformity to the size of the unionid bivalves which is unexpected for a natural death assemblage, suggesting a possible selective agent. Whether this is an artefact of the collection process is difficult to be certain of, though Joordens et al. (2009) give reasons to believe it is not. Analysis of breakage patterns did not rule out predation by hominins. Markings on at least one of the shells appear to be anthropogenic, but further testing is required to confirm this.

This is the first study to examine and compare the mollusc fauna from a relatively large number of ancient hominine sites from a palaeoecological perspective. The study has brought together various data, synthesising them so that they could be analysed, compared and contrasted. The study is very much a preliminary one, and there is great scope for much more detailed and focused studies of the molluscan fauna of hominine sites in the future.

11.3 Further research

Analysis of the data at a community level (treating each assemblage as a specific community), offers great potential (Andrews et al. 1979), but was beyond the scope of this thesis. Preliminary research for such a study would include analysis of the make-up of molluscan taxa common to a particular habitat in terms of diversity and combination. A wetland habitat, for example, with regular connections to a larger permanent drainage system might be characterised by a particular community of molluscan taxa, including a certain number of gastropods and bivalves. If this type of data were found to have some consistency amongst types of habitats, the known combinations could be compared to fossil assemblages to see if there were any similarities. This method is curretnly used in many areas of biology, but has not been attempted on a large scale for mollusc assemblages from hominine sites.

A few sites in this study contained molluscs, but no detailed information about these has been published, probably because the priority for palaeoanthropologists in the field is not always to collect molluscs. Areas of the Middle Awash Valley, Ethiopia, for example, including the Hata, Daka and Herto Members of the Bouri Formation, have very few published details concerning the molluscs within their sediments, even though both gastropods and bivalves have been recorded throughout this Formation (WoldeGabriel et al. 2008). Better knowledge of the bivalves and gastropods of this Formation could lead to a better understanding of the palaeoecology of the area, an area of great significance from a palaeoanthropological context.

References

Abbate, E., Woldehaimanot, B., Bruni, P., Falorni, P., Papini, M., Sagri, M., Girmay, S. & Tecle, T.M. (2004) Geology of the *Homo*-Bearing Pleistocene Dandiero Basin (Buia Region, Eritrean Danakil Depression). *Rivista Italiana di Paleontologia e Stratigrafia* **110 (supplement)**: 5-34.

Abell, P.I., Awramik, S.M., Osborne, R.H. & Tomellini, S. (1982) Plio-Pleistocene Lacustrine Stromatolites from Lake Turkana, Kenya: Morphology, Stratigraphy and Stable Isotopes. *Sedimentary Geology* **32**: 1-26.

Ahmed, M. & Raut, S.K. (2005) Food values in some molluscs. *Environment and Ecology (Kalyani)* **23S (Special 4)**: 762-765.

Aigner, J. (1981) *Archaeological Remains in Pleistocene China*. Verlag C.H.Beck: Munchen.

Albianelli, A. & Napoleone, G. (2004) Magnetostratigraphy of the *Homo*-Bearing Pleistocene Dandiero Basin (Danakil Depression, Eritrea). *Rivista Italiana di Paleontologia e Stratigrafia* **110 (supplement)**: 35-44.

Alemseged, Z. & Geraads, D. (2000) A new Middle Pleistocene fauna from the Busidima-Telalak region of the Afar, Ethiopia. *Comptes Rendus de l'Académie des Sciences* **331**: 549-556.

Alemseged, Z., Spoor, F., Kimbel, W.H., Bobe, R., Geraads, D., Reed, D. & Wynn, J.G. (2006) A juvenile early hominin skeleton from Dikika. *Nature* **443**: 332-336.

Alemseged, Z., Wynn, J.G., Kimbel, W.H., Reed, D., Geraads, D. & Bobe, R. (2005) A new hominin from the Basal Member of the Hadar Formation, Dikika, Ethiopia, and its geological context. *Journal of Human Evolution* **49**: 499-514.

Anderson, D.T. (1998) *Invertebrate Zoology*. Oxford University Press: Melbourne.

Anderson, J.M. (1981) *Ecology for environmental sciences: biosphere, ecosystems and man*. Halstead Press: New York.

Andrewartha, H.G. & Birch, L.C. (1954) *The ecological web: more on the distribution and abundance of animals*. Chicago University Press: Chicago.

Andrews, P. (1989) Paleoecology of Laetoli. *Journal of Human Evolution* **18**: 173-181.

Andrews, P. (1995) Mammals as palaeoecological indicators. *Acta Zoologica Cracoviensia* **38**: 59-72.

Andrews, P. (2006) Taphonomic effects of faunal impoverishment and faunal mixing. *Palaeogeography, Palaeoclimatology, Palaeoecology* **241**: 572–589.

Andrews, P. & Bamford, M. (2008) Past and present vegetaion ecology of Laetoli, Tanzania. *Journal of Human Evolution* **54**: 78–98.

Andrews, P., Lord, J.M., & Nesbit Evans, E.M. (1979) Patterns of ecological diversity in fossil and modern mammalian faunas. *Biological Journal of the Linnean Society* **11**: 177–205.

Andrews, P. & Walker, A. (1976) The Primate and Other Fauna from Fort Ternan, Kenya. In Isaac, G. & McCown, R. (eds) *Human Origins: Louise Leakey and the East African Evidence*. Staples Press: Menlo Park, California, (pp. 279-304).

Argue, D. (2003) The Muddle in the Middle: Temporal and Regional Variation in the evolution of *Homo* during the Middle Pleistocene and beyond. A Morphometric approach. *Quaternary Australia* **21 (July 2003)**: 22.

Aronson, J.L., Schmitt, T.J., Walter, R.C., Taieb, M., Tiercelin, J.J., Johanson, D.C., Naeser, C.W. & Nairn, A.E.M. (1977) New geochronologic and palaeomagnetic data for the hominid-bearing Hadar Formation of Ethiopia. *Nature* **267**: 323-327.

Aronson, J.L. & Taieb, M. (1981) Geology and Paleogeography of the Hadar Hominid Site, Ethiopia. In Rapp, G. &. Vondra, C.F. (eds) *Hominid Sites: Their Geological Settings*. Westview Press: Boulder, (pp. 165–195).

Arzarello, M., Marcolini, F., Pavia, G., Pavia, M., Petronio, C., Petrucci, M., Rook, L. & Sardella, R. (2007) Evidence of earliest human occurrence in Europe: the site of Pirro Nord (Southern Italy). *Naturwissenschaften* **94**: 107-112.

Ascenzi, A., Biddittu, I., Cassoli, P.F., Segre, A.G. & Segre-Naldini, E. (1996) A calvarium of late *Homo erectus* from Ceprano, Italy. *Journal of Human Evolution* **31**: 409-423.

Asfaw, B., Gilbert, W., Beyene, Y., Harts, W., Renne, P., WoldeGabriel, G., Vrba, E. & White, T. (2002). Remains of *Homo erectus* from Bouri, Middle Awash, Ethiopia. *Nature* **416**: 317-320.

Asfaw, B., Gilbert, W.H. & Richards, G.D. (2008) *Homo erectus* Cranial Anatomy. In Gilbert, W.H. & Asfaw, B. (eds) Homo erectus*: Pleistocene Evidence from the Middle Awash, Ethiopia*. University of California Press: Berkeley, (pp. 265-311).

Assefa, Z., Yirga, S. & Reed, K.E. (2008) The large mammal fauna from the Kibish Formation. *Journal of Human Evolution* **55**: 501-512.

Avery, D.M. (2003) Early and Middle Pleistocene environments and hominid biogeography; micromammalian evidence from Kabwe, Twin Rivers and Mumbwa Caves in central Zambia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **189**: 55–69.

Bailey, G.N., Flemming, N.C., King, G.C.P., Lambeck, K., Momber, G., Moran, L.J., Al-Sharekh, A. & Vita-Finzi, C. (2007) Coastlines, Submerged Landscapes, and Human Evolution: The Red Sea Basin and the Farasan Islands. *Journal of Island & Coastal Archaeology* **2**: 127–160.

Balaparameswara Rao, M. & Subba Rao, K. (1985) Inter and intra-specific variation of the shell of two species of the tropical freshwater snail *Bellamya* (Mollusca: Prosabranchia). *Journal of Molluscan Studies* **51**: 1-7.

Banarescu, P. (1990). *Zoogeography of Fresh Waters*. Wiesbaden: AULA-Verlag.

Bartstra, G.-J. (1982) *Homo erectus erectus*: The Search for his Artifacts. *Current Anthropology* **23**: 318-320.

Bar-Yosef, O. (1987) Prehistory of the Jordan Rift. *Israel Journal of Earth Science* **36**: 107-119.

Bar-Yosef, O. (1994) The Lower Paleolithic of the Near East. *Journal of World Prehistory* **8**: 211-265.

Bar-Yosef, O. & Tchernov, E. (1972) *On the Palaeo-Ecological History of the Site of 'Ubeidiya.* The Israel Academy of Sciences and Humanities: Jerusalem.

Bar-Yosef Mayer, D.E. (2005) The Exploitation of Shells as Beads in the Palaeolithic and Neolithic of the Levant. *Paleorient* **31**: 176-185.

Beadle, L. C. (1981) *The inland waters of tropical Africa.* Longman: London.

Begum, S. & Khan, R.A. (2002) Assessment of the habitat and diversity of malaco-fauna of Kosi River system, North Bihar. *Records of the Zoological Survey of India* **100**: 161-175.

Behrensmeyer, A.K. (1991) Terrestrial vertebrate accumulations. In Allison, P.A. & Briggs, D.E.G. (eds) *Taphonomy: Releasing the Data Locked in the Fossil Record.* Plenum: New York.

Behrensmeyer, A.K., Alemseged, Z. & Bobe, R. (2007) Finale and Future: Investigating faunal evidence for hominin palaeoecology in East Africa. In Bobe, R., Alemseged, Z. & Behrensmeyer, A.K. (eds.) *Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence.* Springer: Dordrecht, (333-345).

Behrensmeyer, A.K., Deino, A.L., Hill, A., Kingston, J.D. & Saunders, J.J. (2002) Geology and geochronology of the middle Miocene Kipsaramon site complex, Muruyur Beds, Tugen Hills, Kenya. *Journal of Human Evolution* **42**: 11-38.

Belmaker, M. (2010) The presence of a large cercopithecine (cf. *Theropithecus* sp.) in the 'Ubeidiya formation (Early Pleistocene, Israel). *Journal of Human Evolution* **58**: 79-89.

Belmaker, M., Tchernov, E., Condemi, S. & Bar-Yosef, O. (2002) New evidence for hominid presence in the Lower Pleistocene of the Southern Levant. *Journal of Human Evolution* **43**: 43-56.

Bequaert, J. (1943) Fresh-water shells from cave deposits in the Southern Shan States, Burma. *Transactions of the American Philosophical Society* **32**: 431-437.

Bernard, F.R., Cai, Y., Morton, B. (1993) *Catalogue of the living marine bivalve molluscs of China*. Hong Kong University Press: Hong Kong.

Bernor, R.L. & Scott, R.S. (2003) New interpretations of the systematics, biogeography and paleoecology of the Sahabi hipparions (latest Miocene) (Libya). *Geodiversitas* **25**: 279-319.

Bettis, E.A.III., Zaim, Y., Larick, R., Ciochon, R., Suminto, Rizal, Y., Reagan, M. & Heizler, M. (2004) Landscape development preceding *Homo erectus* immigration into Central Java, Indonesia: the Sangiran Formation Lower Lahar. *Palaeogeography, Palaeoclimatology, Palaeoecology* **206**: 115-131.

Betzler, C. & Ring, U. (1995) Sedimentology of the Malawi Rift: Facies and stratigraphy of the Chiwondo Beds, northern Malawi. *Journal of Human Evolution* **28**: 23-35.

Birdsell, J.B. (1972) *Human Evolution: An introduction to the New Physical Anthropology*. Rand McNally & Company: Chicago.

Binford, L.R. (1989). Isolating the transition to cultural adaptations: an organizational approach. In Trinkaus, E. (ed.) *The Emergence of Modern Humans: Biocultural Adaptations in the Later Pleistocene*. Cambridge University Press: Cambridge, (pp. 18-41).

Bhamrah, H.S. & Juneja, K. (2001) *Introduction to Mollusca*. Anmol Publications: New Delhi.

Bishop, L. (1999) Suid Paleoecology and Habitat Preferences at African Pliocene and Pleistocene Times. In Bromage, T. & Schrenk, F. (eds) *African Biogeography, Climate Change & Human Evolution*. Oxford University Press: New York, (pp. 226-52).

Blumenschine, R.J., Peters, C.R., Masao, F.T., Clarke, R.J., Deino, A.L., Hay, R.L., Swisher, C.C., Stanistreet, I.G., Ashley, G.M., McHenry, L.J., Sikes, N.E., van der Merwe, N.J., Tactikos, J.C., Cushing, A.E., Deocampo, D.M., Njau. J.K. & Ebert, J.I. (2003) Late Pliocene *Homo* and Hominid Land Use from Western Olduvai Gorge, Tanzania. *Science* **299**: 1217-1221.

Boaz, N.T. (1980) A hominoid clavicle from the Mio-Pliocene of Sahabi, Libya. *American Journal of Physical Anthropology* **53**: 49-54.

Boaz, N.T. (1987) Sahabi and Neogene Hominoid Evolution. In Boaz, N.T., El-Arnauti, A., Gaziry, A., de Heinzelin, J. & Boaz, D. (eds) *Neogene Paleontology and Geology of Sahabi*. Liss: New York, (pp. 129-134).

Boaz, N.T. & Almquist, A.J. (1997) *Biological Anthropology: A Synthetic Approach to Human Evolution*. Prentice Hall: Upper Saddle River, New Jersey.

Boaz, N.T., Gaziry, A.W. & El-Arnauti, A. (1979) New fossil finds from the Libyan Upper Neogene site of Sahabi. *Nature* **280**: 137-140.

Bogan, A.E. & Hoeh, W.R. (2000) On becoming cemented: evolutionary relationships among the genera in the freshwater bivalve family Etheriidae (Bivalvia: Unionoida). In, Harper, E.M., Taylor, J.D. & Crame, J.A. (eds) *The Evolutionary Biology of the Bivalvia*. Geological Society, London, Special Publications, **177**, (pp. 159-168).

Boisserie, J.-R. (2004) A new species of Hippopotamidae (Mammalia, Artiodactyla) from the Sagantole Formation, Middle Awash, Ethiopia. *Bulletin de la Societe Geologique de France* **175**: 525-533.

Boisserie, J.-R. & Gilbert, W.H. (2008) Hippopotamidae. In Gilbert, W.H. & Asfaw, B. (eds) Homo erectus: *Pleistocene Evidence from the Middle Awash, Ethiopia*. University of California Press: Berkeley, (pp. 179-191).

Boisserie, J.-R. & Haile-Selassie, Y. (2009) Hippopotamidae. In Haile-Selassie, Y. & WoldeGabriel, G. (eds) Ardipithecus kadabba: *late miocene evidence from the Middle Awash*. University of California Press: Berkeley & Los Angeles, (pp. 373-387).

Boisserie, J.-R., Lihoreau, F. & Brunet, M. (2005) The position of Hippopotamidae within Cetartiodactyla. *Proceedings of the National Academy of Sciences* **103**: 1537–1541.

Bonnefille, R. (1995) A Reassessment of the Plio-Pleistocene Pollen Record of East Africa. In Vrba, E., Denton, G., Partridge, T. & Burckle, L. (eds) *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press: New Haven and London, (pp. 297-310).

Bonnefille, R. & Riollet, G. (1987) Palynological spectra from the Upper Laetoli Beds. In Leakey, M. & Harris, J. (eds) *Laetoli: A Pliocene Site in Northern Tanzania*. Clarendon Press: Oxford, (pp. 52-61).

Bouchet, P. & Rocroi, J.-P. (2005) Classification and nomenclature of gastropod families. *Malacologia: International Journal of Malacology* **47**: 1-397.

Boucot, A.J. (1982) Ecophenotypic or genotypic. *Nature* **296**: 609-610.

Bowler, J.M., Jones, R., Allan, H. & Thorne, A.G. (1970) Pleistocene human remains from Australia: a living site and human cremation from Lake Mungo, western New South Wales. *World Archaeology* **2**: 39-60.

Brain, C. (1981) *The Hunters or the Hunted?* University of Chicago Press: Chicago.

Brain, C. (1985) interpreting early hominid death assemblages: the rise of taphonomy since 1925. In Tobias, P. (ed.) *Hominid Evolution: Past, Present and Future*. A.R. Liss: New York, (pp. 41-46).

Bramble, D.M. & Lieberman, D.E. (2004) Endurance running and the evolution of *Homo*. *Nature* **432**: 345-352.

Branson, B.A. (1981) The Sphaeriacean Pelecypods of Oklahoma. *Proceedings of the Oklahoma Academy of Science* **61**: 1–6.

Braun, D.R., Harris, J.W.K., Levin, N.E., McCoy, J.T., Herries, A.I.R., Bamford, M.K., Bishop, L.C., Richmond, B.G. & Kibunjia, M. (2010) Early hominin diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya. *Proceedings of the National Academy of Sciences* **107**: 10002-10007.

Broadhurst, C. L., Wang, Y., Crawford, M., Cunnane, S., Parkington, J. & Schmidt, W. (2002) Brain specific lipids from marine, lacustrine, or terrestrial food resources: potential impact on early African *Homo sapiens*. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology* **131**: 653-673.

Brockwell, S. & Akerman, K. (2007) Bone Points from the Adelaide River, Northern Territory. *Australian Aboriginal Studies* **1**: 83-97.

Bromage, T., Schrenk, F. & Juwayeyi, Y. (1995) Paleobiogeography of the Malawi Rift: Age and vertebrate paleontology of the Chiwondo Beds, northern Malawi. *Journal of Human Evolution* **28**: 37-57.

Brown, D.S. (1978) Pulmonate molluscs as intermediate hosts for digenetic trematodes. In Fretter, V. & Peake, J. (eds) *Pulmonates*. Academic Press: London, (pp. 287–333).

Brown, D.S. (1980) *Freshwater Snails of Africa and their Medical Importance*. Taylor & Francis: London.

Brown, F. & Feibel, C. (1991) Stratigraphy, Depositional Environments and Palaeogeography of the Koobi Fora Formation. In Harris, J. (ed.) *Koobi Fora Research Project Volume 3, The Fossil Ungulates: Geology, Fossil Artiodactyls, and Palaeoenvironments*. Clarendon Press: Oxford, (pp. 1-30).

Bruggemann, J., Buffler, R., Guillaume, M., Walter, R.C., von Cosel, R., Ghebretensae, B.N. & Berhe, S.M. (2004) Stratigraphy, palaeoenvironments and model for the deposition of the Abdur Reef Limestone: context for an important archaeological site from the last interglacial on the Red Sea coast of Eritrea. *Palaeogeography, Palaeoclimatology, Palaeoecology* **203**:179-206.

Brumm, A., Aziz, F., van den Bergh, G.D., Morwood, M.J., Moore, M.W., Kurniawan, I., Hobbs, D.R. & Fullagar, R. (2006) Early stone technology on Flores and its implications for *Homo floresiensis*. *Nature* **441**: 624-628.

Brumm, A., Jensen, G.M., van den Bergh, G.D., Morwood, M.J., Kurniawan, I., Aziz, F. & Storey, M. (2010) Hominins on Flores, Indonesia, by one million years ago. *Nature* **464**: 748-752.

Brunet, M., Guy, F., Pilbeam, D., Mackaye, H.T., Likius, A., Ahounta, D., Beauvilain, A., Blondel, C., Bocherens, H., Boisserie, J.-R., De Bonis, L., Coppens, Y., Dejax, J., Denys, C., Duringer, P., Eisenmann, V., Fanone, G., Fronty, P., Geraads, D., Lehmann, T., Lihoreau, F., Louchart, A., Mahamat, A., Merceron, G., Mouchelin, G., Otero, O., Campomanes, P.P., Ponce De Leon, M., Rage, J.-C., Sapanet, M., Schuster, M., Sudre, J., Tassy, P., Valentin, X., Vignaud, P., Viriot, L., Zazzo, A. & Zollikofer, C. (2002) A new hominid from the Upper Miocene of Chad, Central Africa. *Nature* **418**: 145-151.

Brusca, R.C. & Brusca, G.J. (1990) *Invertebrates*. Sinauer Associates: Sunderland, Massachusetts.

Bruton, M.N. (1979) The survival of habitat desiccation by air breathing clariid catfishes. *Environmental Biology of Fishes* **4**: 273-280.

Bunje, P.M. & Lindberg, D.R. (2007) Lineage divergence of a freshwater snail clade associated with post-Tethys marine basin development. *Molecular Phylogenetics and Evolution* **42**: 373–87.

Burky, A.J. (1983) Physiological Ecology of Freshwater Bivalves. In Russell-Hunter, W.D. (ed.) *The Mollusca: Volume 6, Ecology*. Academic Press: Orlando, (pp. 281-327).

Burlakova, L.E. & Karatayev, A.Y. (2007) The effect of invasive macrophytes and water level fluctuations on unionids in Texas impoundments. *Hydrobiologia* **586**: 291-302.

Butzer, K.W. (1969) Geological interpretation of two Pleistocene hominid sites in the Lower Omo Basin. *Nature* **222:** 1138–1140.

Butzer, K.W., Brown, F.H. & Thurber, D.L. (1969) Horizontal sediments of the Lower Omo Valley: the Kibish Formation. *Quaternaria* **11**: 15-29.

Butzer, K.W. & Thurber, D.L. (1969) Some Late Cenozoic sedimentary formations of the Lower Omo Basin. *Nature* **222**: 1138-1143.

Byrne, M., Phelps, H., Church, T., Adair, V., Selvakumaraswamy, P. & Potts, J. (2000) Reproduction and development of the freshwater clam *Corbicula australis* in southeast Australia. *Hydrobiologia* **418**: 185–197.

Campbell, B. & Lack, E. (1985) *A Dictionary of Birds*. T. & A.D. Poyser: Calton, Staffordshire, U.K.

Carbonell, E., Bermudez de Castro, J.M., Pares, J.M., Perez-Gonzalez, A., Cuenca-Bescos, G., Olle, A., Mosquera, M., Huguet, R., van der Made, J., Rosas, A., Sala, R., Vallverdu, J., Garcia, N., Granger, D.E., Martinon-Torres, M., Rodriguez, X.P., Stock, G.M., Verges, J.M., Allue, E., Burjachs, F., Caceres, I., Canals, A., Benito, A., Diez, C., Lozano, M., Mateos, A., Navazo, M., Rodriguez, J., Rosell, J. & Arsuaga, J.L. (2008) The first hominin of Europe. *Nature* **452**: 465-469.

Cerling, T.E., Levin, N.E., Quade, J., Wynn, J.G., Fox, D.L., Kingston, J.D., Klein, R.G. & Brown, F.H. (2010) Comment on the Paleoenvironment of *Ardipithecus ramidus*. *Science* **328**: 1005-d.

Cheng, G., Li, S. & Lin, J. (1977) Discussion of the age of *Homo erectus yuanmouensis* and the event of early Matuyama. *Scientia Geologica Sinica* **1**: 34-43.

Choi, K. & Driwantoro, D. (2007) Shell tool use by early members of *Homo erectus* in Sangiran, central Java, Indonesia: cut mark evidence. *Journal of Archaeological Science* **34**: 48-58.

Christian, A.D., Smith, B.N., Berg, D.J., Smoot, J.C. & Findlay, R.H. (2004). Trophic position and potential food sources of 2 species of unionid bivalves (Mollusca: Unionidae) in 2 small Ohio steams. *Journal of North American Benthological Society* **23**: 101-113.

Chua, M., Sivasothi, N. & Teo, R. (2009) Rediscovery of greater mouse deer, *Tragulus napu* (Mammalia: Artiodactyla: Tragulidae) in Pulau Ubin, Singapore. *Nature in Singapore* **2**: 373–378.

Churcher, C.S. (1970) Two new Upper Miocene Giraffids from Fort Ternan, Kenya, East Africa: *Palaeotragus primaevus* n.sp. and *Samotherium africanum* n.sp. In Leakey, L.S.B. & Savage, R.J.G. (eds) *Fossil Vertebrates of Africa, Volume 2*. Academic Press: London.

Ciochon, R. (2009) The mystery ape of Pleistocene Asia. *Nature* **459**: 910–911.

Ciutti, F. & Cappelletti, C. (2009) First record of *Corbicula fluminalis* (Muller, 1774) in Lake Garda (Italy), living in sympatry with *Corbicula fluminea* (Muller, 1774). *Journal of Limnology* **68**: 162–165.

Clark, J., Asfaw, B., Assefa, G., Harris, J.W.K., Kurashina, H., Walter, R.C., White, T.D., & Williams, M.A.J. (1984) Palaeoanthropological discoveries in the Middle Awash Valley, Ethiopia. *Nature* **307**: 423-428.

Clark, J., de Heinzelin, J., Schick, K., Hart, W., White, T., WoldeGabriel, G., Walter, R., Suwa, G., Asfaw, B., Vrba, E. & Haile-Selassie, Y. (1994) African *Homo erectus*: Old Radiometric Ages and Young Oldowan Assemblages in the Middle Awash Valley, Ethiopia. *Science* **264**: 1907-1910.

Clarke, L.R. & Clarke, A.H. (1980) Zooarchaeological analysis of mollusc remains from Yoquot, British Columbia. *History and Archaeology* **43**: 37-57.

Clarkson, E.N.K. (1993) *Invertebrate Palaeontology and Evolution (Third Edition)*. Chapman & Hall: London.

Claassen, C. (1998) *Shells*. Cambridge University Press: Cambridge.

Coffing, K., Feibel, C., Leakey, M. & Walker, A. (1994) Four-Million-Year-Old Hominids From East Lake Turkana, Kenya. *American Journal of Physical Anthropology* **39**: 55-65.

Conroy, G.C., Jolly, C.J., Cramer, D. & Kalb, J.E. (1978) Newly discovered fossil hominid skull from the Afar depression, Ethiopia. *Nature* **276**: 67-70.

Copeland, S.R. (2007) Vegetation and plant food reconstruction of lowermost Bed II, Olduvai Gorge, using modern analogs. *Journal of Human Evolution* **53**: 146-175.

Cowie, R.H. (2002) Apple Snails (Ampullariidae) as Agricultural Pests: their Biology, Impacts and Management. In Barker, G.M. (ed.) *Molluscs as Crop Pests*. CABI Publishing: New York, (pp. 145–192).

Cunnane, S.C. & Crawford, M.A. (2003) Survival of the fattest: fat babies were the key to evolution of the large human brain. *Comparative Biochemistry and Physiology. Part A, Molecular and Integrative Physiology* **136**: 17–26.

Curnoe, D. (2010) A review of early *Homo* in southern Africa focusing on cranial, mandibular and dental remains, with the description of a new species (*Homo gautengensis* sp. nov.) *Journal of Comparative Human Biology* **61**: 151-177.

Curnoe, D. & Tobias, P.V. (2006) Description, new reconstruction, comparative anatomy, and classification of the Sterkfontein Stw 53 cranium, with discussions about the taxonomy of other southern African early *Homo* remains. *Journal of Human Evolution* **50**: 36-77.

Darlington, J.P.E.C. (2005) Distinctive fossilised termite nests at Laetoli, Tanzania. *Insectes Sociaux* **52**: 408-409.

Dart, R. (1925) *Australopithecus africanus*: The Man-Ape of South Africa. *Nature* **115**: 195-199.

Deacon, H.J. (1976) *Where Hunters Gathered: A Study of Holocene Stone Age People in the Eastern Cape*. South African Archaeological Society Monograph Series, No. 1: Claremont, South Africa.

Dean, D. & Delson, E. (1995) *Homo* at the gates of Europe. *Nature* **373**: 472–473.

De Francesco, C.G. & Hassan, G.S. (2009) The significance of molluscs as palaeoecological indicators of freshwater systems in central-western Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* **274**: 105-113.

de Heinzelin, J. & Verniers, J. (1996). Realm of the Upper Semliki (Eastern Zaire): An essay on historical geology. *Annales-Sciences Géologiques* **102**, 1-87.

Deino, A. & Potts, R. (1990) Single-Crystal $^{40}Ar/^{39}Ar$ Dating of the Olorgesailie Formation, Southern Kenya Rift. *Journal of Geophysical Research* **95**: 8453-8470.

Delfino, M. & Bailon, S. (2000) Early Pleistocene Herpetofauna from Cava Dell'Erba and Cava Pirro (Apulia, Southern Italy). *Herpetological Journal* **10**: 95-110.

Delfino, M., Segid, A., Yosief, D., Shoshani, J., Rook, L. & Libsekal, Y. (2004) Fossil reptiles from the Pleistocene *Homo*-bearing locality of Buia (Eritrea, Northern Danakil Depression). *Rivista Italiana di Paleontologia e Stratigrafia* **110 (supplement)**: 51-60.

deMenocal, P. (2004). African climate change and faunal evolution during the Pliocene-Pleistocene. *Earth and Planetary Science Letters* **220**: 3-24.

Dennell, R.W. (2004) *Early Hominin Landscapes in Northern Pakistan: Investigations in the Pabbi Hills*. British Archaeological Reports International Series 1265.

Dennell, R.W. (2008) The taphonomic record of Upper Siwalik (Pinjor stage) landscapes in the Pabbi Hills, northern Pakistan, with consideration regarding the preservation of hominin remains. *Quaternary International* **192**: 62-77.

Dennell, R.W., Coard, R. & Turner, A. (2006) The biostratigraphy and magnetic polarity zonation of the Pabbi Hills, northern Pakistan: An Upper Siwalik (Pinjor Stage) Upper Pliocene-Lower Pleistocene fluvial sequence. *Palaeogeography, Palaeoclimatology, Palaeoecology* **234**: 168-185.

Dennell, R. & Roebroeks, W. (2005) An Asian perspective on early human dispersal from Africa. *Nature* **438**: 1099-1104.

de Vos, J. (1989) The Environment of *Homo erectus* from Trinil H.K. In Giacobini, G. (ed.) *Hominidae: Proceedings of the 2nd International Congress of Human Paleontology*. Editoriale Jaca Books: Milan, (pp. 225-228).

de Vos, J. & Sondaar, P. (1994) Dating Hominid Sites in Indonesia. *Science* **266**: 1726-1727.

De Winter, A. (2008) Redefinition of *Thapsia* Albers, 1860, and description of three more helicarionoid genera from western Africa (Gastropoda, Stylommatophora) *Zoologische Mededelingen* **82:** http://www.zoologischemededelingen.nl/82/nr02/a41.

Dillon, R.T. (2000) *The ecology of freshwater molluscs*. Cambridge University Press: Cambridge.

Duckworth, J.W., Timmins, R.J. & Muddapa, D. (2008) *Viverricula indica.* In: IUCN 2009. IUCN Red List of Threatened Species. Version 2009.2. <www.iucnredlist.org>. Viewed 10 November 2009.

Dudgeon, D. (1999) *Tropical Asian Streams: Zoobenthos, Ecology and Conservation.* Hong Kong University Press: Hong Kong.

Easteal, S. & Herbert, G. (1997) Molecular Evidence from the Nuclear Genome for the Time Frame of Human Evolution. *Journal of Molecular Evolution* **44 (Supplement 1)**: S121–S132.

Eberz, G.W., Williams, F.M. & Williams, M.A.J. (1988) Plio-Pleistocene volcanism and sedimentary facies changes at Gadeb prehistoric site, Ethiopia. *Geologische Rundschau* **77**: 513-527.

Elewa, A.M.T. (2008) *Mass Extinctions*. Springer-Verlag: Heidelberg.

El Rayah, E.A., Constantinou, C. & Cloudsley-Thompson, J.L. (1984) Environmental Adaptations of the African Snail *Limicolaria festiva* Martens. *International Journal of Biometeorology* **28**: 327-331.

Elton, S. (2002) A reappraisal of the Locomotion and Habitat Preference of *Theropithecus oswaldi. Folia Primatologica* **73**: 252-280.

Erlandson, J. (1988) The Role of Shellfish in Prehistoric Economies: A Protein Perspective. *American Antiquity* **53**: 102–109.

Erlandson, J. (2001) The Archaeology of Aquatic Adaptations: Paradigms for a New Millennium. *Journal of Archaeological Research* **9**: 287-350.

Ersoy, B. & Sereflisan, H. (2010) The Proximate Composition and Fatty Acid Profiles of Edible Parts of Two Freshwater Mussels. *Turkish Journal of Fisheries and Aquatic Sciences* **10**: 71-74.

Estes, R. (1991) *The Behavioural Guide to African Mammals*. University of California Press: Berkeley.

Etler, D.A., Crummett, T.L. & Wolpoff, M.H. (2001) Longgupo: Early *Homo* Colonizer or Late Pliocene *Lufengpithecus* Survivor in South China? *Human Evolution* **16**: 1-12.

Falgueres, C., Bahain, J.-J., Yokoyama, Y., Arsuaga, J.L., Bermudez de Castro, J.M., Carbonell, E., Bischoff, J.L. & Dolo, J.-M. (1999) Earliest humans in Europe: the age of TD6 Gran Dolina, Atapuerca, Spain. *Journal of Human Evolution* **37**: 343-352.

Feibel, C.S. (1993) Freshwater stingrays from the Plio-Pleistocene of the Turkana Basin, Kenya and Ethiopia. *Lethaia* **26**: 359-366.

Feibel, C.S. (2003) Stratigraphy and Depositional Setting of the Pliocene Kanapoi Formation, Lower Keiro Valley, Kenya. *Contributions in Science* **498**: 9-20.

Feibel, C.S., Brown, F.H. & McDougall, I. (1989) Stratigraphic Context of Fossil Hominids From the Omo Group Deposits: Northern Turkana Basin, Kenya and Ethiopia. *American Journal of Physical Anthropology* **78**: 595-622.

Feibel, C.S., Harris, J. & Brown, F.H. (1991) Palaeoenvironmental Context for the Late Neogene of the Turkana Basin. In Harris, J. (ed.) *Koobi Fora Research Project Volume 3: The Fossil Ungulates: Geology, Fossil Artiodactyls, and Palaeoenvironments*. Clarendon Press: Oxford, (pp. 321-370).

Fernandes, M. (1991) Tool use and predation of oysters by the tufted capuchin in brackish water mangrove swamp. *Primates* **32**: 529-531.

Fernandez-Jalvo, Y. & Andrews, P. (1992) Small Mammal Taphonomy of Gran Dolina, Atapuerca (Burgos), Spain. *Journal of Archaeological Science* **19**: 407-428.

Fernandez-Jalvo, Y., Denys, C., Andrews, P., Williams, T., Dauphin, Y. & Humphrey, L. (1998) Taphonomy and palaeoecology of Olduvai Bed I (Pleistocene, Tanzania). *Journal of Human Evolution* **34**: 137-172.

Florea Luiza, D. (2008) The Evolution of Freshwater Fish Feeding Groups in Danube River, Braila Areas. *Bulletin UASVM, Agriculture* **65**: 82-87.

Fiore, I., Bondioli, L., Coppa, A., Macchiarelli, R., Russom, R., Kashay, H., Solomon, T., Rook, L. & Libsekal, Y. (2004) Taphonomic analysis of the late Early Pleistocene bone remains from Buia (Dandiero Basin, Danakil Depression, Eritrea): Evidence for large mammal and reptile butchering. *Rivista Italiana di Paleontologia e Stratigrafia* **110 (supplement)**: 89-97.

Findlater, I.C. (1978) Isochronous surfaces within the Plio-Pleistocene sediments east of Lake Turkana. *Geological Society, London, Special Publications* **6**: 415-420.

Fleagle, J.G. (1988) *Primate Adaptation and Evolution*. Academic Press: New York.

Fleagle, J.G., Assefa, Z., Brown, F.H., Shea, J.J. (2008) Paleoanthropology of the Kibish Formation, southern Ethiopia: Introduction. *Journal of Human Evolution* **55**: 360-365.

Frost, S.R., Plummer, T., Bishop, L.C., Ditchfield, P., Ferraro, J. & Hicks, J. (2003) Partial Cranium of *Cercopithecoides kimeui* Leakey, 1982 From Rawi Gully, Southwestern Kenya. *American Journal of Physical Anthropology* **122**: 191-199.

Fuller, S.L.H. (1974) Clams and mussels (Mollusca: Bivalvia). In Hart, C.W., Jr & Fuller, S.L.H. (eds) *Pollution Ecology of Freshwater Invertebrates*. Academic Press: New York, (pp. 215-273).

Gabunia, L., Anton, S., Lordkipanidze, D., Vekua, A., Justus, A. & Swisher, C. (2001) Dmanisi and Dispersal. *Evolutionary Anthropology* **10**: 158-170.

Gabunia, L. Vekua, A. & Lordkipanidze, D. (2000) The environmental contexts of early human occupation of Georgia (Transcaucasia). *Journal of Human Evolution* **38**: 785-802.

Gao, X., Wei, Q., Shen, C. & Keates, S. (2005) New Light on the Earliest Hominid Occupation in East Asia. *Current Anthropology* **46**: S115-S120.

Garcia, N. & Howell, F (2008) New discovery of a large mustelid - *Pannonictis* cf. *nestii* - (carnivora: mammalia) from the early Pleistocene locality of Sima del Elefante (Sierra de Atapuerca, Spain). *Palaeontographica, Abteilung A: Palaozoologie – Stratigraphie* **284**: 1-16.

Gautier, A. (1970) The freshwater mollusks from the Chiwondo Beds (Malawi): Preliminary Report. *Quaternaria* **13**: 325-329.

Gautier, A. (1976) Assemblages of Fossil Freshwater Mollusks from the Omo Group and Related Deposits in the Lake Rudolf Succession. In Coppens, Y., Howell, F.C., Isaac, G. & Leakey, R.E.F. (eds) *Earliest Man and Environments in the Lake Rudolf Basin*. University of Chicago Press: Chicago, (pp. 383-401).

Gentry, A.W. (1970) The Bovidae (Mammalia) of the Fort Ternan fossil fauna. In Leakey, L.S.B. & Savage, R.J.G. (eds) *Fossil Vertebrates of Africa, Volume 2*. Academic Press: London, (pp. 243-324).

Gentry, A.W. & Gentry, A. (1978) Fossil Bovidae (Mammalia) of Olduvai Gorge, Tanzania, Parts 1 and 2. *Bulletin of the British Museum (Natural History) Geological Series* 29 and 30.

Geraads, D., Alemseged, Z., Reed, D., Wynn, J. & Roman, D.C. (2004) The Pleistocene fauna (other than primates) from Asbole, lower Awash Valley, Ethiopia, and its environmental and biochronological implications. *Geobios* **37**: 697-718.

Gibert, J., Gibert, L., Ribot, F., Ferrandez, C., Sanchez, F., Iglesias, A., Gubert, P. & Gonzalez, F. (2004) Human remains in the early Pleistocene deposits of Orce and Cueva Victoria (SE Spain). *BAR International Series* **1272**: 157-166.

Gibert, J. & Palmqvist, P. (1995) Fractal analysis of the Orce skull sutures. *Journal of Human Evolution* **28**: 561-575.

Gilbert, C.C., McGraw, W.S. & Delson, E. (2009) Brief Communication: Plio-Pleistocene Eagle Predation on Fossil Cercopithecids From the Humpata Plateau, Southern Angola. *American Journal of Physical Anthropology* **139**: 421-429.

Gilbert, W.H. (2008a) Ecological and Biogeographical Context of the Daka Member. In Gilbert, W.H. & Asfaw, B. (eds) Homo erectus: *Pleistocene Evidence from the Middle Awash, Ethiopia.* University of California Press: Berkeley and Los Angeles, (pp. 397-411).

Gilbert, W.H. (2008b) Introduction. In Gilbert, W.H. & Asfaw, B. (eds) Homo erectus: *Pleistocene Evidence from the Middle Awash, Ethiopia.* University of California Press: Berkeley and Los Angeles, (pp. 1-12).

Gilbert, W.H. & Asfaw, B. (2008) Homo erectus: *Pleistocene Evidence from the Middle Awash, Ethiopia.* University of California Press: Berkeley and Los Angeles.

Gilbert, W.H. & Stidham, T. (2008) Rare Taxa. In Gilbert, W.H, & Asfaw, B. (eds) Homo erectus: *Pleistocene Evidence from the Middle Awash, Ethiopia.* Berkeley: University of California Press (pp. 261-264).

Giovanelli, A., Coelho da Silva, C.L.P.A., Leal, G.B.E. & Baptista, D.F. (2005) Habitat preference of freshwater snails in relation to environmental factors and the presence of the competitor snail *Melanoides tuberculata* (Muller, 1774). *Memorias do Instituto Oswaldo Cruz* **100**: 169-176.

Glaubrecht, M. (2006) Independent evolution of reproductive modes in viviparous freshwater Cerithioidea (Gastropoda, Sorbeoconcha) — a brief review. *Basteria* **69 (supplement 3)**: 23-28.

Glaubrecht, M., Feher, Z. & Rintelen, T. (2006) Brooding in *Corbicula madagascariensis* (Bivalvia, Corbiculidae) and the repeated evolution of viviparity in corbiculids. *Zoological Scripta* **35**: 641-654.

Glover, E. (1981) Leang Burung 2: Shell Analysis. *Modern Quaternary Research in Southeast Asia* **6**: 45-50.

Glover, I.C. (1978) Survey and excavation in the Maros District, South Sulawesi, Indonesia: the 1975 field season. *Bulletin of the Indo-Pacific Prehistory Association* **1**: 60-103.

Good, S.C. (2004) Paleoenvironmental and paleoclimatic significance of freshwater bivalves in the Upper Jurassic Morrison Formation, Western Interior, USA. *Sedimentary Geology* **167**: 163-176.

Gooders, J. (1975) *Birds: an illustrated survey of the bird families of the world.* Landsdowne Press: Melbourne.

Grabarkiewicz, J. & Davis, W. (2008) *An introduction to freshwater mussels as biological indicators*. EPA-260-R-08-015. U.S. Environmental Protection Agency, Office of Environmental Information: Washington, DC.

Graf, D.L. & Cummings, K.S. (2006a) Freshwater mussels (Mollusca: Bivalvia: Unionoida) of Angola, with description of a new species, *Mutela wistarmorrisi. Proceedings of the Academy of Natural Sciences of Philadelphia* **155**: 163-194.

Graf, D.L. & Cummings, K.S. (2006b) Palaeoheterodont diversity (Mollusca: Trigonioida + Unionoida): what we know and what we wish we knew about freshwater mussel evolution. *Zoological Journal of the Linnean Society* **148**: 343-394.

Graf, D.L. & Cummings, K.S. (2007) Review of the systematic and global diversity of freshwater mussel species (Bivalvia: Unionoida). *Journal of Molluscan Studies* **73**: 291-314.

Griffen, D.L. (2006) The late Neogene Sahabi rivers of the Sahara and their climatic and environmental implications for the Chad Basin. *Journal of the Geological Society, London* **163**: 905-921.

Grossu, A.V. (1984) Biography of the non-marine molluscs of Romania. In Solem, A. & Van Bruggen, A.C. (eds) *World-Wide Snails.* E.J. Brills: Leiden, (pp. 93-106).

Groves, C. (1989) *A Theory of Human and Primate Evolution.* Clarendon Press: Oxford.

Groves, C. (2009) Human evolution: fossils surprising, fossils predicted. Presented at Charles Darwin Symposium: National Museum of Australia, 26 February 2009.

Groves, C.P. & Mazak, V. (1976) An approach to the taxonomy of the Hominidae: gracile Villafranchian hominids of Africa. *Casopis Pro Mineralogii a Geologii* **20**: 225–247.

Gumus, B.A. (2010) The Land Snails of Kahta, Adiyaman, Turkey (Mollusca: Gastropoda: Pulmonata). *Munis Entomology & Zoology* **5**: 286-289.

Gurung, K.K. & Singh, R. (1996) *Field Guide to the Mammals of the subcontinent.* Academic Press: San Diego.

Gutierrez, M., Guerin, C., Lena, M. & Piedade da Jesus, M. (2001) Exploitation d'un grand cétacé au Paléolithique ancien: le site de Dungo V à Baia Farta (Benguela, Angola). *Comptes Rendus de l'Académie des Sciences* **332**: 357-362.

Haile-Selassie, Y., Suwa, G. & White, T.D. (2004) Late Miocene teeth from Middle Awash, Ethiopia, and early hominid dental evolution. *Science* **303**: 1503-1505.

Hailemichael, M., Aronson, J.L., Savin, S., Tevesz, M.J.S. & Carter, J.G. (2002) Delta^{18}0 mollusk shells from Pliocene Lake Hadar and modern Ethiopian lakes: implications for history of the Ethiopian monsoon. *Palaeogeography, Palaeoclimatology, Palaeoecology* **186**: 81-99.

Hardouin, J. (1995) Minilivestock: from gathering to controlled production. *Biodiversity and Conservation* **4**: 220–232.

Hardy, A. (1960) Was man more aquatic in the past? *New Scientist* **7**: 642-645.

Harman, W.N. (1970) Benthic substrate: their effect on freshwater mollusca. *Ecology* **53**: 271-277.

Harper, E.M. (1991) The role of predation in the evolution of cementation in bivalves. *Palaeontology* **34**: 455-460.

Harper, E.M., Taylor, J.D. & Crame, J.A. (2000) *The Evolutionary Biology of the Bivalvia*. Geological Society, London, Special Publications **177**.

Harries, H.C. 91979) Nuts to the Garden of Eden. *Principes* **23**: 143–148.

Harris, D.R. (1992) Human diet and subsistence. In Jones, R., Martin, R. & Pilbeam, D. (eds) *The Cambridge Encyclopedia of Human Evolution*. Cambridge University Press: Cambridge, (pp. 69–74).

Harris, J. (1987) Summary. In Leakey, M. & Harris, J. (eds) *Laetoli: A Pliocene Site in Northern Tanzania*. Clarendon Press: Oxford, (pp. 524-31).

Harris, J. (1991) *Koobi Fora Research Project Volume 3: The Fossil Ungulates: Geology, Fossil Artiodactyls, and Palaeoenvironments*. Clarendon Press: Oxford.

Harris, J.M. & Cerling, T.E. (2002) Dietary adaptations of extant and Neogene suids. *Journal of Zoology* **256**: 45-54.

Harris, J.M., Leakey, M.G. & Cerling, T.E. (2003) Early Pliocene Tetrapod Remains From Kanapoi, Lake Turkana Basin, Kenya. *Contributions in Science* **498**: 31-113.

Harris, J.W.K., Williamson, P.G., Verniers, J., Tappen, M.J., Stewart, K., Helgren, D., de Heinzelin, J., Boaz, N.T. & Bellomo, R.V. (1987) Late Pliocene hominid occupation in Central Africa: the setting, context, and character of the Senga 5A site, Zaire. *Journal of Human Evolution* **16**: 701-728.

Harrison, T. & Baker, E. (1997) Paleontology and Biochronology of Fossil Localities in the Manonga Valley, Tanzania. In Harrison, T. (ed.) *Topics in Geobiology*. Plenum Press: New York, (pp. 361-93).

Harrison, T. & Msuya, C.P. (2005) Fossil struthionid eggshells from Laetoli, Tanzania: Taxonomic and biostratigraphic significance. *Journal of African Earth Sciences* **41**: 303-315.

Harrison, T., Verniers, J., Mbago, M.L. & Krigbaum, J. (1993) Stratigraphy and mammalian Palaeontology of Neogene Sites in the Manonga Valley, Northern Tanzania. *Discovery and Innovation* **5**: 269-275.

Hay, R.L. (1976) Environmental Setting of Hominid Activities in Bed I, Olduvai Gorge. In Isaac, G. & McCown, E. (eds) *Human Origins: Louis Leakey and the East African Evidence*. W.A. Benjamin: Menlo Park, California, (pp. 209-225).

Hay, R.L. (1981) Lithofacies and Environment of Bed I, Olduvai Gorge, Tanzania. In Rapp, G. & Vondra, C. (eds) *Hominid Sites: Their Geological Settings*. Westview Press: Boulder, (pp. 25-55).

Heller, J. (1984) Deserts as refugia for relict land snails. In Solem, A. & Van Bruggen, A.C. (eds) *World-Wide Snails*. E.J. Brills: Leiden, (pp.107-123).

Heller, J. & Sivan, N. (2002). *Melanopsis* from the Pliocene site of 'Erq el-Ahmar, Jordan Valley (Gastropoda: Cerithioidea). *Journal of Conchology* **37**: 607-626.

Hernandez Fernandez, M. & Vrba, E.S. (2006) Plio-Pleistocene climatic change in the Turkana Basin (East Africa): Evidence from large mammal faunas. *Journal of Human Evolution* **50**: 595-626.

Hillaire-Marcel, C., Taieb, M., Tiercelin, J.J. & Page, N. (1982) A 1.2-Myr record of isotopic changes in a late Pliocene Rift Lake, Ethiopia. *Nature* **296**: 640-642.

Hinch, S.G., Bailey, R.C. & Green, R.H. (1986) Growth of *Lampilis radiata* (Bivalvia, Unionidae) in sand and mud: a reciprocal transplant experiment. *Canadian Journal of Fisheries and Aquatic Sciences* **43**: 548-552.

Hobolth, A., Christensen, O.F., Mailund, T. & Schierup, M.H. (2007) Genomic Relationships and Speciation Times of Human, Chimpanzee, and Gorilla Inferred from a Coalescent Hidden Markov Model. *PLoS Genetics* **3**: e7.

Hoffman, H.J. (1973) Stromatolites: Characteristics and Utility: *Earth-Science Reviews* **9**: 339-373.

Horowitz, A. (1979) *The Quaternary of Israel*. Academic Press: New York.

Howell, F.C. (1968) Omo research expedition. *Nature* **219:** 567–572.

Huang, W., Ciochon, R., Gu, Y., Larick, R., Fang, Q., Schwarcz, H., Yonge, C., de Vos, J. & Rink, W. (1995) Early *Homo* and associated artefacts from Asia. *Nature* **378**: 275-278.

Huang, W. & Hu, Y. (1997) Archaeological evidence for the first human colonization of East Asia. *Bulletin of the Indo-Pacific Prehistory Association* **16**: 3-12.

Huffman, O.F. (2001). Geologic context and age of the Perning/Mojokerto *Homo erectus*, East Java. *Journal of Human Evolution* **40**: 353-362.

Huffman O.F. & Zaim, Y. (2003) Mojokerto Delta, East Jawa: Paleoenvironment of *Homo modjokertensis*-First Results. *Journal of Mineral Technology* **10 (2)**: The Faculty of Earth Sciences and Mineral Technology, Institute Technology, Bandung.

Huffman, O.F., Zaim, Y., Kappelman, J., Ruez, D., de Vos, J., Rizal, Y., Aziz, F. & Hertler, C. (2006) Relocation of the 1936 Mojokerto skull discovery site near Perning, East Java. *Journal of Human Evolution* **50:** 431-451.

Hurcombe, L. (2004) The stone artefacts from the Pabbi Hills. In Dennell, R. (ed.) *Early Hominin Landscapes in Northern Pakistan: Investigations in the Pabbi Hills*. British Archaeological Reports International Series **1265**: 222-292.

Hyodo, M., Nakaya, H., Urabe, A., Saegusa, H., Shunrong, X., Jiyun, Y. & Xuepin, J. (2002) Paleomagnetic dates of hominid remains from Yuanmou, China, and other Asian sites. *Journal of Human Evolution* **43**: 27-41.

Indriati, E. & Anton, S.C. (2008) Earliest Indonesian facial and dental remains from Sangiran, Java: a description of Sangiran 27. *Anthropological Science* **116**: 219-229.

Isaac, G. (1977). *Olorgesailie: Archaeological Studies of a Middle Pleistocene Lake Basin in Kenya*. University of Chicago Press: Chicago.

Isaac, G. (1978) The Olorgesailie Formation: Stratigraphy, tectonics and the palaeogeographic context of the middle Pleistocene archaeological sites. In Bishop, W. (ed.) *Geological Background to Fossil Man: Recent research in the Gregory Rift Valley, East Africa.* Scottish Academic Press: Edinburgh, (pp. 173-206).

Jia, L. (1980) *Early Man in China*. Foreign Language Press: Beijing.

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.

Johanson, D.C., Taieb, M., Gray, B.T. & Coppens, Y. (1978) Geological framework of the Pliocene Hadar Formation (Afar, Ethiopia) with notes on paleontology including hominids. In, Bishop, W.W. (ed.) *Geological Background to Fossil Man.* Scottish Academic Press: Edinburgh, (pp. 549-564).

Jonkinen, E.H., Guerette, J. & Kortmann, R.W. (1982) The natural history of an ovoviviparous snail *Viviparus georgianus* in a soft water eutrophic lake. *Freshwater Invertebrate Biology* **1**: 2–17.

Joordens, J., Wesselingh, F., de Vos, J., Vonhof, H. & Kroon, D. (2009) Relevance of aquatic environments for hominins: a case study from Trinil (Java, Indonesia). *Journal of Human Evolution* **57**: 656-671.

Kalb, J.E. (1993) Refined Stratigraphy of the Hominid-Bearing Awash Group, Middle Awash Valley, Afar Depression, Ethiopia. *Newsletters on Stratigraphy* **29**: 21-62.

Kalb, J.E., Jolly, C.J., Mebrate, A., Tebedge, S., Smart, C., Oswald, E.B., Cramer, D., Whitehead, P., Wood, C.B., Conroy, G.C., Adefris, T., Sperling, L. & Kana, B. (1982). Fossil mammals and artefacts from the Middle Awash Valley, Ethiopia. *Nature* **298**: 25-29.

Kalb, J.E., Oswald, E.B., Tebedge, S., Mebrate, A., Tola, E. & Peak, D. (1982) Geology and stratigraphy of Neogene deposits, Middle Awash Valley, Ethiopia. *Nature* **298**: 17-25.

Kalb, J.E., Wood, C.B., Smart, C., Oswald, E.B., Mebrate, A., Tebedge, S. & Whitehead, P. (1980) Preliminary Geology and Palaeontology of the Bodo D'ar Hominid Site, Afar, Ethiopia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **30**: 107-120.

Kafumu, P.D. (2004) Paleoclimatical significance of the palaeosol levels occurring in the Miocene-Pleistocene stratigraphy of the Manonga-Wembere Valley in Central Tanzania. *Episodes* **27**: 107-111.

Kaiser, T.M. (2000) Proposed Fossil Insect Modification to Fossil Mammalian Bone from Plio-Pleistocene Hominid –Bearing Deposits of Laetoli (Northern Tanzania). *Annals of Entomological Society of America* **93**: 693-700.

Kat, P.W. (1987) Biogeography and Evolution of African Freshwater Molluscs: Implications of a Miocene Assemblage from Rusinga Island, Kenya. *Palaeontology* **30**: 733–742.

Kaufulu, Z.M. & Stern N. (1987) The first stone artefacts to be found in situ within the Plio-Pleistocene Chiwondo Beds in northern Malawi. *Journal of Human Evolution* **16**: 729-740.

Kautsky, N. & Kiibus, M. (1997) Biomass, ecology and production of benthic fauna in Lake Kariba. In Moreau, J. (ed.) *Advances in the Ecology of Lake Kariba.* University of Zimbabwe Publications: Harare, Zimbabwe, (pp. 162-182).

Keates, S.G. (2003) Biostratigraphy, Taphonomy, Palaeoenvironment and Hominid Diet in the Middle and Late Pleistocene of China. In *Current Research in Chinese Pleistocene Archaeology*, BAR International Series **1179**. Archaeopress: Oxford, (pp. 37-56).

Kennedy, G.E. (1985) Bone thickness in *Homo erectus*. *Journal of Human Evolution* **14**, 699-708.

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

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

Kingdon, J. (2003) *Lowly Origins: Where, When, and Why Our Ancestors First Stood Up*. Princeton University Press: Princeton.

Kingston, J.D. & Harrison, T. (2007) Isotopic dietary reconstructions of Pliocene herbivores at Laetoli: Impication for early hominin paleoecology. *Palaeogeography, Palaeoclimatolgy, Palaeoecology* **243**: 272–306.

Klein, R. (1983) The Stone Age Prehistory of Southern Africa. *Annual Review of Anthropology* **12**: 25-48.

Klein, R. (1999) *The Human Career: Human Biological and Cultural Origins*. University of Chicago Press: Chicago.

Klein, R., Avery, G., Cruz-Uribe, K., Halkett, D., Parkington, J., Steele, T., Volman, T. & Yates, R. (2004) The Ysterfontein 1 Middle Stone Age site, South Africa, and early human exploitation of coastal resources. *Proceedings of the National Academy of Sciences of the USA* **101**: 5708-5715.

Kohler, F. & Glaubrecht, M. (2006) A Systematic Revision of the Southeast Asian Freshwater Gastropod *Brotia* (Cerithioidea: Pachychilidae). *Malacologia* **48**: 159-251.

Koops, K., Humle, T., Sterck, E.H.M. & Matsuzawa, T. (2006) Ground-nesting by the chimpanzee of the Nimba Mountains, Guinea: environmentally or socially determined? *American Journal of Primatology* **69**: 407-419.

Koravic, K. & Andrews, P. (2007) Bovid postcranial ecomorphological survey of the Laetoli palaeoenvironment. *Journal of Human Evolution* **52**: 663-680.

Korniushin, A.V. (2002) Morphological characters analysis, the intergroup phylogenetic relationships and possible outgroups of the family Sphaeriidae (Mollusca, Bivalvia). *Vestnik zoologii* **36**: 3-22.

Korniushin, A.V. & Glaubrecht, M. (2002) Phylogenetic analysis based on the morphology of viviparous freshwater clams of the family Sphaeriidae (Mollusca, Bivalvia, Veneroida). *Zoologica Scripta* **31**: 415-459.

Korniushin, A.V. & Glaubrecht, M. (2003) Novel reproductive modes in freshwater clams: brooding and larval morphology in Southeast Asian taxa of *Corbicula* (Mollusca, Bivalvia, Corbiculidae). *Acta Zoologica* **84**: 293-315.

Korzeniak, J., Zajac, K. & Zajac, T. (2004) Relations between Unionids Occurrence, In-Steam Vegetation and Morphology of the Channel in the Nida River. *Nature Conservation* **60**: 23-29.

Krolopp, E. & Sumegi, P. (1995) Palaeoecological Reconstruction of the Late Pleistocene, Based on Loess Malacofauna in Hungary. *GeoJournal* **36**: 213-222.

Kullmer, O., Sandrock, O., Abel, R., Schrenk, F., Bromage, T. & Juwayeyi, M. (1999) The first *Paranthropus* from the Malawi Rift. *Journal of Human Evolution* **37**: 121-127.

Kuman, K. & Clarke, R.J. (2000) Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5. *Journal of Human Evolution* **38**: 827-847.

Landau, M. (1984) Human Evolution as Narrative. *American Scientist* **72**: 262-268.

Larick, R., Ciochon, R., Zaim, Y., Sudijono, Suminto, Rizal, Y. & Aziz, F. (2000) Lithostratigraphic Context for Kln-1993.05-SNJ, a Fossil Colobine Maxilla from Jokotingker, Sangiran Dome. *International Journal of Primatology* **21**: 731-759.

Larick, R., Ciochon, R., Zaim, Y., Sudijono, Suminto, Rizal, Y., Aziz, F., Reagan, M. & Heizler, M. (2001) Early Pleistocene ^{40}Ar/^{39}Ar ages for Bapang Formation hominins, Central Jawa, Indonesia. *PNAS* **98**: 4866-4871.

Leakey, L.S.B. (1965) *Olduvai Gorge 1951-61 Volume 1: A Preliminary Report on the Geology and Fauna*. Cambridge University Press: Cambridge.

Leakey M.D. (1971) *Olduvai Gorge Volume 3: Excavations in Beds I and II, 1960-1963*. Cambridge University Press: Cambridge.

Leakey, M.D. (1976) A Summary and Discussion of the Archaeological Evidence from Bed I and Bed II, Olduvai Gorge, Tanzania. In Isaac, G. & McCown, E. (eds) *Human*

Origins: Louis Leakey and the East African Evidence. W.A. Benjamin: Menlo Park, California, (pp. 431-459).

Leakey, M.D. (1979) *Olduvai Gorge: My Search for Early Man.* Collins: London.

Leakey, M.D. & Harris, J.M. (1987) *Laetoli: A Pliocene Site in Northern Tanzania.* Clarendon Press: Oxford.

Leakey, M.D. (1994) *Olduvai Gorge Volume 5: Excavations in Beds III, IV and the Masek Beds, 1968-1971.* Cambridge University Press: Cambridge.

Leakey, M.D. & Hay, R.L. (1979) Pliocene footprints in the Laetoli Beds at Laetoli, northern Tanzania. *Nature* **278**: 317-323.

Leakey, M.G., Feibel, C.S., Bernor, R.L., Harris, J.M., Cerling, T.E., Stewart, K.M., Storrs, G.W., Walker, A., Werdelin, L. & Winkler, A.J. (1996). Lothagam: A Record of Faunal Change in the Late Miocene of East Africa. *Journal of Vertebrate Paleontology* **16**: 556-570.

Leakey, M.G., Feibel, C.S., McDougall, I. & Walker, A. (1995) New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* **376**: 565-571.

Leakey, M.G., Feibel, C.S., McDougall, I., Ward, C. & Walker, A. (1998) New specimens and confirmation of an early age for *Australopithecus anamensis*. *Nature* **393**: 62-66.

Leakey, M.G. & Harris, J.M. (2003) *Lothagam: The Dawn of Humanity in Eastern Africa.* Columbia University Press: New York.

Leakey, M.G., Spoor, F., Brown, F.H., Gathogo, P.N., Kiarie, C., Leakey, L.N. & McDougall, I. (2001) New hominin genus from eastern Africa shows diverse middle Pliocene lineages. *Nature* **410**: 433-440.

Leakey, R.E. (1969) Early *Homo sapiens* remains from the Omo River region of south-west Ethiopia. *Nature* **222**: 1137-1138.

Lewis, M. (1997) Carnivoran paleoguilds of Africa: implications for hominid food procurement strategies. *Journal of Human Evolution* **32**: 257-88.

Li, P., Chien, F., Ma, H., Pu, C., Hsing, L. & Chu, S. (1977) Preliminary Study on the Age of Yuanmou Man by Palaeomagnetic Technique. *Scientia Sinica* **20**: 645-664.

Lieberman, D.E., Bramble, D.M., Raichlen, D.A. & Shea, J.J. (2007) The evolution of endurance running and the tyranny of ethnography: A reply to Pickering and Bunn (2007). *Journal of Human Evolution* **53**: 439-442.

Lihoreau, F., Boisserie, J.-R., Viriot, L., Coppens, Y., Likius, A., Mackaye, H.T., Tafforeau, P., Vignaud, P. & Brunet, M. (2006) Anthracothere dental anatomy reveals a late Miocene Chado-Libyan bioprovince. *Proceedings of the National Academy of Science of the USA* **103**: 8763-8767.

Livshits, G., Fishelson, L. & Wise, G.S. (1984) Genetic similarity and diversity of parthenogenetic and bisexual populations of the freshwater snail *Melanoides tuberculata* (Gastropoda: Prosobranchia). *Biological Journal of the Linnean Society* **23**: 41-54.

Lordkipanidze, D., Vekua, A., Ferring, R., Rightmire, G., Zollikofer, C., Ponce de Leon, M., Agusti, J., Kiladze, G., Mouskhelishvili, A., Nioradze, M. & Tappen, M. (2006) A Fourth Hominin Skull From Dmanisi, Georgia. *The Anatomical Record Part A* **228A**: 1146-1157.

Lordkipanidze, D., Jashashvili, T., Vekua, A., Ponce de Leon, M., Zollikofer, C., Rightmire, G., Pontzer, H., Ferring, R., Oms, O., Tappen, M., Bukhsianidze, M., Agusti, J., Kahlke, R., Kiladze, G., Martinez-Navarro, B., Mouskhelishvili, A., Nioradze, M. & Rook, L. (2007) Postcranial evidence from early *Homo* from Dmanisi, Georgia. *Nature* **449**: 305-310.

Loreau, M. & Baluku, B. (1991) Shade as a means of ecological control of *Biomphalaria pfeifferi*. *Annals of Tropical Medicine and Parasitology* **85**: 443–446.

Louchart, A. (2008) Fossil birds of the Kibish Formation. *Journal of Human Evolution* **55**: 513-520.

Louchart, A., Wesselman, H., Blumenschine, R.J., Hlusko, L.J., Njau, J.K., Black, M.T., Asnake, M. & White, T.D. (2010) Taphonomic, Avian, Small-Vertebrate Indicators of *Ardipithecus ramidus* Habitat. *Science* **326**: 66e1-66e4.

Lubell, D. (2004) Prehistoric edible land snails in the circum-Mediterranean: the archaeological evidence. In Brugal, J.-P. & Desse, J. (eds) *Petits Animaux et Sociétés Humaines: du Complément Alimentaire aux Ressources Utilitaires, XXIVe Rencontres Internationales d'Archéologie et d'Histoire d'Antibes*. Éditions APDCA, Antibes, (pp. 77-98).

Macdonald, D. (2001) *The Encyclopedia of Mammals*. Facts On File: New York.

MacDonald, K. (2006) *The Ecology and Evolution of Hominin Geographic Ranges*. Bar International Series 1550, Archaeopress: Oxford.

Madar, S.I. (2007) The postcranial skeleton of early Eocene pakicetid cetaceans. *Journal of Paleontology* **81**: 176-200.

Maier, W. & Nkini, A. (1985) The Phylogenetic Position of Olduvai Hominid 9, Especially as Determined From Basicranial Evidence. In Delson E. (ed.) *Ancestors: The Hard Evidence*. Alan R. Liss: New York, (pp. 249-54).

Majid, Z. (2005) *The Perak Man and other prehistoric shelters of Malaysia*. Penerbit Universiti: Palau, Penang.

Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., Panha, S., Cheewatham, C. & Hamada, Y. (2007) Stone-Tool Usage by Thai Long-Tailed Macaques (*Macaca fascicularis*). *American Journal of Primatology* **69**: 227-233.

Mallegni, F., Carnieri, E., Bisconti, M., Tartarelli, G., Ricci, S., Biddittu, I. & Segre, A. (2003) *Homo cepranensis sp. nov.* and the evolution of African-European Middle Pleistocene hominids. *Comptes Rendus Palevol* **2**: 153-159.

Mallol, C. (2006). What's in a beach? Soil micromorphology of sediments from the Lower Paleolithic site of Ubeidiya, Israel. *Journal of Human Evolution* **51**: 185-206.

Mania, D. & Vlcek (1981) *Homo erectus* in middle Europe: the discovery from Bilzingsleben. In Sigmon, B. & Cybulski, J. (eds) Homo erectus*: Papers in honor of Davidson Black*. University of Toronto Press: Toronto, (pp. 131-151).

Manser, J.M. (2007) *Morphological Analysis of the Human Burial Series at Niah Cave: Implications for Late Pleistocene-Holocene Southeast Asian Human Evolution*. Pro Quest: Ann Arbor, Michigan.

Manzi, G., Mallegni, F. & Ascenzi, A. (2001) A cranium for the earliest Europeans: Phylogenetic position of the hominid from Ceprano, Italy. *Proceedings of the National Academy of Sciences* **98**: 10011-10016.

Marean, C., Bar-Matthews, J., Fisher, E., Goldberg, P., Herries, A., Jacobs, Z., Jerardino, A., Karkanas, P., Minichillo, T., Nilssen, P., Thompson, E., Watts, I., Williams, H. (2007) Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. *Nature* **449**: 905-908.

Martin, J.W. & Trautwein, S. (2003) Fossil Crabs (Crustacea, Decapoda, Brachyura) from Lothagam. In Leakey, M.G. & Harris, J.M. (eds) *Lothagam: The Dawn of Humanity in Eastern Africa*. Columbia University press: New York, (pp. 67-73.)

Martinez-Navarro, B., Rook, L., Segid, A., Yosief, D., Ferretti, M., Shoshani, J., Tecle, T. & Libsekal, Y. (2004) The large fossil mammals from Buia (Eritrea): Systematics, Biochronology and Paleoenvironments. *Rivista Italiana di Paleontologia e Stratigrafia* **110 (supplement)**: 61-68.

Martini, F., Libsekal, Y., Filippi, O., Ghebre/her, A., Kashay, H., Kiros, A., Martino, G., Okubatsion, D., Segid, A., Solomon, T., Teka, Z., Yosief, D. & Yamane, S. (2004) Characterization of lithic complexes from Buia (Dandiero Basin, Danakil Depression, Eritrea). *Rivista Italiana di Paleontologia e Stratigrafia* **110 (supplement)**: 99-132.

Mazza, P.P.A., Martini, F., Sala, B., Magi, M., Colombini, M.P., Giachi, G., Landucci, F., Lemorini, C., Modugno, F. & Ribechini, E. (2006) A new Palaeolithic discovery: tar-hafted stone tools in a European Mid-Pleistocene bone-bearing bed. *Journal of Archaeological Science* **33**: 1310–1318.

McBrearty, S. & Jablonski, N.G. (2005) First fossil chimpanzee. *Nature* **437**: 105-108.

McDougall, I. & Brown, F. (2006) Precise ^{40}Ar/^{39}Ar geochronology for the upper Koobi Fora Formation, Turkana Basin, northern Kenya. *Journal of the Geological Society* **163**: 205-220.

McDougall, I., Brown, F.H. & Fleagle, J.G. (2005) Stratigraphic placement and age of modern humans from Kibish, Ethiopia. *Nature* **433**: 733-736.

McDougall, I. & Feibel, C.S. (1999) Numerical age control from the Miocene-Pliocene succession at Lothagam, a hominoid-bearing sequence in the northern Kenya Rift. *Journal of the Geological Society, London* **156**: 731-745.

McMahon, R.F. (1983) Ecology of an Invasive Pest Bivalve, *Corbicula*. In Russell-Hunter, W.D. (ed.) *The Mollusca: Volume 6, Ecology*. Academic Press: Orlando, (pp.505-561).

McPherron, S.P., Alemseged, Z., Marean, C.W., Wynn, J.G., Reed, D., Geraads, D., Bobe, R. & Bearat, A. (2010) Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* **466**: 857–860.

Medway, L. (1972) Quaternary Mammals of Malesia; a review. In Ashton, P. & Ashton, M. (eds) *The Quaternary Era in Malesia*. Department of Geography, University of Hull, Miscellaneous Series No. 13: 1-122.

Meehan, B. (1982) *Shell Bed to Shell Midden*. Australian Institute of Aboriginal Studies: Canberra.

Meylan, P. (1987) Fossil snakes from Laetoli. In Leakey, M. & Harris, J. (eds) *Laetoli: A Pliocene Site in Northern Tanzania*. Clarendon Press: Oxford, (pp. 78-82).

Mishra, S., Mishra, R.K., Sahu, B.K., Nayak, L. & Senga, Y. (2008) Differential growth of the freshwater mussel, *Lamellidens marginalis* in relation to certain drugs. *Environmental Toxicology* **23**: 379-386.

Mitchell, T. (1839) *Three expeditions into the interior of Eastern Australia.* T. &W. Boone: London.

Moore, R.C. (1969) *Treatise on Invertebrate Paleontology: Part N, Volume 1 (of 3), Mollusca 6, Bivalvia.* The Geological Society of America and University of Kansas Press: New York.

Morrison, J.P.E. (1942) Preliminary report on mollusks found in the shell mounds of the Pickwick Landing Basin in the Tennessee River valley. *Bulletin of the Bureau of American Ethnology* **129**: 337-392.

Morton, B. (1969) Studies on the Biology of *Dreissena polymorpha* Pall. I. General Anatomy and Morphology. *Journal of Molluscan Studies* **38**: 301–321.

Morton, J.E. (1979) *Molluscs*. Hutchinson: London.

Morton, B. (1986) *Corbicula* in Asia – an updated synthesis. *American Malacological Bulletin, Special Edition* **2**: 113-124.

Morwood, M.J., O'Sullivan, P.B., Aziz, F. & Raza, A. (1998) Fission-track ages of stone tools and fossils on the east Indonesian island of Flores. *Nature* **392**: 173-176.

Morwood, M.J., Aziz, F., O'Sullivan, P., Nasruddin, Hobbs, D.R. & Raza, A. (1999) Archaeological and palaeontological research in central Flores, east Indonesia: results of fieldwork 1997-98. *Antiquity* **73**: 273-286.

Moya- Sola, S. & Kohler, M. (1997) The Orce skull: anatomy of a mistake. *Journal of Human Evolution* **33**: 91-97.

Moyle, P. & Cech, J. (1982) *Fishes: An Introduction to Ichthyology.* Prentice-Hall: New Jersey.

Musiba, C., Magori, C., Stoller, M., Stein, T., Branting, S., Vogt, M., Tuttle, R., Hallgrimsson, B., Killindo, S., Mizambwa, F., Ndunguru, F. & Mabulla, A. (2007) Taphonomy and paleoecological context of the Upper Laetolil Beds (Localities 8 and 9), Laetoli in northern Tanzania. In Bobe, R., Alemseged, Z. & Behrensmeyer, A.K. (eds)

Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence. Springer: Dordrecht, The Netherlands, (pp. 257-278).

Muttoni, G., Scardia, G., Kent, D.V., Swisher, C.C. & Manzi, G. (2009) Pleistocene magnetochronology of early hominin sites at Ceprano and Fontana Ranuccio, Italy. *Earth and Planetary Science Letters* **286**: 255-268.

Nagaoka, S., Katoh, S., WoldeGabriel, G., Sato, H., Nakaya, H., Beyene, Y. & Suwa, G. (2005) Lithostratigraphy and sedimentary environments of the hominid bearing Pliocene-Pleistocene Konso Formation in the southern Main Ethiopian Rift, Ethiopia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **216**: 333-357.

Nagel, K.-O. (2000) Testing hypotheses on the dispersal and evolutionary history of freshwater mussels (Mollusca: Bivalvia: Unionidae). *Journal of Evolutionary Biology* **13**: 854-865.

Ndifon, G.T. & Ukoli, F.M.A. (1989) Ecology of freshwater snails in south-western Nigeria. I: Distribution and habitat preferences. *Hydrobiologia* **171**: 231-253.

Nehring, S. (2006) NOBANIS – Invasive Alien Species fact Sheet – *Crassostrea gigas* – From: Online Database of the north European and Baltic network on Invasive Alien Species- NOBANIS www.nobanis.org. Date of access 01/09/10.

Ninkovich, D. & Burckle, L. (1978) Absolute age of the base of the hominid-bearing beds in Eastern Java. *Nature* **275**: 306-308.

Noskova, N.G. (2001) Elasmotherians – evolution, distribution and ecology. In *The World of Elephants, Proceedings of the First International Congress, 16–20 October 2001, Rome*, (pp. 126–128).

O'Connor, S. & Sullivan, M. (1994) Distinguishing middens and cheniers: a case study from the southern Kimberley, W.A. *Archaeology in Oceania* **29**: 16–28.

Ossa, P., Marshall, B. & Webb, C. (1995) New Guinea II Cave: A Pleistocene site on the Snowy River, Victoria. *Archaeology in Oceania* **30**: 22–35.

O'Sullivan, P.B., Morwood, M., Hobbs, D., Aziz Suminto, F., Situmorang, M., Raza, A. & Maas, R. (2001) Archaeological implications of the geology and chronology of the Soa Basin, Flores, Indonesia. *Geology* **29**: 607-610.

Pace, G.L. (1973) The freshwater snails of Taiwan (Formosa). *Malacologist Review* **Supplement 1**: 118.

Pain, T. & Woodward, F.R. (1961) A revision of the freshwater mussels of the family Etheriidae. *Journal of Conchology* **25**: 2-8.

Parfitt, S.A., Barendregt, R.W., Breda, M., Candy, I., Collins, M.J., Coope, G.R., Durbidge, P., Field, M.H., Lee, J.R., Lister, A.M., Mutch, R., Penkman, K.E.H., Preece, R.C., Rose, J., Stringer, C.B., Symmons, R., Whittaker, J.E., Wymer, J.J. & Stuart, A.J. (2005) The earliest record of human activity in northern Europe. *Nature* **438**: 1008-1012.

Parmalee, P.W. & Klippel, W.E. (1974) Freshwater Mussels as a Prehistoric Food Resource. *American Antiquity* **39**: 421-434.

Partridge, T. (1985) Spring flow and tufa accretion at Taung. In P. V. Tobias (ed.) *Hominid Evolution. Past, present and future*. Liss: New York, (pp. 171-187).

Patil, S.G. & Talmale, S.S. (2005) A Checklist of Land and Freshwater Mollusca of Maharashtra State. *Zoos' Print Journal* **20**: 1912-1913.

Patnaik, R. & Schleich, H.H. (1993) Fossil crocodile remains from the Upper Siwaliks of India. *Mitteilungen der Bayerischen Staatsammlungen Palaontologisch-historische Geologie* **33**: 91-117.

Patterson, B., Behrensmeyer, A.K. & Sill, W.D. (1970) Geology and Fauna of a New Pliocene Locality in North-western Kenya. *Nature* **226**: 918-921.

Patterson, N., Richter, D.J., Gnerre, S., Lander, E.S. & Reich, D. (2006) Genetic evidence for complex speciation of humans and chimpanzees. *Nature* **441**: 1103-1108.

Perrins, C. & Middleton, A. (1985) *The Encyclopedia of Birds*. Facts On File: New York.

Petr, T. (2000) *Interactions between Fish and Aquatic Macrophytes in Inland Waters: A Review*. Rome: Food and Agriculture Organisation of the United Nations.

Petter, G., Pickford, M. & Howell, F.C. (1991) The Pliocene otter of Nyaburogo and Nkondo (Uganda, East Africa): *Torolutra ougandensis* n.g., n.sp., Mammalia, Carnivora. *Comptes Rendus – Academie des Sciences, Serie II: Sciences de la Terre et des Planetes* **312**: 949-955.

Pickford, M. (1984) Fossil mollusca from the Sumburu Hills, Northern Kenya. *African Study Monographs* **Supplementary Issue 2**: 141-145.

Pickford, M. (1987) Fossil terrestrial gastropods from the Namurungule Formation, Kenya. *African Study Monographs* **Supplementary Issue 5**: 155-156.

Pickford, M. (1995) Fossil land snails of East Africa and their palaeoecological significance. *Journal of African Earth Sciences* **20**: 167-226.

Pickford, M. (2004) Palaeoenvironments of Early Miocene hominid-bearing deposits at Napak, Uganda, based on terrestrial molluscs. *Annales de Paleontologie* **90**: 1-12.

Pickford, M., Mein, P. & Senut, B. (1992) Primate bearing Plio-Pleistocene cave deposits of Humpata, Southern Angola. *Human Evolution* **7**: 17-33.

Pickford, M., Sawada, Y., Tayama, R., Matsuda, Y., Itaya, T., Hyodo, H. & Senut, B. (2006) Refinement of the age of the Middle Miocene Fort Ternan Beds, Western Kenya, and its implications for Old World Biochronology. *Comptes Rendus Geoscience* **338**: 545-555.

Pickford, M. & Senut, B. (2001) The geological and faunal context of Late Miocene hominid remains from Lukeino, Kenya. *Comptes Rendus de l'Academie des Sciences, Paris, Earth and Planetary Sciences* **332**: 145–152.

Pickford, M. & Senut, B. (2005) Hominoid teeth with chimpanzee and gorilla like features from the Miocene of Kenya: Implications for the chronology of ape-human divergence and biogeography of Miocene hominoids. *Anthropological Science* **113**: 95-102.

Plaziat, J.-C. & Younis, W.R. (2005) The modern environments of Molluscs in southern Mesopotamia, Iraq: A guide to paleogeographical reconstructions of Quaternary fluvial, palustrine and marine deposits. *Carnets de Geologie*: Article 2005/01 (CG2005-A01).

Plummer, T.W., Ditchfield, P.W., Bishop, L.C., Kingston, J.D., Ferraro, J.V., Braun, D.R., Hertel, F. & Potts, R. (2009) Oldest Evidence of Toolmaking Hominins in a Grassland-Dominated Ecosystem. *PLoS ONE* **4**: e7199.

Poirier, F.E. (1987) *Understanding Human Evolution*. Prentice-Hall: Englewood Cliffs.

Ponder, W.F. & Lindberg, D.R. (1997) Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of the Linnean Society* **119**: 83-265.

Pope, G.G. (1989) Hominid paleoenvironments in the Far East. In Giacobani, G. (ed.) *Hominidae: Proceedings of the 2nd International Congress of Human Paleontology*. Editoriale Jaca Book: Milan, (pp. 231-235).

Potts, R., Behrensmeyer, A.K. & Ditchfield, P. (1999) Paleolandscape variation and Early Pleistocene hominid activities: Members 1 and 7, Olorgesailie Formation, Kenya. *Journal of Human Evolution* **37**: 747-788.

Potts, R., Behrensmeyer, A.K., Deino, A., Ditchfield, P. & Clark, J. (2004) Small Mid-Pleistocene Hominin Associated with East African Acheulean Technology. *Science* **305**: 75-78.

Preston, H. (1915) *The Fauna of British India: Mollusca*. Taylor & Francis: London.

Quade, J., Levin, N., Semaw, S., Stout, D., Renne, P., Rogers, M. & Simpson, S. (2004) Paleoenvironments of the earliest stone toolmakers, Gona, Ethiopia. *Geological Society of America Bulletin* **116**: 1529-1544.

Quade, J., Levin, N.E., Simpson, S.W., Butler, R., McIntosh, W.C., Semaw, S., Kleinasser, L., Dupont-Nivet, G., Renne, P. & Dunbar, N. (2008) The Geology of Gona, Afar, Ethiopia. In Quade, J. & Wynn, J. (eds) *The Geology of Early Humans in the Horn of Africa*. The Geological Society of America, Special Paper 446: Boulder, (pp. 1-31).

Qian, F. & Zhou, G. (1991) *Quaternary Geology and Paleoanthropology of Yuanmou, Yunnan, China*. Science Press: Beijing.

Raikow, D.F. & Hamilton, S.K. (2001). Bivalve Diets in a Midwestern U.S. Stream: A Stable Isotope Enrichment Study. *Limnology and Oceanography* **46**: 514-522.

Raut, S.K. & Barker, G.M. (2002) *Achatina fulica* Bowdich and other Achatinidae as Pests in Tropical Agriculture. In Barker, G.M. (ed.) *Molluscs as Crop Pests*. CABI Publishing: Wallingford, (pp. 55-114).

Reed, K. (1997) Early hominid evolution and ecological change through the African Plio-Pleistocene. *Journal of Human Evolution* **32**: 289-322.

Relethford, J. (1990) *The Human Species: An introduction to biological anthropology*. Mayfield Publishing Company: Mountain View, California.

Rightmire, G.P. (1996) The human cranium from Bodo, Ethiopia: evidence for speciation in the Middle Pleistocene? *Journal of Human Evolution* **31**: 21-39.

Robba, E., Di Geronimo, I., Chaimanee, N., Negri, M.P. & Sanfilippo, R. (2002) Holocene and Recent shallow soft bottom mollusks from the northern Gulf of Thailand area: Bivalvia. *Bollettino Malacologico* **38**: 49-132.

Robba, E., Di Geronimo, I., Chaimanee, N., Negri, M.P. & Sanfilippo, R. (2003) Holocene and Recent shallow soft-bottom mollusks from the northern Gulf of Thailand area. Scaphopoda, Gastropoda additions to Bivalvia. *La Conchiglia* **35 (Suppl. 309)**: 1-289

Roche, H., Delagnes, A., Brugal, J.-P., Feibel, C., Kibunjia, M., Mourre, V. & Texier, P.-J. (1999) Early hominid stone tool production and technical skill 2.34 Myr ago in West Turkana, Kenya. *Nature* **399**: 57-60.

Ron, H. & Levi, S. (2001) When did hominids first leave Africa?: New high-resolution magnetostratigraphy from the Erk-el-Ahmar Formation, Israel. *Geology* **29**: 887-890.

Rosas, A., Huguet, R., Perez-Gonzalez, A., Carbonell, E., Bermudez de Castro, J.M., Vallverdu, J., van der Made, J., Allue, E., Garcia, N., Martinez-Perez, R., Rodriguez, J., Sala, R., Saladie, P., Benito, A., Martinez-Maza, C., Bastir, M., Sanchez, A. & Pares, J.M. (2006) The "Sima del Elefante" cave site at Atapuerca (Spain). *Estudios Geologicos* **62**: 327-348.

Rose, K.D. (1981) Composition and species diversity in Paleocene and Eocene mammal assemblages: an empirical study. *Journal of Vertebrate Paleontology* **1**: 367-388.

Russell-Hunter, W.D., (1978) Ecology of Freshwater Pulmonates. In Fretter, V. & Peake, J. (eds) *Pulmonates*. Academic Press: London, (pp. 335-383).

Sághy, M. & Hornung, E. (2001) Updated Checklist of Grassland Gastropods in the South-Hungarian Plain. *Malacological Newsletter* **19**: 103-107.

Sahnouni, M. (1998) *The Lower Palaeolithic of the Maghreb: Excavations and analyses at Ain Hanech, Algeria*. Bar International Series, Archaeopress: Oxford.

Sahnouni, M. & de Heinzelin, J. (1998) The Site of Ain Hanech Revisited: New Investigations at this Lower Pleistocene Site in Northern Algeria. *Journal of Archaeology Science* **25**: 1083-1101.

Sahnouni, M., Hadjouis, D., van der Made, J., Derradji, A., Canals, A., Medig, M., Belahrech, H., Harichane, Z. & Rabhi, M. (2002) Further research at the Oldowan site of Ain Hanech, North-eastern Algeria. *Journal of Human Evolution* **43**: 925-937.

Sanchez-Marco, A. (1999) Implications of the avian fauna for paleoecology in the Early Pleistocene of the Iberian Peninsula. *Journal of Human Evolution* **37**: 375-388.

Santoso, U., Kubo, K., Ota, T., Tadokoro, T. & Maekawa, A. (1996) Nutrient composition of *kopyor* coconuts (*Cocos nucifera* L.). *Food Chemistry* **57**: 299-304.

Sarac, G. & Sen, S. (2005) Chalicotheriidae (Mammalia, Perissodactyla) from the late Miocene of Akkasdagi, Turkey. In Sen, S. (ed.) Geology, mammals and environments at Akkasdagi, late Miocene of central Anatolia. *Geodiversitas* **27**: 591-600.

Sarmiento, E.E. (2010) Comment on the Paleobiology and Classification of *Ardipithecus ramidus*. *Science* **328**: 1105-b.

Sauer, C.O. (1962) Seashore – Primitive Home of Man? *Proceedings of the American Philosophical Society* **106**: 41-47.

Sawada, Y., Pickford, M., Senut, B., Itaya, T., Hyodo, M., Miura, T., Kashine, C., Chujo, T. & Fujii, H. (2002) The age of *Orrorin tugenensis*, an early hominid from the Tugen Hills, Kenya. *Comptes Rendus Palevol* **1**: 293-303.

Scholz, H. & Hartman, J.H. (2007) Paleoenvironmental Reconstruction of the Upper Cretaceous Hell Creek Formation of the Williston Basin, Montana, USA: Implications From the Quantitive Analysis of Unionid Bivalve Taxonomic Diversity and Morphologic Disparity. *Palaios* **22**: 24-34.

Schrenk, F., Bromage, T., Betzler, C., Ring, U. & Juwayeyi, Y. (1993) Oldest *Homo* and Pliocene biography of the Malawi Rift. *Nature* **365**: 833-936.

Schrenk, F., Bromage, T., Gorthner, A. & Sandrock, O. (1995) Paleoecology of the Malawi Rift: Vertebrate and invertebrate faunal contexts of the Chiwondo Beds, northern Malawi. *Journal of Human Evolution* **28**: 59-70.

Schrenk, F., Kullmer, O., Ring, U., Betzler, C., Sandrock, O. & Abel, R. (1997) Geologie, Palaontologie und Palaoanthropologie des Malawi-Rifts. In Betzler, C. & Hussner, H. (eds) Vogel-Festschrift. *Courier Forschungsinstitut Senckenberg* **201**: 409-419.

Scott, G.R., Gibert, L. & Gibert J. (2007) Magnetostratigraphy of the Orce region (Baza Basin), SE Spain: New chronologies for Early Pleistocene faunas and hominid occupation sites. *Quaternary Science Reviews* **26**: 415-435.

Seed, R. (1969) The Ecology of *Mytilus edulis* L. (Lamellibranchiata) on Exposed Rocky Shores. *Oecologia* **3**: 317-350.

Semaw, S., Simpson, S.W., Quade, J., Renne, P.R., Butler, R.F., McIntosh, W.C., Levin, N., Dominguez-Rodrigo, M. & Rogers, M.J. (2005) Early Pliocene hominids from Gona, Ethiopia. *Nature* **433**: 301-305.

Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K. & Coppens, Y. (2001) First hominid from the Miocene (Lukeino Formation, Kenya). *Comptes Rendus, de l'Academie des Sciences, Series IIA – Earth and Planetary Science* **332**: 137-144.

Shea, J.J. (2008) The Middle Stone Age archaeology of the Lower Omo Valley Kibish Formation: Excavations, lithic assemblages, and inferred patterns of early *Homo sapiens* behavior. *Journal of Human Evolution* **55**: 448-485.

Shikov, E.V. (1984) Effects of land use changes on the land mollusc fauna in the central portion of the Russian plain. In Solem, A. & Van Bruggen, A.C. (eds) *World-Wide Snails.* E.J. Brills: Leiden, (pp. 237-248).

Shreeve, J. (1996). *The Neandertal Enigma.* Morrow: New York.

Sickel, J.B. (1986) *Corbicula* population mortalities: factors influencing population control. *American Malacological Bulletin (Special Edition)* **2**: 89-94.

Sikes, N.E., Potts, R. & Behrensmeyer, A.K. (1999) Early Pleistocene habitat in Member 1 Olorgesailie based on paleosol stable isotopes. *Journal of Human Evolution* **37**: 721-746.

Solounias, N. & Dawson-Saunders, B. (1988) Dietary adaptations and paleoecology of the late Miocene ruminants from Pikermi and Samos in Greece. *Palaeogeography, Palaeoclimatology, Palaeoecology* **65**: 149-172.

Smith, D. (2001) *Pennak's Freshwater Invertebrates of the United States: Porifera to Crustacea, Fourth Edition.* John Wiley & Sons: New York.

Soes, D.M., Gloer, P. & de Winter, A.J. (2009) *Viviparus acerosus* (Bourguignat, 1862) (Gastropoda: Viviparidae), a new exotic snail species for the Dutch fauna. *Aquatic Invasions* **4**: 373-375.

Songtham, W., Ugai, H., Imsamut, S., Maranate, S., Tansathien, W., Meesook, A. & Saengsrichan, W. (2005) Middle Miocene molluscan assemblages in Mae Moh Basin, Lampang Province, northern Thailand. *Science Asia* **31**: 183-191.

Stanley, S.M. (1992) An ecological theory for the origin of *Homo*. *Paleobiology* **18**: 237-257.

Stauffer, R.L., Walker, A., Ryder, O.A., Lyons-Weiler, M. & Hedges, S.B. (2001) Human and Ape Molecular Clocks and Constraints on Paleontological Hypotheses. *The Journal of Heredity* **92**: 469-474.

Stewart, C.B. & Disotell, T.R. (1998) Primate Evolution – in and out of Africa. *Current Biology* **8**: R582-R588.

Stewart, K. (2003) Fossil Fish Remains From the Pliocene Kanapoi Site, Kenya. *Contributions in Science* **498**: 21-38.

Stiner, M. (1994) *Honor Among Thieves*. New Jersey: Princeton University Press: Princeton.

Strayer, D.L., Downing, J.A., Haag, W.R., King, T.L. Layzer, J.B., Newton, T.J. & Nichols, S.J. (2004) Changing Perspectives on Pearly Mussels, North America's Most Imperiled Animals. *BioScience* **54**: 429–439.

Strayer, D.L. (2008) *Freshwater Mussel Ecology: Multifactor Approach to Distribution and Abundance*. University of California Press: Berkeley & Los Angeles.

Stringer, C.B., Finlayson, J.C., Barton, R.N.E., Fernández-Jalvo, Y., Cáceres, I., Sabin, R.C., Rhodes, E.J., Currant, A.P., Rodríguez-Vidal, J., Giles-Pacheco, F. & Riquelme-Cantal, J.A. (2008) Neanderthal exploitation of marine mammals in Gibraltar. *Proceedings of the National Academy of Sciences USA* **105**:14319-14324

Sturm, R. (2007) freshwater molluscs in mountain lakes of the Eastern Alps (Austria): relationship between environmental variables and lake colonization. *Journal of Limnology* **66**: 160–169.

Su, D.F., Ambrose, S.H., DeGusta, D. & Haile-Selassie, Y. (2009) Palaeoenvironment. In Haile-Selassie, Y. & WoldeGabriel, G. (eds) Ardipithecus kadabba: *Late Miocene Evidence from the Middle Awash, Ethiopia*. University of California Press: Berkely and Los Angeles, (521-547).

Sulianti, A. (2008*)* Cooking *Echinostoma*-infected *Bellamya javanica* for Safe Consumption. *Proceedings of the ASEAN Congress of Tropical Medicine and Parasitology* **3**: 28-32.

Supian, Z. & Ikhwanuddin, A.M. (2002) Population Dynamics of Freshwater Molluscs (Gastropod: *Melanoides tuberculata*) in Crocker Range Park, Sabah. *ASEAN Review of Biodiversity and Environmental Conservation* **July-September**: 1-9.

Suryanarayanan, H. & Alexander, K. M. (1972) Biochemical investigations on edible molluscs of Kerala. 1. A study on the nutritional value of some bivalves. *Fishery Technology* **9**: 42-47.

Suwa, G., Nakaya, H., Asfaw, B., Saegusa, H., Amzaye, A., Kono, R.T., Beyene, Y. & Katoh, S. (2003) Plio-Pleistocene terrestrial mammal Assemblage from Konso, Southern Ethiopia. *Journal of Vertebrate Paleontology* **23**: 901-916.

Suwa, G., Kono, R.T., Katoh, S., Asfaw, B. & Beyene, Y. (2007) A new species of great ape from the late Miocene epoch in Ethiopia. *Nature* **448**: 921-924.

Swisher, C., Curtis, G., Jacob, T., Getty, A., Suprijo, A. & Widiasmoro (1994) Age of the Earliest Known Hominids in Java, Indonesia. *Science* **263**: 1118-1121.

Szabó, K. (2007) Comments on the molluscan remains from Batadomba-Lena. Unpublished report prepared for Nimal Perera, Department of Archaeology and Anthropology, Australian National University.

Szabó, K., Ramirez, H., Anderson, A. & Bellwood, P. (2003) Prehistoric Subsistence Strategies on the Batanes Islands, Northern Philippines. *Bulletin of the Indo-Pacific Prehistory Association* **23**: 163-171.

Taieb, M., Johanson, D.C., Coppens, Y. & Aronson, J.L. (1976) Geological and palaeontological background of Hadar hominid site, Afar, Ethiopia. *Nature* **260**: 289-293.

Tang, Y., You, Y. & Li, Y. (1981) Several Paleolithic and Early Pleistocene Mammalian Localities in Yangyuan and Yuxian Counties, Hebei Province. *Vertebrata PalAsiatica* **19**: 256-267.

Tappen, M. (1995) Savanna Ecology and Natural Bone Deposition: Implications for Early Hominid Site Formation, Hunting, and Scavenging. *Current Anthropology***36**: 223–260.

Tchernov, E. (1968) *A Preliminary Investigation of the Birds in the Pleistocene Deposits of 'Ubeidiya*. The Israel Academy of Sciences and Humanities: Jerusalem.

Tchernov, E. (1973) *On the Pleistocene Molluscs of the Jordan Valley*. The Israel Academy of Sciences and Humanities: Jerusalem.

Tchernov, E. (1987) The age of the 'Ubeidiya Formation, an Early Pleistocene Hominid Site in the Jordan Valley, Israel. *Israel Journal of Earth Science* **36**: 3-30.

Thorpe, S.K.S., Holder, R.L. & Crompton, R.H. (2007) Origin of Human Bipedalism As an Adaptation for locomotion on Flexible Branches. *Science* **316**: 1328–1331.

Trapani, J. (2008) Quaternary fossil fish from the Kibish Formation, Omo Valley, Ethiopia. *Journal of Human Evolution* **55**: 521-530.

Turner, A., Bishop, L.C., Denys, C. & McKee, J.K. (1999) A Locality-based Listing of African Plio-Pleistocene Mammals. In Bromage, T. & Schrenk, F. (eds) *African Biogeography, Climate Change & Human Evolution*. Oxford University Press: New York, (pp. 369-399).

Uboh, F.E., Ebong, P.E. & Mbi, E. (2010) Cultural discrimination in the Consumption of black snail (*Archachatina marginata*) and white snail (*Achatina achatina*); and scientific justification? *International Research Journal of Microbiology* **1**: 13–17.

Urabe, M. (2000) Phenotypic Modulation by the Substratum of Shell Sculpture in *Semisulcospira reiniana* (Prosobranchia: Pleuroceridae). *Journal of Molluscan Studies* **66**: 53-59.

Urabe, A., Nakaya, H., Muto, T., Katoh, S., Hyodo, M. & Shunrong, X. (2001) Lithostratigraphy and depositional history of the Late Cenozoic hominid-bearing successions in the Yuanmou Basin, southwest China. *Quaternary Science Reviews* **20**: 1671-1681.

Van Benthem Jutting, T. (1937) *Non marine mollusca from horizons in Java with special reference to the Trinil fauna*. E.J. Brill: Leiden.

Van Bocxlaer, B. & Van Damme, D. (2009) Palaeobiology and Evolution of the Late Cenozoic Freshwater Molluscs of the Turkana Basin: Iridinidae Swainson, 1840 and Etheriidae Deshayes, 1830 (Bivalvia: Etherioidea). *Journal of Systematic Palaeontology* **7**: 129-161.

Van Bocxlaer, B., Van Damme, D. & Feibel, C.S. (2008) Gradual versus punctuated equilibrium evolution in the Turkana Basin molluscs: Evolutionary events or biological invasions? *Evolution* **62**: 511-520.

Van Couvering, J.A.H. & Van Couvering, J.A. (1976) Early Miocene Mammal Fossils from East Africa: Aspects of geology, faunistics, and palaeoecology. In Isaac, G. & McCown, E, (eds) *Human Origins: Louis Leakey and the East African Evidence*. Staples Press: Menlo Park, (pp. 55-207).

Van Damme, D. (1984) *The Freshwater Mollusca of Northern Africa: Distribution, Biogeography and Palaeoecology*. Dr. W. Junk Publishers: Dordrecht.

Van Damme, D. & Gautier, A. (1997) Late Cenozoic Freshwater Mollusks of Wembere-Manonga Valley, Tanzania. In Harrison, T. (ed.) *Neogene Paleontology of Manonga Valley, Tanzania: A window into the evolutionary history of East Africa*. Plenum Press: New York, (pp. 351-360).

Van Damme, D. & Pickford, M. (2003) The late Cenozoic Thiaridae (Mollusca, Gastropoda, Cerithioidea) of the Albertine Rift Valley (Uganda-Congo) and their bearing on the origin and evolution of the Tanganyikan thalassoid malacofauna. *Hydrobiologia* **498**: 1-83.

van den Bergh, G., de Vos, J. & Sondaar, P. (2001) The Late Quaternary palaeogeography of mammal evolution in the Indonesian Archipelago. *Palaeogeography, Palaeoclimatology, Palaeoecology* **171**: 385-408.

van Kolfschoten, T. (1992) Aspects of the migration of mammals to northwestern Europe during the Pleistocene, in particular the reimmigration of *Arvicola terrestris*. *Courier Forschungsinstitut Senckenberg* **153**: 213-220.

Vekua, A., Lordkipanidze, D., Rightmire, G., Agusti, J., Ferring, R., Maisuradze, G., Mouskhelishvili, A., Nioradze, M., Ponce de Leon, M., Tappen, M., Tvalchrelidze, M. & Zollikofer, C. (2002) A New Skull of Early *Homo* from Dmanisi, Georgia. *Science* **297**: 85-89.

Venette, R.C. & Larson, M. (2004) *Mini Risk Assessment Giant African Snail,* Achatina fulica *Bowdich (Gastropoda: Achatinidae)*. Department of Entomology: University of Minnesota.

Verdcourt, B. (1972) The zoogeography of the non-marine mollusca of East Africa. *Journal of Conchology* **27**: 291-348.

Verdcourt, B. (1984) Discontinuities in the distribution of some East African land snails. In Solem, A. & Van Bruggen, A.C. (eds) *World-Wide Snails*. E.J. Brill: Leiden, (pp. 134-155).

Verdcourt, B. (1987) Mollusca from the Laetoli and Upper Ndolanya Beds. In Leakey, M. & Harris, J. (eds) *Laetoli: A Pliocene Site in Northern Tanzania*. Clarendon Press: Oxford, (pp. 438-450).

Viegas, J. (2010) Toothy tree-swinger may be earliest human. *Discovery News* http://news.discovery.com/human/human-ancestor-tree-swinger.html (viewed 19/10/10).

Vignaud, P., Duringer, P., Mackaye, H.T., Likius, A., Blondel, C., Boisserie, J.-R., de Bonis, L., Eisenmann, V., Etienne, M.-E., Geraads, D., Guy, F., Lehmann, T., Lihoreau, F., Lopez-Martinez, N., Mourer-Chauvire, C., Otero, O., Rage, J.-C., Schuster, M., Viriot, L., Zazzo, A. & Brunet, M. (2002) Geology and Palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad. *Nature* **418**: 152-155.

Vrba, E. (1974) Chronological and ecological implications of the fossil Bovidae at the Sterkfontein Australopithecine site. *Nature* **250**: 19-23.

Vrba, E. (1988) Late Pliocene climatic events and hominid evolution. In Grine, F.E. (ed.) *Evolutionary History of the "Robust" Australopithecines*. Aldine de Gruyter: New York, (pp. 405-426).

Vrba, E. (1999) Habitat Theory in Relation to the Evolution in African Neogene Biota and Hominids. In Bromage, T. & Schrenk, F. (eds) *African Biogeography, Climate Change & Human Evolution*. Oxford University Press: New York, (pp. 19-34).

Walker, A. (1993) Taphonomy. In Walker, A. & Leakey, R. (eds) *The Nariokotome* Homo erectus *Skeleton*. Harvard University Press: Cambridge, (pp. 40-53).

Walter, R.C. & Aronson, J.L. (1993) Age and source of the Sidi Hakoma Tuff, Hadar Formation, Ethiopia. *Journal of Human Evolution* **25**: 229-240.

Walter, R.C., Manega, P.C., Hay, R.L., Drake, R.E. & Curtis, G.H. (1991) Laser-fusion ^{40}Ar/^{39}Ar dating of Bed I, Olduvai Gorge, Tanzania. *Nature* **354**: 145-149.

Ward, C.V., Leakey, M.G. & Walker, A. (2001) morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. *Journal of Human Evolution* **41**: 255–368.

Warren, R.E. (1991) Freshwater Mussels as Paleoenvironmental Indicators: A Quantitative Approach to Assemblage Analysis. In Purdue, J.R., Klippel, W.E. & Styles, B.W. (eds) *Beamers, Bobwhites, and Blue-Points: Tributes to the Career of Paul W. Parmalee*. Illinois State Museum Scientific Papers 23: Springfield, Illinois, (pp. 23-66).

Waselkov, G.A. (1987) Shellfish gathering and shell midden archaeology. *Advances in Archaeological Method and Theory* **10**: 93-210.

Watters, G.T. & O'Dee, S.H. (1998) Metamorphosis of Freshwater Mussel Glochidia (Bivalvia: Unionidae) on Amphibians and Exotic Fishes. *American Midland Naturalist* **139**: 49-57.

Wesselingh, F.P., Cadee, G.C. & Renema, W. (1999) Flying high: on the airborne dispersal of aquatic organisms as illustrated by the distribution histories of the gastropod genera *Tryonia* and *Planorbarius*. *Geologie en Mijnbouw* **78**: 165–174.

White, T.D., Ambrose, S.H., Suwa, G., Su, D.F., DeGusta, D., Bernor, R.L., Boisserie, J.-R., Brunet, M., Delson, E., Frost, S., Garcia, N., Giaourtsakis, I.X., Haile-Selassie, Y., Howell, F.C., Lehmann, T., Likius, A., Pehlevan, C., Saegusa, H., Semprebon, G., Teaford, M. & Vrba, E. (2009a) Macrovertebrate Paleontology and the Pliocene Habitat of *Ardipithecus ramidus*. *Science* **326**: 87-93.

White, T.D., Ambrose, S.H., Suwa, G. & WoldeGabriel, G. (2010) Response to Comment on the Paleoenvironment of *Ardipithecus ramidus*. *Science* **328**: 1105-e.

White, T.D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C.O., Suwa, G. & WoldeGabriel, G. (2009b) Ardipithecus ramidus and the Paleobiology of Early Hominids *Science* **326**: 75-86.

White, T.D., Suwa, G., Richards, G., Watters, J.P. & Barnes, L.G. (1983) "Hominoid Clavicle" From Sahabi Is Actually a Fragment of Cetacean Rib. *American Journal of Physical Anthropology* **61**: 239-244.

White, T.D., WoldeGabriel, G., Asfaw, B., Ambrose, S., Beyene, Y., Bernor, R.L., Boisserie, J.-R., Currie, B., Gilbert, H., Haile-Selassie, Y., Hart, W.K., Hlusko, L.J., Clark Howell, F., Kono, R.T., Lehmann, T., Louchart, A., Lovejoy, C.O., Renne, P.R., Saegusa, H., Vrba, E.S., Wesselman, H. & Suwa, G. (2006) Asa Issie, Aramis and the origin of *Australopithecus*. *Nature* **440**: 883–889.

Whitton, B. (1982) *Rivers, Lakes and Marshes*. Hodder & Staughton: London.

Williams, M.A.J., Williams, F.M., Gasse, F., Curtis, G.H. & Adamson, D.A. (1979) Plio-Pleistocene environments at Gadeb prehistoric site, Ethiopia. *Nature* **282**: 29-33.
Williamson, P.G. (1981) Palaeontological documentation of speciation in Cenozoic molluscs from Turkana Basin. *Nature* **293**: 437-443.

Williamson, P.G. (1982) Molluscan biostratigraphy of the Koobi Fora hominid-bearing deposits. *Nature* **295**: 140-142.

Williamson, P.G. (1985a) Evidence for an early Plio-Pleistocene rainforest expansion in East Africa. *Nature* **315**: 487-489.

Williamson, P.G. (1985b) Punctuated equilibrium, morphological stasis, and the paleontological documentation of speciation. *Biological Journal of the Linnean Society of London* **26**: 307-324.

Willis, J. (1966) *A Dictionary of the Flowering Plants and Ferns*. Cambridge University Press: Cambridge.

Wright, C.A. (1977) Co-evolution of bulinid snails and African schistosomes. In Gear, J.H. (ed.) *Medicine in a tropical environment*. Balkema: Capetown, (pp. 291-300).

WoldeGabriel, G., Ambrose, S.H., Barboni, D., Bonnefille, R., Bremond, L., Currie, B., DeGusta, D., Hart, W.K., Murray, A.M., Renne, P.R., Jolly-Saad, M.C., Stewart, K.M. & White, T.D. (2009) The Geological, Isotopic, Botanical, Invertebrate, and Lower Vertebrate Surroundings of *Ardipithecus ramidus*. *Science* **326**: 65e1-65e5.

WoldeGabriel, G., Gilbert, W.H., Hart, W.K., Renne, P.R. & Ambrose, S.H. (2008) Geology and Geochronology. In Gilbert, W.H, & Asfaw, B. (eds) Homo erectus*: Pleistocene Evidence from the Middle Awash, Ethiopia.* University of California Press: Berkeley, (pp. 13-43).

WoldeGabriel, G., Haile-Selassie, Y, Renne, P.R., Hart, W.K., Ambrose, S.H., Asfaw, B., Heiken, G. & White, T. (2001) Geology and palaeontology of the Late Miocene Middle Awash valley, Afar rift, Ethiopia. *Nature* **412**: 175-178.

WoldGabriel, G., Hart, W.K., Renne, P.R., Haile-Selassie, Y. & White, T. (2009) Stratigraphy of the Adu-Asa Formation. In Haile-Selassie, Y. & WoldeGabriel, G. (eds) Ardipithecus kadabba: *Late Miocene Evidence from the Middle Awash, Ethiopia.* University of California Press: Berkely and Los Angeles, (pp. 27-61).

Wood, B. & Collard, M. (1999) The Human Genus. *Science* **284**: 65–71.

Wrangham, R. (2005) The Delta Hypothesis: Hominoid Ecology and Hominin Origins. In Lieberman, D., Smith, R. & Kelley, J. (eds) *Interpreting the Past: Essays on Human,* *Primate and Mammal Evolution in Honor of David Pilbeam.* Brill Academic Publishers: Boston, (pp. 231-242).

Wrangham, R. Cheney, D., Seyfarth, R. & Sarmiento, E. (2009) Shallow-Water Habitats as Sources of Fallback Foods for Hominins. *American Journal of Physical Anthropology* **140**: 630-642.

Wu, M., Wu, Q., Wang, Y. & Xue, D. (2003) A land snail species *Cathaica* (*Pliocathaica*) *radiata*, facing extinction in China. *Tentacle* **11**: 6-7.

Wu, X. (2000) Longgupo Hominoid Mandible Belonged to Ape. *Acta Anthropologica Sinica* **19**: 1–10.

Wu, X. & Poirier, F.E. (1995) *Human Evolution in China: A Metric Description of the Fossils and a Review of the Sites*. Oxford University Press: Oxford.

Wynn, J.G. (2000) Paleosols, stable carbon isotopes, and paleoenvironmental interpretation of Kanapoi, Northern Kenya. *Journal of Human Evolution* **39**: 411-432.

Wynn, J., Alemseged, Z., Bobe, R., Geraads, D., Reed, D. & Roman, D. (2006) Geological and palaeontological context of a Pliocene juvenile hominin at Dikika, Ethiopia. *Nature* **443**: 332-336.

Wynn, J., Roman, D., Alemseged, Z., Reed, D., Geraads, D. & Munro, S. (2008) Stratigraphy, depositional environments, and the basin structure of the Hadar and Busidima Formations at Dikika, Ethiopia. *Geological Society of America Special Papers* **446**: 87-118.

Yildirim, M.Z. (2004) The Gastropods of Lake Egirdir. *Turkish Journal of Zoology* **28**: 97-102.

Yildirim, M.Z., Koca, S.B. & Kebapci, U. (2006) Supplement to the Prosobranchia (Mollusca: Gastropoda) Fauna of Fresh and Brackish Waters of Turkey. *Turkish Journal of Zoology* **30**: 197-204.

Yin, G.M., Zhao, H., Yin, J.H. & Lu, Y.C. (2002) Chronology of the stratum containing the skull of the Dali Man. *Chinese Science Bulletin* **47**: 1302-1307.

Yonge, C.M. (1960) *Oysters*. Collins: London.

Yonge, C.M. (1962) On *Etheria elliptica* Lam. and the Course of Evolution, Including Assumption of Monomyarianism, in the Family Etheriidae (Bivalvia: Unionacea). *Philosophical Transactions of the Royal Society of London B* **244**: 423-458.

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

Zhu, R.X., Potts, R., Pan, Y.X., Yao, H.T., Lu, L.Q., Zhao, X., Gao, X., Chen, L.W., Gao, F. & Deng, C.L. (2008) Early evidence of the genus *Homo* in East Asia. *Journal of Human Evolution* **55**: 1075-1085.

Zhu, R., Potts, R., Xie, F., Hoffman, K., Deng, C., Shi, C., Pan, Y., Wang, H., Shi, R., Wang, Y., Shi, G. & Wu, N. (2004) New evidence on the earliest human presence at high northern latitudes in northeast Asia. *Nature* **431**: 559-562.

Zihlman, A.L. & Lowenstein, J.M. (1996) A Spanish Olduvai? *Current Anthropology* **37**: 695-697.

Appendix 1

A1: Damage patterns of *Pseudodon* bivalves from Trinil

A1.1 Introduction

The early Pleistocene site of Trinil from the lower Bapang (Kabuh) Formation of Java has yielded molluscs of a now extinct sub-species of unionid bivalve *Pseudodon vondembuschianus trinilensis* (Van Benthem Jutting 1937). These shells are generally well preserved and often paired. The outer surface of the shells seems abraded, but this apparently is a chemical and not a physical feature.

The *Pseudodon* specimens have similar fracture patterns with those seen in more recent Holocene assemblages from Sampung Cave (Figure A1.1.1), which are most probably the remains of food consumption by modern human populations (Van Benthem Jutting 1932).

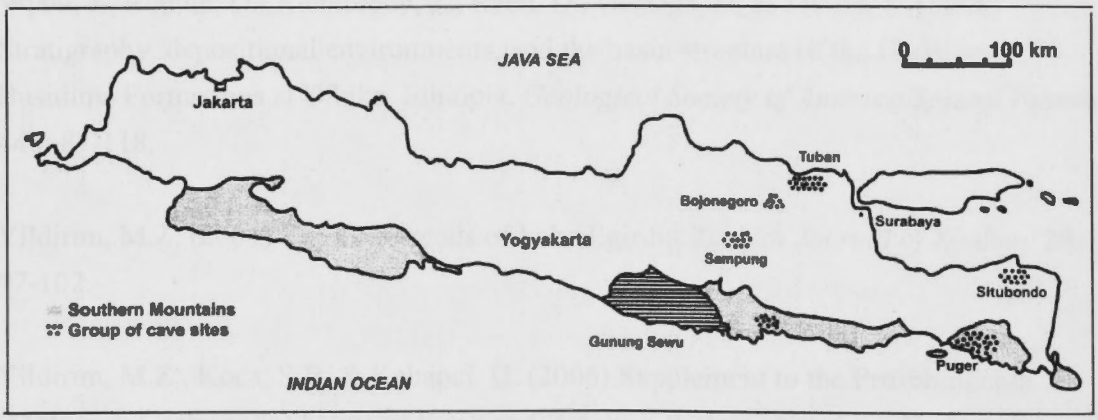


Figure A1.1.1: Map of Java showing location of Sampung Caves (Simanjuntak & Asikin 2004)

Since *Homo erectus* at Sangiran 1.5Ma was using thick shelled bivalves as tools to butcher large mammals (Choi & Driwantoro 2007), and since freshwater bivalves are a common food resource for modern human populations, the idea that some of the damage observed on the *Pseudodon* shells might have been caused by hominin predation is here examined.

A1.2 Methods and material

The *Pseudodon* specimens were collected by Eugene Dubois between 1890 and 1900, and now form part of the Dubois collection stored at Naturalis (The National Museum of Natural History, The Netherlands), Leiden. The specimens are typically large (c.100 x 60mm) and the valve walls thick. The specimens include articulated shells, single valves and fragments. Each valve, and each fragment either including the umbo, or measuring more than 50mm, was photographed and each photograph examined for fractures and notches.

Venerupis aurea, from Eemian (last glacial c.125 ka) beach deposits in the Netherlands, were subjected to the same analysis, because it was noted (by Gerhard Cadée, after discussion with Frank Wesselingh) that these shells had similar breakage characteristics to the *Pseudodon* assemblage. This sample includes only single valves, including undamaged as well as fractured and notched specimens. An outline of each valve was sketched to include fractures and notches. These bivalves are typically smaller (50 x 30mm) than the *Pseudodon* specimens, not as thick walled, but of relatively similar shape.

Elongaria bivalves from the Neolithic Cave site of Sampung were also subjected to the same analysis. These shells were analysed because of the strong possibility that they represent the remains of human predated bivalves and therefore could be directly compared to the other two assemblages examined. The Sampung shells almost certainly have a cultural context, with evidence suggesting human agency in transporting the shells to the cave, and associated consumption and possible tool use. Specimens were photographed and analysed using the same method as that used for the *Pseudodon* and *Venerupis* assemblages. The *Elongaria* shells are also smaller than the *Pseudodon* specimens (larger specimens typically 70 x 30mm), and are closer in size to the *Venerupis* shells, but generally more elongated. The presence of more than one taxonomic group within the assemblage is distinctly possible.

Each of the three bivalve assemblages include shells that are morphologically similar in that the umbo is closer to the anterior margin than to the midline, and pointing anteriorly (see Figure A1.2.1 for shell terminology).

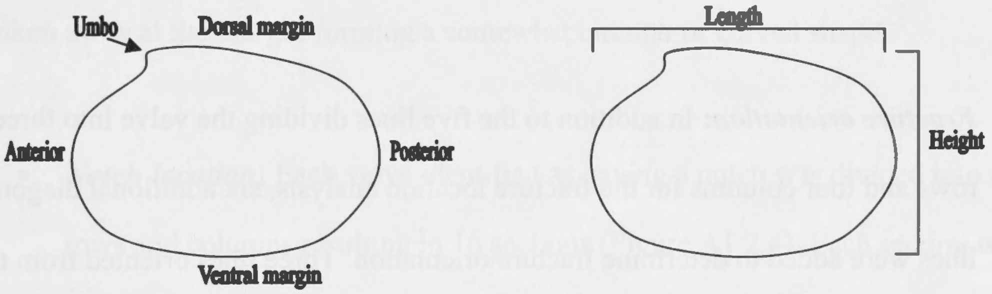


Figure A1.2.1: Morphological terminology used in this chapter

A1.2.1 Fractures

Valves with five or fewer fractures were subject to analysis; valves consisting of more than five fractures were considered too fragmentary. Valve fragments where less than half the original valve remained were not included in the fracture analysis study.

- ***Fracture location*:** Each valve was divided into 12 sections with three vertical lines dividing the shell into four columns, and two horizontal lines dividing the shell into three rows, with the divisions relative to the size of each specimen. Each valve was therefore divided into 12 potential locations in which fractures could occur (Figure A1.2.2). For each valve all locations in which at least one fracture occurred was recorded.

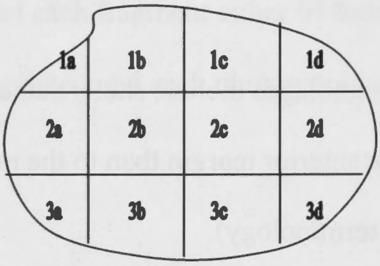


Figure A1.2.2: Potential locations in which fractures could occur

- ***Fracture orientation***: In addition to the five lines dividing the valve into three rows and four columns for the fracture location analysis, six additional diagonal lines were added to determine fracture orientation. Three lines oriented from the dorsal-anterior margin to the ventral-posterior margin, and three lines from the dorsal-posterior margin to the ventral-anterior margin (Figure A1.2.3). Each fracture was then evaluated and matched to the line that it most closely paralleled. Because some valves have more than one fracture, and because many fractures are not straight lines, it is possible that both valves and fractures can have multiple fracture lines of orientation. This method relies on approximate estimations of the major axis of a fracture.

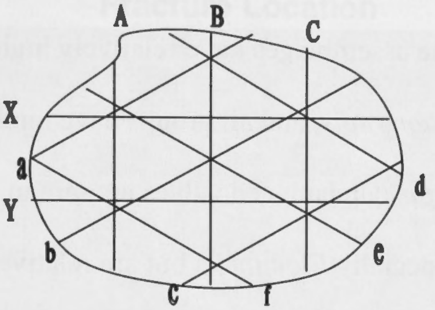


Figure A1.2.3: Lines used for fracture orientation locations

A1.2.2 Notches

Notches are small indentations in the margin of the shell, not fractures, and not chipped margins. Notches essentially represent the hole left where a portion of shell has been broken away at the margin forming a somewhat circular or curved shape.

- ***Notch location***: Each valve identified as having a notch was divided into four rows and columns resulting in 16 sections (Figure A1.2.4). Each section where a notch occurred was then recorded. Because notches occur only along the margin of the shell, the four locations of the shell that do not occur on the margin (2b, 2c, 3b 3c) are disregarded, leaving 12 possible locations where notches could occur.

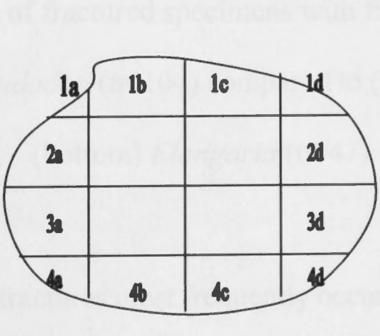


Figure A1.2.4: Valve divided into 16 sections, 12 of which occur on the margin.

A1.3 Results

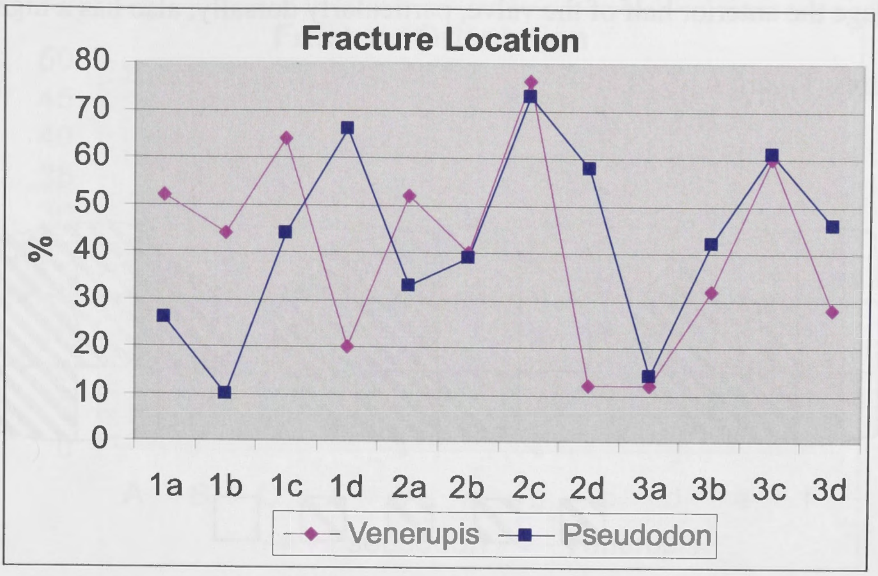
The results show that all the assemblages have relatively high frequencies of fractures, especially *Elongaria* and *Venerupis*, and all groups have moderately high frequencies of notches, especially *Venerupis*. Undamaged valves are rare in the *Venerupis* and *Elongaria* assemblages, especially *Elongaria*, but are relatively common in the *Pseudodon* assemblage (Table A1.3.1).

Table A1.3.1: Types of damage for each assemblage, *Pseudodon* (n=270); *Venerupis* (n=48); *Elongaria* (n=82)

	Undamaged	Fractured	Notched
Pseudodon	90 (33%)	104 (39%)	57 (21%)
Venerupis	6 (12%)	25 (52%)	26 (54%)
Elongaria	2 (2%)	49 (60%)	26 (32%)

A1.3.1 Fracture location

When the *Pseudodon* fracture location results are compared with the other assemblages there are certain similarities to both, but they are more similar to the *Elongaria* assemblage (Figure A1.3.1).



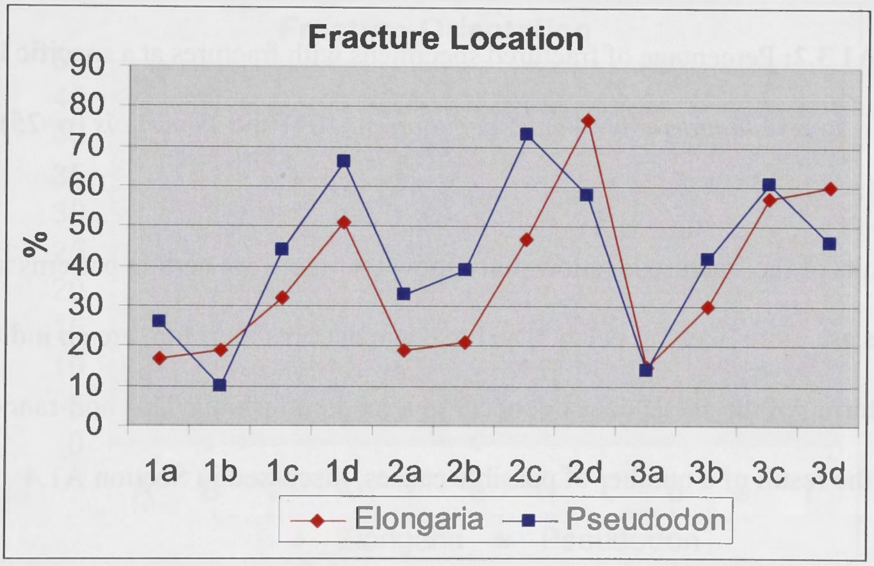


Figure A1.3.1*:* Percentage of fractured specimens with fractures at a specific location (see Figure A1.2.2): *Pseudodon* (n=104) compared to (top) *Venerupis* (n=25) and (bottom) *Elongaria* (n=47)

The areas of the shell where fractures most frequently occur are in the posterior half of the shell in both the *Elongaria* and *Pseudodon* assemblages, whereas in the *Venerupis* assemblage the anterior half of the valve, particularly dorsally, also has a high frequency of fractures (Figure A1.3.2).

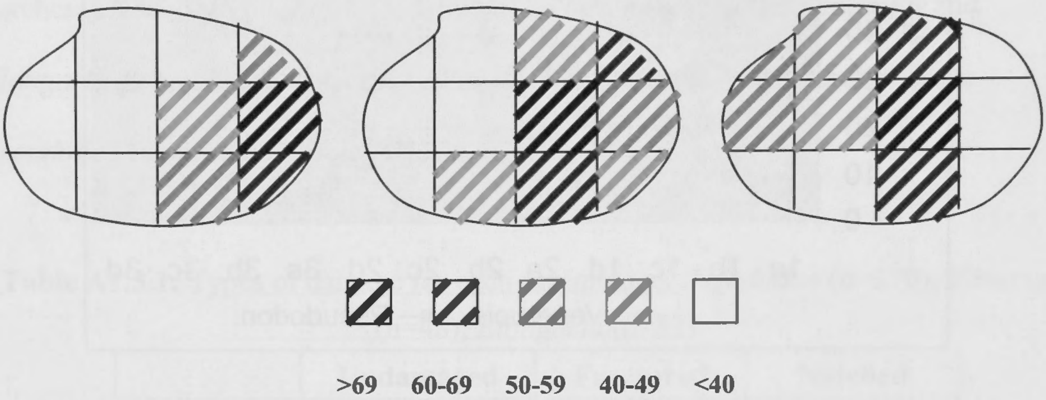
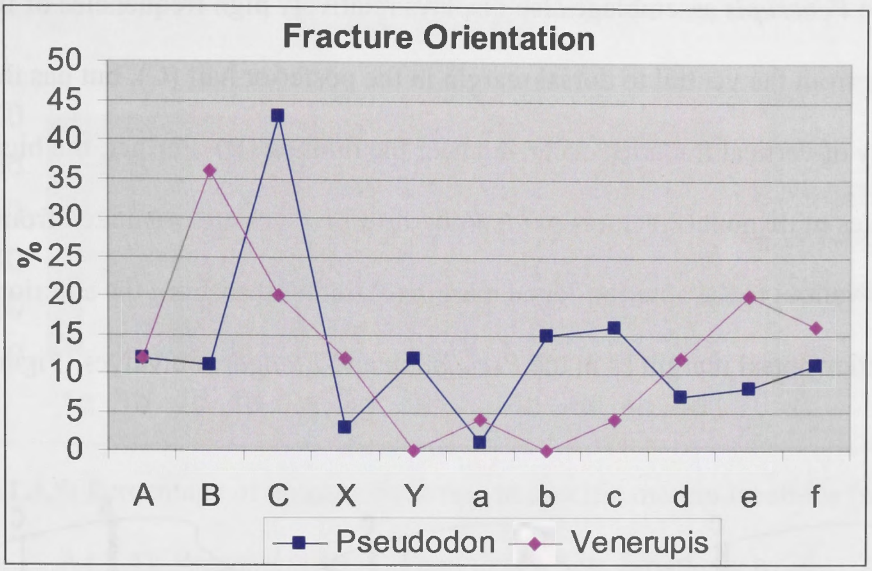


Figure A1.3.2: Percentage of fractured specimens with fractures at a specific location: (L to R) *Elongaria* (n =47), *Pseudodon* (n=104) and *Venerupis* (n=25).

The results of the fracture location study show that there are certain patterns as to where fractures are more likely to occur. The breakage patterns therefore are an indication that the fracturing of the shells does not occur in a random fashion. This non-random pattern may be the result of a number of possible causes, discussed in Section A1.4.

A1.3.2 Fracture orientation

The *Pseudodon* assemblage shows more similarity to the *Elongaria* assemblage in terms of fracture orientation than to the *Venerupis* assemblage, though there is a general pattern that all three assemblages conform to (Figure A1.3.3).



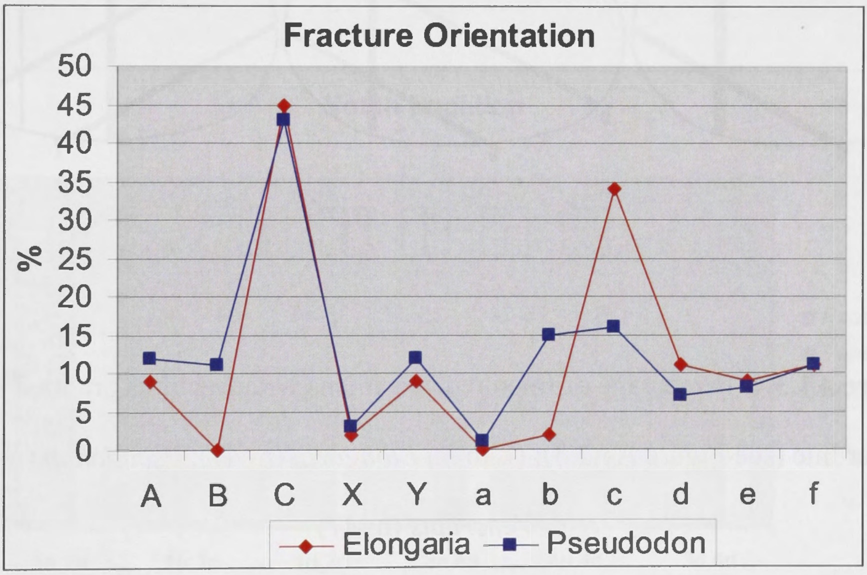


Figure A1.3.3: Percentage of fractured specimens with fractures oriented along a particular line (see Figure A1.2.3): *Pseudodon* (n=103) compared to (top) *Venerupis* (n=23), and (bottom) *Elongaria* (n=47).

The *Pseudodon* and *Elongaria* assemblages have higher frequencies of fractures oriented vertically from the dorsal to ventral margin in the posterior half of the valve (C), while *Elongaria* also has higher frequencies of fractures oriented diagonally from the ventral/anterior margin to the dorsal/posterior margin (c) than most other areas of the shell. The *Venerupis* assemblage also displays relatively high frequencies of fractures vertically from the ventral to dorsal margin in the posterior half (C), but has the highest frequency of vertical fractures occurring near the midline (B). Further, the highest frequencies of diagonal fractures in the *Venerupis* bivalves are orientated from the posterior/ventral to the anterior/dorsal margin (e), rather than from the anterior/ventral to the posterior/dorsal margin as in the *Pseudodon* and *Elongaria* bivalves (Figure A1.3.4).

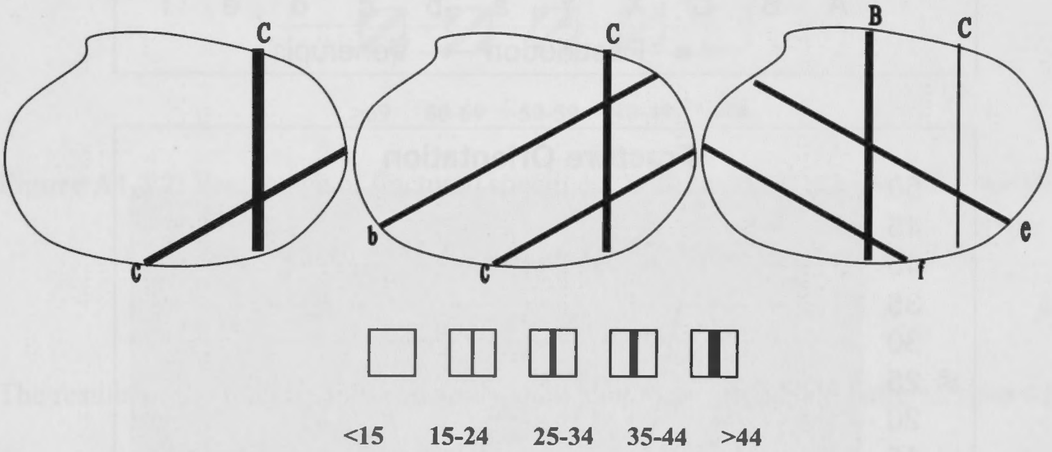


Figure A1.3.4: Percentage of fractured specimens with fractures oriented along a particular line (see Figure A1.2.3): (L to R) *Elongaria* (n=47), *Pseudodon* (n=103) and *Venerupis* (n=47)

8.3.3 Notches

The notch locations of all three assemblages display a certain pattern with one location in particular, on the dorsal anterior margin (2a), being the dominant location for notches in both the *Pseudodon* and *Venerupis* specimens, and the most frequent location for notches in the *Elongaria* specimens (Figure A1.3.5).

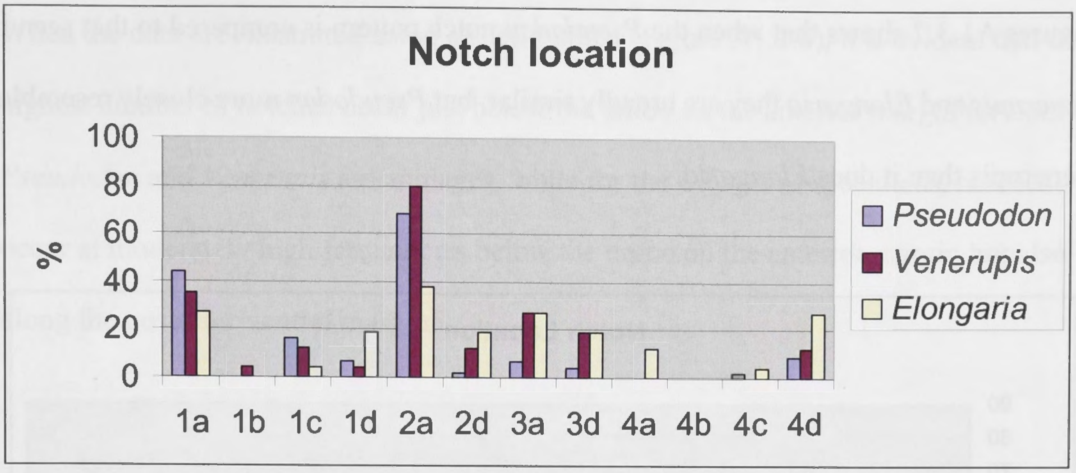


Figure A1.3.5: Percentage of notches occurring at specific margin locations (see Figure A1.2.4): *Pseudodon* n=57, *Venerupis* n= 26, *Elongaria* n=26

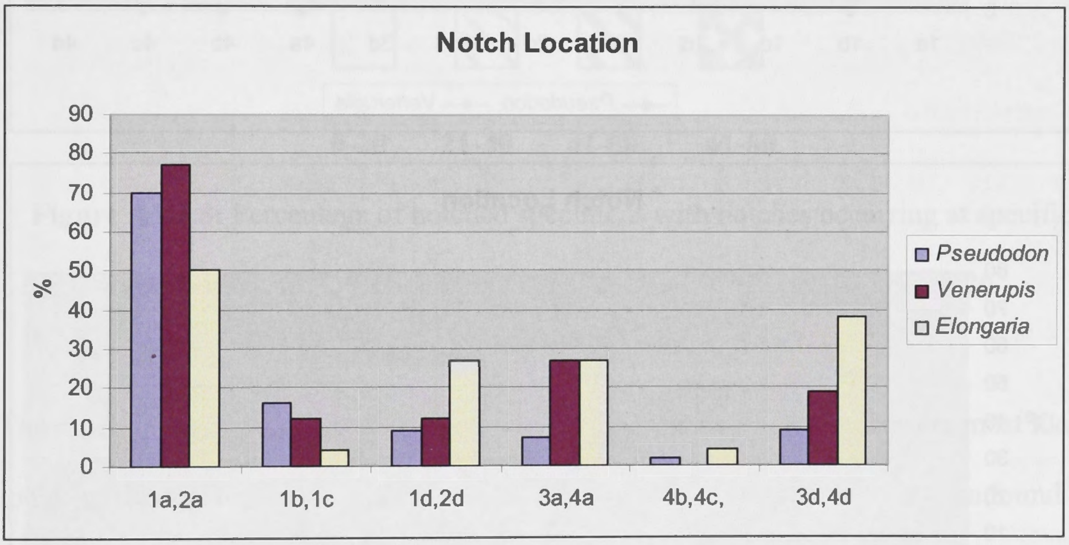


Figure A1.3.6: Percentage of notched specimens with notches occurring at particular margin locations (see Figure 8.2.4): *Pseudodon* n=57, *Venerupis* n= 26, *Elongaria* n=26

Figure A1.3.6 combines notch areas according to their margin location. The anterior region close to the dorsal margin, below the umbo, has the highest incidence of notches for all assemblages.

Figures A1.3.7 shows that when the *Pseudodon* notch pattern is compared to that seen in *Venerupis* and *Elongaria* they are broadly similar, but *Pseudodon* more closely resembles Venerupis than it does *Elongaria*.

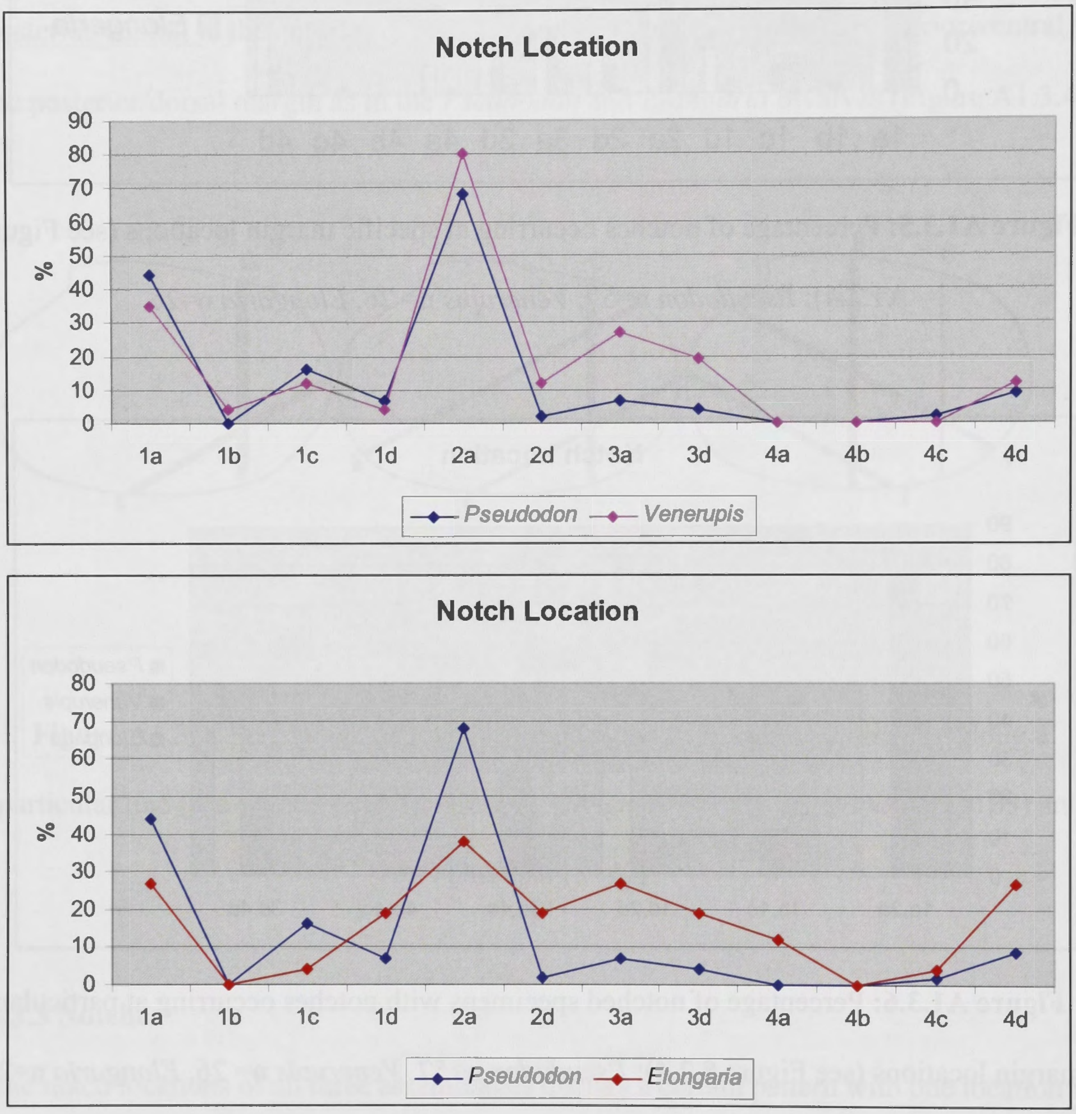


Figure A1.3.7: Percentage of notched specimens with notches occurring at specific locations (see Figure A1.2.4): *Pseudodon* n=57 compared to (top) *Venerupis* n= 26, and (bottom) *Elongaria* n=26

When the data are illustrated using a shell outline (Figure A1.3.8), it is evident that the highest number of notches occur just below the umbo on the anterior margin for both the *Pseudodon* and *Venerupis* assemblages, while for the *Elongaria* specimens, notches occur at moderately high frequencies below the umbo on the anterior margin but also along the posterior/ventral margin.

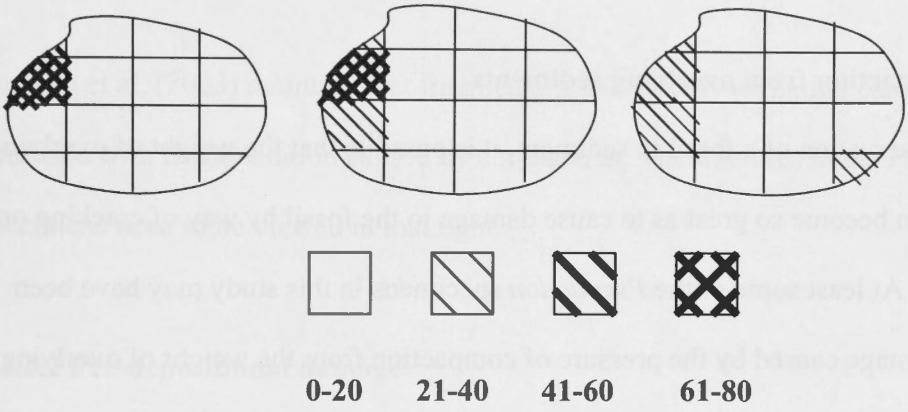


Figure A1.3.8: Percentage of notched specimens with notches occurring at specific locations: (L to R) *Pseudodon* n=57, *Venerupis* n= 26, *Elongaria* n=26

The notch location study shows a clear pattern in terms of where notches are most likely to occur; relative to a random set of results. Certain patterns therefore have been found for the three types of damage examined; fracture location, fracture orientation and notch location, with varying degrees of similarity when the three assemblages are compared.

In the next section the possible causes for the patterns observed will be examined and discussed.

A1.4 Possible causes

Shells can be damaged in a number of ways including during life and after death. Some of the ways in which a shell can be damaged are discussed here in relation to the above results.

A1.4.1 Post depositional damage

- **Compaction from overlying sediments**

After the preservation of a fossil in sediment, it is possible that the weight of overlying sediments can become so great as to cause damage to the fossil by way of cracking or deformation. At least some of the *Pseudodon* specimens in this study may have been subject to damage caused by the pressure of compaction from the weight of overlying sediments. The observed pattern of the fractures in this case could be accounted for by natural weak points in the shell.

While some of the specimens may be the result of compaction from overlying sediment, there are a number of reasons to think that this process may not have been the cause of all fractures in the assemblage. One such reason is that a number of the valves are fragmented so that they preserve only part of the original valve. If the fractures resulted from *in situ* fragmentation of whole shells by sediment compaction, then we would expect the shell fragments to be preserved together in their original position within the sediment (Zuschin & Stanton 2001).

Fragmentation from sediment compaction is more likely to occur when shells are in contact with other hard objects, such as other shells, or with coarse grains (Zuschin & Stanton 2001), otherwise the mechanism of compaction tends to yield distorted shells associated with subtle fractures (Zuschin et al. 2003). The percentage of undamaged bivalves (33%: see Table A1.3.1) within the assemblage is indicates that sediment compaction, if it did occur, did not affect all the shells within the beds.

Zuschin et al. (2003) maintain that fragmentation caused by predation can be easily confused with fragmentation caused by compaction. The fractures in the *Pseudodon* specimens need to be viewed in that light.

A1.4.2 Pre-depositional damage

- **Water transport**

Transport by water in the form of tides, waves and river currents can cause damage to shells by causing them to impact with other shells or hard objects such as stones and reefs. Newell et al. (2007) conclude that *in situ* fragmentation of bivalves in river channels can be caused by the impact of sediment carried by the river's current, and that, because bivalves orientate themselves in a predictable way in relation to the direction of the current, the shells show characteristic damage including fracturing. This particular process can be ruled out as a possible agent for the *Pseudodon*, *Venerupis* and *Elongaria* shells, however, because none of these display the characteristic fracture or abrasion patterns that are associated with the *Unio* shells in the study by Newell et al (2007).

Wave action might possibly be responsible for some of the fractures observed in the *Venerupis* specimens, because a few of these show some signs of having been transported (slightly rounded edges). The notches are less likely to be explained by this process, however, because in this case we would expect the notches to be more evenly distributed around the shell's margin, although natural weak points in the shell at that particular point could be a contributing factor for the high frequency of notches.

For the *Pseudodon* specimens it is less likely that water transport played a role in the observed damage; because these are such large shells, any transporting agent would have to have been of rather high energy. If this were the case we would expect other signs of water transport such as rounded edges, but there is little evidence of rounded edges in the *Pseudodon* specimens, or indeed in other parts of the Trinil mollusc assemblage, which at least in part indicates "a rapid and undisturbed fossilization" (Van Benthem Jutting 1937: 164). In fact the vast majority of fragments (97%) have characteristically angular or sharp edges not at all consistent with water transport (Figure A1.4.2).

Experiments in which shells were tumbled in a barrel with other sediments resulted in fragments with abraded rather than angular or sharp margins (Oji et al. 2003). Bivalve fragments with sharp margins without signs of abrasion are therefore interpreted as indicating durophagous predation (Oji et al. 2003). Further, the presence of incomplete shells together with complete shells indicates the possibility of selection from durophagous predators.

Figure A1.4.2: *Pseudodon* fragment displaying sharp, angular edges (scale 10mm)

- **Trampling**

Trampling from large mammals has to be considered a possibility for some of the damage observed in the *Pseudodon* assemblage. It would probably be expected, however, that more comprehensive damage to the shells would be present than is observed in many of the specimens in this assemblage. Damage such as that seen in Figure A1.4.3, for example, appears unlikely to have been caused by large mammal trampling, but there may be other examples in the assemblage more consistent with animal trampling.

Figure A1.4.3: *Pseudodon* specimen displaying a fracture unlikely to be caused by trampling (scale 10mm)

- **Predatory damage**

A number of animals prey on bivalves using various methods to gain access to the edible soft tissue, and some of these methods can result in damage of a characteristic nature (Carter 1968, Zuschin et al. 2003). There are therefore some circumstances in which it is possible to infer whether or not a bivalve specimen was preyed upon, and even by which animal, by examining the shell damage, though caution must also be shown here due to the difficulties involved in distinguishing various damage types.

  - **Gastropods**

A number of gastropods are known to prey on bivalves by drilling holes through the shell to gain access to the meat. Both mechanical (e.g., rasping) and chemical secretion are used by gastropods to drill holes (Carter 1968). Drilling leaves characteristic damage that is different from the fracture and notch damage observed in this study.

Another less common method used by some gastropods to prey on bivalves involves the forcing apart of the two valves using the edge of the gastropod's shell. This can result in chipping of the shell margin and it is also not uncommon that one or both valves can become badly cracked during this process. At least some predators known to employ this method show a marked tendency to target thin shelled bivalves (Carter 1968), which perhaps makes it less likely that this gastropod predation method could account for the notches observed in the thick walled *Pseudodon* specimens. A number of gastropod species are known from Trinil, but none of these is known to prey on bivalves.

- **Octopuses**

Bivalves are preyed on by octopuses which use various techniques to extract meat, including breaking the shell of fragile mussels, pulling the valves apart, drilling with the radula, or chipping with the beak. Octopuses are also known to inject poison into bivalves to weaken the adductor muscle, and apparently have an ability to directly attack this muscle (Mather & Anderson 2000). Interestingly, and perhaps significantly, the location in which notches occur most frequently in the *Venerupis*, *Pseudodon* and *Elongaria* shells (see Figure A1.3.8) corresponds with the position of the anterior adductor muscle (Figure A1.4.4).

Figure A1.4.4: Internal view of a *Pseudodon* valve, showing pallial line running parallel with ventral margin and scars where anterior (left) and posterior (right) adductor muscles attach (scale 10mm)

It is conceivable that predation by octopuses on bivalves deliberately targeting this part of the shell could leave notch patterns such as those seen in the *Venerupis*, *Elongaria* and *Pseudodon* specimens, however, since octopuses are restricted to marine environments, it is virtually impossible for them to have been responsible for the damage inflicted on the *Pseudodon* and *Elongaria* specimens, which are strictly freshwater inhabitants.

- **Crabs**

Certain crabs prey on bivalves by breaking away the margin of the shell with their claws before extracting the meat. The shore crab *Carcinus maenas* has been observed using at least four different techniques to predate the mussel *Mytilus edulis*. These include crushing of smaller shells (less than 1cm), crushing the umbo or posterior part of intermediate sized shells (1-3cms), boring the hinge ligament of larger shells and chipping the posterior margin of shells that could not be crushed (Elner 1978).

Boring of the hinge ligament is the most time consuming and therefore least efficient method employed by crabs, and is used only when no other method is successful or where no other more suitable sized prey is available. The crabs appear to target weak points of the shell, with vulnerable areas occurring where the shell is thin and brittle through erosion, especially at the umbo, and areas where the nacreous layers are absent because of the insertion of posterior and anterior adductor muscles (Elner 1978).

- **Lobsters**

Lobsters are also known to predate bivalves, crushing them with their pincers (Carter 1968). Experiments show that size has a limiting factor on predation and in some mussel species fracture patterns correspond with shell weak points (Griffiths & Seiderer 1980). Both shell shape and size play an important role in limiting predation, and fracture patterns can occur as a result of these factors. The mussel *Choromytilus meridionalis* showed consistent fracturing in the posterior dorsal region (Griffiths & Seiderer 1980).

While the *Venerupis* and *Elongaria* specimens may have been of a size suitable for crab or lobster predation, the *Pseudodon* shells were probably too large and their shells too thick walled to have been predated on by these predators. The notches, however, do correspond to an area where the adductor muscles attached, and this appears to be a favoured area for crab boring. The above observations involve marine species, and therefore the likelihood of predation on the freshwater *Pseudodon* and *Elongaria* specimens is low, though the *Venerupis* shells were found in a marine context.

- **Starfish**

Perhaps the most common predators of bivalves are starfish, which use two methods to consume their prey. The first method involves swallowing bivalves whole, digesting the meat and ejecting the empty shell; this usually occurs in deeper water where bivalves are generally small and thin shelled. The other method involves the predator inserting its stomach into the bivalve between the two valves, and digesting the flesh (Carter 1968). Neither method results in consistent morphological damage. Since starfish occur only in marine environments they can be ruled out as a cause for the damage observed in the *Pseudodon* specimens.

- **Fish**

A number of fish are known to prey on bivalves using numerous methods to extract and/or digest the meat: crushing the shell with teeth, grinding palate, hard parts of the throat or in the gizzard; or simply ingesting the shell whole, digesting the meat and then ejecting the shell undamaged (Carter 1968, Zuschin et al. 2003). Some fish are also known to bite off the siphon of a bivalve which can leave characteristic damage to the posterior margin. None of these predatory methods seems able to account for the damage observed in the specimens examined in this study.

- **Birds**

A number of birds prey on bivalves using various methods for meat extraction and some of these methods can result in characteristic shell damage (Stempien 2007). The oystercatcher *Haematopus*, for example, employs at least two different methods to extract meat from bivalves. The first involves plunging the beak into the bivalve while it is still open, and the second involves hammering the shell with the beak, forcing a hole, often through the umbo, or else along the commissure. This latter method can result in characteristic damage to the anterior margin of the shell (Zuschin et al. 2003, Stempien 2007), and sometimes to the margin corresponding to the site of siphon extrusion (Carter 1968). The brown teal duck *Anas chlorotis* has also been observed 'jackhammering' cockles of the species *Austrovenus stutchburyi* with its beak in order to open them and extract the meat (Moore & Battley 2003).

Cadée (2000) reports on the characteristic fracturing inflicted on razor clams *Enis directus* by herring gulls *Larus argentatus* which shake the shell in their beak. Razor clams, however, have a very different shape to the bivalves in this study, being more rod-like, elongated lengthwise and relatively narrow in terms of height.

Herring gulls, like a number of other birds, also drop bivalves from heights in order to crack them open (Cadée 1995). Limiting factors for birds employing this method include both small and large size; shells that are too small tend not to shatter, while shells that are too large can be too heavy to lift (Vermeij 1983). In a study of transported bivalves in the Wadden Sea, however, Cadée (1989) found that only large mussels were transported by herring gulls. Bird predation of bivalves appears to be more intense in temperate and polar regions than in the tropics (Zuschin et al. 2003).

The *Venerupis* shells display damage that may well be the result of predation by birds. The anterior fractures (see Carter 1968 figure 2b, also Zuschin et al. 2003 fig 14E) occur at a location of the margin corresponding to the position of the adductor muscle, a possible target area for predatory birds such as oystercatchers. The fact that the most common fracture is orientated across growth lines is a further indication that bird predation may be responsible (Stempien 2007). Whether birds would have the strength to use hammering methods to fracture the much larger *Pseudodon* species is questionable. The fact that bird predation in tropical regions is rarer than in temperate and polar regions makes it less likely that birds were responsible for the damage observed in the *Pseudodon* assemblage.

- **Pinnipeds**

The walrus *Odobenus rosmarus* and bearded seals *Erignathus barbatus* are known to eat molluscs, and although they may occasionally crush these shells they more commonly suck the contents out with their mouths, without causing damage to the shell (Carter 1968). Walruses and bearded seals are both restricted today to arctic or sub-arctic waters and in combination with their being marine are unlikely to be responsible for the damage observed in the *Pseudodon* shells.

- **Otters**

Sea otters *Enhydra* use tools to open hard shelled prey such as bivalves. After collecting a bivalve from the sea bottom, sea otters return to the surface where they float on their back with a usually flat stone resting on their chest, which they pound the bivalve against until it opens. Where stones are not available sea otters use other bivalves as anvils on which to pound their prey (Macdonald 2001). This method of predation could conceivably account for the fracture patterns (but not the notches) seen in the *Venerupis* and *Pseudodon* specimens, but sea otters today are confined to temperate waters and are fully marine, making them unlikely agents for the *Pseudodon* damage. A number of otter genera are known from Java at the time of the Trinil deposits, including *Lutra* and *Amblonyx* (Medway 1972), but neither of these is known to crack open bivalves with tools.

Freshwater otters such as the smooth-coated otter *Lutrogale* generally feed on fish rather than molluscs, and when they do consume molluscs they crush them with their teeth (Gurung & Singh 1996), which is unlikely to cause the sort of damage observed in the *Pseudodon* specimens.

- **Primates**
  - **Monkeys**

Both the platyrrhine (new world) and catarrhine (old world) monkeys contain species that are known to prey on bivalves. Capuchin monkeys *Cebus apella* have been observed removing and opening oysters *Crassostrea rhizophorae* attached to mangrove trees by manipulating them with oyster shells (Fernandes 1991), and the long tailed macaque

Macaca fascicularis has been observed opening bivalves by cracking them with stones (Malaivijitnond et al. 2007).

While capuchins obviously were geographically incapable of predating on mussels from Java, macaques, specifically *Macaca fascicularis*, were present at Trinil (Medway 1972), and therefore need to be considered as potential bivalve predators. Interestingly, Carpenter (1887) reports that macaques observed off the coast of Burma had developed a method of opening oysters that involved dislocating the valves by a blow to the base of the upper valve, thus breaking the shell over the attaching muscle. This implies that primates such as macaques are capable of learning how to open bivalves by targeting a particular part of the shell with a hard object.

The fracture pattern observed in the *Pseudodon* assemblage, in which fractures most commonly occur in the posterior half of the shell at a location close to where the posterior adductor muscle attaches, could therefore conceivably be explained as targeting by a tool using primate.

- ***Homo erectus***

Evidence of stone tool manufacture and use by *Homo erectus* and related early humans is well known from a wide range of locations from Africa, Europe and Asia throughout the Pleistocene. Human populations from various regions around the world today collect and consume bivalves as ethnographic records demonstrate. One problem, however, with applying ethnographic observations to prehistoric populations is that modern humans commonly use heat in the form of fire or boiling water to open bivalves (Meehan 1982).

Before the use of fire (and it remains uncertain exactly when fire use became widespread in prehistoric populations), it is likely that humans would have had to resort to other methods in order to extract the meat of bivalves, including:

- Extracting the meat while the bivalve is open (in the manner that oystercatchers do)
- Leaving the shells in the sun until they open (as some birds do).
- Prising them open with a sharp object such as another shell, stick or stone flake (as the ethnographic record shows humans do, see e.g., Mann 1883)
- Pounding them with a hard object such as a stone or shell (as otters, capuchins and macaques do)

Important points to consider in relation to human consumption of bivalves include the fact that humans can, and still often do, consume bivalves raw. Also, human bivalve consumption is often associated with shell middens; however, it is possible that shell middens only became widespread after the invention of carrying bags which allowed large numbers of bivalves to be transported to a particular location for processing and consumption at a single time. Before the invention of bags it is possible that the consumption of bivalves by humans occurred more spontaneously, where bivalves were gathered rather than at the same central location returned to over and over again. This would make the creation of shell mounds less likely.

Shells recovered from the Neolithic Sampung Cave site, Central Java, have characteristic fractures suggesting that they may have been opened for the purpose of consumption; the bivalves invariably have the posterior part of the shell missing, and according to Van Benthem Jutting (1932: 105) this may have been the result of "pounding with a large stone". Baker (1981: 64) states that shells associated with human consumption (middens) tend to have "characteristic fracture marks where they have been broken open", but gives no detail as to what these characteristic fractures are.

Marine gastropods consumed by Mousterian inhabitants of the Mediterranean coast, show characteristic damage in which "usually a portion of the shell wall was sheared away by a sharp clean blow" (Stiner 1994: 178). Bivalve shells associated with flint tools at the Mousterian cave site of Moscerini, Italy, are highly fragmented and the break edges are "clean, square and fresh looking" (Stiner 1994: 184), as opposed to shells occurring in naturally occurring beach deposits from the same cave, which are rarely fragmented but exhibit damage characteristic of surf action including extensive polishing and punched out umbos. In a study of shells associated with middens in northern Australia, Esposito (2005) contemplated whether the consistent damage to the distal (posterior-ventral) margin of *Marcia hiantina* and *Anadara antiquate* may have been caused by their being prised open after not having fully opened during cooking, but lack of comparative samples made it difficult to answer.

The fractures in the *Pseudodon* specimens examined here could conceivably have been the result of intentional pounding with hard objects by *Homo erectus,* which might account for at least some of the fracture patterns. The notches, on the other hand, could conceivably be the result of attempts to prise open the bivalves by using sharp objects on the anterior margin near the adductor muscle (Figure 8.4.5). Mann (1883) reports observing Andaman Islanders inserting bivalve shell fragments and sharp pieces of wood between the valves of certain bivalves to prise them open in order to extract the meat and Waselkov (1987) reports the use of broken shells to shuck bivalves.

Figure A1.4.5: Typical fracture (top) and anterior notch (bottom) found in the *Pseudodon* sample (scale 10mm).

Another possibility is that bivalves may have been deliberately broken by early hominins such as *Homo erectus* in order to create sharp edged tools. Bivalve shells are known to have been used as tools in both prehistoric (Stiner 1994, Szabo et al. 2007) and more recent contexts (Cooper 1988, Lima et al. 1986, Mann 1883). Studies of cut marks found on the bones of large bovids (*Bos*) from early Pleistocene Sangiran deposits indicate that *Homo erectus* was using thick shelled bivalves to butcher mammals (Choi & Driwantoro 2006) and it is possible that thick shelled bivalves were also used as tools in some early Pleistocene East African locations (Toth & Woods 1989).

A1.7 Conclusion

Shells can be damaged in a number of ways including before and after death. Some of the ways in which a shell can be damaged include by predators, by physical erosion, or by the pressure of overlying sediment.

The shell assemblages examined here display certain characteristics which indicate that they may have been caused by some type of predation, but the differences between the assemblages suggest possibly different methods of predation, different predators, or both. Reasons to believe predation may have been a factor as an accumulating agent include:

1. The uniform size of the individuals in all assemblages (especially *Pseudodon*)
2. The notch location patterns which correlated strongly in all assemblages with the location of the anterior adductor muscle (though in *Elongaria* the ventral/posterior margin was also heavily notched)
3. The large amount of damage in each assemblage (though roughly a third of the *Pseudodon* specimens were undamaged)
4. The morphology of the braeks (i.e., sharp edges, not rounded as would be expected in shells transported by water)
5. The pattern of fractures, with vertical breaks most common down the posterior half of the shell, near the posterior adductor muscle (though *Venerupis* differs from *Elongaria* and *Pseudodon* in this trait).

There are a number of different animals that prey on molluscs, and specifically bivalves, but the methods used vary depending on the predator. The *Elongaria* specimens, having been found in cave deposits, are almost certainly part of a kitchen midden, and therefore it is highly probable that they were consumed by humans (Van Benthem Jutting 1937, Joordens et al. 2009). The context of the *Venerupis* shells is not known, but they were possibly predated on by sea birds.

For the breakage patterns found in the *Pseudodon* assemblage there are a number of possible candidates including otters and macaques, both of which were present on Java at the time. The possibility that *Homo erectus* may have been the responsible accumulating agent is not contradicted by the breakage pattern data.

Three further independent factors suggest bivalves may have been consumed by early hominins on Java. Firstly, *Homo erectus* was known to be using thick shelled bivalves as tools at Sangiran not far from Trinil (Choi & Driwantoro 2007). Secondly, *Homo erectus* would have benefited from having large bivalves in the diet, since these are known to contain omega 3 fatty acids such as DHA, important for brain growth and maintenance (Broadhurst et al. 2002, Ersoy & Sereflisan 2010). And thirdly, the markings found on a number of shells at Trinil, especially those shown in Figure 9.8.1, are best explained as anthropogenic markings. Further research and more comparative samples, however, are required to further test this hypothesis.

References Appendix 1

Baker, R. (1981) *The Aboriginal and Environmental History of the Chambers Bay Coastal Plains*. BA Honours Thesis, Australian National University: Canberra.

Barton, R.N.E., Currant, A.P., Fernandez-Jalvo, Y., Finlayson, J.C., Goldberg, P., MacPhail, R., Pettitt, P.B. & Stringer, C.B. (1999) Gibraltar Neanderthals and results of recent excavations in Gorham's, Vanguard and Ibex Caves. *Antiquity* **77**: 13-23.

Broadhurst, C. L., Wang, Y., Crawford, M., Cunnane, S., Parkington, J. & Schmidt, W. (2002) Brain specific lipids from marine, lacustrine, or terrestrial food resources: potential impact on early African *Homo sapiens. Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology* **131**: 653-673.

Cadee, G (1989) Size-selective transport of shells by birds and its palaeoecological implications. *Palaeontology* **32**: 429-437.

Cadee, G. (1995) Birds as producers of shell fragments in the Wadden Sea, in particular the role of the Herring gull. *Geobios* **18**: 77-85.

Cadee, G. (2000) Herring gulls feeding on a recent invader in the Wadden Sea, *Enis directus*. In Harper, E.M., Taylor, J.D. & Crame, J.A. (eds) *The Evolutionary Biology of the Bivalvia*. Geological Society, London, Special Publications **177**: 459-464.

Carpenter, A. (1887) Monkeys opening oysters. *Nature* **36**: 53.

Carter, R.M. (1968) On the Biology and Palaeontology of Some Predators of Bivalved Mollusca. *Palaeogeography, Palaeoclimatology, Palaeoecology* **4**: 29-65.

Choi, K. & Driwantoro, D. (2007) Shell tool use by early members of *Homo erectus* in Sangiran, central Java, Indonesia: cut mark evidence. *Journal of Archaeological Science* **34**: 48-58.

Cooper, Z. (1988) Shell Artefacts from the Andaman Islands. *Australian Archaeology* **26**: 24-41.

Elner, R. (1978) The mechanics of predation by the Shore Crab, *Carcinus maenas* (L.), on the Edible Mussel, *Mytilus edulis* L. *Oecologia* **36**: 333-344.

Esposito, V. (2005) *Sorting Shells: An examination of archaeological criteria used to identify cultural shell material*. BA Honours Thesis, Australian National University: Canberra.

Ersoy, B. & Sereflisan, H. (2010) The Proximate Composition and Fatty Acid Profiles of Edible Parts of Two Freshwater Mussels. *Turkish Journal of Fisheries and Aquatic Sciences* **10**: 71-74.

Fernandes, M. (1991) Tool use and predation of oysters by the tufted capuchin in brackish water mangrove swamp. *Primates* **32**: 529-531.

Griffiths, C.L. & Seiderer, J.L. (1980) Rock-Lobsters and Mussels – Limitations and Preferences in a Predator-Prey Interaction. *Journal of Experimental Marine Biology and Ecology* **44**: 95-409.

Joordens, J., Wesselingh, F., de Vos, J., Vonhof, H. & Kroon, D. (2009) Relevance of aquatic environments for hominins: a case study from Trinil (Java, Indonesia). *Journal of Human Evolution* **57**: 656-671.

Lima, T.A., Botelho de Mello, E.M. & Pinheiro da Silva, R.C (1986) Analysis of molluscan remains from the Ilha de Santana site, Macae, Brazil. *Journal of Field Archaeology* **13**: 83-97.

Macdonald, D. (2001) *The Encyclopedia of Mammals*. Facts On File: New York.

Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., Panha, S., Cheewatham, C. & Hamada, Y. (2007) Stone-Tool Usage by Thai Long-Tailed Macaques (*Macaca fascicularis*). *American Journal of Primatology* **69**: 227-233.

Mann, E.H. (1883) On the Aboriginal Inhabitants of the Andaman Islands (Part III). *The Journal of the Anthropological Institute of Great Britain and Ireland* **12**: 327-434.

Mather J. & Anderson R. (2000) Octopuses are Smart Suckers!? First published on the Man and Mollusc web site. The Cephalopod Page http://www.thecephalopodpage.org/ Wood, J.B. Webmaster, viewed 17 March 2008.

Medway, L. (1972) Quaternary Mammals of Malesia; a review. In Ashton, P. & Ashton, M. (eds) *The Quaternary Era in Malesia.* Department of Geography, University of Hull, Miscellaneous Series No. 13: 1-122.

Meehan, B. (1982) *Shell Bed to Shell Midden.* Australian Institute of Aboriginal Studies: Canberra.

Moore, S. & Battley, P. (2003) Cockle-opening by a Dabbling Duck, the Brown Teal. *Waterbirds* **26**: 331-334.

Newell, A., Gower, D., Benton, M. & Tverdokhlebov, V. (2007) Bedload abrasion and the *in situ* fragmentation of bivalve shells. *Sedimentology* **54**: 835-845.

Oji, T., Ogaya, C. & Sato, T. (2003) Increase of shell-crushing predation recorded in fossil shell fragmentation. *Paleobiology* **29**: 520-526.

Simanjuntak, T. & Asikin, I.N. (2004) Early Holocene Human Settlement in Eastern Java. *Indo-Pacific Prehistory Association Bulletin* **24**: 13-19.

Stempien, J. (2007) Detecting avian predation on bivalve assemblages using indirect methods. *Journal of Shellfish Research* **26**: 271-280.

Stiner, M. (1994) *Honor Among Thieves.* New Jersey: Princeton University Press: Princeton.

Szabó, K., Brumm, A. & Bellwood, P. (2007) Shell Artefact Production at 32,000-28,000 BP in Island Southeast Asia. *Current Anthropology* **48**: 701-723.

Toth, N. & Woods, M. (1989) Molluscan shell knives and experimental cut marks on bones. *Journal of Field Archaeology* **16**: 250-255.

Van Benthem Jutting, T. (1932) On prehistoric shells from Sampoeng Cave (Central Java). *Treubia* **14**: 103-108.

Van Benthem Jutting, T. (1937) *Non marine mollusca from horizons in Java with special reference to the Trinil fauna*. E.J. Brill: Leiden.

Vermeij, G.J. (1983) Shell-Breaking Predation through Time. In Tevesz, M.J.S. & McCall, P.L. (eds) *Biotic Interactions in Recent and Fossil Benthic Communities*. Plenum Press: New York, (pp. 649-669).

Waselkov, G.A. (1987) Shellfish gathering and shell midden archaeology. *Advances in Archaeological Method and Theory* **10**: 93-210.

Zuschin, M., Stachowitsch, M. & Stanton, R.J. (2003) Patterns and processes of shell fragmentation in modern and ancient marine environments. *Earth Science Reviews* **63**: 33-82.

Zuschin, M. & Stanton, R. J. (2001) Experimental Measurement of Shell Strength and its Taphonomic Interpretation. *Palaios* **16**: 161-170.

Appendix 2 (Mollusc Data)

ORDER **Family** *Genus species*	FT	Lu	Lo	Ka	AD	MV	La	Ha	Ch	**KF** Bu	**KF** KB	Hu	**OG** I	**OG** II	**OG** IV	5A	Ek	Ub	Dm	PH	Mo	Tr	Ni	Da	Ol	Bu	So	Bo	Ce	Yu	Pa	Ki
GASTROPODA																																
Unidentified																								x				x				
CYCLONERTIMORPHA																																
Neritidae																																
Theodoxus jordani																	x	x														
SORBEOCONCHA																																
Hydrobiidae																																
Hydrobia longiscata																	x															
Falsipyrgula barroisi																	x															
Pachychilidae																																
Brotia testudinara																						x					x					
Brotia s.l. sp.																					x											
Potadoma				x																												
Cerithiidea																																
Cerithium cf. *torresi*																						x										
Thiaridae																																
Melanoides tuberculata		x			x			x	x	x	x					x	x	x								x	x					
aff. *tuberculata*																						x										
dadianus																	x															
jordanicus																	x															
aff. *anomala*						x																										
sp.		x	x	x																		x										
sp. B											x																					
sp. C											x																					
Melanoides? tuburculata?																					x											
cf. Melanoides tuberculata													x	x																		
Tarebia granifera																						x										
Tarebia? granifera?																											x					
Cleopatra				x																												
bulimoides								x								x																
ferruginea										x																						
aff. *ferruginea*						x																										
sp.					x				x																							
sp. A										x																						
Thiara zollingeri																						x										

ORDER **Family** *Genus species*	FT	Lu	Lo	Ka	AD	MV	La	Ha	Ch	**KF** Bu	**KF** KB	Hu	**OG** I	**OG** II	**OG** IV	5A	Ek	Ub	Dm	PH	Mo	Tr	Ni	Da	Ol	Bu	So	Bo	Ce	Yu	Pa	Ki
Thiara scabra																						x										
cf. *tjemoroensis*																						x										
Melanopsidae																																
Melanopsis praemorsa																	x	x														
doriae																	x															
LITTORINIMORPHA																																
Bithyniidae																																
Bithynia syriaca																	x															
multicostata																	x															
hawaderiana																		x														
neumanni																									x							
troscheli																															x	
Gabbiella aff. *humerosa*						x																										
senarriensis										x																						
sp.									x																							
Jubaia sp.								x																								
Digoniostroma truncatum																						x										
Stenothryridae																																
Stenothyra sp.																						x										
NEOGASTROPODA																																
Melongenidae																																
Melongena sp.																						x										
ARCHITAENIOGLOSSA																																
Viviparidae																																
Viviperidea (?)																				x												
Viviparus unicolor																	x															
apamea																	x	x														
sp.																														x	x	
Bellamya unicolor					x			x		x																						
aff. *capillata*						x																										
capillata									x																							
javanica																						x										
cf. *robertsoni*									x																							
cf. *trochlearis*									x																							
cf. *pagodiforms*									x																							
sp. B										x																						
sp.				x							x									x												
Bellamya? sp.			x																													

ORDER **Family** *Genus species*	FT	Lu	Lo	Ka	AD	MV	La	Ha	Ch	**KF** Bu	**KF** KB	Hu	**OG** I	**OG** II	**OG** IV	5A	Ek	Ub	Dm	PH	Mo	Tr	Ni	Da	Ol	Bu	So	Bo	Ce	Yu	Pa	Ki
Ampullaridae																																
Ampullaria wernie			x																													
Lanistes carinatus			x																													
ovum						x																										
sp.									x	x																						
Pila ovata						x										x																
conica																						x										
sp.																					x											
Maizanidae																																
Maizania	x																															
HETEROBRANCHIA																																
Valvatidae																																
Valvata sp. A										x																						
sp.																													x		x	
goldfussiana																															x	
Pyramidellidae																																
Quirella cf. *lyngei*																						x										
Cingulina sp.																						x										
Retusidae																																
Didontoglossa cf. *decoratoides*																						x										
BASOMMATOPHORA																																
Indet.																											x					
Lymnaeidae																																
Lymnaea natalensis														x																		
lagotis																	x	x														
javanica																						x										
sp.																							x								x	
Radix sp.																														x		
Ameria duboisi																						x										
Planorbidae																																
Planorbinae											x														x							
Anisus natalensis														x																		
Gyraulus piscinarum																	x	x														
chihliensis																							x									
convexiusculus																						x										
sp.																														x		
cf. *Gyraulus*					x																											
Planorbis planorbis																		x														

ORDER **Family** *Genus species*	FT	Lu	Lo	Ka	AD	MV	La	Ha	Ch	**KF** Bu	**KF** KB	Hu	**OG** I	**OG** II	**OG** IV	5A	Ek	Ub	Dm	PH	Mo	Tr	Ni	Da	Ol	Bu	So	Bo	Ce	Yu	Pa	Ki
Planorbis youngi																							x									
Bulinus truncatus								x		x																						
aff. *truncatus*													x																			
tropicus													x	x																		
sp.									x		x																					
sp. Indet																x																
Acroloxidae																																
Acroloxus lacustris																		x														
STYLOMMATOPHORA																					x											
Enidae																																
Edouardia												x																				
Edouardia laetoliensis							x																									
Cerastua	x																															
Jaminia sp.																			x													
Pseudochondrula																			x													
Subulinidae												x																				
Homorus	x																															
sp.													x																			
Subulona pseudinvoluta							x																									
Pseudoglessula cf gibbonsi							x																									
Euonyma leakeyi							x																									
Achatinidae																																
Achatina									x			x																				
Achatina ?zanzibarica							x																									
cf. Achatina														x																		
Burtoa nilotica	x						x																									
Limicolaria							x																									
cf. *Limicolaria*															x																	
Streptaxidae																																
Gulella	x																															
Streptostele sp.							x						x																			
Bradybaenidae																																
Cathaica sp.																														x		
Hygromiidae																																
Helicopsis sp.																			x													
Trichia																															x	
Helicidae																																
Helix aff. *pomatia*																			x													

ORDER **Family** *Genus species*	FT	Lu	Lo	Ka	AD	MV	La	Ha	Ch	**KF** Bu	**KF** KB	Hu	**OG** I	**OG** II	**OG** IV	5A	Ek	Ub	Dm	PH	Mo	Tr	Ni	Da	Ol	Bu	So	Bo	Ce	Yu	Pa	Ki
Limacidae																																
Deroceras																															x	
Euconulidae																																
Thapsia												x																				
Helicarionidae																																
Trodonania	x																															
Urocyclidae																																
Trochonanina spp. A & B							x																									
Indet.													x																			
Urocyclinae spp.							x																									

BIVALVIA

Indet.																								x				x				
NUCULOIDA																																
Nuculanidae																																
Jupiteria sp.																						x										
UNIONOIDA																																
Iridinidae																																
Iridina subelongata		x		x																												
moharensis		x																														
omoensis										x																						
browni										x	x																					
Chambardia wahlbergi						x		x																								
rubens										x	x																					
feibeli										x																						
nyassaensis									x																							
Aspatharia cf. *rugifera*				x																												
Pleiodon bentoni										x	x																					
Unionidae					x																											
Pseudodon vondembuschianus																						x										
Coelatura bakeri																x																
sp. B										x																						
sp.									x		x																					
Coelatura ?sp. A			x																													
Unio elongatulus								x																								
subrectangularis																	x															
terminalis																		x														

ORDER **Family** *Genus species*	FT	Lu	Lo	Ka	AD	MV	La	Ha	Ch	**KF** Bu	**KF** KB	Hu	**OG** I	**OG** II	**OG** IV	5A	Ek	Ub	Dm	PH	Mo	Tr	Ni	Da	Ol	Bu	So	Bo	Ce	Yu	Pa	Ki
Unio semirugatus																		x														
sinuata																													x			
pictorum																															x	
Unio sp.															x																	
spp.																															x	
Anodonta anatina																															x	
Pseudobovaria										x	x																					
Pseudodiplodon										x																						
Elongaria orientalis																					x	x										
Leguminaia chantrei																		x														
Indonaia sp.																				x												
Lamellidens sp.																				x												
Parreysia sp.																				x												
Lamprotula																							x									
Cuneopsis																							x									
Rectidens sumatrensis																						x										
Etheriidae																																
Etheria				x							x																					x
elliptica			x						x																							
MYTILOIDA																																
Mytlidae																																
indet.																						x										
ARCOIDA																																
Arcidae																																
Anadara cf. *granosa*																						x										
OSTEOIDA																																
Ostreidae																																
Crassostrea																					x											
VENEROIDA																																
Corbiculidae																																
Corbicula consobrina								x		x	x																					
fluminalis																		x														
sp.									x				x										x							x		
africana														x																		
pullata																						x										
gerthi																						x										
Geloina sp.																						x										
Polymesoda ? cf. *coaxans*																					x											

ORDER **Family** *Genus species*	FT	Lu	Lo	Ka	AD	MV	La	Ha	Ch	**KF** Bu	**KF** KB	Hu	**OG** I	**OG** II	**OG** IV	5A	Ek	Ub	Dm	PH	Mo	Tr	Ni	Da	Ol	Bu	So	Bo	Ce	Yu	Pa	Ki
Pisidiidae																																
Eupera sp. B										x																						
Pisidium casertanum																	x															
amnicum																													x		x	
clessini																															x	
supinum																															x	
henslowanum																															x	
moitessierianum																															x	
spp.																															x	
sp.																							x									
Sphaerium bulleni																															x	
rivicola																															x	
spp.																															x	
Semelidae																																
Theora lata																						x										
Psammobidae																																
Gari sp.																						x										
Montacutidae																																
Tellimya sp.																						x										
Ungulinidae																																
Cycladicama cumingii																						x										
Tellinidae																																
Acropagia pudica																						x										
yemensis																						x										
Lucinidae																																
Eamesiella aff. *corrugata*																						x										
Dreissenidae																																
Dreissena chantrei																	x															

SCAPHOPODA

DENTALIIDA																																
Denteliidae																																
Dentalium sp.																						x										