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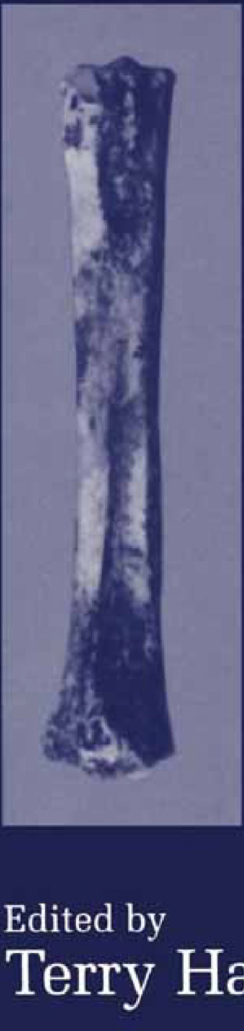
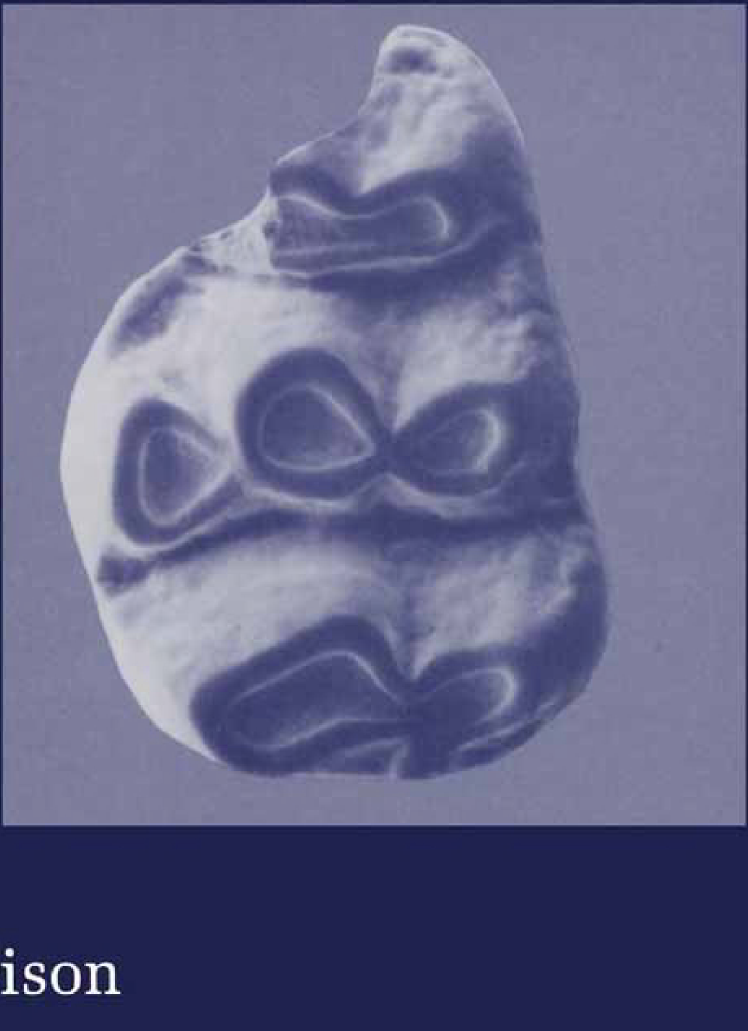
Neogene Paleontology of the Manonga Valley, Tanzania

A Window into the Evolutionary History of East Africa





Edited by
Terry Harrison

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TOPICS IN GEOBIOLOGY

Series Editors: **Neil H. Landman,** American Museum of Natural History,
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Edited by

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To the people of Tanzania
who welcomed me into their country
and shared their knowledge and wisdom

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Preface

In spite of the dedication and resourcefulness shown by paleontologists and paleoanthropologists over the past seventy years in their quest to find new fossil hominids, it is clear that, in the enterprise of reconstructing the evolutionary history of humans (and other mammals), we still have much to accomplish. It is true that we have made significant advances, with the help of some remarkable fossil discoveries, in documenting the main phylogenetic strands, but we know very little about the detailed anatomy or paleobiology of these lineages, or about the critical events that led to their divergence and subsequent evolutionary changes. Our image of the early evolutionary history of our own species is based on a montage of snapshots obtained from fleeting glimpses of the phylogenetic tree as seen through a few narrow temporal and spatial windows provided us by the fossil record. If our objective is not simply to fill in the missing gaps, and thereby document the configuration of the major branches of the human evolutionary tree, but rather to gain some real insight into early hominid diversity in space and time, and to explain this diversity in terms of the complexity of ecological, geographic, and evolutionary factors that produced it, then we need a broader perspective. We should strive to improve the quality (not just the quantity) of the hominid fossil record, so that it includes a wider geographic coverage and a finer temporal resolution. In order to achieve this objective, the search for new paleontological sites in Africa, and elsewhere, must be considered as a high priority. Paleontology is inherently a risky business, with no guarantee of returns on one's investment, but given the right balance of effort, perseverance, funding, and good fortune, significant advances in our knowledge of human evolution can be made. Exciting new finds of Plio-Pleistocene hominids from Ethiopia, Eritrea, Kenya, Malawi, and Chad provide tangible evidence of such successes.

The people of Tanzania are justifiably proud of the fact that some of the most important fossil and archaeological finds pertaining to the earliest stages of human evolution have been discovered in their country. Olduvai Gorge and Laetoli are famous throughout the world, and fossil discoveries at these sites have made a significant contribution toward helping to piece together the evolutionary history of humankind over the past four million years. Today, Tanzania is celebrated internationally as a leading center for paleoanthropological studies. Even so, only three sites in Tanzania have yielded the remains of early fossil hominids, Olduvai Gorge, Laetoli, and Peninj, all located in the Serengeti Plains in the northeastern part of the country. This limited distribution is primarily a consequence of geological factors. The sites cluster at the southern extremity of the Gregory Rift, where the eastern branch of the East African Rift valley splays out around the margin of the resistant Tanganyika shield. The rift valley, and its associated volcanism, provides an ideal geological setting for the preservation and recovery of fossils. Indeed, almost all of the spectacular early hominid fossil finds in East Africa are from sites located within the Eastern Rift.

However, another significant factor is that the sites in northern Tanzania are easily accessible, especially from Kenya. The full paleontological potential of Olduvai Gorge was not realized until the 1950s, when Louis and Mary Leakey were able to intensify their explorations from their base in Nairobi. Today it is relatively easy for expeditions and tourist buses to reach Olduvai Gorge, but when Louis Leakey began his pioneering work there in the early 1930s, it was a major logistical problem. Louis Leakey's initial paleontological experiences in the southern part of Tanzania give some indication of the past difficulties and dangers involved in mounting major expeditions to the more remote regions of the country. In 1924, Louis Leakey took part in an ill-fated expedition to the Jurassic site of Tendaguru, where W. E. Cutler, the leader of the expedition, succumbed to blackwater fever. Our knowledge of the paleontology and archaeology of most of Tanzania is quite limited, especially when compared with that of neighboring Kenya, which has been much more extensively explored. Geologists interested in locating economically important minerals and deposits have surveyed much of Tanzania, and in the process they have reported finding further sites with fossils, but very few paleontologists or archaeologists have ever visited these sites. As a consequence, a large number of potentially important paleontological sites remain unexplored.

With this in mind, I began to consider the possibility of developing new initiatives in Tanzania with the aim of searching for new paleontological sites. By the early 1980s, I had identified several areas that might prove worthwhile for further investigation, but it was not until the spring of 1985 that concrete plans for an expedition began to crystallize. At that time, Michael Mbago from the National Museums of Tanzania, who was enrolled as a graduate student in New York University's Museum Studies program, visited my office to introduce himself, and to announce his interest in studying human evolution. Over the next few months, Michael and I discussed the prospects of working in Tanzania, and initially identified the Lake Rukwa basin or the region of Lake Malawi south of Mbeya as potential areas for exploration. In the summer of 1986, I was able to make a brief visit to many of the paleontological and archaeological sites in Tanzania, and to study previous collections of East African fossil mammals in England. The Natural History Museum in London had a small collection of unaccessioned fossils made by geologists in the 1920s from the site of Tinde in the Manonga Valley. This material had never been formally described, although A. T. Hopwood had made reference to it in a brief note published in 1931. Hopwood and subsequent workers considered this material to be of Pleistocene age. However, my preliminary study of the material indicated that the fossils were probably late Miocene to Pliocene age. Tinde looked like a promising site, and one that deserved further attention. It was apparently a productive locality yielding fossils that were at least as old as those from Laetoli, with a fauna containing species that were not well known from other sites in Africa, and located in a region of Tanzania that had not been surveyed since the late 1920s. Published accounts of the regional geology further indicated that the Manonga Valley would be a good place to begin the search for productive new sites, with the potential to yield evidence that might possibly pertain to the earliest phases of human evolution.

The Manonga Valley in north-central Tanzania, the focus of this volume, represents a large and previously almost unexplored lake basin, with well-exposed and richly fossiliferous sediments. The sequence of deposits range in estimated age from late Miocene to early Pliocene (~5.5–4.0 Ma), a slice of time that is generally poorly represented in other parts of Africa. In addition, the Manonga Valley is of special interest in that it is located in a geographic province that lies just beyond the immediate confines of the rift valley. With its unique combination of characteristics (i.e., it has the oldest fossil mammal localities in Tanzania, apart from the Jurassic site of Tendaguru, an estimated age range for the stratigraphic sequence that is generally not well represented in other parts of Africa, and it has the southernmost localities in East Africa associated with, but located just outside, the Eastern Rift), the Manonga Valley offers an important new window into the evolutionary history of Africa.

In 1990, I organized the first Wembere–Manonga Paleontological Expedition (WMPE), and this was followed by full-scale expeditions in 1992 and 1994. As director of the expedition I soon learned that establishing a field project at a site that has little or no prior research history has its problems. To develop a rational plan of research one needs basic information on the site's geology and paleontology. However, this inevitably leads one to a conundrum that is commonly encountered by researchers. To convince granting agencies to give funds to support new paleontological endeavors one needs to provide them with the kind of information that one is requesting money for in the first place! Knowing these limitations, the goals of the Manonga Valley project have been relatively simple—to find out as much as possible about the geology and paleontology of the area. This information has provided the necessary empirical foundation on which to establish a more theoretical, problem-oriented approach. Our initial objectives for the Manonga Valley project were therefore: (1) to survey for new paleontological localities; (2) to assess the nature of the geological context of the major localities; (3) to reconstruct the geological history of the Manonga basin; (4) to make paleontological collections that would contribute to a better understanding of the systematics, zoogeography, and evolutionary history of East African faunas; (5) to obtain more secure estimates of the age ranges of the fossil-bearing sediments; (6) to reconstruct the paleoecological and paleoenvironmental setting of the lake basin; and (7) to assess the potential of the Manonga Valley for paleoanthropological research.

The contributions in this volume represent the outcome of these research goals. Chapter 1 provides an overview of the history of research, geology, and paleontology in the Manonga Valley. Chapters 2 and 3 present details of the stratigraphy, mineralogy, and geomorphology, and Chapter 4 provides a preliminary synthesis of the taphonomy and paleoecology of the key paleontological sites. Chapters 5–12 are primarily accounts of the anatomy, systematics, and paleobiology of the fossils collected, including formal descriptions of several new species. Chapter 13 provides an overview of the Manonga Valley fauna, and attempts to establish a biochronological framework on which age estimations can be based. The volume concludes with a brief commentary on the importance of sites such as the Manonga Valley for studies of human evolution. The chapters in this volume not only lay the foundation for future geological, paleontological, and paleoecological research in the Manonga Valley, but they also offer new insights into the evolutionary history, taxonomy, paleobiology, ecology, and zoogeographic relationships of African faunas in general. Since we are just beginning in the Manonga Valley, and because there is still a great deal of basic paleontological and geological research that needs to be done in East Africa, we anticipate that this project will be a vital and ongoing concern for the foreseeable future. Fossil hominids have not yet been found in the Manonga Valley, but we have not given up the search. With just a few scraps known from other sites in East Africa to document the hominid fossil record prior to 4.5 Ma, there are certainly still some major surprises lurking up the elongated sleeves of our ancestors older than 5 million years. I suspect that the dusty, acacia-lined gullies of the Manonga Valley are a good place to look for these ancestors.

The success of the Manonga Valley project over the past six years owes much to the dedication and effort of my collaborators in the field. The WMPE teams consisted of the following individuals: 1990—D. C. Katunge, Christine Kiyembe, Bernadetha Kokusima, John Krigbaum, Michael Mbago, and Jacques Verniers; 1992—Bereket Haileab, Eugene Harris, Christine Kiyembe, Amandus Kweka, Michael Mbago, Charles Msuya, Varsha Pilbrow, Bill Sanders, and Kathy Stewart; 1994—Mayassa Abubakar, Eric Baker, Wendy Dirks, John Kappelman, Christine Kiyembe, Amandus Kweka, Avelin Malyango, Michael Mbago, Charles Msuya, Medard Mutakyahwa, Bill Sanders, Kathy Stewart, Machteld Van Schandevijl, and Jacques Verniers. It is never an easy task directing a major overseas research project, and I am indebted to numerous people and institutions in Tanzania that have helped out in many practical ways, both in the field and behind the scenes. There are obviously too many people to acknowledge individually, but the following deserve special mention: William Bongo, J. K. Chande, C. C. Magori, Michael Mbago, Paul Msemwa, Esto Mtui, Martha Mvungi, Raju Nathwani, Abel Nkini, Tobias Lubulila, Hamisi Salum, Charles Saanane, Ali Tonondo, and Simon Waane. I am grateful to the Tanzanian Commission for Science and Technology and to the Unit of Antiquities for granting permission to conduct research in Tanzania, and to the staff of the National Museums of Tanzania for their assistance and hospitality during my visits to Dar es Salaam. The Regional and District Development and Cultural Officers of Singida, Tabora, and Shinyanga Regions have been most enthusiastic in their support of my research and have always been willing to help. Although the main goal of our expeditions has been to uncover clues to the past, it is the friendship and generosity of the people, and the majesty of the scenery of today's Tanzania, that perhaps leave the most memorable impressions on visitors to the Manonga Valley.

In addition to those colleagues and students who actually took part in the fieldwork, a number of individuals outside of Tanzania have assisted in many ways with this project. These include Peter Andrews, Ray Bernor, Laura Bishop, David Brown, Frank Brown, Rufus Churcher, Basil Cooke, Eric Delson, C. Denys, Alan Gentry, John Harris, Judith Harris, Linda Heusser, Andrew Hill, Jerry Hooker, F. Clark Howell, Clifford Jolly, Jean-Jacques Jaeger, Jon Kalb, Mary Leakey, Meave Leakey, Todd Olson, Martin Pickford, Richard Tedford, and John Van Couvering. Lastly, special thanks go to my family for their patience, encouragement, and support. My wife, Terri, served as the unofficial, unpaid, and overworked administrative assistant of the Manonga Valley project, while my two sons, Chris and Ben, were able to add fieldwork in Tanzania to their already impressive resumé of paleontological credentials.

Research in the Manonga Valley has been generously supported by grants from the National Geographic Society (1991, 1994), the Research Challenge Fund at New York University (1990), the L.S.B. Leakey Foundation (1991, 1994), and the Boise Fund (1989, 1990, 1991, 1993, 1994), as well as by a Small Grant for Exploratory Research from the National Science Foundation (DBS9120882).

Terry Harrison

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Chapter 1

Introduction: Paleontological and Geological Research in the Manonga Valley, Tanzania

TERRY HARRISON and MICHAEL L. MBAGO

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1. Introduction

During the summer of 1990, a small international team, representing the first Wembere–Manonga Paleontological Expedition (WMPE), initiated a long-term field program of geological and paleontological research in the Manonga Valley of north-central Tanzania (Fig. 1). Although the occurrence of fossil sites in the Manonga Valley was first recognized in 1929 (Stockley, 1930; Grace and Stockley, 1931), there was little subsequent paleontological exploration, and the 1990 expedition represented the first concerted effort to document in detail the geology and paleontology of the region (Harrison, 1991a, b; Harrison *et al.*, 1993; Harrison and Verniers, 1993). The expedition recovered vertebrate fossils from

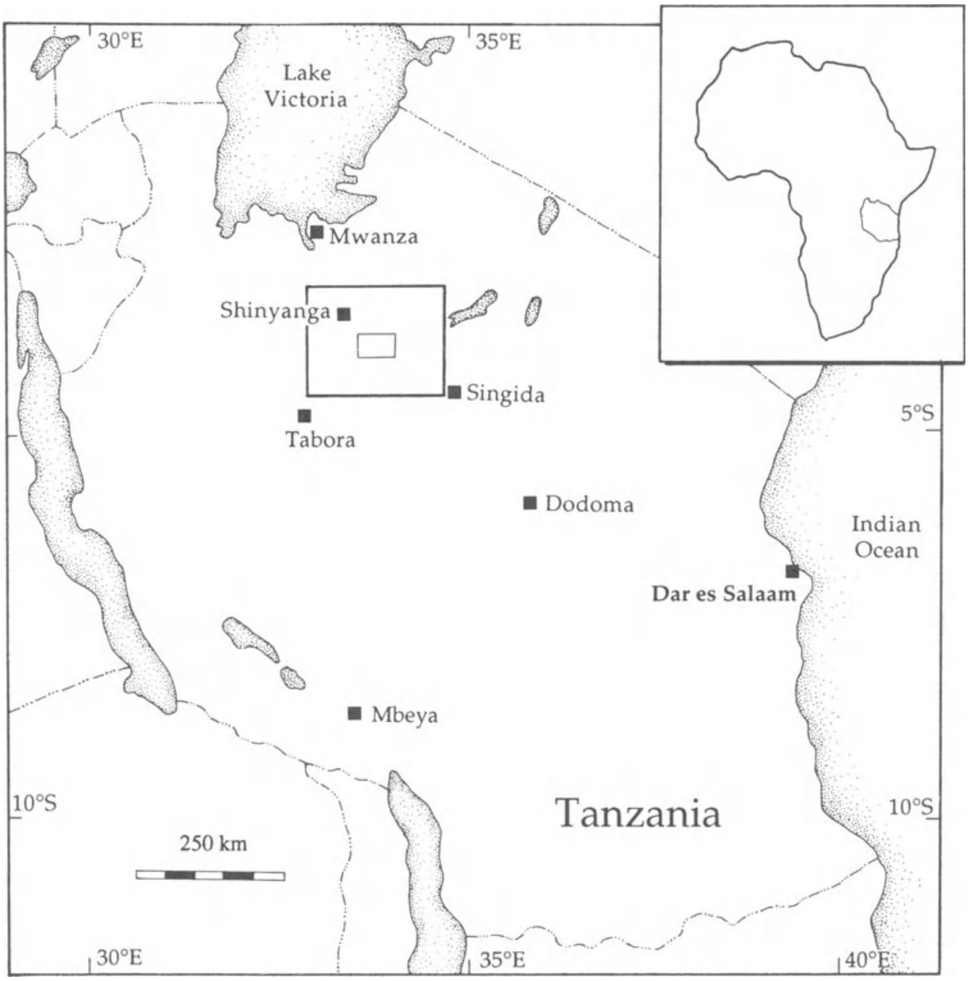

FIGURE 1. Map showing the location of the main research area in north-central Tanzania. See Figs. 2 and 3 for detail of large and small insets, respectively.

10 different localities, and preliminary studies of the fauna confirmed initial observations based on the 1929 collections in the Natural History Museum in London, that the sediments probably ranged in age from late Miocene to early Pliocene (Hopwood, 1931; Harrison, 1991a, b; Harrison *et al.*, 1993; Harrison and Verniers, 1993). The 1990 survey was sufficiently promising that full-scale expeditions were organized in 1992 and 1994. A total area of over 1000 km^2 has now been explored, and more than 30 productive paleontological sites have been identified (Table I). Brief preliminary reports on the 1990 and 1992 expeditions have been published (Harrison, 1991b, 1993a, b, 1994; Harrison and Verniers, 1993; Haileab and Harrison, 1993; Winkler, 1993; Harrison *et al.*, 1993), but the present volume represents the first detailed account of the history of research (Chapter 1), geology (Chapter 2 and 3), paleoecology and taphonomy (Chapter

Table I. List of Fossil Localities in the Manonga Valley

Name of locality	SASES No[a]	Coordinates	Year of discovery
Tinde West	Hi Ix/1	4°02′S 33°46′E	1929
Tinde East	Hi Ix/2	4°02′S 33°46′E	1929
Mwambiti 1	Hi Ix/3	4°01′S 33°50′E	1990
Mwambiti 2	Hi Ix/4	4°01′S 33°50′E	1990
Mwambiti 3	Hi Ix/5	4°02′S 33°47′E	1992
Mwambiti 4	Hi Ix/6	4°02′S 33°47′E	1992
Mwambiti 5	Hi Ix/7	4°01′S 33°49′E	1994
Lubeho	Hi Ix/8	4°02′S 33°45′E	1994
Kiloleli 1	Hh Iw/1	3°51′S 33°42′E	1990
Kiloleli 2	Hh Iw/2	3°52′S 33°43′E	1930s
Kiloleli 3	Hh Iw/3	3°52′S 33°42′E	1990
Kiloleli 4	Hh Iw/4	3°52′S 33°42′E	1990
Shoshamagai 1	Hh Iw/5	3°53′S 33°42′E	1990
Shoshamagai 2	Hh Iw/6	3°53′S 33°42′E	1990
Ipembe	Hh Iw/7	3°56′S 33°37′E	1992
Inolelo 1	Hh Iw/8	3°53′S 33°43′E	1992
Inolelo 2	Hh Iw/9	3°54′S 33°44′E	1992
Inolelo 3	Hh Iw/10	3°54′S 33°44′E	1992
Kalitu	Hh Iw/11	3°54′S 33°45′E	1992
Ngofila 1	Hh Ix/1	3°55′S 33°47′E	1992
Ngofila 2	Hh Ix/2	3°55′S 33°49′E	1992
Ngofila 3	Hh Ix/3	3°55′S 33°49′E	1992
Ngofila 4	Hh Ix/4	3°54′S 33°49′E	1992
Ngofila 5	Hh Ix/5	3°53′S 33°49′E	1992
Beredi North	Hh Ix/6	3°53′S 33°51′E	1992
Beredi South 1	Hh Ix/7	3°55′S 33°52′E	1992
Beredi South 2	Hh Ix/8	3°55′S 33°52′E	1992
Beredi South 3	Hh Ix/9	3°56′S 33°52′E	1992
Beredi South 4	Hh Ix/10	3°55′S 33°53′E	1992
Beredi South 5	Hh Ix/13	3°55′S 33°53′E	1994
Nyawa	Hh Ix/11	3°50′S 33°58′E	1959
Kininginila	Hh Ix/12	3°59′S 33°56′E	1992
Mihama	Hh Ix/14	3°53′S 3°55′E	1994

[a] Standardized site enumeration system for Africa.

4), vertebrate and invertebrate paleontology (Chapters 5–13), and paleoanthropological significance (Chapter 14) of the Manonga Valley.

2. The Modern Geographic Context

The Manonga River originates near the village of Igunda, northwest of Isaka, and flows eastward through the Manonga Valley to discharge into Lake Kitangiri (Fig. 2). The river represents the boundary between Shinyanga and Tabora Regions, the two main administrative provinces that encompass the Manonga Valley. The Manonga Valley is between 10 and 20 km wide, and is bordered to the north and south by low cliffs and slopes no more than 30 m in height. The general area has a low relief, ranging in elevation from 1000 m to 1200 m above sea level. The presence of a number of small hills, formed by remnants of the Precambrian basement, results in a gently undulating terrain. Formation of the valley was presumably initiated by the action of the Manonga River as it cut through the underlying Neogene lake sediments, but the continued retreat of its margins is due to active erosion of the exposed faces of the cliffs by heavy seasonal rains.

The region is hot and dry, with unreliable rainfall. The average annual precipitation is slightly more than 800 mm, which is generally considered close to the minimum to support intensive grazing and cultivation. From June to November, during the dry season, ephemeral streams and rivers, including the Manonga River, are completely dry, except for small stagnant ponds excavated and maintained by the local inhabitants. Tracks and river gullies are impassable during the rainy season (January to April), making it impractical to conduct fieldwork at this time of the year. In the course of three summer field seasons (May to August), WMPE has recorded no rainfall whatsoever in the Manonga Valley. Mean ambient temperatures range between 21–25°C, but there is considerable daily and seasonal variation.

The vegetation is predominantly dry thornbush, composed of *Acacia–Commiphora–Lannea* association, and grasslands with a sparse covering of *Combretum* and gall acacia (Grantham *et al.*, 1945). Toward the eastern margin of the basin, where the Manonga Valley grades into the Eyasi–Wembere depression, a flat, treeless expanse of grassland occurs, representing the southernmost extension of the Serengeti Plains. The western portion of the Manonga basin, where human population densities are generally much lower, miombo woodland predominates. This type of woodland, dominated by several species of trees belonging to *Julbernardia, Isoberlinia*, and *Brachystegia*, is typical of the Central Plateau of Tanzania (Gillman, 1949; Kingdon, 1974; Lind and Morrison, 1974). Woodland habitats were probably more widespread in the Manonga Valley in the recent past, but rapid population growth in the last 60 years, and the subsequent increased demand for firewood and suitable agricultural and grazing lands, has led to wide-scale clearance (see Harrison and Baker, this volume, Chapter 13). In some areas, overgrazing and poor agricultural management have caused extensive soil erosion and badlands formation.

The Manonga Valley is largely populated by the Wasukuma, the largest tribal group in Tanzania. The closely related Wanyamwezi are also encountered in the western and southern portions of the valley, and Iramba and Nilotic pastoralist peoples belonging to the Tatoga group (known locally as Taturu) are found in the Wembere–Eyasi Steppe, at the eastern margin of the Manonga Valley. Population densities in the area are quite low, usually not exceeding 30 persons/km^2, but are often as sparse as 10 persons/km^2 (Thomas, 1971).

The Sukuma are industrious agriculturalists and cattle herders. Shinyanga Region, which represents the heart of Usukuma, has the highest concentration of cattle in Tanzania (supporting more than 25% of the nation's cattle), along with sheep and goats (Moore, 1971). This success is due to a combination of skilled husbandry, the availability of good grazing lands, and the absence of tsetse flies (*Glossina* spp.). Staple crops include millet, sorghum, maize, beans, sweet potato, and cassava. In addition, rice, groundnuts, and cotton are grown as cash crops. The cotton industry has proved extremely profitable for the Sukuma, whose use of cattle as draught animals has greatly enhanced their capability to transport cotton harvests to centralized ginneries. Additional

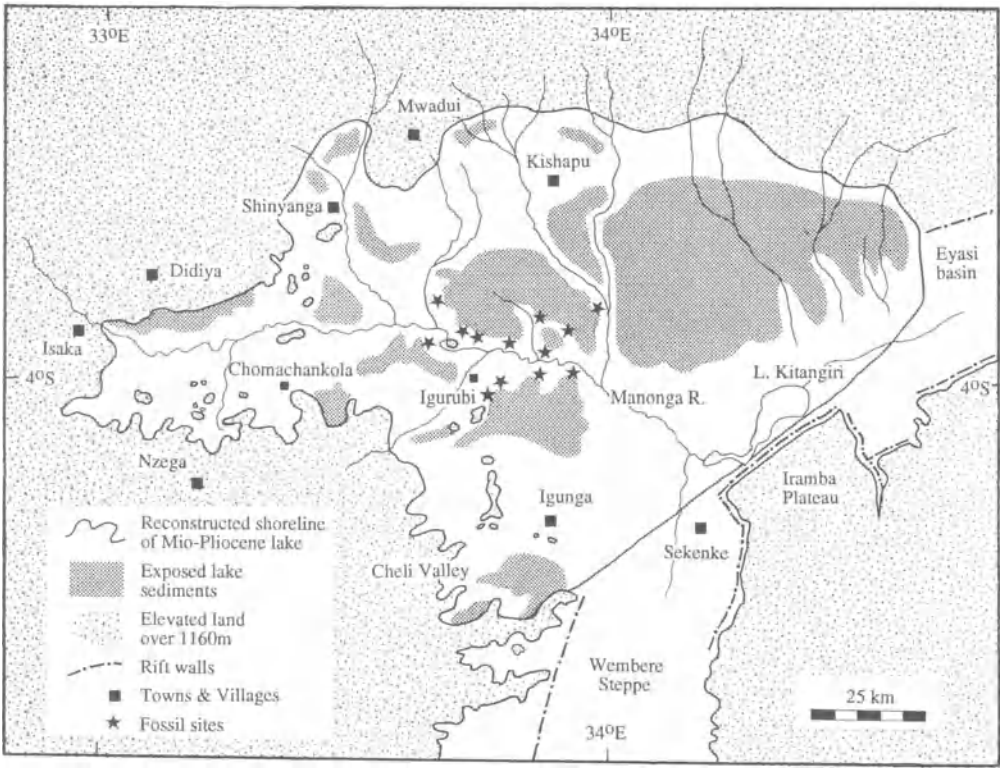

FIGURE 2. Reconstruction of the extent of the paleolake in the Manonga basin during the late Miocene and early Pliocene (after Harrison, 1993).

sources of income are derived from the collection of natural resources, such as honey, beeswax, and gum arabic. A major commercial diamond company is located at Mwadui in Shinyanga District, and itinerant prospectors also operate small-scale concerns in the region in search of gold and diamonds, but with very little return. Abandoned quarries in the vicinity of Shinyanga and elsewhere indicate that the extraction of limestone was formerly a viable concern, but the difficulties of transportation have served to limit its economic potential (Williams and Eades, 1939).

Igurubi, close to the center of the Manonga Valley, is a small market town that provides the focal point for communication with other parts of the region. Situated on the main road from Singida to Shinyanga, Igurubi is located 40 km north of Igunga and 80 km south of Shinyanga (Figs. 2 and 3). Because of the sparse vegetation cover, the flatness of the terrain, and the network of small oxcart tracks that crisscross the valley, most areas of the Manonga basin are easily

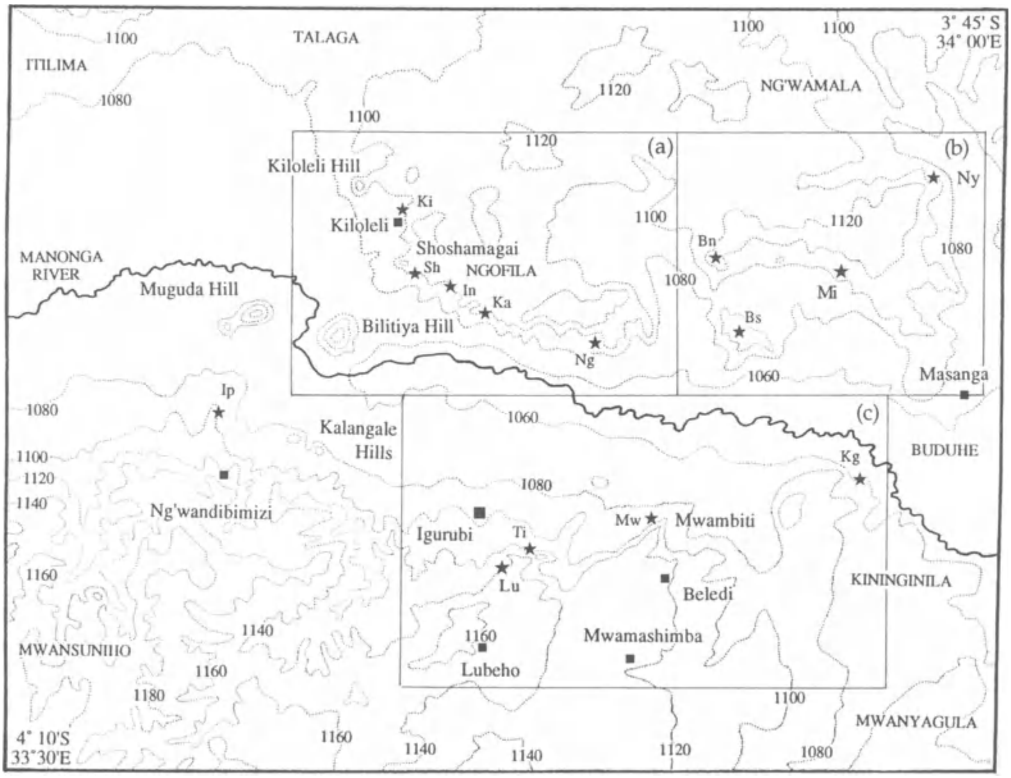

FIGURE 3. Topographic map of the center of the Manonga basin showing the location of the main paleontological site complexes (marked by stars). See Figs. 7–9 for details of insets (c), (a), and (b), respectively. Abbreviations: Bn, Beredi North; Bs, Beredi South; In, Inolelo; Ip Ipembe; Ka, Kalitu; Kg, Kininginila; Ki, Kiloleli; Lu, Lubeho; Mi, Mihama Mw, Mwambiti; Ng, Ngofila; Ny Nyawa; Sh, Shoshamagai; Ti, Tinde.

reachable by car (or by foot) from Igurubi, at least during the dry season. Since 1990, WMPE has been based at temporary tented camps, located 5 km east of Igurubi on the south side of the Manonga River, close to the village of Mwamakona.

3. History of Research

Fossils were first discovered in the Manonga Valley in 1929 by C. Grace, a geologist who was mapping the area for a Belgian mining syndicate. Grace made a small collection of fossils from a locality close to the village of Tinde,* just to the east of Igurubi (Stockley, 1930; Grace and Stockley, 1931). The site was located at a distinct break or gap in a line of bluffs situated about 2 km south of the Sakamaliwa–Nzega road. Grace was later joined by G. M. Stockley of the Geological Survey of Tanganyika Territory, and together they collected further specimens at Tinde, and attempted several trial excavations without much success. Fossils were recovered mainly from the surface, after having eroded out of the cliff face. Excavations showed, however, that the fossils were all derived from a single horizon, a nodular limestone band interposed between "stiff greenish clays" (Grace and Stockley, 1931). Stockley (1930) and Grace and Stockley (1931) described these beds as the Tinde beds, and referred to the fossil horizon as the Tinde bone-bed.

These collections were forwarded by Dr. E. O. Teale of the Geological Survey to the Natural History Museum in London, where they were examined by A. T. Hopwood. In a letter to Teale, dated 12 September 1929, Hopwood, referring to the Tinde fossils, stated:

> So far as I can say at present there is nothing very startling among them, but, all the same, they are interesting as being the first fossil mammals, so far as I know, which have been collected in Tanganyika. [Hopwood was evidently unaware of Reck's material from Olduvai Gorge (Reck, 1914a, b; Dietrich, 1916, 1925, 1928).] They are chiefly remains of Hippopotamus but there is one piece of Elephant which may be important later on and there are in addition fragments of fish and turtles. The age is very late, I don't see any possibility of an earlier date than the middle of the Pleistocene. The Hippo does not help at all in this respect, it all turns on the Elephant, and there isn't sufficient of him.

Hopwood (1931) later published a brief report on the fauna from Tinde. He made passing reference to a species of *Hippopotamus*, which he suggested was prob-

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*The location of the village of Tinde is clearly shown on Grace and Stockley's (1931) sketch map as being very close to the fossil site. However, it should be noted that no village exists in this location today, and that the present village of Tinde is located at some distance. Moreover, local inhabitants have no recollection of a nearby village called Tinde, although they do identify a small river gully further to the northeast by this name. This is not surprising, given the ephemeral nature of small villages in the area, and the fact that the main Nzega–Sakamaliwa road today follows an entirely different course. The name Tinde, however, seems to recur throughout the region, and although the etymology is uncertain, local Sukuma informants suggest that the name implies the stump of a large tree.

ably *H. amphibius*, and a medium-sized antelope, but he was most intrigued by the lower jaw fragment of a juvenile proboscidean, mentioned in his correspondence, which he referred to as *Elephas* sp. Hopwood noted its primitive molar morphology and the presence of a fragment of an unerupted P_4 still preserved in its crypt, and he compared it most favorably with elephantids from the Siwalik Hills and Kaiso (see Sanders, this volume, Chapter 9, for further discussion of the taxonomy of this specimen). Hopwood (1931) tentatively assigned a Pleistocene age to the material.

Williams and Eades (1939) presented a detailed account of the geology in the area of Shinyanga, which includes the northwest quadrant of the Manonga Valley. They outlined a geological succession in the region, and included the Tinde beds of Grace and Stockley (1931) into a broader stratigraphic unit, the Manonga–Wembere lake beds. The latter comprised an extensive series of calcareous lake sediments in the center of the basin, along with sandy littoral facies (Teale, 1931; Williams, 1939). Williams and Eades (1939) suggested that the Manonga–Wembere lake beds were laid down sometime during the Plio-Pleistocene, prior to the formation of the Eyasi trough, and that this latter event led to the eventual degradation of the earlier terrestrial and lacustrine sediments in the Manonga Valley. They also briefly reported the discovery of a fossil assemblage, similar to that from Tinde, recovered from marl bluffs along the Negezi–Igurubi road, about 3 km north of Shoshamagai. The exact location of the site is not given, but based on the evidence presented, it would seem to be equivalent to the locality identified as Kiloleli 2 by WMPE (see 5.3 below).

In 1959 the area was visited briefly by Kleindienst and Haldemann, who made small paleontological collections at the sites of Tinde, Kiloleli, and Nyawa. Several fragmentary specimens from each of these sites were sent to K. P. Oakley at the Natural History Museum in London, as possible samples for absolute dating. As far as we can discover, however, the samples were never analyzed. In correspondence with Oakley, dated 2 February, 1960, Kleindienst stated:

> The sediments are fine tuffs, silty-clays, and sands with several definite red marker beds that have not been previously recorded. They could well be Lower-Middle Pleistocene. I was unable to find any associated artifacts, although some Middle-Late Stone Age occurs on the surface.

At a later date, Kleindienst was contacted by Shirley Savage (née Coryndon), who had made a brief study of the fauna. In a letter dated 4 October, 1973, Savage writes:

> I'm afraid all the material is very scrappy and contains few diagnostic items. There is only one specimen which would suggest an age earlier than Upper Pleistocene/Holocene, and that is two small fragments of elephant tooth which have rather thick enamel and widely separated plates—as far as one can see any detail on a worn couple of fragments. Otherwise the fauna appears to contain living genera and probably species.

However, it seems likely that at least part of this fauna was derived from the superficial mbuga clay layer, which is much younger than the late Neogene Manonga–Wembere lake beds (see below, and Harrison and Baker, this volume, Chapter 13).

Finally, in 1976, while Mary Leakey was working at Laetoli in northern Tanzania, Philip Leakey and a geologist, Mark Monaghan, made a brief reconnaissance trip to the Manonga Valley. They recovered a small collection of fossils, which are currently stored in the Laetoli lab at Olduvai Gorge (M. D. Leakey, personal communication).

As can be seen from this brief review, the Manonga Valley was largely unexplored when WMPE mounted its first expedition in 1990. The initial idea to work in the Manonga Valley stems from discussions between the coauthors of this chapter in New York in 1985, about the potentials and prospects of conducting paleontological research in Tanzania. Following brief visits to study fossil collections in the Natural History Museum in London and the National Museums of Tanzania in Dar es Salaam in 1986, a collaborative research effort between New York University and the National Museums of Tanzania was established.

One of the major problems with establishing a long-term field program in the Manonga Valley was that there was little or no background information already available on the geology, vertebrate paleontology, or age of the sites. This had serious implications for scientific planning, field logistics, and the fund-raising potential of the project, and meant that initial stages of the research would need to concentrate on a number of basic issues and problems (Harrison, 1992). Several key objectives were identified, as follows: (1) to relocate the known paleontological sites in the Manonga Valley, and to prospect for additional productive localities; (2) to make intensive surface collections and excavations for fossils from these sites to improve on the very limited data available on fossil faunas from the Manonga Valley; (3) to make detailed studies of these fossils for taxonomic, phylogenetic, biogeographic, and biochronological purposes; (4) to conduct geological investigations at both the local and regional levels, and to assess the nature of the geological context of the major fossil localities to obtain a detailed understanding of the local stratigraphy and geological history of the Manonga Valley; (5) to obtain more secure estimates of the age range of the fossil-bearing sediments through faunal correlation, paleomagnetic stratigraphy, and, if possible, radiometric dating; and (6) to attempt to reconstruct the paleoecology of the Manonga basin using evidence from geological studies and paleontology.

4. Geological Context

The basement rocks in the Manonga Valley are part of the Precambrian-age Nyanzian System, formerly referred to as the Upper Basement Complex (Stockley, 1935, 1943; Grantham and Temperley, 1939; Grantham *et al.*, 1945; Teale and Oates, 1946; Quennell *et al.*, 1956). They consist primarily of a series of acidic and basic volcanic rocks, schists of sedimentary origin, and banded ironstones, up to 7500 m thick (Grace and Stockley, 1931; Eades, 1936; Eades and Reeve, 1938; Williams and Eades, 1939; Grantham *et al.*, 1945; Stockley, 1947; Quennell *et al.*, 1956; Cahen *et al.*, 1984; Borg, 1992; Walraven *et al.*, 1994). The sediments are not highly metamorphosed, in contrast to those of the earlier Dodoman

System (formerly the Lower Basement Complex), which occur in other parts of Tanzania (Quennell *et al.*, 1956).

The most distinctive component of the Nyanzian System is the Banded Ironstone Formation (BIF), with a U-Pb zircon age of 2.7 Ga (Borg, 1992; Walraven *et al.*, 1994). Owing to its resistant nature, the banded ironstone, consisting of a chert with magnetite-rich laminae, is commonly found as irregular pebbles among the surface debris at Precambrian outcrops. The Nyanzian beds were subject to several episodes of batholithic intrusion of granitoid rocks, principally migmatites, biotite gneisses, gneissose granites, and biotite granites, commonly associated with dykes or sills of pegmatite, acidic volcanics, quartz veins, and other minor intrusions (Kuntz, 1909; Eades, 1936; Wade, 1937; Stockley, 1948; Quennell *et al.*, 1956). Rb-Sr and K-Ar dating of the granitoids indicates a widespread event of migmatization at ca. 2.4–2.6 Ga (Old and Rex, 1971; Dodson *et al.*, 1975; Cahen *et al.*, 1984; Walraven *et al.*, 1994). The oldest granites are dated at 2.85–3.12 Ga, which establishes the younger limit for the Nyanzian (Cahen *et al.*, 1984). As a consequence of these intrusions, the Nyanzian shows evidence of contact metamorphism and steep isoclinal folding (Quennell *et al.*, 1956; Walraven *et al.*, 1994). The resulting granitoid shield occupies a major portion of the Central Plateau, leaving a series of roof pendants of the Nyanzian System as isolated outcrops of limited extent (Grantham *et al.*, 1956; Cahen *et al.*, 1984).

The Nyanzian was subsequently disrupted by the intrusion of dykes of olivine dolerite and kimberlite pipes (Williams, 1939). The kimberlites in the vicinity of Nzega, just to the southwest of the Manonga depression, has a U-Pb date of 53 Ma, placing the intrusive event in the early Tertiary, close to the Paleocene–Eocene boundary (Dawson, 1970; Mitchell, 1986).

During the later Tertiary, the Central Plateau was subject to peneplanation, which resulted in the accumulation of extensive terrestrial deposits in shallow valleys and depressions (Teale, 1931; Williams and Eades, 1939; Grantham *et al.*, 1945). The terrain at this time was of relatively uniform relief, except for low, rounded inselbergs formed from outcrops of the more resistant granitic and basement rocks. The combination of arid conditions and low elevations resulted in broad, shallow valleys that quickly became filled with coarse, poorly sorted granitic brash and metamorphic detritus of local origin (Williams, 1939; Williams and Eades, 1939; Harrison and Verniers, 1993). These aggradational sediments are generally not bedded, but are cemented together by a calcareous, siliceous, or ferruginous matrix. Similar terrestrial sediments appear to be quite widespread on the Central Plateau, and may include the "Kilimatinde cement" (Krenkel, 1925; Wade, 1937; Quennell *et al.*, 1956; Pickering, 1958) and the ferruginous "cement" of the Gila Hills (Eades and Reeve, 1938). Evidence from boreholes has shown that these deposits may be up to 60 m in thickness (Grantham *et al.*, 1945).

By the end of the Miocene, initiation of regional rifting led to distant warping of the basement complex, which produced a shallow lake basin in the Manonga depression (Stockley, 1930; Williams and Eades, 1939). At its maximum, the lake covered an area in excess of 10,000 km^2—which today would rank it as Africa's fifth largest lake (Harrison, 1993a, 1994; Fig. 2). However, it is evident from the nature of the sediments, especially in the lower part of the sequence, that the lake underwent periods of regression, during which the floor of the lake emerged subaerially. The Precambrian hillocks of the Tertiary peneplain remained sufficiently elevated to form small, low-lying islands. Fine calcareous clays were deposited toward the center of the lake basin, and these have yielded the fossilized remains of vertebrates and invertebrates that lived in and around the lake during the Neogene (Grace and Stockley, 1931; Williams and Eades, 1939; Harrison, 1991b, 1993a, 1994; Haileab and Harrison, 1993; Harrison *et al.*, 1993; Harrison and Verniers, 1993). Coarser sandy and pebbly littoral facies were produced along the shorelines of the lake. The Sekenke conglomerates, composed of quartz pebbles with ferruginous staining and cherty beds, represent a localized occurrence along the flanks of the Sekenke ridge at the eastern margin of the Wembere depression (Kuntz, 1909; Eades, 1936; Eades and Reeve, 1938; Williams and Eades, 1939). The particles are medium-size, well rounded or subangular, and they are derived locally from the underlying Nyanzian complex (Eades, 1936). These conglomerates have been interpreted as shoreline or shoal accumulations, and they possibly represent the easternmost extent of the Manonga lake basin (Pickering, 1958). No fossils have yet been recovered from these sediments.

The regional geology has not yet been studied in sufficient detail to allow the reconstruction of the hydrographic relationships of the Manonga basin. Nevertheless, some interesting clues can be garnered from analyses of the biogeographic associations of the fish fauna (Stewart, this volume, Chapter 11) and mollusks (Gautier and Van Damme, this volume, Chapter 12), as well as from inferences about possible paleodrainage patterns. This is a topic of considerable interest given the location of the Manonga basin close to the great divide between the Zaïre (Atlantic), East Rift/east coast (Indian Ocean) and Nile (Mediterranean) drainage systems (Fig. 4).

There is no evidence to suggest that Lake Manonga was a dischargeless basin, comparable to that of Lake Eyasi today. Instead, the geomorphological and paleontological evidence both suggest that there was at least a periodic connection of the Manonga basin with the east coast and the Nile hydrological provinces during the late Neogene. It has been noted previously that Lake Manonga may have drained eastward into the Indian Ocean via the Pangani River system prior to the development of the Eastern Rift in northern Tanzania (Cooke, 1958). This is certainly a possibility, but there is very little empirical support for such an inference, and the geological evidence runs counter to such a suggestion. The subsequent formation of the southern end of the Gregory Rift in northern Tanzania has obscured the topographical and geomorphological relationships of the eastern portion of the Manonga basin. Today, the Manonga basin and Pangani Valley are separated by the Eyasi–Wembere troughs and the main southern axis of the Gregory Rift. It is, therefore, difficult to reconstruct the hydrological relationship between the east coast and Lake Manonga during the later Neogene, prior to regional rifting. It is evident, however, that the modern-day Pangani River

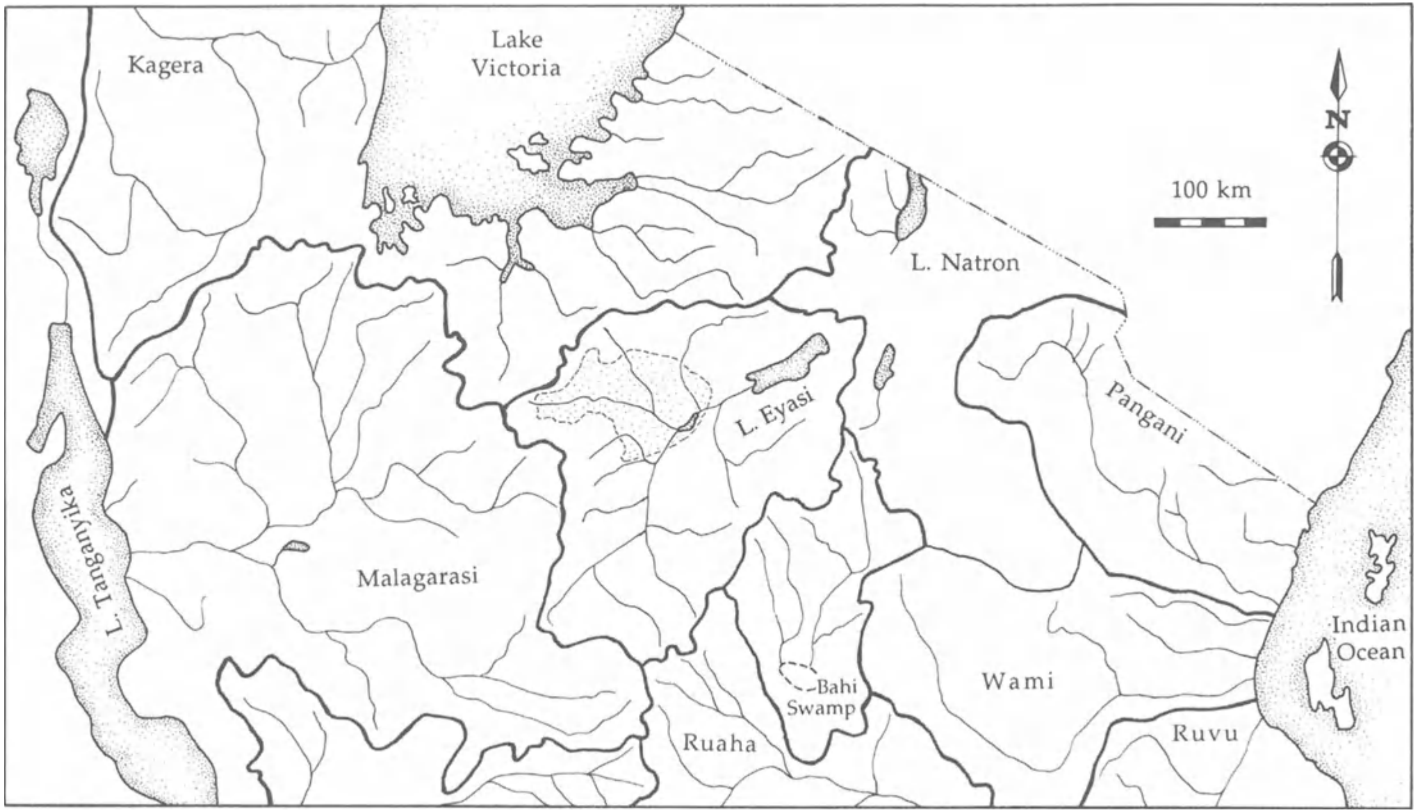

FIGURE 4. Hydrological map showing the main river basins in northern Tanzania. The Manonga River, which passes through the center of the Manonga basin (shown in light stipple in the center of the figure) is part of the present-day Lake Eyasi drainage basin, but it is located close to the divide between the Lake Victoria (Nile) and Lake Tanganyika (Zaire) drainage systems. Adapted from Berry (1972).

is a product of the rifting process itself, and that its current pattern of drainage antedates the depositional sequence in the Manonga Valley.

Nevertheless, a connection between the Manonga Valley and the east coast province is implied by the zoogeographic relationships of the fish faunas (Stewart, this volume, Chapter 11). It would seem that this connection was extant during the early part of the sequence, when Lake Manonga was relatively shallow, but that its drainage toward the east was eventually impeded by the development of the rift valley (Williams and Eades, 1939). In the western portion of the basin, away from the extreme margins of the Tanzanian craton, and where the effects of rift formation have been minimal, it is possible to reconstruct more precisely the topographic and hydrological relationships of Lake Manonga during the late Neogene. Presently, the lowest point in the divide between the Manonga basin and the Lake Victoria basin is at Igundu, 1154 m above sea level, and only 20 m above the present-day level of Lake Victoria. Lake sediments in the Manonga Valley currently range in elevation from just over 1000 m to about 1160 m (Williams and Eades, 1939; Verniers, this volume, Chapter 2). Even taking into consideration the slight tilting of the lake beds and changes in the position and elevation of the divide, we can infer that when Lake Manonga reached its maximum extent it overspilled into what is now the Lake Victoria basin. At the time, the latter basin was occupied by an extensive river system (the Kagera–Katonga basin), now largely submerged under the present-day lake (Cooke, 1958; Kendall, 1969; Kingdon, 1989; Pickford *et al.*, 1993). Water flowed into the center of the basin from the east and south, and eventually fed into the Kagera River. This then flowed west, presumably into the developing Western Rift via Lake Rutanzige (Lake Edward), and was eventually captured by the Nile River system (see Pickford *et al.*, 1993, for discussion of drainage in the Western Rift). Smith Sound and Stuhlmann Sound, which enter the Mwanza Gulf along the southern margin of Lake Victoria, represent the remains of deep channels cut by major rivers that flowed northwest into the Kagera–Katonga basin (Cooke, 1958). It seems likely that these were major drainage outlets from the Manonga basin during the early Pliocene, when Lake Manonga was at its deepest (but see Pickford *et al.*, 1993, for an alternative explanation of the formation of "Lake Wembere").

The Eastern Rift in northern Tanzania is deflected around the resistant craton to produce a 300-km-wide fracture zone of diverging faults and downwarps, (King, 1970, 1978; Baker *et al.*, 1972; McConnell, 1967, 1972; Williams, 1978; Fig. 5). Rifting and active volcanism at the southern end of the Gregory Rift appear to have occurred much later than that along the main axis of the rift. The Sonjo–Eyasi fault, which is partly buried by volcanics dated at 3.2 Ma (i.e., the Mozonik tuff at Peninj), is most probably early Pliocene in age (Isaac, 1967; King, 1970; Baker, 1986), while the faults in the central part of the divergence zone are slightly younger, probably late Pliocene to Pleistocene in age. Nevertheless, based on an assessment of the local paleo-drainage patterns, Hay (1987) has suggested that the Eyasi fault scarp did not exist at 3.5 Ma when the Laetolil Beds were deposited, and that most or all of the displacement occurred subsequent to the eruption of the Ogol lavas at 2.41 Ma. However, a critical review of the stream

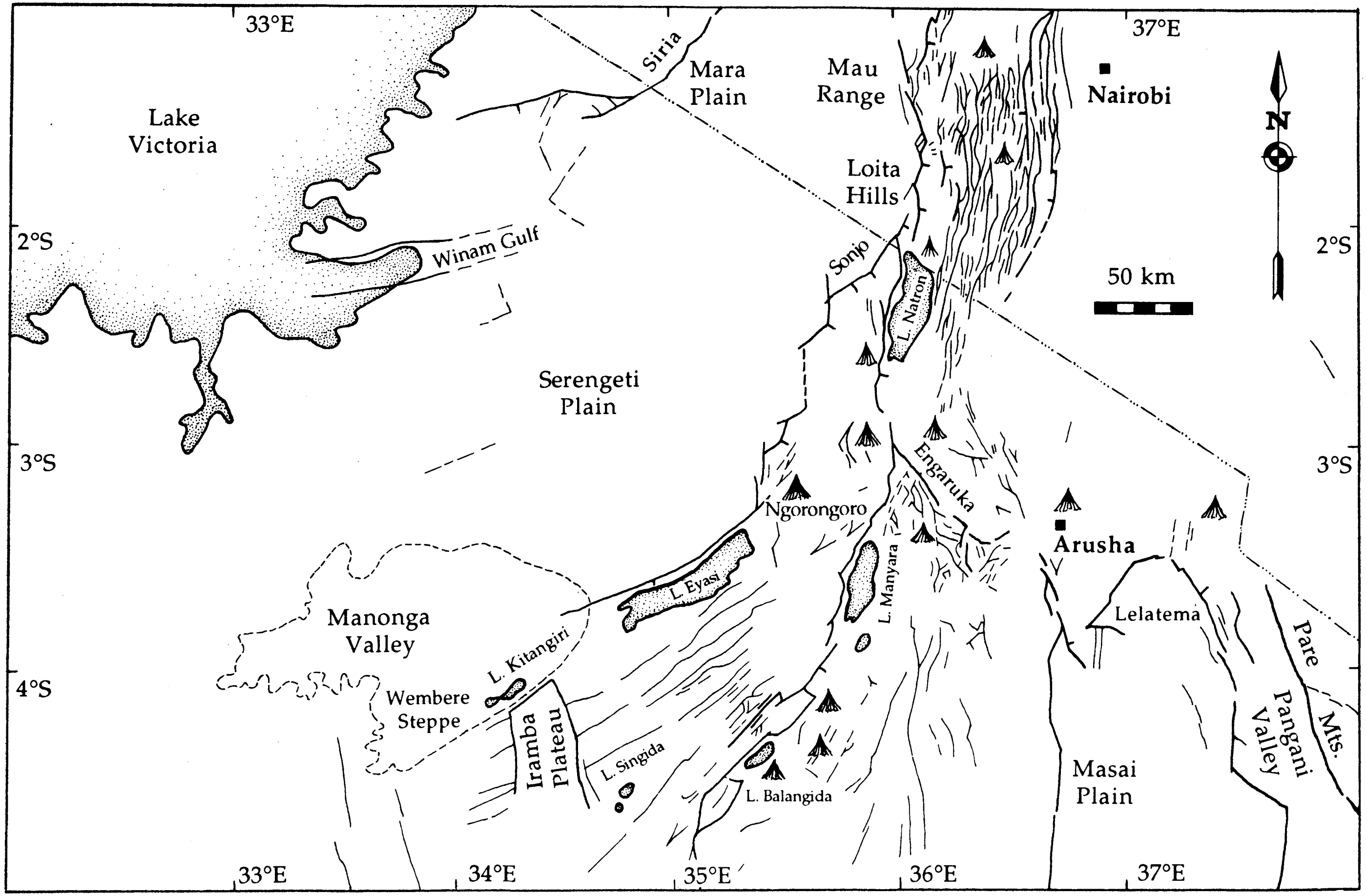

FIGURE 5. Map showing the fault pattern and major volcanic centers in southern Kenya and northern Tanzania in relation to the Manonga basin. Adapted from King (1970).

system of the present-day Eyasi basin, as revealed from aerial photographs and topographic maps, shows a complex pattern of directionality, one that would not readily provide convincing evidence today for the existence of a fault scarp along the northern margin of lake, especially when viewed at a local level. We can, therefore, conclude that development of the Eyasi trough, just to the northeast of the Manonga Valley, was probably initiated at the beginning of the Pliocene. The occurrence of a tuff, outcropping in a scarp near Olpiro, 15 km southeast of Laetoli, dated at 4.32 Ma, certainly confirms that volcanism, associated with the rift valley, was active in the region at this time (Drake and Curtis, 1987; Brown, 1994).

With the development of the Eyasi–Wembere grabens during the early Pliocene, Lake Manonga drained toward the northeast into the deeper Eyasi trough. The rifting process also apparently produced a slight downwarping of the Manonga lake beds. This directed the Manonga River eastward through the center of the depression toward Lake Kitangiri and Lake Eyasi, thus initiating the development of the modern Wembere–Manonga drainage system (Harrison and Verniers, 1993). Although the Manonga Valley is located at some distance from the major volcanic centers of the Eastern Rift, it is still affected by tectonic movements, with seismic activity reported up to several times a year (Eades, 1936). In fact, during the summer of 1990, the expedition experienced a strong tremor at the base camp.

Since the mid-Pliocene, the Neogene lake sediments have been exposed at cliff faces and eroded by the action of the Manonga River and its tributaries, as well as by heavy seasonal rains. The Manonga Valley, which cuts through the center of the lake basin, is associated with the most productive fossil sites.

The Neogene beds are overlain in places by quite extensive layers of undifferentiated alluvial sands and mbuga clays, which probably accumulated during the late Pleistocene and Holocene (Williams and Eades, 1939). Lake Victoria was formed during the middle to late Pleistocene, as a consequence of sagging of the Tanzanian craton to the north of the Manonga Valley, and by uplift in the west through continued maturation of the shoulders of the Western Rift. This led to tectonic back-ponding of westward flowing rivers, and subsequent drowning of the Kagera–Katonga river systems (Kendall, 1969). The height of Lake Victoria is now 1134 m above sea level,* some 20 m below the height of the Victoria–Manonga divide. However, evidence from ancient lake terraces and from lake cores suggests that at about 12,000 years ago Lake Victoria may have reached levels more than 20 m higher than the present lake (Temple, 1964, 1966, 1967; Kendall, 1969; Livingstone, 1975; Hamilton, 1982). This occurred at a time (12,700–11,100 BP) when climatic conditions in East Africa were warmer and wetter, and before significant down-cutting of the Nile outlet at Jinja in Uganda had developed (Kendall, 1969; Livingstone, 1975; Roberts *et al.*, 1993). Lake Victoria may have overspilled into the Manonga Valley at this time, thereby

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*This is the pre-1961 level of Lake Victoria, since which time it has risen several meters (Kendall, 1969).

forming part of a huge system of swamps and shallow lakes across much of northern Tanzania. It is possible that some of the superficial sediments in the Manonga Valley, including the mbuga clays, are the result of inundation by higher water levels in the Victoria basin (Verniers, this volume, Chapter 2), or alternatively they were deposited by shallow lakes and swamps that formed in the previous lake basin as a consequence of wetter conditions than those prevailing today. Further evidence of contact with the Victoria basin is confirmed by the common occurrence of large bivalve mollusks in the mbuga clays (see Gautier and Van Damme, this volume, Chapter 12; Harrison and Baker, this volume, Chapter 13).

Verniers (this volume, Chapter 2) presents a revised stratigraphy of the Manonga basin, following the initial studies of Harrison and Verniers (1993) and Harrison *et al.* (1993). A generalized stratigraphic scheme, based on the revised interpretation of Verniers is presented in Fig. 6. The Tertiary sediments are divided into two formations, the Mwansarara Formation and the Wembere–Manonga Formation, the latter of which is further subdivided into three members, the Ibole, Tinde, and Kiloleli. To date, no fossils have been recovered from the Mwansarara Formation, but they are well represented in each of the major stratigraphic subunits of the Wembere–Manonga Formation. Biostratigraphic analysis of the mammalian fauna (Harrison and Baker, this volume, Chapter 13) indicates an age estimation of ~4.0–5.5 Ma for the Wembere–Manonga Formation.

Estimated age	Stratigraphic unit		Fossil mammal localities
Late Pleistocene or Holocene	Mbuga clays, yellow clays		Ipembe, Kalitu, Ngofila 1–2, Nyawa, Shoshamagai Hill, Shoshamagai 2, Inolelo 1–3, Tinde West, Kiloleli 2–3, Beredi South 1, Kininginila, Ngofila 2
Early Pliocene ~4.0–4.5 Ma	Wembere–Manonga Formation	Kiloleli Member	Kiloleli 1–4, Ngofila 1–5, Beredi South 1–3
Early Pliocene ~4.5–5.0 Ma		Tinde Member	Tinde East, Tinde West, Mwambiti 1, 2, 5, Ipembe, Shoshamagai 1–2, Ngofila 1–5, Beredi North, Mihama, Kininginila, Nyawa
Late Miocene ~5.0–5.5 Ma		Ibole Member	Inolelo 1–3, Shoshamagai 2, Mwambiti 3–4, Lubeho, Beredi South 5, Kalitu, Ngofila 1–2, 5
?Miocene	Mwansarara Formation		
Precambrian	Nyanzian System		

FIGURE 6. Generalized stratigraphic scheme of the sediments in the Manonga basin, and the stratigraphic distribution of fossil mammal localities.

5. Paleontological Localities in the Manonga Valley

As the majority of fossil sites in the Manonga Valley have not been formally described, a brief review of each collecting locality is presented below. Additional information about their geographic location, stratigraphic position, and the fossil material recovered is presented in Table I and Fig. 6. Figures 2 and 3 illustrate the location of the main collecting areas in the Manonga Valley. All of the fossil sites are located in the center of the Manonga basin, not far from the Manonga River.

5.1. Tinde

The site of Tinde, first described by Stockley (1930) and Grace and Stockley (1931) is located in Igunga District (Tabora Region), about 7 km southeast of the village of Igurubi (Fig. 7). It is situated close to the center of the Manonga depression, about 10 km south of the Manonga River. The site consists of two low bluffs, less than 10 m high, separated by a flat gap, about 110 m wide. Owing to the spatial separation of the fossil-producing beds, it was considered convenient to divide the former site into two separate collecting localities, Tinde East and Tinde West, situated on the eastern and western side of the gap, respectively (Harrison, 1991b, 1993a; Harrison and Verniers, 1993; Harrison *et al.*, 1993).

As this locality represents the type locality for the Tinde Member (=Tinde Beds), geological and paleontological work was initiated here during the 1990 season. Detailed geological mapping was untaken in order to provide a standard stratigraphy for regional comparison. Fossils *in situ* are restricted to a single horizon, about 1 m in thickness, consisting of a light gray calcareous clay layer impregnated with a hard honeycomblike calcite matrix. Almost all of the fossils obtained from this site have been recovered by surface collection after they have eroded out of the fossiliferous layer.

The two sites at Tinde are among the most productive localities in the Manonga Valley. To date, almost two thousand taxonomically identifiable large mammals have been recovered, representing 48% of the collections from all localities in the Manonga Valley. Further details of the paleoecology, taphonomy, and vertebrate paleontology of Tinde are presented by Harrison (this volume, Chapter 4) and Harrison and Baker (this volume, Chapter 13).

5.2. Mwambiti

Five fossil localities have been designated in the vicinity of Mwambiti point, a distinct promontory on the southern edge of the Manonga Valley, located 5.4 km south of the Manonga River and 7.6 km northeast of Tinde West. The sites are associated with an arc of cliffs, 10.7 km long, that run from Tinde West to Mwambiti point. Intensive exploration of these cliffs and the neighboring valley since 1990 has shown that the sediments are mostly unfossiliferous. Nevertheless, several areas of rather limited extent have produced vertebrate fossils.

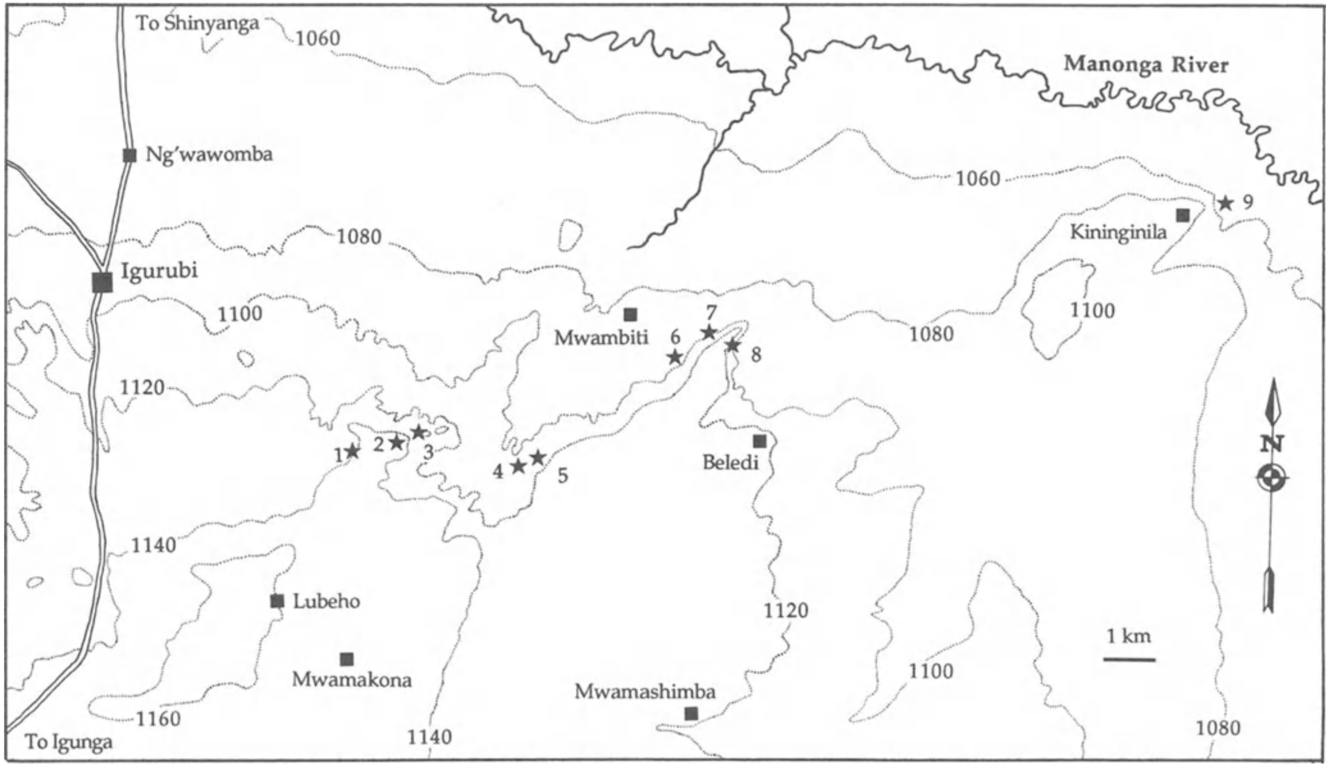

FIGURE 7. Topographic map showing the location of the fossil localities (marked by stars) at Lubeho, Tinde, Mwambiti, and Kininginila: 1, Lubeho; 2, Tinde West; 3, Tinde East; 4, Mwambiti 4; 5, Mwambiti 3; 6, Mwambiti 5; 7, Mwambiti 1; 8, Mwambiti 2; 9, Kininginila. Detail of inset (c) from Fig. 3.

In 1990, two sites, Mwambiti 1 and Mwambiti 2, were discovered on the northwestern and eastern flanks of Mwambiti point, respectively (Fig. 7). Fossils were recovered from the surface debris, having previously eroded out of a hard calcareous band close to the top of the cliff, intercalated within sediments equivalent to the Tinde Member. Fragmentary fossils were also recovered from a thin red clay layer at the base of the cliff, initially designated as the Mwambiti Member (Harrison, 1991b, 1993a; Harrison and Verniers, 1993; Harrison *et al.*, 1993), but now subsumed into the Ibole Member. A widened search of the general area in 1992, with teams prospecting as far as 2 km from the cliffs, led to the discovery of two further sites, Mwambiti 3 and Mwambiti 4 (Fig. 7). Mwambiti 3 is a relatively restricted locality situated quite close to the base of the cliffs, 5.2 km southwest of Mwambiti point, and 2.8 km east of Tinde West. Mwambiti 4 is located about 1 km north of the cliffs, 5.7 km southwest of Mwambiti point, and 2.3 km east of Tinde West. Fossils from both of these sites were found eroding out of a thick layer of red calcareous clays within the Ibole Member. They are exposed and concentrated in small ephemeral river gullies that have cut down several meters into the floor of the valley. In addition, at Mwambiti 3, fossils were also recovered from the cliff face, derived from calcareous clays of the Tinde Member.

In 1994, a further site, Mwambiti 5, was discovered 2 km southwest of Mwambiti point (Fig. 7). The locality consists of a low denuded hillock, situated less than 100 m north of the main cliffs. The hillock, which rises only about 5 m above the general surface of the valley floor, exposes an alternating series of hard calcareous clays and softer swelling clays of the Tinde Member. Fossil vertebrates are extremely rare, but well-preserved jaws and associated postcranial elements of a small species of rodent were recovered after having washed out of a light gray and reddish-tinged swelling clay at the base of the hillock. The number of large mammals known from the localities at Mwambiti is relatively small, representing less than 1% of the total material from the Manonga Valley.

5.3. Kiloleli

In 1990, several productive fossil localities were discovered along a line of low cliffs situated just west of the main Igurubi–Shinyanga road, in the vicinity of the village of Kiloleli. The sites have been subdivided geographically into four collecting localities, Kiloleli 1 through Kiloleli 4. Kiloleli 1 is located just north of the village of Kiloleli, while Kiloleli 2–4 are located south of the village (Fig. 8). The sites are located in Shinyanga District (Shinyanga Region), beginning 6.8 km north of the Manonga River, 14.0 km north of Igurubi, and 19.1 km northwest of the site of Tinde West. Williams and Eades (1939) made reference to a fossil site just north of Shoshamagai, but gave no specific information on its location. From the evidence available, however, it seems likely that the locality is equivalent to Kiloleli 2, as defined by WMPE (Harrison, 1991b).

The best exposures at Kiloleli consist of low slopes and cliffs, which rise to less than 15 m above the valley floor. Careful examination of the surface exposures has revealed that fossils are eroding out of a series of hard calcareous bands intercalated within a thick bed of swelling clays, representing the Kiloleli Member. At least two of the hard layers at Kiloleli 2 have yielded fossils *in situ*. The faunas from each layer are identical, and there is no reason to assume that a significant time interval elapsed between their deposition. However, quarrying activities for suitable raw material for brick-making by the local inhabitants has recently exposed a layer of yellow clay at the top of the Kiloleli sequence that yields what appears to be a much younger fauna. The bones and teeth from this horizon, which have a distinctively yellowish coloration and friable texture, tend to be more complete and better preserved than the more heavily mineralized and brittle fossils from the underlying Kiloleli Member. Although very little material has been recovered from this upper clay horizon, the identifiable taxa can probably be referred to modern species, implying a late Pleistocene or Holocene age (see Harrison and Baker, this volume, Chapter 13).

It is worth noting that when Kiloleli was first visited by WMPE in 1990, brick-making activities at the southern end of Kiloleli 2 made it impossible to obtain fossils because of the disturbed stratigraphy and the superficial coverage by excavated debris. Following discussions with the local authorities at Kiloleli,

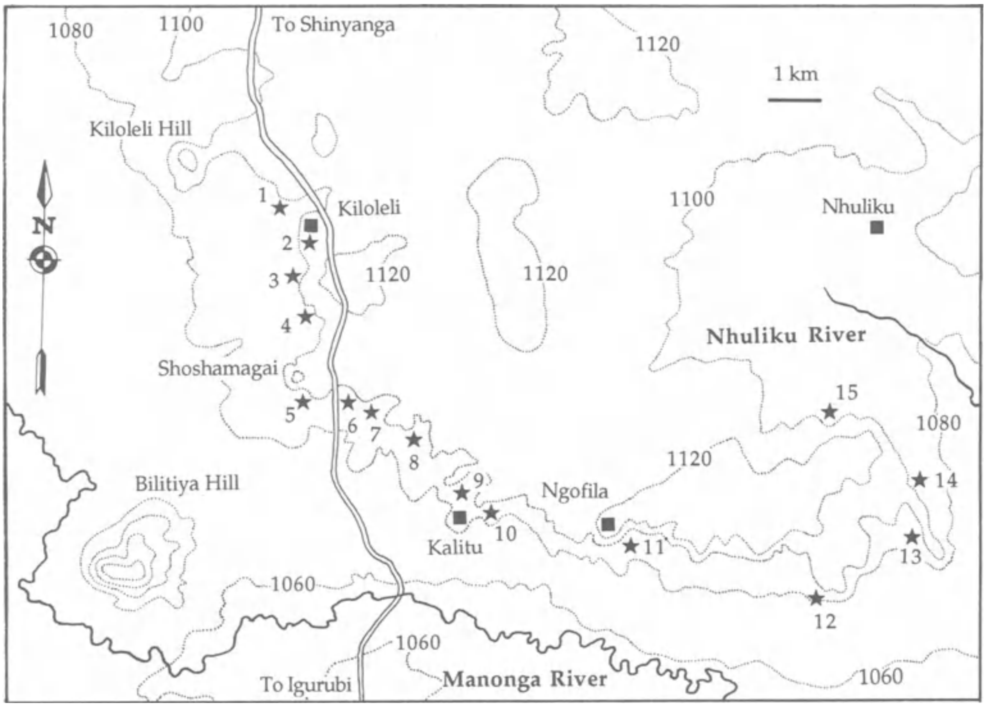

FIGURE 8. Topographic map showing the location of the fossil localities (marked by stars) at Kiloleli, Shoshamagai, Inolelo, Kalitu, and Ngofila: 1, Kiloleli 1; 2, Kiloleli 2; 3, Kiloleli 3; 4, Kiloleli 4; 5, Shoshamagai 1; 6, Shoshamagai 2; 7, Inolelo 1; 8, Inolelo 2; 9, Inolelo 3; 10, Kalitu; 11, Ngofila 1; 12, Ngofila 2; 13, Ngofila 3; 14, Ngofila 4; 15, Ngofila 5. Detail of inset (a) from Fig. 3.

a ban was imposed on brick-making in an attempt to conserve the site, and these restrictions were still in effect when WMPE returned in 1992. However, by the time of our next visit in 1994 excavation of the clays had resumed, and, in fact, exploitation had intensified. Although this has led, at least initially, to a higher yield of fossils on the surface, the increased breakage and the lack of primary stratigraphic association associated with indiscriminate excavation has undermined the utility of the collections.

The localities at Kiloleli, especially Kiloleli 2, are among the most productive fossil localities in the Manonga Valley. Together they have produced 17.3% of the taxonomically identifiable large mammals, second only in importance to the sites at Tinde.

5.4. Ipembe and Lubeho

In 1992 and 1994, WMPE conducted a brief survey in the region of the Kalangale Hills, an elevated series of Precambrian outcrops, located on the southwestern margin of the Manonga basin. A search of the exposed sediments in the vicinity of the villages of Ng'wandibimizi and Ipembe led to the discovery of a single new fossil locality. The site of Ipembe is located 1.8 km southwest of the village of Ipembe, 12 km northwest of Igurubi, and 7.3 km south of the Manonga River. The locality consists of a low plateau, less than 10 m high, with east- and west-facing cliffs that meet at a precipitous north-facing promontory. Mammalian fossils were not abundant. They were found scattered along the entire length of the eastern flank of the plateau, derived from light gray calcareous clays of the Tinde Member.

The site of Lubeho was first discovered in 1994. It is located just to the north of the village of Lubeho, 2.3 km southwest of Tinde West, and 6.6 km southeast of Igurubi (Fig. 7). The low, northwest-facing cliffs at the site grade gently down to a series of shallow gullies in the valley floor that expose the red clays of the Ibole Member. The contact between the light gray swelling clays of the Tinde Member and the red beds of the Ibole Member are obscured by a thick sheet of mbuga clays. Initial prospecting of the site led to the discovery of a partial mandible of an elephantid, still *in situ* in the Ibole beds. A subsequent visit to the site led to the recovery of further proboscidean remains, presumably belonging to the same individual, but no additional fossils (apart from an equid molar from the mbuga clays) were found. It would appear that the elephantid remains are an isolated occurrence at this site.

5.5. Shoshamagai

In 1990, a preliminary survey of the exposed sediments at the foot of Shoshamagai Hill, about 2 km south of Kiloleli village, revealed that the deposits were fossiliferous. Shoshamagai is subdivided into two collecting localities, Shoshamagai 1 and Shoshamagai 2 (Fig. 8).

Shoshamagai 1 is situated on the southern flank of Shoshamagai Hill to the western side of the main Igurubi–Shinyanga road. The sediments consist of a thick blanket of undifferentiated light gray to olive swelling clays, with several thin intercalated lenticular layers of hard white powdery calcareous clay. These sediments are assigned to the Tinde Member. The surface exposures in close proximity to the hill are littered with coarse, angular nodules of banded ironstone and other detritus derived from the Precambrian basement. Further from the hill, the sediments are better exposed, and the lake beds are deeply excised by small ephemeral drainage channels that radiate out from the base of the hill. Shoshamagai 1 is poorly fossiliferous. Recovered remains consist mainly of fish and aquatic reptiles, although isolated bones and teeth of large mammals do occur.

Shoshamagai 2 is adjacent to Shoshamagai 1, but is situated on the eastern side of the Igurubi–Shinyanga road, just to the southeast of Shoshamagai Hill. The Tinde beds at Shoshamagai 2 are the lateral equivalent of those at Shoshamagai 1, but they are better exposed, with steep-sided cliffs up to 10 m in height. Fossils are quite rare, however, and the Tinde beds in this area are much less productive than those at Tinde. Further from the cliffs at Shoshamagai 2, a rich concentration of fossils was found in sediments situated lower down in the local sequence, associated with the red beds of the Ibole Member (Harrison and Verniers, 1993; Verniers. this volume, Chapter 2). This site has yielded more than 11% of the large mammals from the Manonga Valley, and is one of only three sites to have yielded samples of micromammals (Winkler, 1993, this volume, Chapter 10).

5.6. Inolelo

From Shoshamagai Hill, a continuous series of low cliffs extends eastward for about 15 km, forming the northern margin of the Manonga Valley. These cliffs end at the Nhuliku Valley, formed by a shallow, ephemeral river that runs from the northwest, and eventually drains into the Manonga River. The cliffs form distinct promontories, which conveniently allow demarcation of the northern portion of the Manonga Valley into a series of eight geographically contiguous localities. Starting east of the Igurubi–Shinyanga road with Shoshamagai 2, discussed above, the collecting localities passing from east to west are Inolelo 1, Inolelo 2, Inolelo 3, Kalitu, Ngofila 1, Ngofila 2, and Ngofila 3 (Fig. 8).

The sites at Inolelo extend southeast along the northern margin of the Manonga valley for a distance of 5 km from Shoshamagai Hill. As at Shoshamagai 2, few fossil mammals have been obtained eroding out of the cliff faces from horizons within the Tinde Member. Most of the fossils, and certainly the best-preserved material, have been recovered from the Ibole Member, exposed on the surface of the Manonga Valley or in shallow gullies located up to 500 m from the cliffs. The red beds, which may be up to 6 m in thickness, consist of a laterized calcareous clay, grading down from light gray in color through gray-green, orange, pink, to bright red at its base. Fossils appear to be concentrated, but not exclusively found, in the upper portion of this layer. The red beds are overlain in places by mbuga clays, which support a sparse vegetation dominated by gall acacia. These vegetated patches serve to demarcate the eroded fossiliferous exposures into separate collecting localities. The fossils recovered from the red beds at Inolelo are derived from the same horizon as those from Shoshamagai 2, and the material obtained from all four sites can be considered as representing a single fauna.

Inolelo 1 is the largest exposure, and the most productive of the three sites. It is centered around a single main gully, up to 3 m in depth. Along with Shoshamagai 2, Inolelo 1 represents the most productive locality sampling fossils from the Ibole Member. In addition, an intensive program of screening at the site, directed by Dr. Kathlyn Stewart (Canadian Museum of Nature), has yielded a small, but important, collection of microvertebrates, including teeth and isolated bones of rodents, small carnivores, and several species of fish (see Winkler, this volume, Chapter 10; Stewart, this volume, Chapter 11). Inolelo 2 consists of three parallel gullies, much shallower than that at Inolelo 1 and heavily choked with mbuga clay and superficial sediments. Inolelo 3 extends eastward as far as the village at Kalitu, where a shallow gully and surface exposures of the red beds, some located only 10 m from the nearest house, have yielded well-preserved fossil mammals. The sites at Inolelo have yielded 10.6% of all of the large mammals from the Manonga Valley.

5.7. Kalitu

This site is situated northeast of the village of Kalitu, 1.3 km north of the Manonga River and 10 km northeast of Igurubi (Fig. 8). The site extends eastward for 2.3 km from the village of Kalitu to the village of Ngofila. A search of the exposed sediments of the Ibole Member in the village itself and to the east of the village has failed to yield any indications that fossils are present. However, a few fossils were recovered from the base of the cliffs nearby, and these are presumably derived from the swelling clays of the Tinde Member. The Neogene sediments at the base of the cliff are covered by patches of mbuga clay of variable thickness. A sample of isolated teeth of large mammals, presumably of late Pleistocene or Holocene age, was recovered from these latter deposits (Harrison and Baker, this volume, Chapter 13).

5.8. Ngofila

Ngofila is a continuation of the series of fossil localities that follow the line of cliffs on the northern side of the Manonga Valley, extending from Shoshamagai Hill in the west to the Nhuliku Valley in the east. The localities begin at the cliffs just below the village of Ngofila and continue east and north into the Nhuliku Valley (Fig. 8). A series of five collecting localities have been designated, based on geographic features and the distribution of fossils. These sites have yielded 6.4% of the large mammal specimens from the Manonga Valley.

Ngofila 1 is contiguous with the locality of Kalitu to the west, and comprises a series of low cliffs that extend eastward from the village of Ngofila for 4.3 km (Fig. 8). Its eastern boundary is demarcated by a low eroded hillock ("Ngofila Hill") that rises from the valley floor, and it is located less than 1 km west of Ngofila school. Few fossils have been recovered, and these are largely derived from beds of the Tinde Member. In 1994, a collection of fossil mammals was obtained from equivalent beds at Ngofila Hill.

Ngofila 2 is located east of Ngofila 1, and comprises a line of south- and east-facing cliffs, about 3 km in length, that pass below Ngofila school (Fig. 8). These cliffs reach a maximum elevation of 15 m above the valley floor, but eastward they descend to a low, densely bush-covered saddle, forming the boundary between Ngofila 2 and 3. Fossils from this locality derive from several horizons. A number of darkly stained and heavily mineralized bones and teeth were collected at the base of the cliff, presumably eroded out of a resistant calcareous clay band, located midway up the cliff, and the underlying swelling clays. These are best correlated with the Tinde Member. Directly above this is a yellowish-brown pebbly clay horizon, densely packed with gastropods, and capped by a thin grey limestone, equivalent to one of the uppermost horizons of the Kiloleli Member. On a narrow ledge very close to the top of the cliff at Ngofila 2 were a large number of poorly mineralized bones and teeth, creamy white in color, with bright yellow adhering matrix. These bones are identical in preservation to the similar occurrence at Kiloleli discussed above. Some of these bones exhibit signs of human activity in the form of butchering marks, but no stone tools were found in association. A few bones also show evidence of having been gnawed by rodents, an indication that they were exposed on the surface prior to burial. Since these fossils can be attributed to modern species, they are almost certainly late Pleistocene or Holocene in age (Harrison and Baker, this volume, Chapter 13).

Ngofila 3 consists of west-facing cliffs, separated from Ngofila 2 by a low, bush-covered saddle (Fig. 8). The cliffs, which extend for 1.5 km, are quite low to the north, but increase in elevation as they pass south, ending at a precipitous promontory at least 15 m high. The site is not richly fossiliferous, but a thin scatter of vertebrate fossils was found eroding out of beds in the Kiloleli Member. Of some taphonomic interest was the incidental recovery at Ngofila 3 of modern bone samples derived from spotted eagle owl nests, as well as from porcupine and hyena lairs. These samples are currently being prepared and studied by Wendy Dirks and Erin Dooley (New York University).

Ngofila 4 is located 7 km east of the village of Ngofila, and 4.5 km southwest of the village of Beredi (Fig. 8). Located 2 km from the Nhuliku River, the locality consists of northeast-facing cliffs, 3.3 km long, that form the western flank of the Nhuliku Valley. The low cliffs, less than 20 m high, are generally poorly fossiliferous. Fossils appear to be derived from both the Tinde and Kiloleli Members, although the best concentrations of fossil mammals were derived from horizons within the Kiloleli Member.

Ngofila 5 is located 6 km northeast of the village of Ngofila, 4.5 km southwest of the village of Beredi, and 4.1 km south of the village of Nhuliku (Fig. 8). The cliffs face northward and form the southern margin of the Nhuliku Valley, 2.5 km from the Nhuliku River. From its boundary with Ngofila 4, the cliffs extend west for more than 2 km before grading into a series of low slopes with dense vegetation cover and poorly exposed sediments. Fish and turtle remains were recovered from a narrow pink clay horizon at the base of the Tinde Member, but most of the fossil mammals were derived from the Kiloleli Member.

5.9. Beredi North and Mihama

Beredi North is located 2.7 km southeast of the village of Beredi, 9.3 km east of the village of Ngofila, and 7.5 km northwest of the village of Mihama (Fig. 9). The site consists of a low triangular plateau, bounded on the southwest and southeast by low cliffs that extend for about 4 km. The southwestern cliffs form the eastern margin of the Nhuliku Valley, 2.3 km east of the Nhuliku River. Beredi North is separated from Ngofila 4 on the western side of the valley by a flat plain about 4 km wide. Most of the cliffs are rather thickly vegetated, so erosion occurs slowly, and relatively few fossils have weathered out. Most of the fossils have been recovered from the southern tip of the plateau, where an elevated promon-

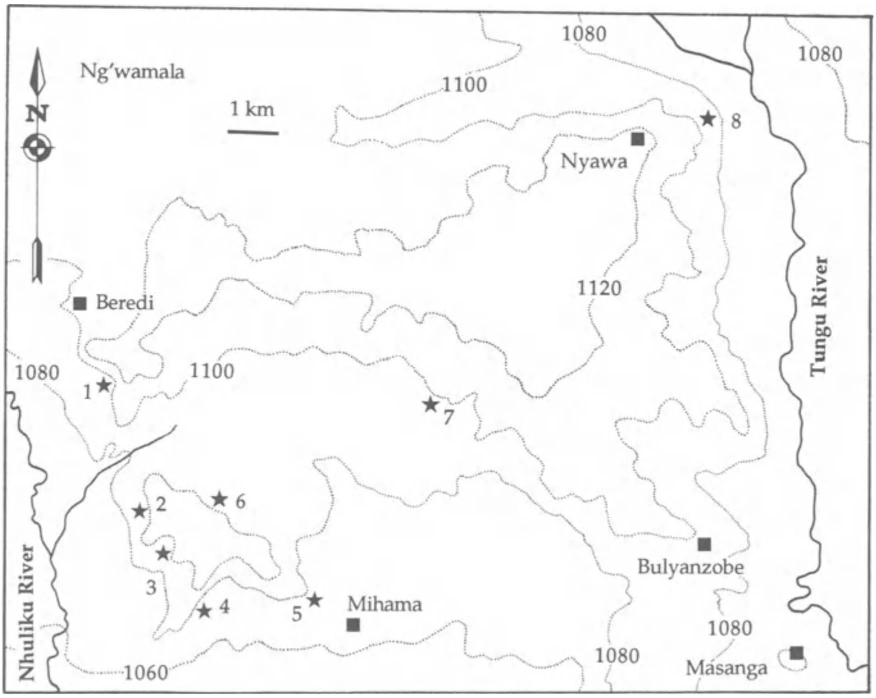

FIGURE 9. Topographic map showing the location of the fossil localities (marked by stars) at Beredi North, Beredi South, Mihama, and Nyawa: 1, Beredi North; 2, Beredi South 1; 3, Beredi South 2; 4, Beredi South 3; 5, Beredi South 4; 6, Beredi South 5; 7, Mihama; 8, Nyawa. Detail of inset (b) from Fig. 3.

tory has well-exposed sediments. Nevertheless, even here, fossils appear to be relatively uncommon.

In 1994, WMPE spent several days prospecting along the cliffs and low hills to the east of Beredi North, running from the village of Ng'wang'wika to the village of Bulyanzobe on the western flank of the Tungu River valley, about 5 km north of Mihama (Fig. 9). The slopes are poorly exposed, and are mostly covered with grass and sparse thickets. A few teeth of fossil mammals have been recovered from the surface. One specimen was collected from the mbuga clay, and is presumably Holocene or late Pleistocene in age, while the remaining material is derived from the Tinde Member.

5.10. Beredi South

Beredi South is a low plateau located 3.8 km southeast of the village of Beredi, 10.5 km east of Ngofila and 2.4 km northwest of the village of Mihama (Fig. 9). The plateau is separated from Beredi North by a flat plain 1.2 km wide. The southern and western margins of the plateau end at steep cliffs, which delimit the northern and eastern flanks of the Manonga and Nhuliku Valleys, respectively. Beredi South is located less than 2 km from the Manonga River and 1.8 km from the Nhuliku River. The cliffs forming the edge of the plateau have been subdivided into five separate collecting localities, Beredi South 1 through 5.

Beredi South 1 is located on the northwestern side of the plateau, overlooking the Nhuliku Valley and facing Ngofila 4. It is the most productive of the localities at Beredi South, and consists of a steep cliff exposing a series of well-stratified sediments. Fossils have been recovered from a number of different horizons. A hard calcareous clay, intercalated within a thick layer of swelling clays at the base of the cliff, represents the Tinde beds. This has yielded the remains of fossil fish and mollusks. Higher up the sequence, in the Kiloleli Member, a rich concentration of fossil mammals has been recovered, including a skull and forelimb skeleton of *Eurygnathohippus* (see Bernor and Armour-Chelu, this volume, Chapter 8). In addition, poorly mineralized and friable bones are derived from a yellow clay layer at the top of the cliff. This is presumably the lateral equivalent of the lithologically similar layer at Kiloleli 2 and Ngofila 1. The fossils are estimated to be late Pleistocene or Holocene in age (see Harrison and Baker, this volume, Chapter 13).

Beredi South 2 is a small exposure of sediments on a low range of cliffs, just to the southeast of Beredi South 1. The site has yielded fossils from the Kiloleli Member (Fig. 9).

Beredi South 3 is a long line of cliffs on the southeastern flank of the plateau running northeast from the southernmost promontory of Beredi South, close to the village of Buking'wanzuki (Fig. 9). A thin scattering of bones, mostly of fish and aquatic reptiles, was collected from the base of the cliff, derived from the Tinde Member. A rich concentration of fossils was also discovered from the Kiloleli Member, in a thick series of alternating calcareous clays and mudstones toward the top of the cliff.

Beredi South 4 consists of a southwest-facing cliff to the east of Beredi South 3, and 2.3 km northwest of the village of Mihama (Fig. 9). The northern section of the site consists of relatively low slopes, with dense grass and bush cover, and few good exposures. The cliff at the southwestern extreme of the site is more precipitous, with an elevation above the floor of the valley of more than 20 m. At the base of the cliff, small gullies cutting through the floor of the valley have exposed the red beds of the Ibole Member. Above this layer is a thick bed of swelling clays, up to 8 m thick, with at least six intercalated bands of hard calcareous clays. The lowest two bands, each less than 10 cm thick, consist of fine white calcareous clays containing small, well-rounded pink clay nodules. These layers contain a rich concentration of fossil fish, mostly *Clarias*, but the remains are extremely fragmentary and abraded, suggesting fluvial transportation prior to burial. However, they do not exhibit signs of rolling, certainly not to the degree exhibited by the associated pebbles, which have presumably been transported some considerable distance. Above the swelling clays is a series of fluvial sediments, up to 13 m thick, that comprise the Kiloleli Member, but no fossils have yet been recovered from these horizons.

Beredi South 5 is a line of cliffs and low slopes, 4.2 km long, forming the northeast margin of the plateau, and facing the locality of Mihama (Fig. 9). Kiloleli and Tinde Member beds are both represented, but the combination of low inclines and dense vegetation cover provides few good exposures. Fossil remains from these horizons tend to be fragmentary and scarce. At the base of the cliffs the Ibole Member beds are well exposed. These are largely unfossiliferous, but in 1994 a partial skeleton of a massive proboscidean was discovered (see Sanders, this volume, Chapter 9).

5.11. Nyawa

Nyawa is the easternmost of the localities on the northern side of the Manonga Valley (Fig. 9). The site consists of a series of low cliffs and slopes along the western flank of the Tungu Valley, between 1 and 2 km from the Tungu River. The southern end of the cliffs starts just north of the main track that fords the Tungu River leading to the town of Masanga. The main exposures occur in the vicinity of the village of Nyawa, close to the confluence of the Tungu and Mangu Rivers, about 13 km northeast of the village of Beredi. Fossils were first collected at Nyawa by Kleindienst and Haldemann, who made a brief visit to the area in 1959.

Mammalian fossils from the Tinde beds at Nyawa are not common, although the remains of fish, turtles, and crocodiles are ubiquitous. The floor of the valley, immediately to the north of the village of Nyawa, has a series of deep gullies that expose the Ibole Member. These appear to be unfossiliferous. The red beds are covered with a thin layer of mbuga clay that has yielded a good number of bones and teeth of large mammals, associated with quartz artifacts. The association of a Late Stone Age assemblage and modern fauna suggests that the mbuga clays were deposited during the late Pleistocene or Holocene.

5.12. Kininginila

The cliffs and exposed sediments in the vicinity of the village of Kininginila were first prospected during the 1992 field season. The site is situated on the southern edge of the Manonga Valley, less than 1 km from the Manonga River. It is located 11.5 km east of Mwambiti point, 7 km south of the village of Mihama, and 14.3 km northeast of the town of Mwamashimba (Fig. 7). Fossils are scarce, but a number of remains of large mammals, fish, and reptiles have been recovered from the Tinde Member.

6. Significance of Paleontological Research in the Manonga Valley

The recent expeditions to the Manonga Valley have provided evidence of the paleontological potential of the area. The large lake basin, with its extensive, well-exposed sediments and numerous productive fossil localities, can now be considered an important new paleontological research area in eastern Africa. The sequence of fossil-bearing sediments in the Manonga Valley covers an estimated time range (~4.0–5.5 Ma) that is generally poorly represented in sub-Saharan Africa. The paleontological collections, therefore, provide important new information on the evolutionary history, taxonomic diversity, paleobiology, and paleoecology of fossil mammals in East Africa during the late Neogene.

The Manonga Valley is, perhaps, of especial importance for researches into human origins. Even though paleoanthropologists have been painstakingly piecing together an increasingly complete record of human evolutionary history in Africa over the past 70 years, the hominid fossil record prior to 4.5 Ma remains extremely meager. At present, a jaw fragment and two teeth from Lothagam and an isolated tooth from Lukeino, dated at 5–7 Ma, represent the sum total of the evidence available (Patterson *et al.*, 1970; Pickford, 1975; Hill and Ward, 1988; Hill *et al.*, 1992; Hill, 1994; Leakey *et al.*, 1996). Therefore, the eventual recovery of fossil hominids from the Manonga Valley could contribute significantly to our currently limited understanding of the anatomy and paleobiology of the earliest stages of human evolution (see Harrison, this volume, Chapter 14). However, it is important to stress here that there is more at stake than merely extending the human lineage back in time and being able to lay claim to the earliest human ancestor. According to many paleoanthropologists and molecular biologists, 5–6 Ma may be close to the point in time when the human lineage diverged from the other African hominoids (e.g., Weiss, 1987: Hasegawa *et al.*, 1989; Caccone and Powell, 1989; Andrews, 1992; Hasegawa, 1992; Boaz, 1994; Hill, 1994). The discovery of the remains of early hominids from the late Miocene (or perhaps even more intriguingly, the remains of the antecedents of the last common ancestor of humans and African apes) would represent a major advance in our understanding of the evolutionary history of humans. In any event, even if hominid fossils continue to elude us in the Manonga Valley, analysis of the fauna from this poorly understood but critical time period may ultimately allow us to advance new hypotheses concerning the ecological and biogeographic factors, as well as the adaptive consequences, associated with the initial differentiation of the hominids in Africa (Hill, 1987, 1994; Boaz, 1994; Leakey *et al.*, 1996; Harrison, this volume, Chapter 14).

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Chapter 2

Detailed Stratigraphy of the Neogene Sediments at Tinde and Other Localities in the Central Manonga Basin

JACQUES VERNIERS

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1. Introduction

In 1990, during the initial field season of the Wembere–Manonga Paleontological Expedition (WMPE), the main characters of the structure, stratigraphy, paleoenvironment, and geological history of the Neogene lake basin in the Manonga Valley were outlined. As only a small fraction of the extensive lake basin

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(covering approximately 10,000 km^2) could be explored during this brief reconnaissance, lasting only about 15 days, geological work was concentrated at Tinde, and at neighboring paleontological sites in the center of the Manonga Valley. Preliminary results of this research have already been published by Harrison *et al.* (1993) and Harrison and Verniers (1993). More recently, during the summer of 1994, the author was able to study the stratigraphy in most of the outcropping areas in the Manonga Valley. As a consequence, a more detailed review of the stratigraphical results obtained from these two field seasons is presented in this chapter.

2. History of Previous Geological Research

The Neogene sediments in the Manonga Valley were first described in 1930, following the discovery by a mining engineer, C. Grace, of a richly fossiliferous horizon in the region (Stockley, 1930). The site was located at a break or gap in a low line of cliffs near the village of Mwamakona, a distinctive feature that is visible from some distance. The locality was referred to as Tinde—the name of a river to the west, and also the name of a village on that river some 4 km northwest of the site. With the assistance of Stockley (of the Geological Survey of Tanganyika), five pits were dug at Tinde to establish the provenance of the fossils (Grace and Stockley, 1931). The excavations established that only a single layer contained bones *in situ*. The collection of fossils was sent by E. O. Teale (the director of the Geological Survey of Tanganyika) to A. T. Hopwood at the British Museum of Natural History for examination. An unpublished report written by Stockley in 1929 presents a sketch of the gap at Tinde that clearly shows the stratigraphical succession and the position of the excavation pits. Unfortunately, the sketch was not included in the initial publications by Stockley (1930) and Grace and Stockley (1931).

Williams and Eades (1938) and Williams (1939) mapped the area geologically, and postulated the existence of a large lacustrine basin that covered most of the present-day valley of the Manonga River. They noted the occurrence of fine, calcareous sediments in the central part, and littoral, more sandy sediments toward the periphery of the lake. Williams and Eades (1938, p. 8) also recorded a second bone-bearing locality, some 20 km north-north-west of the first site, "below the marl bluffs on the Negezi-Igurubi road about two kilometers north of Shoshamagai." A brief reconnaissance was conducted in the area in 1959 by Kleindienst and Haldemann, and in 1976 by Leakey and Monaghan, without published results (see Harrison and Mbago, this volume, Chapter 1).

Barth of the German *Bundesanstalt für Geowissenschaften und Rohstoffe* was commissioned via the West German Federal Government on behalf of the Ministry of Energy and Minerals, Geological Division (Madini) in Dodoma, to compile a map (1:500,000) to document the geological context of the goldfields around Lake Victoria. Barth's (1989) map, as far as I am aware, was not accompanied by any published text. In the legends to the map, however, he succinctly names several new units of Neogene sediments in the region, and gives a new

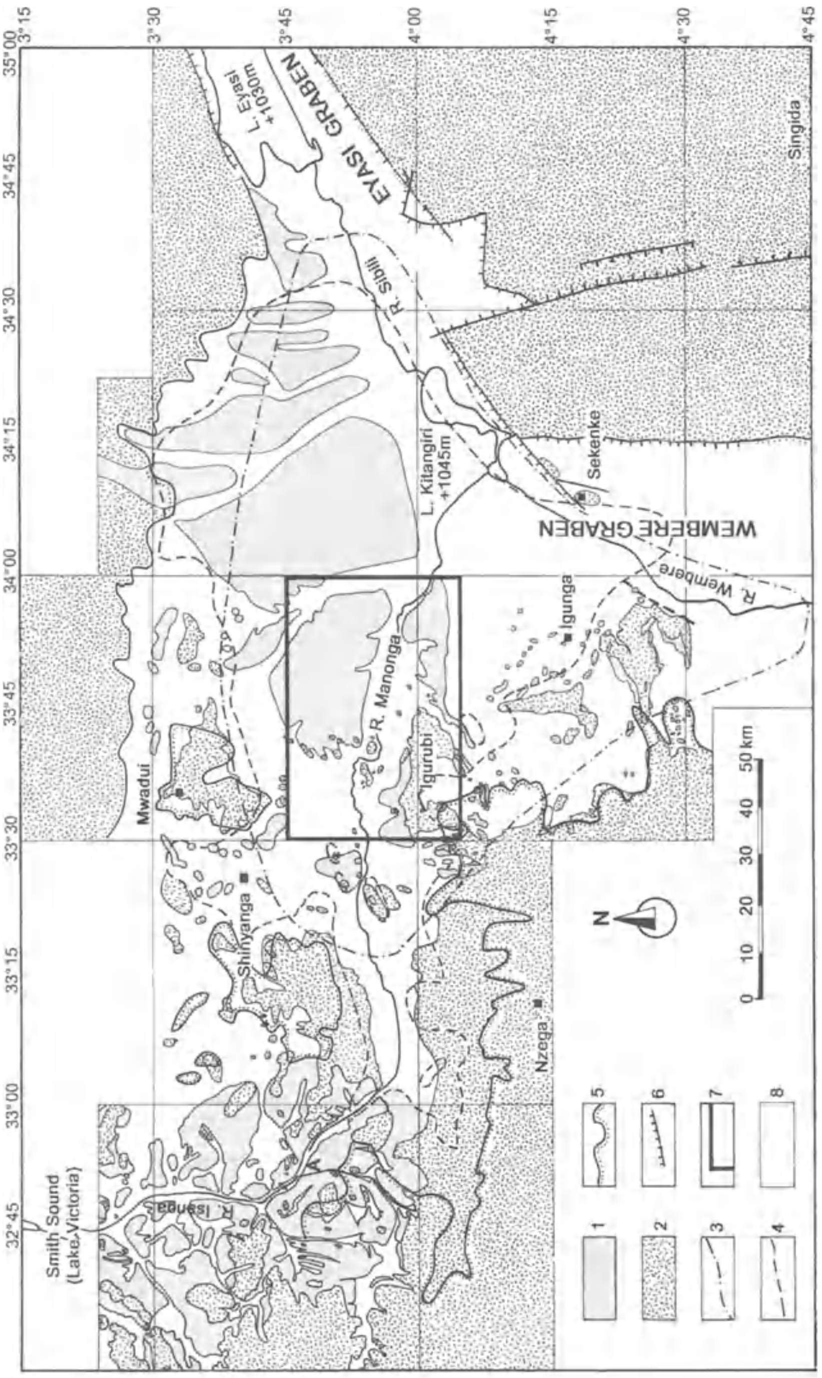


FIGURE 1. Schematic geological map of the late Neogene Wembere–Manonga paleolake area. Note the Eyasi and Wembere rifts and the Manonga Valley as a third aborted arm of that rift system. 1: late Miocene–early Pliocene sediments; 2: Precambrian outcrops or inselbergs; 1 and 2 according to Eades (1936), Eades and Reeve (1938), Williams and Eades (1938), Williams (1939), Grantham *et al.* (1945), Handley (1956), Handley and Harpum (1956), Barth, (1989), and personal observations in the field and on aerial photographs; 3: limit of the Wembere–Manonga lake beds according to Pickering (1958); 4: limit of the Plio-Pleistocene lake according to Williams and Eades (1938); 5: 1170-m contour line and proto–Lake Victoria/Lake Nyanza shoreline according to Barth (1989). For discussion on 3, 4, and 5, see section 2 of text; 6: escarpment faults; 7: limits of central Manonga basin; 8: different Neogene sediments and present-day erosion areas; A: location of the divide between the Isanga and Manonga Rivers at about 1154 m.

interpretation of the extent of the deposits. Although I accept the validity of some of these units, several are rejected, along with their underlying concepts.

Barth assumes that the Tanzanian craton has been extremely stable since the Miocene, and that all Neogene sediments, including those in the Manonga Valley, were deposited horizontally. As a result, he assumes that the 1170-m contour line (associated with the highest elevation at which lake sediments have been found) is a reasonable guide to the limit of the extent of the Wembere–Manonga paleolake. Similarly, the distribution of the "ancient beach flats of proto-Lake Victoria" were drawn by Barth along contour lines. Observations in the field, however, establish that block faulting, associated with the subsequent formation of the Eyasi–Wembere rift grabens, disturbed the Miocene or early Pliocene lake beds, and that the present-day contour lines cannot be used to accurately map the maximal elevation of the Neogene deposits.

Barth (1989) introduced several new concepts on his map, or at least in the legend to his map, but his "Lake Manonga" is clearly a junior synonym of the Manonga–Wembere Lake (Williams and Eades, 1938), while his "proto-Lake Eyasi" and "Lake Nyanza" or "proto-Lake Victoria" are successive lakes of Quaternary age.

In the literature, the Neogene paleolake has received a variety of names: "Lake in the Man(y)onga depression" (Teale, 1931, 1932; Williams, 1939); "deposits of the Manonga–Wembere lake and lake extension" (Williams and Eades, 1938); "Plio-Pleistocene lake" (Williams and Eades, 1938; Williams, 1939); "Wembere Plio-Pleistocene lake" (Grantham *et al.*, 1945, p. 4, misquoting Williams and Eades, 1938); and "Lake Wembere" (Pickford *et al.*, 1993).

The region of the Neogene lake deposits is illustrated in Fig. 1. It includes the following information: (1) the extent of the lake deposits as inferred by Williams and Eades (1938) and by Pickering (1958); (2) the location of the Eyasi and Wembere grabens; (3) the location of marl outcrops, described as "travertines," according to the soil map of Williams and Eades (1938), and corresponding to the Tinde Member (see below); and (4) the extent of the different facies of the other Neogene terrestrial and lacustrine deposits, based on Williams (1939).

3. Geological Structure of the Manonga Basin

3.1. Central Part of the Manonga Basin

Nine sections, combining data from topographic maps (1:50,000), field and/or photogeological observations, and the results of detailed loggings of sections showing the limits of the stratigraphic units, allow a description of the structure of the central part of the Manonga basin. The locations of the sections are shown in Fig. 2, and the sections themselves are illustrated in Fig. 3. Three major features or events are indicated: the presence of a rather flat paleotopography between the low-lying Precambrian hills, prior to the deposition of the lake sediments; the nearly horizontal position of the Neogene strata; and the occur-

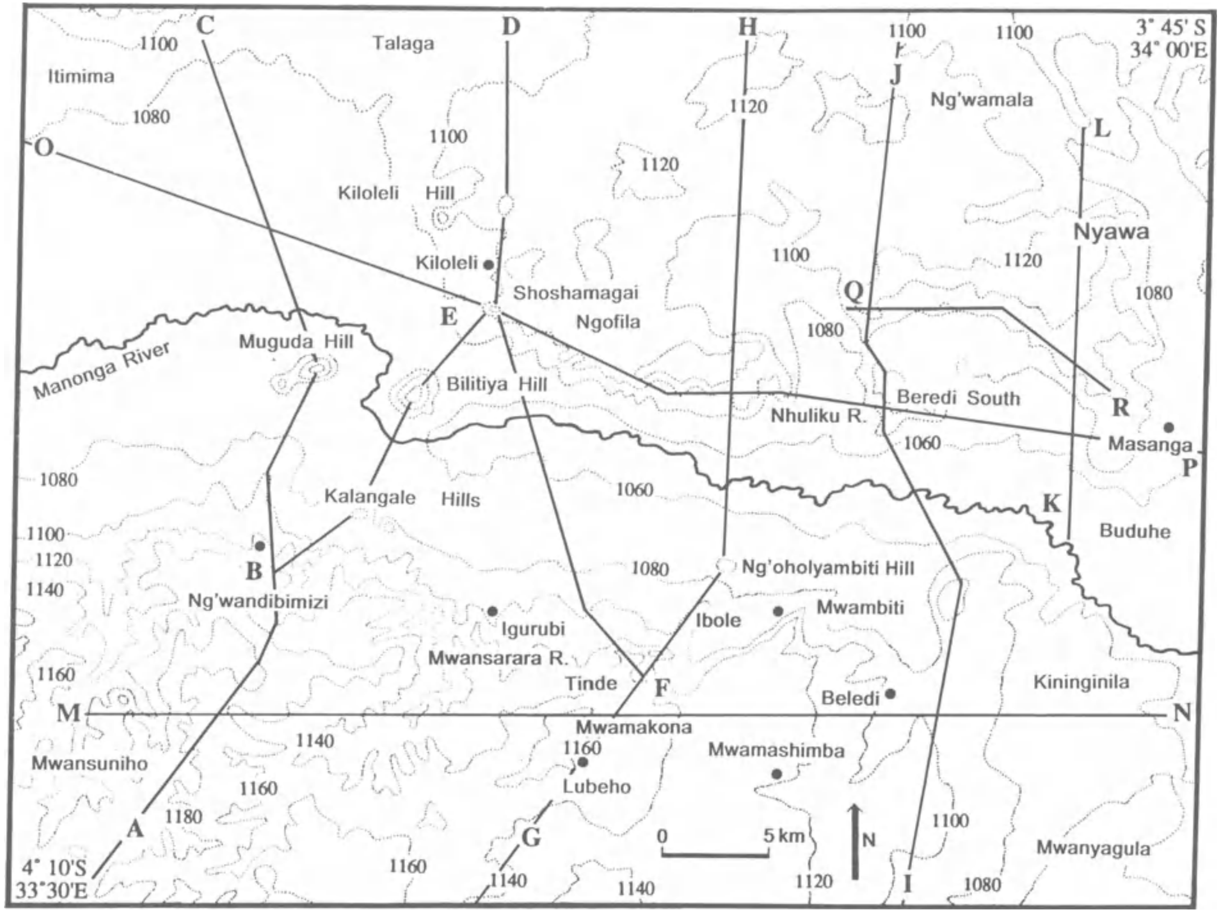
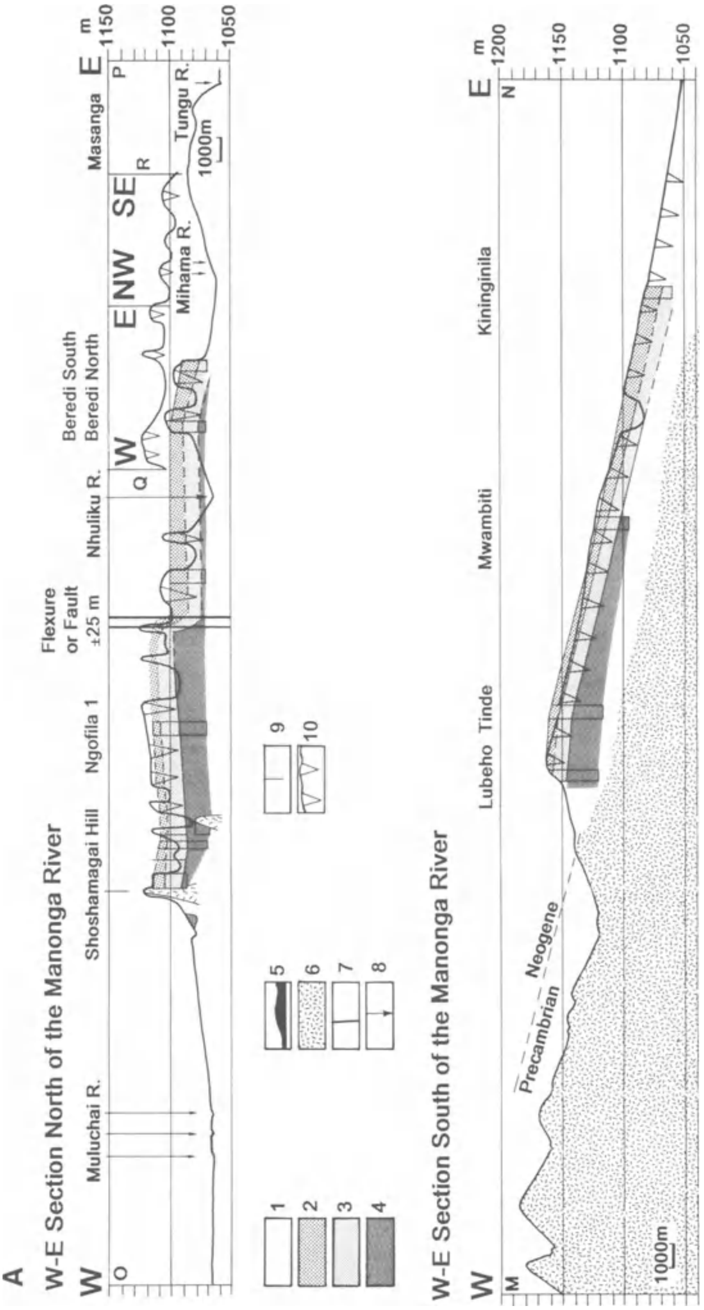


FIGURE 2. Schematic topographic map of the study area, with location of the topographic sections.


A
W-E Section North of the Manonga River
W
E
m
1150
1100
1050
O
Muluchai R.
Shoshamagai Hill
Ngofila 1
Flexure
or Fault
±25 m
Nhuliku R.
Beredi South
Beredi North
Q
W
E
NW
SE
Masanga
R
P
Mihama R.
Tungu R.
1000m
1
2
3
4
5
6
7
8
9
10
W-E Section South of the Manonga River
W
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Mwambiti
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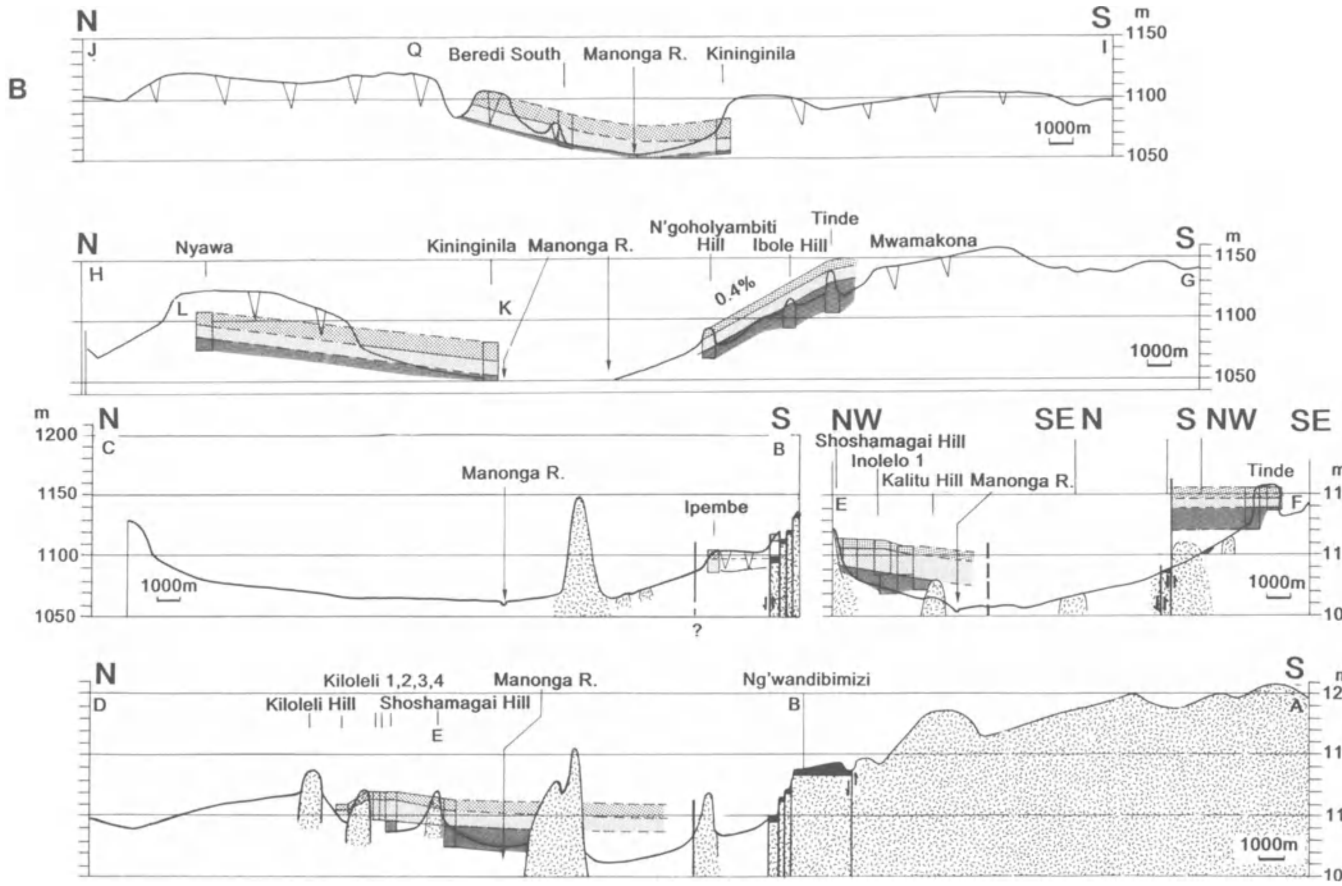


FIGURE 3. Topographic sections through the study area (for further explanation see section 3 of text); (A) sections M–N, O–P and Q–R in W–E direction; (B) sections D–B–A, C–B, E–F, H–G, L–K, and J–I in N–S direction. 1: Wembere–Manonga Formation undifferentiated; 2: Kiloleli Member; 3: Tinde Member; 4: Ibole Member; 5: Mwansarara Formation; 6: Precambrian rocks; 7: faults; 8: location of rivers in the section; 9: location of other topographic features; 10: cliffs, mesa, or cuesta scarps formed in Neogene sediments. In section M–N the unobserved unconformity between the Precambrian basement and the Neogene strata is marked by a blank zone.

rence of an important faulting event, subsequent to the deposition of the lake beds. Each of these is discussed in greater detail below.

A major feature of the area is the presence of Precambrian hills that are sometimes elevated above the Neogene lake beds. Two types of Precambrian outcrops occur. The first type comprises isolated and elevated hills reaching above the present-day surface exposures of the Neogene strata (i.e., Muguda Hill, Bilitya Hill, Kalangale School Hills). These are interpreted as remnants of permanent islands that emerged subaerially above the level of the Neogene paleolake. The second type of outcrop consists of flat hills, no more than 10 m in elevation, located in the bottom of the valley. These features are generally not identified by name on topographic maps. They may have formed low-lying islands, at least during the deposition of the lower units of the Wembere–Manonga Formation, but they were later submerged. Rapid facies change from conglomeratic and sandy deposits at the base of the Precambrian hills to clayey and silty sediments just a few hundred meters away from them confirms their identity as islands.

Another striking feature of the central part of the basin is the remarkable degree of horizontality of the Neogene sediments overlying the Precambrian substratum. As a result of erosion by the Manonga River system, principally during the Quaternary, the almost horizontal sediments are now exposed as prominent mesas. The strata indicate that the topography, prior to the formation of the lake, was an extensive and flat depression with isolated Precambrian hills, a consequence, presumably, of Miocene peneplanation (see Harrison and Mbago, this volume, Chapter 1). The mesa topography proves also, *de visu*, that the Archean Tanzania Craton (Lower Precambrian) behaved as a rigid and tectonically stable crustal unit, at least since the Miocene.

However, there is evidence to indicate that tectonic faulting occurred after deposition of the lake beds. Some very low dips in the lake beds, mostly less than 1%, were measured in the field (Fig. 4) or were deduced from the topographic sections. These allow the identification of six areas or blocks with slightly different dips. In addition, a distinct area within the center of the basin is formed by the Precambrian substratum (Fig. 7). The following units were defined by Harrison and Verniers (1993), but their limits and some of the dips are herein emended, following new observations in 1994: block A: Mwamakona–Kininginila block; block B: Igurubi–Mwansuniho area; block C: Ng'wandibimizi block; block D: Central Manonga Valley block; block E1: Kiloleli–Shoshamagai–Ngofila block; block E2: Nhuliku–Masanga block; block E3: Ng'wabulandi–Ng'wamala block.

The relative position of these blocks can best be appreciated by reference to the three east–west and the six north–south sections (Fig. 3) and to the schematic geological map (Fig. 7). The extreme vertical exaggeration of the sections (×50) serves to enhance the variation in the degree of dip of the Neogene strata.

The north–south sections (H–G and J–I) exemplify the variation in dip of the Neogene strata. The northern cliffs show a southward dip, while the southern cliffs show a northward dip. In these sections, the base of the Neogene strata at the center of the basin is estimated to lie up to 63 m below the same stratigraphic

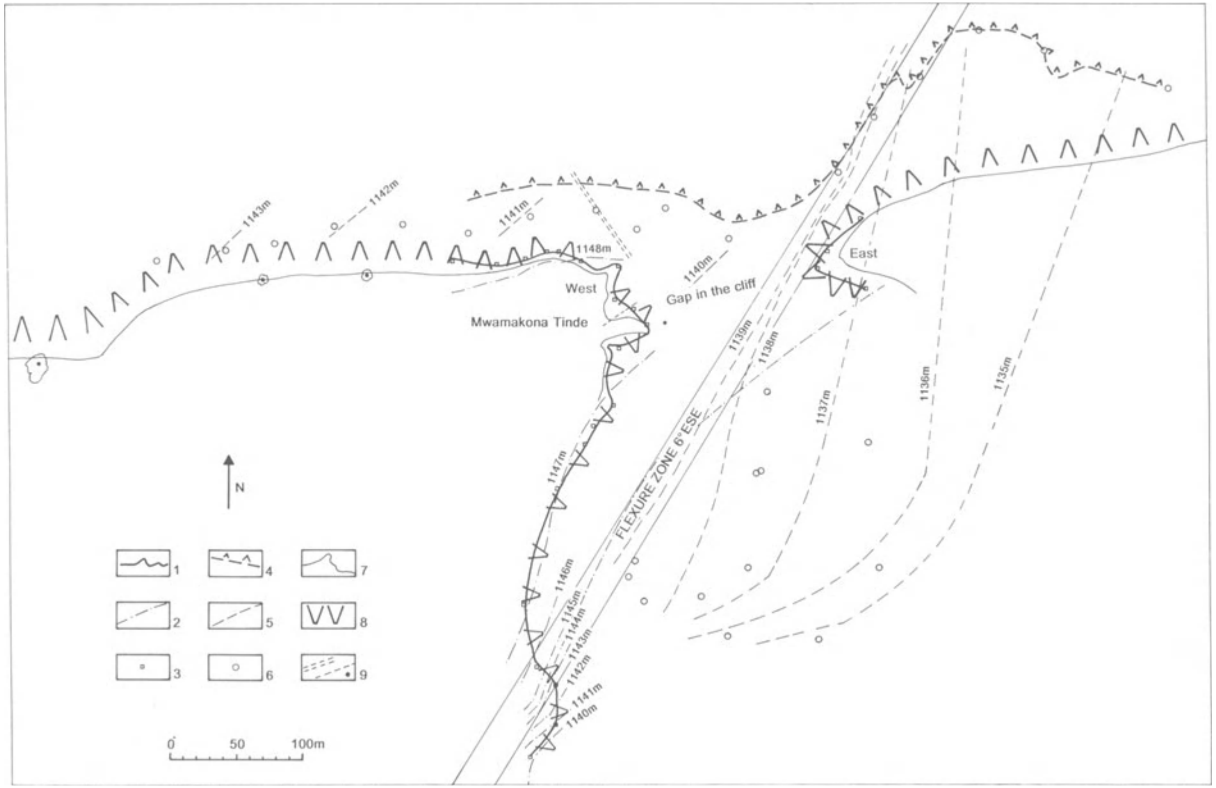


FIGURE 4. Detailed location map of the Tinde area with isohypses of boundaries between the stratigraphic units. The gentle dip to the E and SE is evident as is the flexure zone located at the gap in the cliff with a vertical downthrow of 3.5 to 1.5 m. 1: outcrop of the red soil covering the Tinde bone-bed; 2: isohypses of the top of the same red soil; 3: points of topographic measurement of the same level; 4: top of the small cuesta front formed by the Ibole Member; 5: isohypses of the top of the Ibole Member (red soil and white calcareous nodule level); 6: points of topographic measurement of the same level; 7: top of the prominent cuesta front formed by the Tinde and Kiloleli Members; 8: cuesta front itself formed by a steep hill; 9: road, footpath, and datum point.

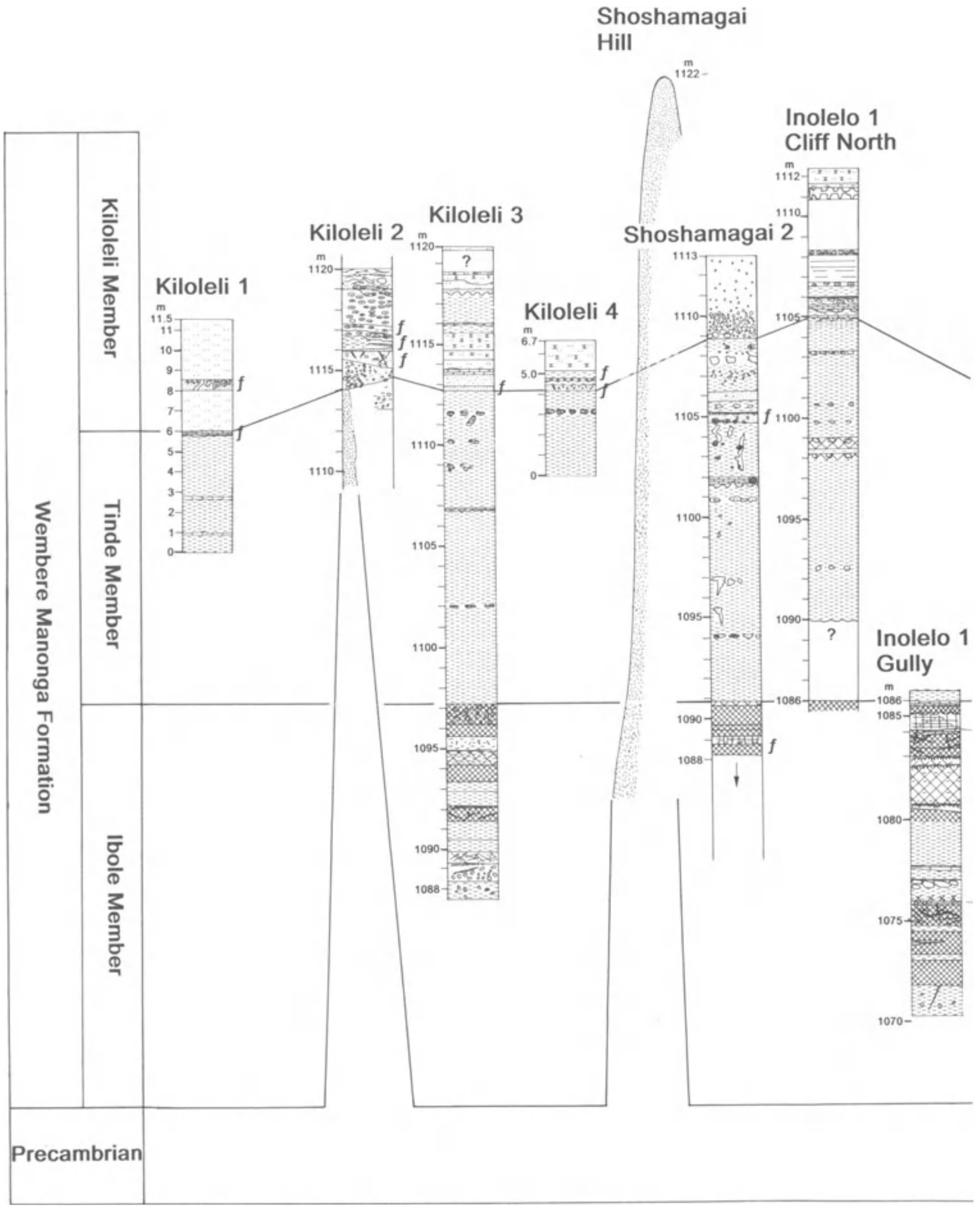


FIGURE 5. Correlation table of detailed stratigraphic columns and lithostratigraphy in the Tinde area and surroundings. 1: olive-colored swelling clay; 2: silt; 3: sand with lenses of coarse sand and fine conglomerate; 4: limestone layer and calcareous sediment; 5: fossil bone or mollusk; 6: calcareous nodule or fissure infilling; 7: calcareous siltstone nodule; 8: fossil level; 9: iron oxide–rich bed; 10: undescribed ferruginous level; 11: calcareous nodule level; 12: ferruginous level (e.g., minor ferruginous level); 13: iron oxide staining of sediment; 14: uncertain lithology or thickness; 15: Precambrian rocks. The heights are in meters above sea level, except for Kiloleli 1, Kiloleli 4, and Bukawa, where height is measured above the base of the outcrop.

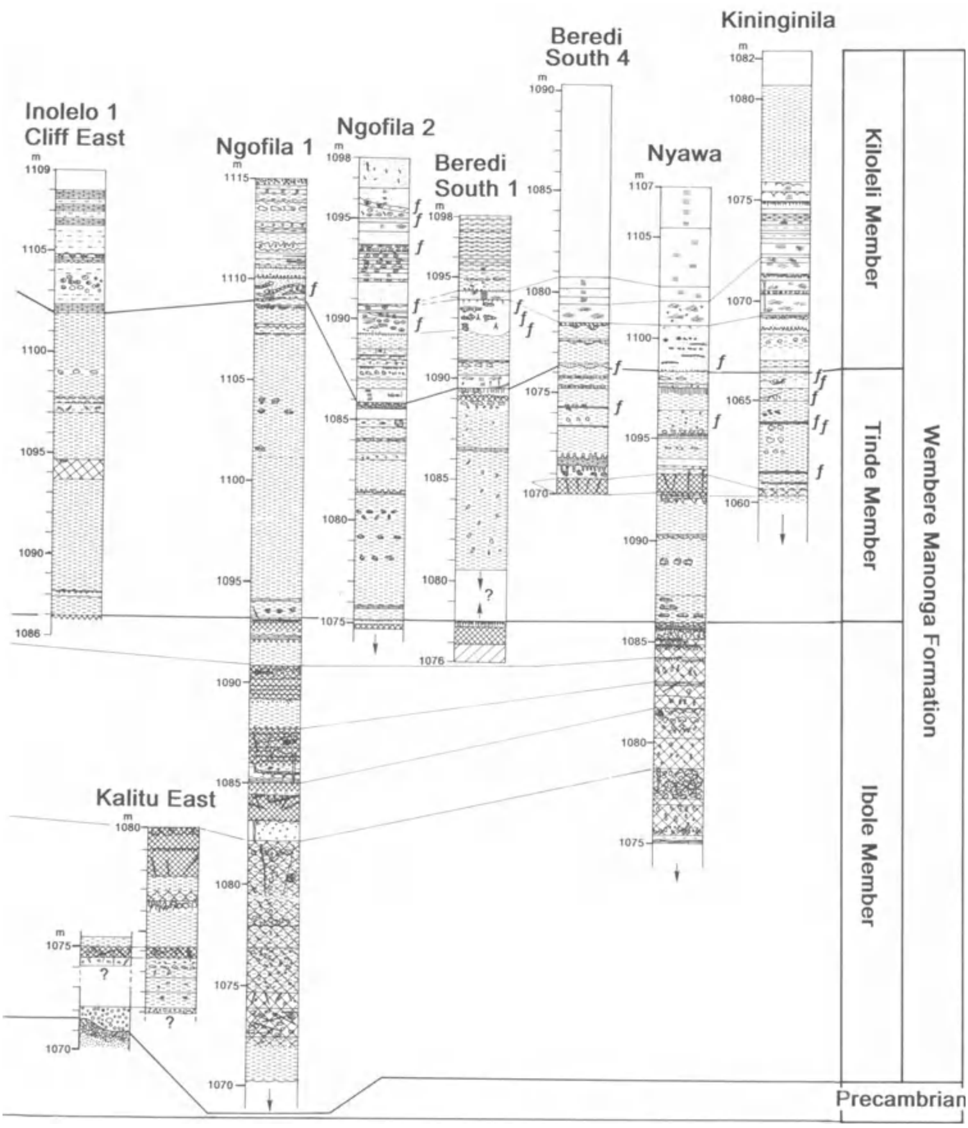


FIGURE 5. Continued

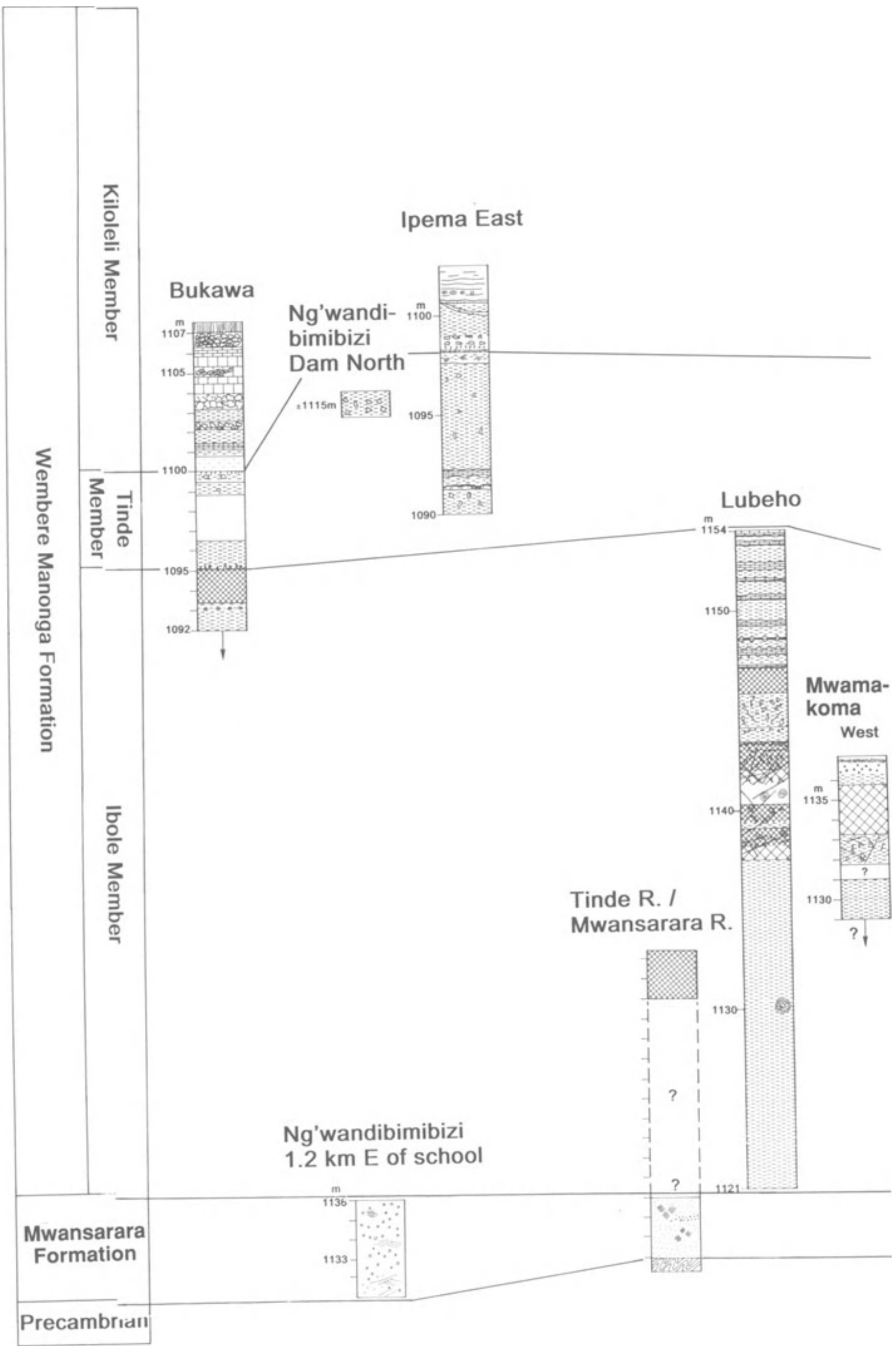


FIGURE 5. Continued

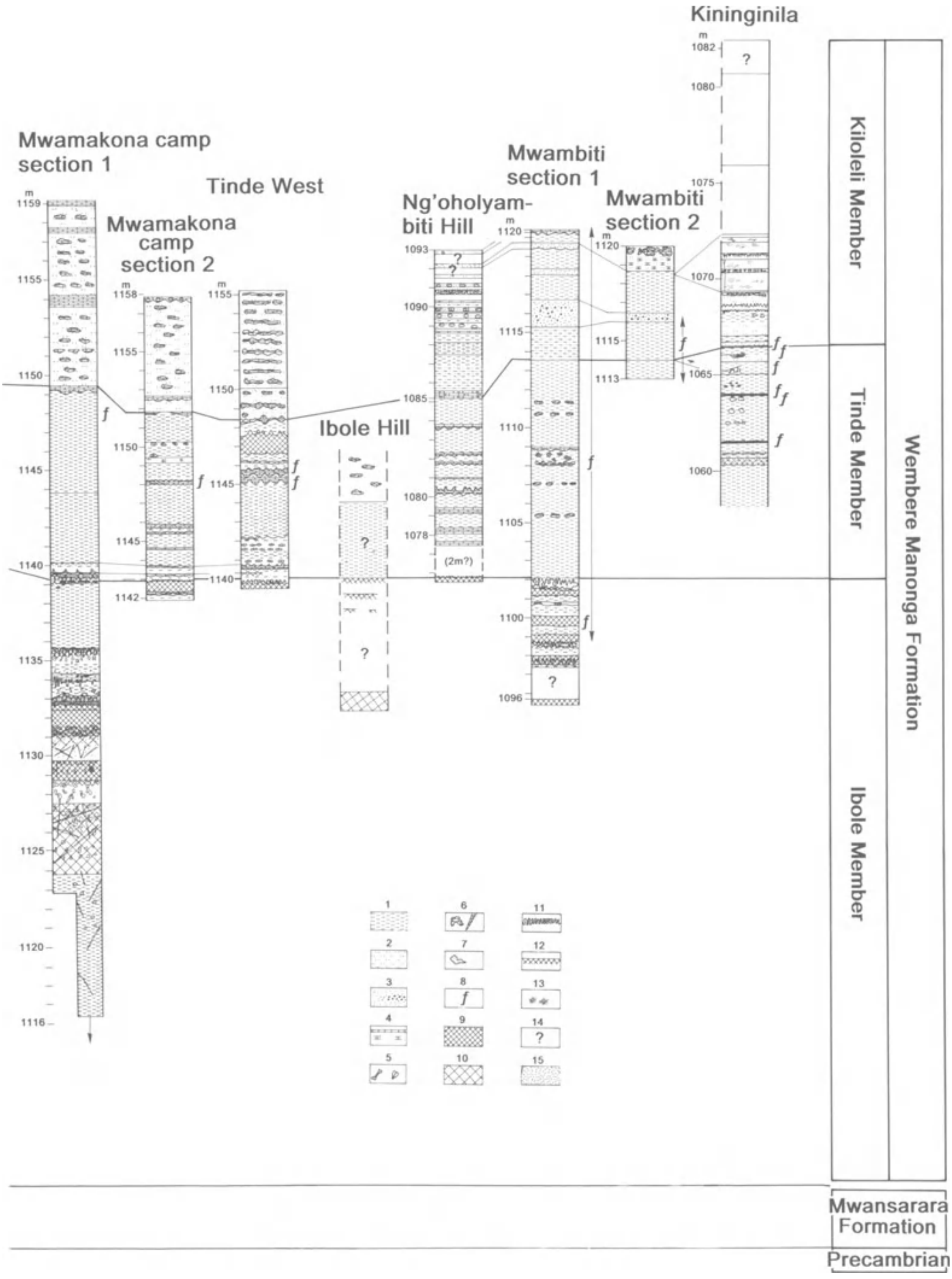


FIGURE 5. Continued

horizon in the north and south. In west–east sections (sections O–P, Q–R, M–N), the strata in the northern blocks are essentially horizontal, except for some slight flexures (section O–P), while in the southern blocks they dip monoclinally to the east (section M–N). The disposition of the Neogene sediments of the northern blocks in relation to those of the southern blocks can be explained only by the presence of a fault or a set of faults close to the line followed by the Manonga River.

In the two southern blocks, the Neogene strata, which dip about 0.3° to the east-south-east in block A, cover the Precambrian basement that outcrops in block B to the west (sections H–G, J–I, and M–N, Figs. 3 and 7). In block A the prominent cliff is noticeably lower toward the east. In section M–N the Neogene strata cover the Precambrian, which outcrops in block B.

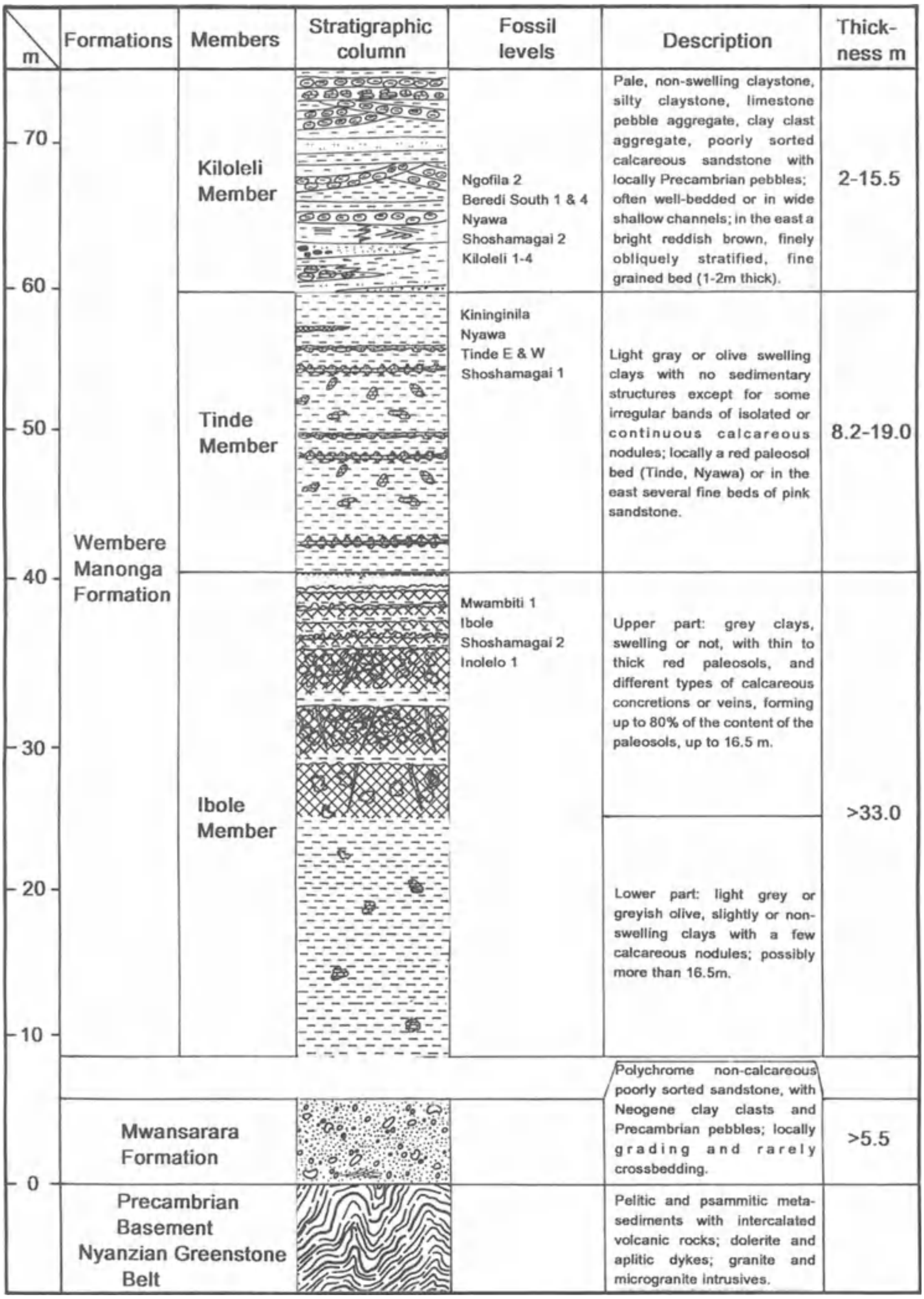
Within block A slight warping and flexures have been identified. In the vicinity of Tinde, detailed mapping and leveling of marker horizons indicate the presence of a gentle flexure zone, about 25 m wide, oriented N31°E, with an eastern downthrow of about 2.0 m to 3.5 m (Fig. 4). An east–west lineament between Ibole and Ng'oholyambiti Hill, north of block A, might be the trace of a fault. However, this could not be confirmed in the field, because suitable outcrops are lacking.

As deduced from aerial photographs, geological maps, and field observations in the area of Igurubi, block B is characterized by Precambrian rocks partly covered by a thin layer of Quaternary sediments. Reaching altimetrically to more than 1200 m, it is the highest block in the study area. Its surface is strongly incised, and it is covered by woodland. This block is limited to the north by a series of east–west directed step faults with a downthrow of at least 50 m. The step faults are observed in the field, with the Mwansarara Formation in the area being disrupted by three faults over a distance of about 200 m, with a total downthrow of more than 38 m (section A–B–C). The downthrow along the fault decreases toward the east, changing into a flexure.

Just north of this fault, block C contains Neogene sediments in mesalike features of different heights, separated by a series of stepfaults. North of the lowermost mesa there is no evidence of faulting. The height of the latter is about the same as the general surface in block E1 to the north.

Block D represents the bottom of the paleolake with most of the lacustrine sediments eroded away, except for the more resistant lowermost horizons (i.e., the Ibole Member, see below). Sections J–I and H–G show the dip of the Neogene deposits in this block northward toward the Manonga River, possibly indicating faults to the north and south of the block.

In the three northern blocks, E1, E2, and E3, the Neogene strata either lie horizontally or dip toward the Manonga River. In blocks E2 and E3, no Precambrian hills emerge through the Neogene strata, but in block E1 the Neogene lake sediments occur between Precambrian islands (sections D–E–B, E–F, and O–P). Field observations show the presence of beach deposits of limited extent around the islands, grading rapidly (in less than 100 m) into fine, deeper lake sediments. In block E2, the Neogene sediments dip slightly toward the Manonga River, as can be deduced from sections H–G, J–I, L–K, O–P, and Q–R. In block E3, the beds



Formations	Members	Stratigraphic column	Fossil levels	Description	Thickness m
Wembere Manonga Formation	Kiloleli Member		Ngofila 2 Beredi South 1 & 4 Nyawa Shoshamagai 2 Kiloleli 1-4	Pale, non-swelling claystone, silty claystone, limestone pebble aggregate, clay clast aggregate, poorly sorted calcareous sandstone with locally Precambrian pebbles; often well-bedded or in wide shallow channels; in the east a bright reddish brown, finely obliquely stratified, fine grained bed (1-2m thick).	2-15.5
	Tinde Member		Kininginila Nyawa Tinde E & W Shoshamagai 1	Light gray or olive swelling clays with no sedimentary structures except for some irregular bands of isolated or continuous calcareous nodules; locally a red paleosol bed (Tinde, Nyawa) or in the east several fine beds of pink sandstone.	8.2-19.0
	Ibole Member		Mwambiti 1 Ibole Shoshamagai 2 Inolelo 1	Upper part: grey clays, swelling or not, with thin to thick red paleosols, and different types of calcareous concretions or veins, forming up to 80% of the content of the paleosols, up to 16.5 m.	>33.0
				Lower part: light grey or greyish olive, slightly or non-swelling clays with a few calcareous nodules; possibly more than 16.5m.	
Mwansarara Formation				Polychrome non-calcareous poorly sorted sandstone, with Neogene clay clasts and Precambrian pebbles; locally grading and rarely crossbedding.	>5.5
Precambrian Basement Nyanzian Greenstone Belt				Pelitic and psammitic meta-sediments with intercalated volcanic rocks; dolerite and aplitic dykes; granite and microgranite intrusives.	

FIGURE 6. General lithostratigraphy of the Neogene sediments in the study area.

of the Neogene are nearly horizontal, or dip slightly to the east, as inferred from sections G–H, I–J, and K–L.

3.2. Section through the Manonga Basin

Detailed study of the geology in the central part of the basin, in conjunction with isolated observations in the vicinity of Igunga and Shinyanga, allow the reconstruction of a northwest–southeast section, 120 km long (Fig. 8). The section is incomplete because of lack of information in several areas. Nevertheless, the available evidence is sufficient to demonstrate that one of the most prominent features of the lake basin is a fault or fault zone close to the Manonga River, with a downthrow of about 60 m, separating two southeast-dipping blocks. This observation, together with the recognition of faults through the Tinde Member at Tinde, and through the Mwansarara Formation at Ng'wandibimizi, are clear proof of a major phase of tectonic faulting subsequent to the deposition of the Wembere–Manonga Formation.

This faulting is probably related to the development of the Eyasi and Wembere grabens at the southern tip of the Eastern Rift. Its southward prolongation was limited by the rigid Archean Tanzania Craton. North of Lake Eyasi the earliest volcanism linked with the rifting is dated at 4.32 Ma (Drake and Curtis, 1987). This could fit with the age of the youngest lake beds in the Kiloleli Member, which, based on faunal correlations, are estimated to be about 4.0 Ma (see Harrison and Baker, this volume, Chapter 13). The Manonga Valley could, therefore, represent an aborted graben, a third branch of the Eyasi–Wembere graben system, with minimal downthrow in relation to the much larger downthrows of both the Eyasi and Wembere grabens.

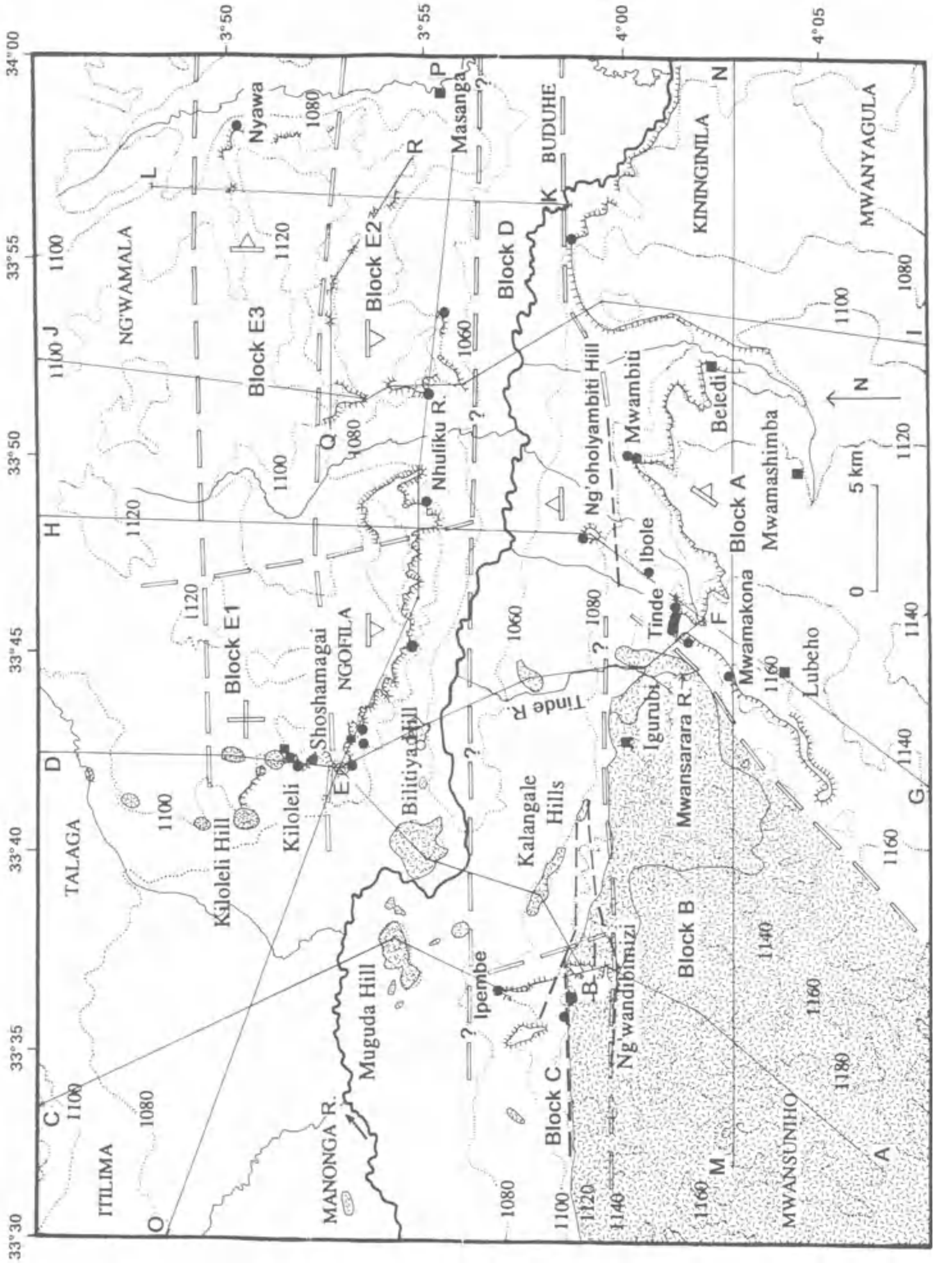
4. Stratigraphy

The stratigraphy of the central part of the Manonga basin was studied in 1990 at 12 localities near Tinde, Ibole, Mwambiti, and Kiloleli, and in 1994 at 20 localities in the vicinity of Ipembe, Ng'wandibimizi, Ibole, Kiloleli, Shoshamagai, Inolelo, Kalitu Hill, Ngofila, Beredi South, Nyawa, and Kininginila. In addition, locations at the periphery of the paleolake were studied in two main areas: around Shinyanga in the northwest and around Igunga in the southwest of the basin.

By measuring topographic sections with a transit (stepped leveling), bed thicknesses were calculated or inferred, following correction for dip, and a partly composite stratigraphic column was constructed. The detailed field description

→

FIGURE 7. Schematic geological map of the study area, with indication of the structural blocks, their dips and limits (in open large broken lines), the Precambrian islands or outcrop area (stippled areas), the major cliffs with outcropping Neogene lake beds (comblike line), the location of sections (black circles), villages (black squares), and the lineaments interpreted as faults (thick broken lines).


34°00
3°50
3°55
4°00
4°05
33°55
33°50
33°45
33°40
33°35
33°30
NG'WAMALA
Block E3
Block E2
Block E1
Block D
Block C
Block B
Block A
NGOFILA
TALAGA
ITILIMA
MANONGA R.
BUDUHE
KININGINILA
MWANYAGULA
MWANSUNIHO
Nyawa
Masanga
Nhuliku R.
Kiloleli Hill
Kiloleli
Shoshamagai
Bilitiya Hill
Kalangale Hills
Muguda Hill
Ipembe
Ng'wandibimizi
Mwansarara R.
Igurubi
Tinde R.
Tinde
Ibole
Ng'oholyambiti Hill
Mwambiti
Beledi
Mwamashimba
Mwamakona
Lubeho
A
B
C
D
E
F
G
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J
K
L
M
N
O
P
Q
R
?
0
5 km
N
1060
1080
1100
1120
1140
1160
1180

for each stratum included the thickness, color (determined by the standard soil color charts of Oyama and Takehara [1970]), lithology, estimated granulometry and sorting, (post-)sedimentologic structures, and diagenetic features. In total about 512 m of sections were recorded. The fossil-bearing levels were precisely located in the columns (Fig. 5).

Based on these columns, photogeology, and other field data obtained in 1990, a preliminary lithostratigraphy was defined for the first time in the study area by Harrison and Verniers (1993; Fig. 6). Results from the 1994 field season have confirmed that the proposed lithostratigraphy generally applies to other areas in the Manonga basin. The additional sections allow a more complete definition of the units and their lateral variations. However, some minor changes in the lithostratigraphy are introduced here.

Further analysis of the Ibole Formation (see Harrison and Verniers, 1993), for example, showed that it was very similar in facies to the Wembere–Manonga Formation. Hence, the Ibole Formation is here reduced in rank to that of a member, and it is included here as the lowermost stratigraphic unit of the latter formation. Furthermore, the distinction between the Ibole and Mwambiti Members has proved difficult to maintain in the light of new evidence from additional sections and observations. The Mwambiti Member is, thus, incorporated into the Ibole Member, the latter of which, when redefined, therefore, continues higher in the stratigraphy. The two thickest measured sections are 45 m and 43 m thick (i.e., Ngofila 1 and Mwamakona Camp section 1, respectively). Adding the maximal observed thickness of each of the three members of the Wembere–Manonga Formation gives a maximum of 66 m for the entire formation (Fig. 6).

5. Lithostratigraphy

This section provides more detailed information on the lithostratigraphy of the Manonga basin. All stratigraphic units previously defined or mentioned in the literature are critically evaluated in relation to the present findings, and based on the recommendations of the *International Stratigraphic Guide* (Hedberg, 1976).

5.1. Mwansarara Formation

5.1.1. Historical Background

Previous studies do not describe this formation in the study area, but similar strata, possibly belonging to the widespread blanket of Neogene continental sediments, were described in other areas, under various informal and formal names: “terrestrial deposits of pre-rifting age” (Teale, 1931); “cement” (Teale 1931; Grantham *et al.*, 1945); “Kilimatinde Conglomerate” (Krenkel, 1925); “Kilimantinde Cement in the Singida region” (Teale in Wade, 1937); “cements” (Wade and Oates, 1938; Eades and Reeve, 1938); “Tertiary terrestrial deposits” (Williams and Eades, 1938); “superficial deposits” (Williams, 1939). The Mwansarara Formation was formally proposed and defined by Harrison and Verniers (1993; see also Harrison *et al.*, 1993).

5.1.2. Description of the Stratotype

The stratotype occurs as outcrops in the Mwansarara River bed, an eastern tributary of the Tinde River, 150 to 350 m upstream from its confluence.

The outcrops are of medium sandstone, very poorly sorted; grains are from fine to coarse, mainly quartz, with some Precambrian fragments, and pink and black minerals, sometimes with subelongated pebbles of mostly quartz (3–25 mm in diameter), laterite pebbles (2–20 mm in diameter), and clay nodules. Colors on dry pieces are light gray (7.5Y7/1 to 8/2) to light green, with large mottles unrelated to recent cracks, yellowish orange (10YR7/8), bright brown (7.5YR5/6), red (10R4/8), and reddish brown (2.5YR4/8). Sometimes bedding is visible, in which subhorizontal layers of pebbly sand alternate with coarse sandy beds. Maximal thickness in the stratotype is 2.5 m. The surface of the outcrops display an irregular, large "cerebrumlike" form. At the stratotype, one sees the formation unconformably overlying the weathered or unaltered Precambrian basement.

5.1.3. Regional Variations

A further outcrop is visible over a distance of 300 m along the Tinde River bed. It is located in a north–south directed paleo-depression or valley, situated between Precambrian hills, close to a complex of water holes also known as Tinde. The formation is also observed between Igurubi and Ng'wandibimizi, where more than 5.5 m of sediments cover the Precambrian rocks. Polychrome pale yellow, bright brown to dark reddish brown, poorly sorted sandstones alternate with conglomerates, which include subelongated to rounded pebbles (0.5–22 cm in diameter) derived from the Precambrian, and cemented with a red matrix. Rare cross-bedding is found at the base of the unit, and irregular or tubular nodules occur higher up. Extensive outcrops of the formation have also been identified at the Mwamapuli Dam, south of Igunga. These comprise bright reddish brown conglomerates with rounded, elongated, to spherical pebbles (2–15 cm in diameter) derived from the Precambrian, alternating with light gray, yellowish, and brownish, very poorly sorted noncalcareous sandstones.

5.1.4. Geological Age

The sediments of the Mwansarara Formation cover, in many places, a supposedly early Miocene peneplain on the Precambrian basement (Grantham *et al.*, 1945). In the central area, the sediments are found only on top of, or close to, block B, not more than a few hundred meters away, and sometimes deposited in what are clearly remnants of paleo-valleys. Block B was evidently elevated land, either directly linked with the mainland or a large island on the lake. Similarly, around Igunga the formation was observed only on top of, or very close to, large Precambrian islands or the mainland. These few observations seem to indicate a possible occurrence in which the deposits fringe the Wembere–Manonga paleolake. Topographic and altimetric observations show that the formation follows the same irregular contours as the Wembere–Manonga Formation. Faults occurring through the Mwansarara Formation certainly confirm a prefaulting age for deposition. However, its stratigraphic relationship to potentially superpositional units, such as the Wembere–Manonga Formation, is still uncertain, because of the lack of direct observations of contact. Hence, two alternative inferences concerning relative stratigraphic position and age of the Mwansarara Formation are possible: (1) It is a stratigraphic unit of undifferentiated Miocene age underlying the Wembere–Manonga Formation or (2) it is a lateral facies of the Wembere–Manonga Formation produced along the shoreline of the paleolake, with an equivalent age of latest Miocene to earliest Pliocene. The latter interpretation is tentatively favored here.

5.2. Wembere–Manonga Formation

5.2.1. Historical Background

As discussed above, the lacustrine deposits that cover a large part of the Manonga basin were first discovered at Tinde by Grace in 1929. This unit was accurately defined and described by Stockley (1930; summarized in Grace and Stockley, 1931), which is not the case for many of the other Neogene units of the area assigned by subsequent authors.

Geologists mapping the area between 1930 and 1957 observed that the lacustrine calcareous facies, referred to as "tuffaceous" or "travertine," are present only in the central part of the Manonga basin. At the margin of the basin are sandy facies that have been interpreted as possibly more littoral in origin.

Teale (1931) described "flat-lying, grey, sandy marls, clays and limestone bands, much dissected by valleys and up to 300 ft in depth," without providing a name for these deposits. The following year Teale described "extensive marly lacustrine strata . . . in the Manonga valley," without giving further details (Teale, 1932). Subsequent authors accepted the foregoing statements as the definition for the "Man(y)onga Lake Beds" (e.g., Quennell *et al.*, 1956, 1957).

The "Manonga–Wembere lake deposits or lake-beds" is the name given by Williams and Eades (1938), with no specified stratotype, although these authors mention two places where the gradational facies between marls and sands could be observed. They described the calcareous facies as marls; it appeared not "to have extended to the shores of the lake, the deep embayments being filled mainly with sandy littoral facies". . . sometimes difficult to distinguish from earlier terrestrial deposits. "Gradational facies between the marls and the sands may be best seen on the Tungu and the Mango rivers" (Williams and Eades, 1938, p. 8). Williams and Eades (1938, p. 9) identified Tertiary terrestrial deposits as underlying units, sediments that are elsewhere called cements. No capping units were recognized, and these authors supposed that subsequent to the deposition of lake sediments a period of laterization occurred. This conclusion is not supported by the present study, mainly because lake beds are seen to overly the thick red soils of the Ibole Member.

Williams and Eades (1938) provide a geological map of the Shinyanga Region showing a reconstruction of the maximum extent of the lacustrine sediments, but exclude, without explanation, outcrops of travertine and gray calcareous loams north of Mwadui (see Fig. 1). They also extend the marls to the east and south, toward the western end of Lake Eyasi, and along the western side of the Wembere depression. They further discuss the presence of the deeper and marly facies in the central part of the Manonga basin and a sandy facies closer to the inferred shoreline. The marly facies reach heights of 3730 ft (1137 m) and sandy facies up to 3800 ft (1158 m). Our observations indicate an even greater height of the marly facies at 1160–1165 m, 7 km south-south-east of Igurubi along the Igurubi–Igunga road.

In the summary of the geology of Tanzania by Quennell *et al.* (1956, 1957), the poor definition of the formation by Williams and Eades (1938) was favored over the well-defined Tinde beds by Stockley (1930). Williams (1939) accurately mapped unnamed "Tertiary and Pleistocene terrestrial and lacustrine sediments" (Fig. 1). Subsequent workers also observed this unit, and proposed several names such as "terrestrial lake-shore accumulations" (Grantham *et al.*, 1945), "lacustrine deposits of Manyonga–Wembere" (Handley, 1956), and "lacustrine deposits of Manyonga–Wembere" (Handley and Harpum, 1956).

Widespread, unnamed red soils and laterites, purportedly of Neogene age, have been described in other areas of Tanzania. These include "red clays on the Iramba plateau" (Eades, 1936), "lateritic ironstone that mantles some part of the country" (Williams and Eades, 1938), "lateritic ironstone" (Eades and Reeve, 1938), "red soils over much of the country around Shinyanga, generally over Tertiary deposits" (Williams, 1939), and "red laterite covered surfaces and valley bottoms with red soils" (Grantham *et al.*, 1945). Harrison and Verniers (1993) described comparable red soils on clays from the Manonga Valley, and these were defined as the Ibole Formation (see also Harrison *et al.*, 1993). However, this unit is here reduced in rank to a member of the Wembere–Manonga Formation.

The Wembere–Manonga Formation was formally defined and subdivided into three members (i.e., the Mwambiti, Tinde, and Kiloleli) by Harrison and Verniers (1993, see also Harrison *et al.*, 1993). In this present study, the Mwambiti Member and the Ibole Formation are grouped into a single unit: the Ibole Member.

5.2.2. Stratotype

The stratotype of the formation is not defined as such, as it consists of the succession of stratotypes of its constituent three members: (1) Ibole Member: the steep gullies, 250–500 m north of the Mwamakona cliff, and in the flanks of the promontory to the west of these gullies, 1–3 km west and west-south-west of the village of Ibole (Mwamakona Camp section 1, in Fig. 5); (2) Tinde Member: the sections west of the gap in the cliff, called Tinde by Grace and Stockley (1931), but presently within the confines of the village of Mwamakona, Igunga district, and at 6 km southeast of the locality of Tinde (Tinde, in Fig. 7; section Tinde West, Mwamakona, in Fig. 5); (3) Kiloleli Member: the cliffs at Kiloleli 2 and 3, just south of the village of Kiloleli, where the calcareous clay is locally used for brick-making (Figs. 1, 7, and section Kiloleli 3 in Fig. 5).

5.2.3. Description of the Wembere–Manonga Formation

The formation consists of lake deposits, with deep marly facies in the central part, divided into three members. The lithology consists mainly of swelling clays in the lower and middle members, and silt and nonswelling clays in the upper member. Red soils occur often in the lower member, while alternating layers containing calcareous nodules occur in all three members. Fossils have been recovered *in situ* from at least six horizons: two in the upper part of the lower member, two in the middle member, and two at the base of the upper member. The contact with the underlying Mwansarara Formation is not observed, and contact with the Precambrian basement is only visible at Kalitu Hill (see below). The upper boundary is unknown because the formation usually represents the eroded surface of the modern-day landscape.

At the margin of the Manonga basin, we have observed the Wembere–Manonga Formation only south of Igunga and north of Shinyanga. In the latter area olive swelling clays alternate with impure clays containing feldspar and quartz grains, coarse sandy clays, and limestone pebble aggregates. These sediments often contain large, dispersed, and irregular calcareous nodules, indicating periodic desiccation. This clayey facies occurs up to 600 m from the Precambrian hill near Old Shinyanga. South of Igunga, limestone quarries that penetrate the Wembere–Manonga Formation show light gray irregularly bedded and faintly laminated limestone, at least 6.5 m in thickness. The marly facies is present up to about 500 m distant from large Precambrian hills nearby. Therefore, the occurrence of sandy littoral facies over a wide area fringing the margin of the paleolake, reported by previous workers, was not observed in these two representative areas. In this case, it is possible that the Mwansarara Formation, with sands and conglomerates laid down in a narrow strip never more than 1 km wide, fringing the shoreline of islands and the lake itself, could be the littoral, lateral facies of the Wembere–Manonga Formation. However, this cannot as yet be resolved, because the exact stratigraphic relationship between the Mwansarara Formation and the Wembere–Manonga Formation is unobserved (see above for further discussion of this issue).

The preliminary study on the mineralogy of the sediments by Mutakyahwa (this volume, Chapter 3) indicates that the sediments are volcano-sedimentary in origin. They were derived from a direct or indirect volcanic source, and additionally from the weathering of Precambrian rocks surrounding the paleolake. Much of the CaO in the calcareous nodules could be derived from the weathering of volcanic glass in the volcano-sedimentary rocks.

Ibole Member. The lowest unit of the Wembere–Manonga Formation is a distinctive and clearly visible unit that outcrops in the floor of the Manonga Valley, and that follows the paleotopography. It comprises two parts. The upper portion consists of up to 16.5 m of red clayey beds, strongly cemented, mostly by different types of calcareous nodules or veins. Reddening occurs in at least three thick clay beds (up to 3.5 m thick), as well as several thinner beds. These calcareous red beds vary considerably in thickness as they extend laterally. However, locally the degree of red coloration and the amount, type, and size of the calcareous concretions are characteristic of beds that can be traced over several kilometers. The colors vary from red (10R4/8), reddish orange (10YR6/6, 7/8), orange (2.5YR7/4, 7/6, 6/6), dull orange (7.5YR7/3), bright reddish brown (2.5YR5/8), reddish brown (2.5Y4/2), to dark reddish brown (2.5YR3/6).

The lower part of the Ibole Member consists of up to 16.5 m of slightly swelling or nonswelling clay, with dispersed silt and fine sands, grayish olive and light gray in color (5Y6/2 to 8/1), with relatively few white round calcareous concretions or veins. The lower boundary is unknown, because its base is always covered by Holocene mbuga or other clays, except at Kalitu Hill, where the sediments are observed to cover the sides of a Precambrian inselberg. However, it is possible that sedimentation began earlier, at some distance from the inselberg. The member was described in 20 profiles (Fig. 5), with a total thickness of 0.5 to 31.5 m, and comprising 20.5 m of red beds above and 16.5 m of gray clays below.

Tinde Member. The middle unit of the formation was originally described by Stockley (1930), Grace and Stockley (1931), and Quennell *et al.* (1956, 1957), and has subsequently been redefined by Harrison and Verniers (1993; see also Harrison *et al.*, 1993). Although the type locality is presently situated within the confines of the village of Mwamakona (Igunga District), the name Tinde is used for historical reasons, because it was the name given to the site by Grace and Stockley (1931; see Harrison and Mbago, this volume, Chapter 1, for a fuller discussion of this subject). The member was described in 11 profiles (Fig. 5), with a thickness of 8.2 to 19.0 m (at Inolelo 1). It consists typically of light gray (5Y8/1, 7/2) to pale yellow (2.5Y8/3, 5Y7/3) swelling clay, slight to noncalcareous, with several levels of large irregular calcareous nodules, more or less continuous or dispersed. No sedimentary structures are observable, but if originally present, they may have been destroyed by the mechanical action of the swelling clays, as indicated by the presence of some laminated clay occurring within a calcareous nodule close to Shoshamagai. Locally at Tinde, Nyawa, Beredi South, and Kininginila a red bed occurs (2.5YR7/4, 6/6 pale reddish orange and dull orange), possibly at the same stratigraphic level or close by. In the eastern part of the basin, some thin layers (just a few centimeters thick) of pinkish (gravelly) sandstone occur.

The Tinde bone-bed defined by Stockley (1930) and Grace and Stockley (1931) is considered a local marker bed of the Tinde Member by Harrison and Verniers (1993). It can be described as a lacustrine clay deposit with a dense bone accumulation. Postsedimentary calcareous infilling of desiccation cracks in the clay protected the bones against mechanical destruction and dissolution in the swelling clays. Locally, a red coloration occurs 1.0 to 1.5 m above the bone-bed, and this is possibly diagenetically related to the calcareous layer.

Kiloleli Member. The upper unit of the formation was formerly referred to as "sandy marls and limestone" (Teale, 1931), "extensive marly lacustrine strata"

(Teale, 1932), "marls . . . calcareous facies" (Williams and Eades, 1938), "travertine outcrops and grey calcareous loam" (soil map of Williams and Eades, 1938), "sediments of proto-Lake Victoria (Igurubi limestone) . . . in the Igurubi cliff" (legend of the geological map by Barth, 1989). The member is observed in 22 sections, with a thickness ranging from 2.0 to 15.5 m (at Kininginila). It consists of several types of sediments: indurated nonswelling claystones and silty claystones, but also limestone pebble aggregates, clay clast aggregates and conglomerates, and poorly sorted calcareous sandstones with small Precambrian pebbles at its base. The beds are well stratified, decimetric or pluridecimetric, often in channels a few to tens of meters wide, and 0.1 to 0.5 m deep. In the eastern part of the basin, midway in the sequence, the member contains a ± 2-m-thick, obliquely stratified bed, well indurated, with a characteristic bright reddish brown to pale yellow color (5Y5/6, 5Y8/3). Its volcano-sedimentary origin has been noted by Mutakyahwa (this volume, Chapter 3).

5.2.4. Geological Age

Hopwood (1931) initially suggested a Pleistocene age for the Tinde bone-bed, after studying the fossil mammals collected by Grace and Stockley. However, restudy of this fauna, and comparisons of the mammalian fauna discovered since 1990 with well-dated East African sites, suggests that the age of the Wembere–Manonga Formation is late Miocene to early Pliocene (Harrison and Verniers, 1993; Harrison *et al.*, 1993; Harrison and Baker, this volume, Chapter 13). More specifically, the data suggest a latest Miocene to earliest Pliocene age for the upper part of the Ibole Member (ca. 5.0–5.5 Ma), and an early Pliocene age for both the Tinde member and lower part of the Kiloleli Member (ca. 4.0–5.0 Ma) (for details see Harrison and Baker, this volume, Chapter 13).

5.3. Post-Wembere–Manonga Paleolake History

Although this study has focused primarily on the Miocene and Pliocene deposits in the Manonga basin, several local observations and regional considerations allow some conclusions concerning the subsequent history of the basin during the Quaternary. Firstly, some terrace gravels have been observed on the sides of the main cliffs in the Manonga Valley. At Inolelo 1, for example, a 1.48-m-thick layer of gravel is present, with its base at 1095.3 m, about 38 m above the present-day river and 13 m below the top of the cliff. This indicates the presence of a Quaternary high lake level located within the confines of the cliffs that form the perimeter of the central study area. Secondly, distributed widely across the floor of the central area of the Manonga Valley is a thin clay cover that has been transformed into mbuga clays. Thirdly, the extremely flat topography of the Manonga Valley, forming a 4-km-wide strip along either side of the Manonga River from Kininginila, and widening toward the east, indicates a dried-out lake floor, which eventually grades into the flat bottom of the Eyasi and Wembere grabens.

Moreover, observations by Wayland (1934) and Stockley (1947) provide evidence that Lake Victoria, now at +1134 m, previously rose to higher levels, as indicated by the presence of terraces at +1138 m and +1146 to +1155 m, and a previous lake level at +1158 m. The origins of the Isanga River, discharging into Lake Victoria, and of the Manonga River, discharging into Lake Kitangiri–Lake Eyasi, are situated on the divide between the two hydrographic basins at +1154 m. This disposition indicates that during the Quaternary, and especially during the early Holocene, highstands of Lake Victoria water probably flowed over this divide into the Eyasi basin. If enough water was available it would have flooded the entire present-day Manonga and Wembere drainage basins to a level well above that of most of the present-day cliffs. The level would have risen to 124 m above the present level of Lake Eyasi. The extent of this vast hypothetical post-Wembere–Manonga paleolake is illustrated on the geological map by Barth (1989) by what he calls the "shoreline of Lake Nyanza, the part of the Proto-Lake Victoria transgressing southwards over the Archean shield following the 1160 m contour line." Our observations in the field, however, do not reveal any gravel or other deposit between 1154 and 1160 m, only much lower at 1095 m in the terrace at Inolelo 1. This supports only the presence of a much smaller lake, recognized by Barth (1989) as proto–Lake Eyasi. The extant Lake Eyasi and Lake Kitangiri are only small remnants of the former proto–Lake Eyasi. The high cliffs characteristic of the central part of the study area are probably the result of the erosion along the lakeshore at the time of deposition of the Inolelo 1 terrace gravel, although later surface erosion and retrograde erosion of the tributaries of the Manonga River over a few tens or hundreds of meters width have contributed to the present-day morphology of the cliffs.

At Shoshamagai 2 and Inolelo 1 a fossiliferous pebbly sandstone bed, 5–20 cm thick, occurs at a height of 1095 m. The bed is remarkably horizontal, possibly reflecting a Holocene lake shoreline, but because it runs along strike, it could structurally belong to the Wembere–Manonga Formation. The bed contains fossils also found in the Ibole Member. It lays on top of layers of the Ibole Member, but nowhere is it covered by other beds of the Ibole Member. Stratigraphically it is not possible to confirm the relation of this fossil-rich bed to a littoral facies of either the Ibole Member or the retreating proto–Lake Eyasi.

6. Paleoenvironment

Stockley (1930) and Stockley and Grace (1931) originally postulated that the Wembere–Manonga Formation consisted of "old lake sediments formed under shallow conditions. They indicate a great extension of fresh water lake conditions." This interpretation has generally been followed by subsequent workers (e.g., Teale, 1931; Eades, 1936; Williams and Eades, 1938; Williams, 1938; Grantham *et al.*, 1945; Pickering, 1958).

Stratigraphic and sedimentologic observations made during the 1990 and 1994 field seasons allow some important conclusions to be drawn about the paleoenvironment of the Neogene sediments in the study area. A lacustrine environment is indicated by the presence of fine-grained clays and silts, with only the rare occurrence of coarser sediments, as well as by the great extent of the members and individual beds, which sometimes can be followed over tens of kilometers. The presence of dramatic facies changes, from fine sediments to sands, over relatively short distances around the Precambrian islands also indicates a lakeside setting.

The lake appears to have been quite shallow, and there are clear indications of periodic recessions, during which the lake dried up for long enough to produce paleosols over large areas of the basin (mainly in the upper part of the Ibole Member and to a lesser degree in the Tinde Member).

Evidence for pedogenesis is indicated by the presence of extensive red beds with differing amounts (estimated at between 5% and 80%) of associated calcareous concretions or nodules. Aspects of the pedogenesis are still under study, but macroscopic observations have already led to the identification of different types of calcareous concretions: rootlike, often branching structures, tubular calcareous concretions, and small spherical to subspherical concretions ranging from 0.5–5.0 cm in diameter. Other calcareous concretions, occurring in levels or continuous beds, indicate periodic emergence of the lake floor under climatic conditions with distinct dry and wet seasons. These include fissures with calcite fillings, such as large, rounded irregular concretions (3–20 cm in diameter and up to more than 50 cm in length); horizontal networks of irregular concretions, forming polygonal ring structures of about 40–70 cm in diameter, 5–10 cm wide, and 10–30 cm high; and calcareous veins or joints dipping in all direction, with horizontal, subhorizontal, steep, subvertical, or vertical dips. Many of the thicker concretions are formed as calcite deposited in cracks in the swelling clay, forming an irregular honeycomblike structure, corresponding in size (0.2–2.0 cm in diameter) to the angular, blocky clay peds of the surrounding clay sediments.

Both the red beds and the layers with calcareous nodules and concretions can be traced laterally over several kilometers. Their thickness can change, but the content and type of calcareous concretions of each layer tend to remain constant. At Tinde East and Tinde West one can observe that the extent of the red bed is more limited than that of the associated calcareous concretion bed below it. A possible mechanism for this could be that after subaerial emergence of a part of the lake bottom, calcite precipitated from evaporating calcareous groundwater about 0.5–1.5 m below the surface, in cracks formed by the drying and shrinking swelling clays. Pedogenetic calcareous concretions were then formed from roots or tubes produced by bioturbation. When subaerial emergence of the sediments occurred over extended periods, oxidation of part of the swelling clay could produce reddening of the layer. The calcite or iron oxides were possibly remobilized after each subsequent emergent phase.

Each formation or member has its own particular paleoenvironmental characteristics. The conglomerates and poorly sorted sandstones with some cross-bedding, which make up the Mwansarara Formation, are geographically located at the fringes of the limestone or calcareous sediments of the Wembere–Manonga paleolake, and they point to a littoral environment passing locally into a terrestrial environment with colluvial or fluvial sediments deposited in paleovalleys.

The thick, homogeneous clays, with occasional calcareous concretions, that form the lower part of the Ibole Member indicate the first stage in the development of the paleolake, during which there were few or no emersions. The red beds with abundant calcareous concretions forming the upper part of the Ibole Member indicate a second stage in the development of the paleolake. During this stage the lake underwent extended periods of emersion under a climate with distinct wet and dry seasons.

The presence in the Tinde Member of extensive swelling clays, occasionally with discontinuous calcareous concretions or continuous polygonal structures, and one or two intercalated red beds, represents the third stage in the formation of the paleolake. This is when the lake was at its deepest, when periodic emersions were relatively rare events. The presence of thin pinkish sandstone beds at the base of this member, located toward the eastern side of the basin, might be considered as the result of small turbidites that descended into the lake from a prodelta front.

The overlying Kiloleli Member shows a dramatic change in facies, with its nonswelling clays, fine silts, clay clast aggregates, and rare sandstones arranged in horizontal beds or filling wide, shallow channels. The transition from the Tinde Member to the Kiloleli Member can be interpreted as part of a general cycle of coarsening upwards—a change from a lake over a prodelta into a delta. Calcareous concretions occur, but no red beds; occasionally some fine crack infillings of calcite, a few millimeters long, are present. They are not typically fluvial sediments. The present-day Manonga River system, with a topographic context and source material similar to that of the Wembere–Manonga paleolake, produces coarse-grained fluvial sediments, while the Kiloleli Member is dominantly fine-grained. This is further support for the interpretation presented here of a prodelta environment, with influx from the eastern side of the lake, where the thickness of sediments is greatest (i.e., at Kininginila). The contact between the Tinde and Kiloleli Members is hence probably diachronous.

It is not known whether the present-day Manonga River passes through the deepest part of the paleolake. In lake settings the thickest strata tend to be present in the central part of the basin. However, no clear pattern can be deduced from the measured thicknesses of the members (Fig. 3). Based on a limited number of observations, the Ibole Member is thickest at Tinde and Lubeho, south of the Manonga River; the Tinde Member is thickest between Kiloleli and Ngofila 1, to the north of the river; and the Kiloleli Member is thickest at Kininginila, situated just south of the river. The present-day depression of the Manonga River in the study area is probably the result of a combination of rifting activity, which produced a downthrow of the Manonga Valley and the blocks to the north, and a retrograde erosion by the Manonga River system during the Quaternary, as it followed the zones of weakness created by faults or fault zones north and south of blocks C and D, respectively (see Fig. 3).

Fossils are absent in the Mwansarara Formation. In the Wembere–Manonga Formation, fossil localities are located 1.0 to 1.5 km from the Precambrian islands

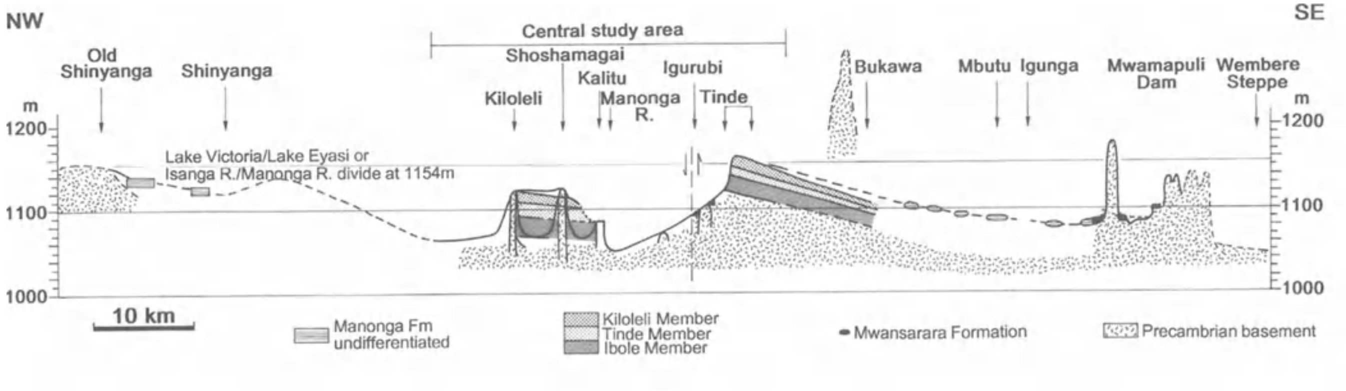

FIGURE 8. Northwest–southeast section through the later Neogene Wembere–Manonga paleolake, from Old Shinyanga to Igunga. It shows the pre-Wembere–Manonga Formation paleotopography with Precambrian hills emerging from the paleolake and post-Wembere–Manonga Formation faulting close to the Manonga River (100 × vertical exaggeration).

in the Ibole Member, less than 4 km from the Precambrian mainland in the Tinde Member, and are located throughout the basin in the Kiloleli Member.

It is possible that fossils were originally more widely distributed throughout the sequence and geographic extent of the basin but that they were destroyed by strong leaching of calcareous materials in the red beds of the Ibole Member and by the mechanical action of expansion and shrinkage of the swelling clays in the Tinde Member. This may explain why fossil occurrences are more common in the Kiloleli Member, where swelling clays do not occur and where the apparently higher calcite content may have preserved fossils against leaching.

7. Schematic Geological Map

The schematic map presented in Fig. 7 summarizes data from field observations, previously published geological and topographic maps, and aerial photographs (at a scale of 1:55,000). The latter were used not only for the accurate location of outcrops, sections, and fossil localities, but also to determine geological boundaries, such as Precambrian islands and lineaments, mainly interpreted as faults, that define structural blocks. Aerial photographs revealed, for instance, the existence of five Precambrian outcrops in the middle of the study area, later verified in the field, that are not shown on previous geological maps. The geological map presented here (Fig. 7) is only schematic; the Pleistocene and Holocene sediments are not represented. It shows the extent of the Precambrian outcrops, the position of the topographic sections, the location of fossil sites and stratigraphic columns, the limits of the structural blocks, and the occurrence of prominent cliffs.

8. Conclusions

The supposedly early Miocene peneplanation over the Archean Tanzania Craton produced a flat paleotopography within the extensive, but shallow, Manonga basin. The harder units of the Precambrian basement resisted erosion, and formed small to large inselbergs on the paleolandscape. Locally, coarse and poorly sorted colluvials of terrestrial sands and gravels were accumulated subaerially in shallow depressions (Eades and Reeve, 1938; Williams and Eades, 1938) to form the Mwansarara Formation (but see below for an alternative interpretation).

During the course of the Miocene, impediment of the drainage system produced flooding of the Manonga basin, thereby forming the Wembere–Manonga paleolake, which was at least 10,000 km^2 at its greatest extent. The cause of the blockage is unknown. The uplift of the Albertine Rift could be one possible contributing factor, but more localized effects cannot be discounted. Sediments deposited in the lake compose the Wembere–Manonga Formation. Up to 66 m of strata have been recorded, laid down horizontally on top of the early Tertiary topography. It is possible that the sediments of the Mwansarara Formation, previously interpreted as being formed prior to the deposition of the lake sediments, represent lateral facies of the Wembere–Manonga Formation being laid down at the fringes of the paleolake. Some of the low-lying Precambrian outcrops were submerged by the lake, but the larger inselbergs produced small islands. Around these, coarse littoral facies were developed, grading laterally to lacustrine facies over short distances of between 100 and 1000 m.

The paleoenvironment of the Wembere–Manonga Formation is that of a shallow lake that dried out periodically. The depth of the lake was in the order of tens of meters. A modern analogue of the Wembere–Manonga paleolake might be either Lake Victoria, only smaller, perhaps one quarter of its size, and less permanent, or Lake Chad, with an extent that varies considerably.

The basic lithostratigraphy of the paleolake deposits established after the first field season by Harrison and Verniers (1993) is herein slightly changed, with more accurate descriptions of the two formations. The Wembere–Manonga Formation can be interpreted as the result of a single transgression–regression cycle. The unfossiliferous lowermost unit, the Mwansarara Formation, is postulated to be either a prelake colluvial and/or fluvial deposit of Miocene age, or possibly a later Neogene littoral facies fringing the paleolake.

The Ibole Member, the lowest of the three members of the Wembere–Manonga Formation, contains in the lower part of its sequence a uniform series of clays with few calcareous concretions, indicating a lake environment with no regressions. The upper portion of the member comprises swelling clays with numerous red beds that are rich in calcareous concretions and veins (formed by evaporation of calcium-rich groundwater), suggesting a cyclical drying of the lake. Emersions were prolonged enough to allow oxidation of the clays and the formation of thick red beds up to 3.5 m thick. At localities such as Inolelo 1–3, Shoshamagai 2, and Lubeho, situated up to 1 km from Precambrian islands, terrestrial fossils occur in horizons situated in the upper part of the member. These fossil are indicative of a latest Miocene or early Pliocene age (see Harrison and Baker, this volume, Chapter 13).

The extensive swelling clays in the Tinde Member, characterized by the occurrence of few calcareous nodular levels and local red beds, indicate that during this time the lake was at its maximal extent, with only occasional and brief periods of emersion. Based on fossils discovered at Tinde and other localities since 1990, the Tinde Member is inferred to be early Pliocene in age (see Harrison and Baker, this volume, Chapter 13). In the eastern portion of the Manonga basin, thin pink sandstone beds are interpreted as the product of small turbidites descending a prodelta front.

The uppermost unit of the Wembere–Manonga Formation, the Kiloleli Member, consists of a series of nonswelling clays and silts, with associated sandstones, cross-bedded silts and clay clast, and limestone pebble aggregates, deposited in horizontal beds or in wide gullies. These deposits indicate a prodelta or delta environment associated with filling of the lake basin with sediments. Fossils from the Kiloleli Member indicate an early Pliocene age (Harrison and Baker, this volume, Chapter 13). The disappearance of the Wembere–Manonga paleolake may be linked to the initial formation of the Eyasi graben at the beginning of the Pliocene.

Slight tectonic movements of the Wembere–Manonga Formation led to tilting and block faulting, which, in turn, created a number of structural blocks that can be defined by their slightly different angles of dip or by the nature of their substratum. This faulting occurred after the deposition of the Wembere–Manonga Formation, probably during the late Pliocene or Pleistocene. It is probably linked with the continued development of the Eyasi–Wembere grabens. The north-northeast-trending Eyasi graben forms an angle with its southward continuation, the south-southeast-trending Wembere graben. The east–west-trending Manonga Valley can be seen as a third, more weakly developed, rift branch of a triple junction. The faults observed in the Manonga basin have downthrows of less than 100 m.

Since the Quaternary, few sediments have been deposited in the Manonga Valley, and these include gravel lags, terrace gravels, mbuga clays, and alluvia along the courses of the larger rivers. These allow only a tentative and poorly dated reconstruction of the Pleistocene and Holocene history of the basin. The presence of a high terrace at different places around Lake Victoria, similar in height to the Isanga–Manonga divide, indicates that the waters of the proto–Lake Victoria may have flowed into the Eyasi–Wembere basin. This would have raised the water level in the latter basin by at least 65 m, creating the proto–Lake Eyasi. It created a terrace and steep cliffs at the lake margin, the latter of which dominate the landscape in the central Manonga basin today. Successive steps in the lowering of the water level brought proto–Lake Eyasi down to its present-day remnants: Lake Kitangiri and Lake Eyasi.

During the later phases in the development of the proto–Lake Victoria (or proto–Lake Nyanza) and of Lake Eyasi, the area was subject to regressive erosion by the Manonga River. This cut back into the soft sediments of the Wembere–Manonga Formation, and laid bare most of the central part of the Manonga Valley, leaving only some outliers of the Wembere–Manonga Formation (e.g., on Ng'oholyambiti Hill) and remnants of the Ibole Member. In some places erosion has penetrated down sufficiently to expose rocks of the Precambrian basement.

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Chapter 3

Mineralogy of the Wembere–Manonga Formation, Manonga Valley, Tanzania, and the Possible Provenance of the Sediments

MEDARD MUTAKYAHWA

1. Introduction

This chapter presents the results of geological fieldwork conducted in the Manonga Valley, northern Tanzania, during the summer of 1994, in conjunction with the stratigraphic and paleomagnetic studies of Drs. Jacques Verniers (University of Gent) and John Kappelman (University of Texas at Austin). The research area and the location of the sites discussed in this chapter are described in detail by Harrison and Mbago (this volume, Chapter 1) and by Verniers (this volume, Chapter 2). Deposits in the Manonga depression consist of a series of fluvio-lacustrine sediments, ranging from 25 to 200 m in thickness (Kassim, 1994; Verniers, this volume, Chapter 2). The lowermost beds consist of a layer of conglomerates, up to 5 m thick, which compose the Mwansarara Formation. This is overlain by a thick series of fine- to medium-grained sediments, primarily

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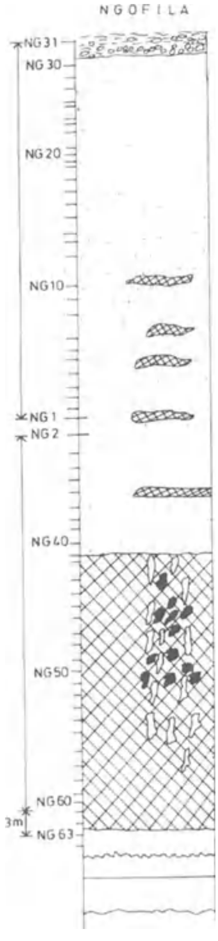
consisting of swelling clays with calcretes and red beds (latosols), that together make up the Wembere–Manonga Formation. The aim of this Chapter is to provide a brief description of rock samples obtained from three naturally exposed profiles of the Wembere–Manonga Formation, and to report on preliminary findings of mineralogical analyses.

2. Ngofila Profile

The site of Ngofila 1 (S3°55′, E33°47′; 1100 m above sea level) consists of a low cliff and a section of the valley floor on the northern side of the Manonga Valley, just to the east of the village of Kalitu. Details of its precise location are given by Harrison and Mbago (this volume, Chapter 1). A total of 63 samples



Pseudo-conglomeratic structures produced by drying in conjunction with the formation of desiccation cracks. Eroded and redeposited in the form clay pebbles cemented by calcified mud.

Well-bedded silts and sands with calcite cement. Sometimes with fossil gastropods and vertebrates. The sediments are generally relatively hard, but vary locally to form friable siltstones and swelling clays.

Alternating greenish-grey swelling clays of variable thickness.

Swelling clays and calcified mudstones with locally occurring red latosols of variable thickness. Hard calcitic nodules occur in the clays and friable siltstone.

Red beds up to 20m in thickness (Ibole Member), occasionally with cross-bedding. Extensive development of calcareous nodules. Fossil roots and termitaria are also observed.

FIGURE 1. Generalized sedimentary profile at Ngofila 1 showing the stratigraphic location of samples discussed in the text.

Table I. Rock Samples from the Ngofila Profile

Sample	Description
NG 1:	Swelling clay. Sample used for XRD analysis.
NG 2:	Honeycombed red clay. Paddy structure well developed.
NG 3:	Calcareous nodules at top of red bed showing paddy structures.
NG 4:	Honeycombed red clay, slightly bleached.
NG 5:	Red clay, weathered or bleached to pinkish brown or tan. Paddy textures present. Abundant evidence of bioturbation and fossil root casts.
NG 6:	Thin white calcareous horizon intercalated between a red clay and a swelling clay.
NG 7:	Swelling clay. Bioturbated, with slickensides.
NG 8:	White calcareous bed. Calcrete development.
NG 9:	Swelling clays with slickensides. Very compact. 10 m thick.
NG 10:	Calcareous nodules within swelling clays.
NG 11:	Swelling clays similar to NG 9 and NG 10. Red spots in the coarse-grained sediments are probably pyroxenes.
NG 12:	Swelling clays (?montmorillonitic).
NG 13:	Whitish calcareous nodular layer in swelling clays. 20 cm thick.
NG 14:	Yellowish calcareous nodule. About 1 m above NG 13.
NG 15:	Swelling clays with scattered calcareous nodules. Much bioturbation.
NG 16:	Swelling clays similar to NG 15.
NG 17:	Calcareous band or concretions intercalated between swelling clays. 20 cm thick.
NG 18:	Calcareous band that pinches out in the swelling clays.
NG 19:	Clays showing variable degrees of calcification. Mn-oxides precipitating out in fissures. Reworked calcareous nodules.
NG 20:	Conglomeratic horizon consisting of reworked clay pebbles of local origin. 35 cm thick. Indicative of a channel-fill structure.
NG 21:	Tan claystone with small clasts or reworked clay pebbles. Calcite crystals along fissures and cracks.
NG 22:	Tan claystone with variegated bedding.
NG 23:	Hard olive green claystone with pronounced exfoliation weathering. 1 m above NG 22.
NG 24:	Hard claystone. 35 cm above NG 33.
NG 25:	Soft olive green clay with bedding. 20 cm thick.
NG 26:	Hard, massive olive green clay. 20 cm thick.
NG 27:	Massive cemented claystone. 20 cm above NG 26.
NG 28:	Massive cemented claystone.
NG 29:	Massive cemented claystone. 1 m above NG 28.
NG 30:	Massive cemented claystone.
NG 31:	Calcareous horizon, with rounded pisolitic calcrete pebbles cemented by calcite.
NG 32:	Tan-red claystone and red clays with calcareous nodules. 1.0–1.5 m thick.
NG 33:	Pink claystone, possibly originally red.
NG 34:	Red clay with sparsely carbonated nodules, containing hematite and calcite. 1 m below NG 33.
NG 35:	Friable brownish red clays with olive green nodules. Saprolitic texture.
NG 36:	Calcareous nodules on top of red bed. 1.2 m below NG 35.
NG 37:	Red claystone with calcite cement. Paddy structures. 1 m below NG 36.
NG 38:	Red claystone. Paddy structures. Similar to NG 2. 0.8 m below NG 37.
NG 39:	Red claystone as in NG 32.
NG 40:	Red claystone with scattered calcareous nodules. 1.1 m below NG 39.
NG 41:	Calcified red claystone. 0.4 m below NG 40.
NG 42:	Highly calcified red bed with calcareous nodules. Fossil termitaries indicate a paleosol. 1.25 m below NG 41.
NG 43:	Hard calcareous red clay. 1 m below NG 42.
NG 44:	Soft red clay. 1.1 m below NG 43.
NG 45:	Calcified red clay with calcareous nodules. 1 m below NG 44.

(*continued*)

Table I. (Continued)

Sample	Description
NG 46:	Poorly calcified red clay with calcareous nodules. Tectonic fissures on lineaments filled with calcified red clay. 1 m below NG 45.
NG 47:	Slightly calcified red-brown clay. 0.8 m below NG 46.
NG 48:	Slightly calcified red-brown clay. 1 m below NG 47.
NG 49:	Slightly calcified red-brown clay.
NG 50:	Calcified red clay, with sheets of calcite filling fissures. 1 m below NG 49.
NG 51:	Slightly calcified red clay with calcareous nodules. 0.8 m below NG 50.
NG 52:	Red sandstone with cross-bedding. 0.8 m below NG 51.
NG 53:	Red clays with scattered calcareous nodules. 0.9 m below NG 52.
NG 54:	Red sandstones with cross-bedding. Cracks filled with calcite.
NG 55:	Calcareous nodule. 1.35 m below NG 54.
NG 56:	Calcareous nodule. 1.3 m below NG 55.
NG 57:	Calcareous nodule. 1.0 m below NG 56.
NG 58:	Calcareous nodule. 1.0 m below NG 57.
NG 59:	Calcareous nodule.
NG 60:	Calcareous nodule, with weblike calcite texture. 1.2 m below NG 59.
NG 61:	Calcareous nodule. 1.05 m below NG 60.
NG 62:	Brown claystone, probably originally red. Cracks filled with calcite. 1.55 m below NG 61.
NG 63:	Red-brown clay with paddy texture. Calcite nodules common. White calcrete crust on top of bed. 2–3 m below NG 62.

were obtained, and their position in the stratigraphic sequence is shown in Fig. 1. Descriptions of the rock samples are given in Table I.

3. Beredi South Profiles

The site of Beredi South (S3°55′ E33°52′; 1100 m above sea level) consists of a series of low cliffs along the elevated flanks of the Nhuliku River valley on the northern side of the Manonga Valley. It is located about 10 km east of Ngofila 1.

Table II. Rock Samples from the Beredi South (BA) Profile

Sample	Description
BA 1:	Brown claystone. Well cemented. Indications of varved bedding.
BA 2:	Pale yellow-tan siltstone/claystone.
BA 3:	Friable green-gray clay. Mottled, with Mn-oxide crusts. Horizon contains fossil gastropods and fish.
BA 4:	Pale tan siltstone/mudstone. Contains fossil fish.
BA 5:	Greenish siltstone/mudstone. Highly bioturbated and friable.
BA 6:	Similar to BA 5, but more compact and more heavily calcified.
BA 7:	Hard mudstone/siltsone.
BA 8:	Well-calcified mudstone/claystone.
BA 9:	Well-calcified mudstone/claystone.
BA 10:	Calcified mudstones with widely separated beds that make the rock friable.
BA 11:	Well-bedded calcified mudstones.
BA 12:	Buff-colored calcified claystone/mudstone.

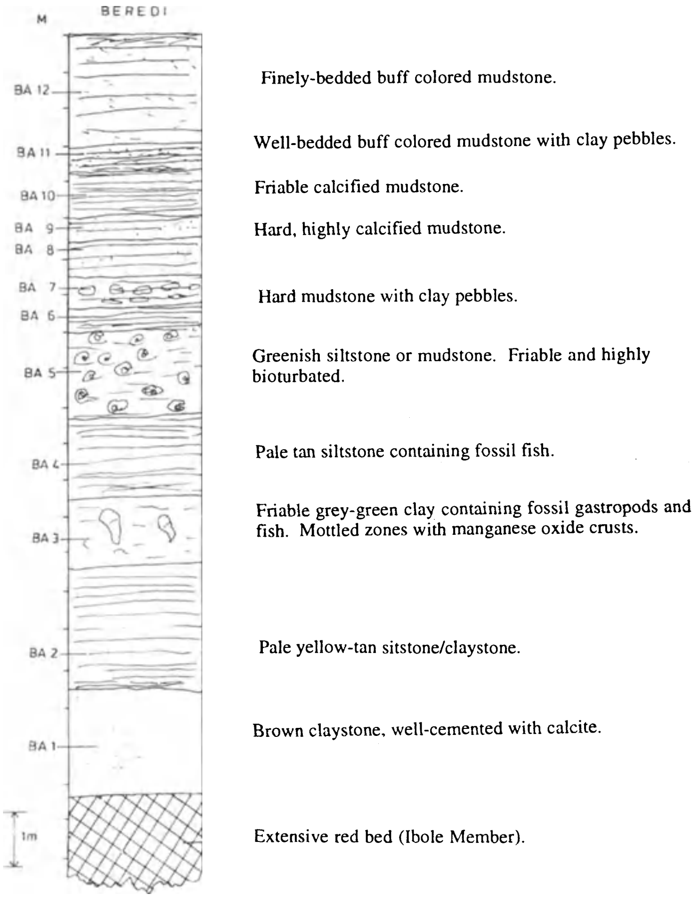


FIGURE 2. Generalized sedimentary profile at Beredi showing the stratigraphic location of the samples discussed in the text.

Details of its location are given in Harrison and Mbago (this volume, Chapter 1). Two profiles were examined at Beredi South, designated Beredi A (BA) and Beredi B (BB), with thicknesses of 21.7 m and 20.1 m, respectively (Fig. 2). The two profiles are essentially the same. Descriptions of the rock samples from Beredi A are given in Table II.

4. Mineralogy

Rock samples obtained from each of the profiles described above were analyzed mineralogically and chemically. Each sample was impregnated with coropox, and then thin-sectioned for microscopic studies.

NG 3 and NG 36: The rock consists mainly of micrite, which acts as a cementing material for feldspars and pyroxenes. It appears that micrite not only

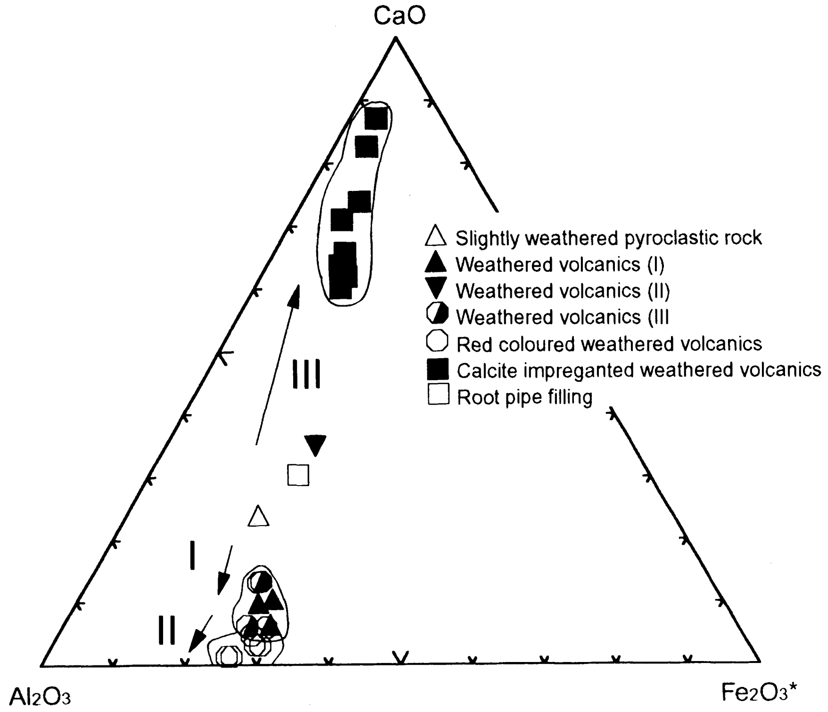


FIGURE 3. Ternary diagram of CaO-Al_2O_3-Fe_2O_3 showing the alteration stages of the Wembere–Manonga volcanic sediments. Symbols represent samples from the Manonga Valley.

is secondarily crystallized, but also results from the replacement of certain minerals, such as feldspars, nepheline, and melilite. Micrite is also found in the clay matrix. Sparite fills in fissures and pores.

NG 23: Minerals include K-feldspars (microcline and anorthoclase), plagioclase, and pyroxene (clinopyroxene). Opaques occur as relict minerals. Feldspars are replaced by calcite (sparite). Rounded volcanic globules are common, ranging in size from 0.1–2.0 mm. These may contain anorthoclase, plagioclase, pyroxenes, hornblende, and opaques. Micrite and brownish yellow clay particles cement together the volcanic globules. The former might be the result of the alteration of volcanic ashes or glasses. Any pores and fissures, produced by solution of minerals such as nepheline or melilite, are filled with sparite. Euhedral rectangular clay pseudomorphs preserve the original texture of the parent volcanic rock. These are crossed by a network of fractures that are filled by micrite or sparite.

NG 27: Volcanic glass of melilitic composition has been altered through a devitrification process to form a yellowish isotropic dense clay. This material is in turn replaced by calcite (micrite), which makes up 60–70% of the total mineralogical content. Sparite, which crystallizes in pores and fissures, and relict minerals (i.e., pyroxenes, plagioclase, and K-feldspars) make up the remainder of the rock.

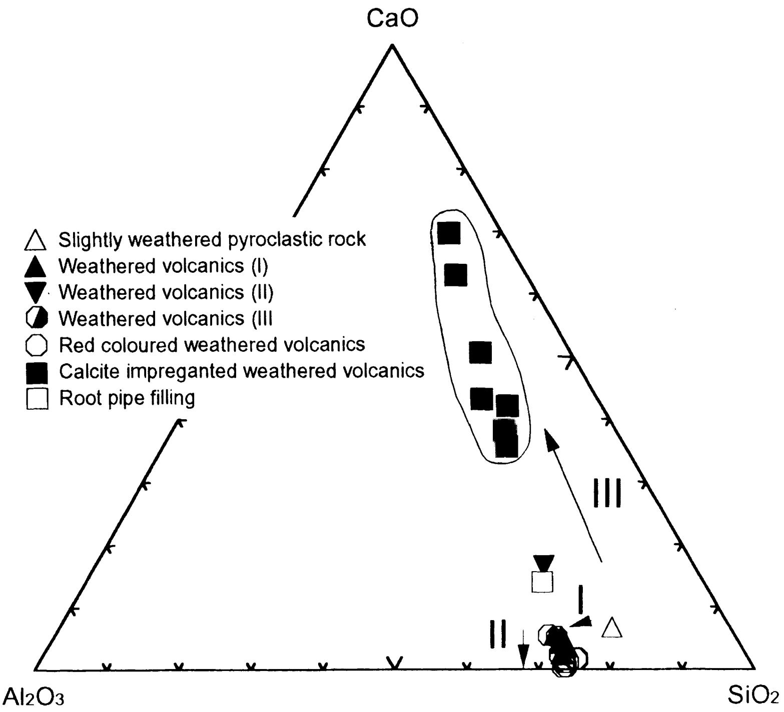


FIGURE 4. Ternary diagram of CaO-Al_2O_3-SiO_2 showing the alteration stages of the Wembere–Manonga volcanic sediments. Symbols represent samples from the Manonga Valley.

NG 20b: Volcanic glass has been altered to a yellowish brown isotropic dense clay, and partly replaced by calcite (micrite). Euhedral rectangular clay pseudomorphs occur. Volcanic globules, ranging in size from 0.01–0.5 mm, consist mainly of K-feldspars, plagioclases, pyroxenes (clinopyroxenes), and hornblende. These may be cemented together by micrite or Mn-oxides.

NG 2 and NG 2a: Includes volcanic globules composed of calcite, with some fresh feldspars and sphene. The globules are well rounded and have a cortex of micrite. Most of the minerals (80–90%) have been altered to calcite (micrite). Sparite fills the fissures and pores. Micrite and hematite form the cementing materials.

BA 2: Similar in composition to NG 2.

BA 11: Brownish yellow isotropic dense clay with disseminated calcite composes 90–95% of the composition. K-feldspars and clinopyroxenes occur as rare components.

BB 3: Similar in composition to BA 11. The brownish yellow isotropic dense clay, which makes up about 95% of the rock, is pseudomorphically replacing melilite. Sparite fills pores and fissures along the ill-defined bedding planes.

X-ray diffraction (XRD) and fluorescence (XRF) analyses were carried out to complement the petrographic results (Fig. 3 and 4). The diffractogram revealed

Table III. Major Element Composition (wt %) of the Volcanic Sediments from the Ngofila and Beredi South Profiles of the Wembere–Manonga Formation

Sample	SiO2	TiO2	Al2O3	Fe2O3	MnO	MgO	CaO	NA2O	K2O	P2O5	LOI
10. CaVolc	29.40	0.48	8.62	2.71	0.14	0.87	27.67	2.94	1.82	0.18	26.08
11. Volc (I)	44.56	0.89	15.66	6.81	0.08	2.29	2.65	5.85	2.79	0.18	19.05
12. RedVolc	47.57	0.89	16.74	6.87	0.09	1.75	0.81	5.25	3.05	0.06	17.67
13. Volc (I)	46.54	0.74	15.57	6.10	0.10	2.26	2.39	4.47	2.55	0.05	19.92
14. CaVolc	29.59	0.53	9.95	4.52	0.12	1.23	23.59	3.36	2.08	0.18	25.93
15. Volc (II)	40.94	0.71	13.74	6.50	0.12	1.72	10.88	3.71	2.68	0.11	19.88
16. CaVolc	20.75	0.38	8.22	3.36	0.15	8.09	22.12	3.60	1.40	0.23	32.85
17. CaVolc	13.56	0.22	4.35	1.75	0.12	0.54	41.03	0.52	0.73	0.11	36.74
18. Volc (III)	47.68	0.76	17.12	6.46	0.04	2.20	1.57	6.05	2.69	0.09	16.06
19. RedVolc	47.35	1.03	17.02	7.36	0.07	1.75	1.57	4.92	3.23	0.11	16.48
20. RootPipe	37.76	0.67	13.30	5.69	0.07	6.01	8.27	4.28	2.06	0.13	22.91
21. Volc (III)	44.36	0.77	16.65	6.42	0.11	2.28	3.56	6.63	2.46	0.14	17.42
22. Volc (III)	45.68	0.71	16.22	6.10	0.06	2.58	3.41	6.38	2.46	0.10	17.39
23. RedVolc	49.99	0.84	16.01	6.33	0.09	1.89	1.13	4.16	2.53	0.04	17.68
24. CaVolc	16.00	0.22	5.77	2.08	0.02	0.88	37.04	1.88	0.78	0.04	33.67
25. RedVolc	49.70	0.92	17.87	6.13	0.06	1.46	0.32	6.26	2.69	0.05	15.20
26. RedVolc	47.03	0.85	16.54	5.88	0.08	1.54	0.31	6.50	2.81	0.03	19.43
27. CaVolc	30.21	0.74	10.44	4.54	0.11	1.26	22.56	3.25	2.16	0.18	24.65
28. Volc (I)	45.79	0.67	16.25	7.22	0.06	1.84	1.62	5.25	3.11	0.35	18.88
29. CaVolc	29.32	0.64	9.94	3.90	0.08	1.35	24.28	3.29	2.17	0.32	26.08
30. SWPR	58.97	1.09	12.57	4.01	0.12	1.22	5.23	4.23	3.40	0.27	9.32
31. RedVolc	48.61	0.73	16.71	7.14	0.10	2.04	0.79	5.47	3.36	0.38	15.50
32. CaVolc	22.70	0.44	7.74	3.37	0.10	1.26	31.24	2.60	1.64	0.06	29.65

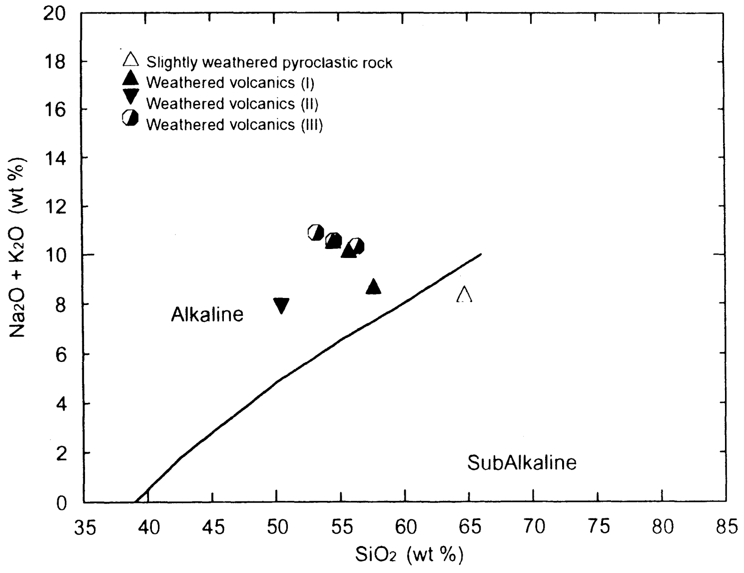


FIGURE 5. Binary diagram plotting $Na_2O + K_2O$ (wt %) against SiO_2 (wt %), following the classification of volcanic rocks proposed by Irvine and Baragar (1971). Symbols represent samples from the Manonga Valley. From Irvine and Baragar (1971).

Table IV. Trace Element Composition (ppm) of the Volcanic Sediments from the Ngofila and Beredi South Profiles of the Wembere–Manonga Formation

Sample	Cr	Ni	Co	V	Cu	Pb	Zn	S	Rb	Ba	Sr	Ga	Nb	Zr	Y	Th	U	La	Ce	Nd
10. CaVolc	91	79	33	140	81	15	45	0.00	64	667	2035	14	43.0	188	124	51.00	0.00	296.00	347.00	145.00
11. Volc (I)	139	81	38	142	97	20	115	0.03	143	977	499	32	63.0	245	24	20.00	4.00	72.00	129.00	56.00
12. RedVolc	151	85	13	83	66	26	89	0.01	157	395	126	30	56.0	252	24	19.00	3.00	70.00	96.00	39.00
13. Volc (I)	162	83	13	67	60	22	83	0.01	141	308	272	26	36.0	186	28	20.00	1.00	57.00	129.00	47.00
14. CaVolc	93	85	33	181	108	16	77	0.02	80	796	2154	22	53.0	194	105	29.00	0.00	201.00	469.00	107.00
15. Volc (II)	117	83	13	94	133	19	108	0.01	122	1672	656	24	70.0	207	32	23.00	5.00	81.00	144.00	53.00
16. CaVolc	94	98	57	89	103	13	66	0.09	54	376	3098	22	17.0	82	51	4.00	1.00	69.00	222.00	57.00
17. CaVolc	71	81	54	42	91	5	30	0.04	19	1099	4804	15	16.0	69	56	0.00	0.00	136.00	142.00	44.00
18. Volc (III)	161	82	17	174	92	18	77	0.03	154	410	513	25	45.0	232	14	14.00	12.00	33.00	64.00	25.00
19. RedVolc	136	77	17	115	73	15	121	0.01	152	394	277	29	90.0	325	28	14.00	0.00	64.00	133.00	46.00
20. RootPipe	139	86	38	154	96	25	92	0.02	103	995	1645	28	48.0	198	38	8.00	0.00	78.00	138.00	53.00
21. Volc (III)	126	79	14	142	72	31	92	0.03	131	349	431	26	55.0	226	26	33.00	8.00	81.00	175.00	60.00
22. Volc (lll)	150	92	25	169	107	19	88	0.02	143	446	494	30	40.0	228	32	14.00	0.00	79.00	115.00	67.00
23. RedVolc	177	77	16	107	97	29	92	0.01	148	597	401	25	58.0	242	30	20.00	3.00	80.00	187.00	58.00
24. CaVolc	88	79	54	92	82	7	30	0.07	4	3835	16000	15	0.0	43	40	0.00	6.00	80.00	25.00	9.00
25. RedVolc	163	74	15	80	60	28	77	0.02	159	377	129	30	53.0	241	24	24.00	6.00	88.00	98.00	50.00
26. RedVolc	153	75	7	66	68	16	84	0.02	153	433	143	27	76.0	270	22	20.00	4.00	81.00	93.00	41.00
27. CaVolc	94	72	10	43	133	9	64	0.01	75	720	2008	18	63.0	186	64	9.00	0.00	167.00	167.00	73.00
28. Volc (I)	157	81	10	50	84	26	130	0.02	143	479	458	29	74.0	262	44	37.00	4.00	120.00	210.00	80.00
29. CaVolc	109	81	28	68	124	13	65	0.01	80	538	1736	22	43.0	193	66	40.00	0.00	140.00	341.00	66.00
30. SWPR	136	62	25	64	85	26	59	0.01	127	791	636	18	73.0	490	53	40.00	9.00	183.00	357.00	117.00
31. RedVolc	156	75	0	74	84	26	117	0.01	146	602	475	25	79.0	268	42	60.00	1.00	100.00	350.00	67.00
32. CaVolc	93	81	29	65	87	9	55	0.01	46	679	4649	22	35.0	130	95	0.00	0.00	227.00	197.00	85.00

Table V. Chemical Composition of Yellowish Brown Paragonite Mineral[a]

Composition	Pseudomorphs (%)	Matrix (%)
Al	13.44	11.66
Fe	11.49	6.61
Ca	4.00	17.71
Mg	2.60	1.66
Cl	2.53	3.23
Ti	1.33	1.57
Si	46.97	39.82
K	9.21	7.58
Na	8.43	10.16
Total	100.00	100.00

[a] Sample 20b from Ngofila.

samples that are purely calcite in composition, including calcrete concretions and calcite-impregnated volcanic pyroclasts with calcite and paragonite minerals. The remaining samples consist of volcanic rocks that have been weathered to varying degrees. These include (1) a red volcanic pyroclast that consists of calcite, paragonite, and goethite; (2) intermediate-weathered volcanic pyroclasts that consist of paragonite and/or poorly crystallized smectite; and (3) slightly weathered volcanic pyroclasts composing relic minerals and paragonite.

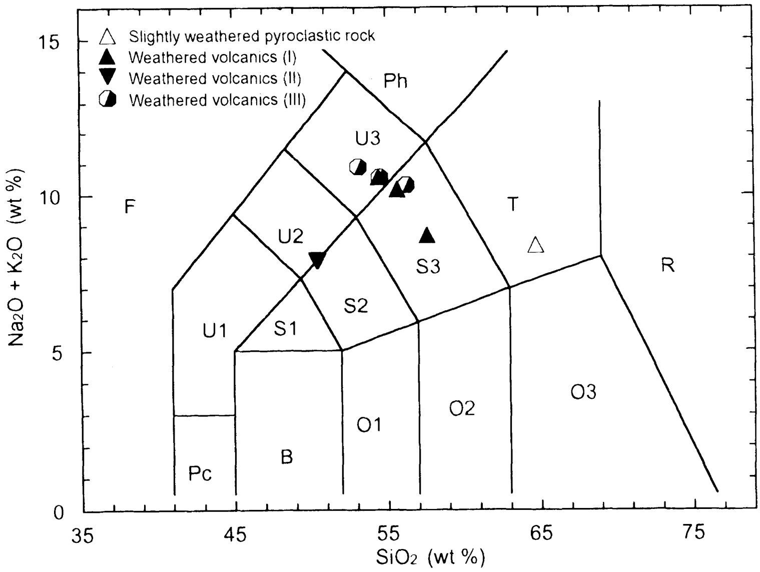


FIGURE 6. Binary diagram plotting $Na_2O + K_2O$ (wt %) against SiO_2 (wt %), following the classification of volcanic rocks proposed by Le Maitre (1989). Abbreviations: B. basalt; F, foidite; O1, basaltic andesite; O2, andesite; O3, dacite; Pc, picro-basalt; Ph, phonolite; R, rhyolite; S2, basaltic trachyandesite; S3, trachyandesite; T, trachyte; U1, tephrite; U2, phono-tephrite; U3, tephriphonolite. Symbols represent samples from the Manonga Valley. From Le Maitre (1989).

Analysis of the major elements and trace elements (Tables III and IV) have provided the basis for the binary and ternary diagrams presented in Figs. 3–6. Figures 3 and 4 show the stages in alteration of the sediments from relatively fresh volcanic pyroclasts. The long arrows indicate calcite development, while the short arrows show the concentration of aluminum weathering. It is also possible to identify the type of volcanic pyroclast using the classifications developed by Irvine and Baragar (1971) and Le Maitre (1989). The samples from the Manonga Valley are subalkaline to alkaline (Fig. 5) and fall into the trachy-andesitic field (Fig. 6). The yellowish brown isotropic matrix (paragonite) and euhedral rectangular clay pseudomorphs (NG 20b) have also been analyzed for major elements, and the results are presented in Table V.

5. Conclusions

The mineralogical composition of the rock samples obtained from the Wembere–Manonga Formation generally suggests a volcanic origin for the sediments. They appear to be waterlain airfall tuffs and fluvially reworked pyroclasts. The development of calcrete in the sediments may be due to carbonate-rich tuffs derived from a carbonatitic volcanic center. These calcretes were formed rapidly, compared with those of semiarid and acidic regions. The well-cemented calcretes contain unaltered feldspars, yellow isotropic dense clays, micrite or sparite pseudomorphs, and nepheline phenocrysts, cemented together by yellow isotropic dense clay with disseminated micrite. These are the result of the alteration of a glassy ground mass of volcanic ashes, similar to that found at Laetoli (Hay, 1978, 1986, 1987). The volcanic glass is initially altered to reddish brown or yellowish brown paragonite, and then to brown montmorillonitic clay. Melilite is principally weathered to a dense orange clay that resembles paragonite. The volcanic globules are rounded, sometimes with a cortex of micrite. Particles are fine to medium grained, and vary greatly in their degree of sorting. Relict minerals include K-feldspars (anorthoclase, microcline, ?sanidine), plagioclase, aegirine-augite (clinopyroxenes), sphene partly altered to anatase, opaques, and rutile. Nepheline is replaced by calcite, clay, and zeolite (phillipsite). Calcite is the principle carbonate mineral. Micrite, sparite, and zeolites (phillipsite, and probably chabazite) may occur individually or in combination.

In sum, the Wembere–Manonga Formation appears to be dominated by volcanic sediments. The thick layers of swelling clays are the result of devitrification of pyroclastic materials, probably derived from windblown volcanic ashes or fluvially reworked tuffs, originating from melilitic and carbonatitic magma centers. The tuffs were probably derived from eruptive centers in the developing rift valley to the northeast of the Manonga basin (Hay, 1978, 1987). The Wembere–Manonga sediments, apparently laid down in a shallow lake, were subsequently periodically exposed subaerially to produce paleosols.

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Chapter 4

Paleoecology and Taphonomy of Fossil Localities in the Manonga Valley, Tanzania

TERRY HARRISON

1. Introduction

One of the major objectives of paleontological fieldwork in the Manonga Valley has been to obtain data that would be relevant for reconstructing the paleoecology and depositional setting of the fossil localities in the region (see Harrison & Mbago, this volume, Chapter 1). It is has become evident in recent years that a sound appreciation of the environmental context is of paramount importance in understanding observed changes in the adaptive strategies of individual mammalian lineages or in the structure of the faunal community in general. Information of this kind might contribute significantly, for example, to the proposal and testing of hypotheses or models that seek to understand the critical environmental factors that underlie the divergence and differentiation of the earliest

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Neogene Paleontology of the Manonga Valley, Tanzania, Volume 14 of *Topics in Geobiology*, edited by T. Harrison, Plenum Press, New York, 1997.

hominids (see Harrison, this volume, Chapter 14). Traditionally, paleoanthropologists have viewed the unique specializations of hominids as adaptations to open country habitats, and this has led to the development of various scenarios in which human ancestors diverged from the forest-dwelling last common ancestor of the African hominoids by exploiting an entirely new set of resources that were available on the grasslands (see Brain, 1981; Vrba, 1985; Hill and Ward, 1988; Hill, 1994). In recent years, this view has been revised with the realization that later Miocene and Pliocene habitats in East Africa do not reflect a wide-scale shift to open grasslands, and that the paleoecology of sites at which the early hominids have been found indicates a more wooded setting (Hill and Ward, 1988; Hill, 1994; Kingston *et al.*, 1994; WoldeGabriel *et al.*, 1994; Andrews, 1995). Even with the limited paleoecological data available, it is apparent that late Miocene and early Pliocene habitats in East Africa consisted of a complex mosaic of forested, woodland, and grassland habitats. Given the paucity of paleontological sites of the appropriate age, especially those that have yielded fossil hominids, it is difficult to make any useful deductions about the possible habitat preferences of the earliest hominids. Clearly, what is needed is a broader regional perspective, and a more synthetic approach to the study of paleoecology in the later Neogene of Africa. With this in mind, the fossil localities in the Manonga Valley, therefore, provide new information that is pertinent to help piece together the diversity of habitats that were available to late Miocene and early Pliocene hominids in East Africa.

The aim here is to briefly review what is known about the paleoecology and taphonomy of the most productive paleontological localities in the Manonga Valley. The most detailed information is from Tinde, but good evidence for comparison has also been obtained from additional site complexes, such as Shoshamagai, Inolelo, Beredi South, Ngofila, and Kiloleli (see Harrison and Mbago, this volume, Chapter 1, for information on these sites). Fossils from these localities are derived from the three major stratigraphic subunits of the Wembere–Manonga Formation (Fig. 1). Comparisons between sites, therefore, provide some indication of the facies and ecological changes that occurred in the Manonga basin through time.

Estimated age	Stratigraphic unit		Paleontological localities
Early Pliocene ~4.0–4.5 Ma	Wembere–Manonga Formation	Kiloleli Member	Kiloleli 1–4, Ngofila 1–5, Beredi South 1
Early Pliocene ~4.5–5.0 Ma		Tinde Member	Tinde East, Tinde West, Kininginila, Ipembe, Nyawa Mwambiti 5
Late Miocene ~5.0–5.5 Ma		Ibole Member	Inolelo 1–3, Shoshamagai 2, Beredi South 5, Ngofila 1–2

FIGURE 1. Generalized scheme of the main stratigraphic units of the Wembere–Manonga Formation, and the stratigraphic position of localities discussed in the text.

2. Geological Context

Only a brief overview of the geology of the Manonga Valley is presented here, as a more detailed account is given by Harrison and Verniers (1993), Harrison and Mbago (this volume, Chapter 1) and Verniers (this volume, Chapter 2).

During the late Miocene, warping of the Precambrian basement, associated with the initiation of regional rifting, produced a lake basin in the region of the present-day Manonga Valley. The lake basin was extensive, covering an area in excess of 10,000 km^2, but it was relatively shallow. Eroded inselbergs derived from the Precambrian basement remained sufficiently elevated to form small, low-lying islands dotted around the lake. Sediments, originally derived from volcanic ashes, were deposited in the center of the lake as a series of calcareous clays and silts. These represent the main fossiliferous beds. Coarser sandstones and conglomerates occur in the vicinity of islands and around the margin of the lake, and probably represent shoreline or shoal accumulations. The series of fine-grained sediments in the center of the basin constitute the Wembere–Manonga Formation, which is subdivided into three members: Ibole, Tinde, and Kiloleli (Fig. 1; Verniers, this volume, Chapter 2).

3. Taphonomy and Paleoecology at Tinde (Tinde Member)

The most productive fossil locality in the Manonga Valley is Tinde (Table I), and, as such, it has been the focus of much of the attention with regard to obtaining detailed taphonomic and paleoecological data. The site consists of two low bluffs separated by a narrow divide. The intervening gap allows the site to

Table I. Number of Specimens Collected at Fossil Sites in the Manonga Valley 1990–94

	Mammals					
Site	Identifiable	Indeterminate	Reptiles	Fish	Other[a]	Total
Tinde East & West	1929	9981	902	8616	12	21,440
Kiloleli 1–4	691	856	247	209	6	2009
Mwambiti 1–5	36	71	34	199	5	345
Shoshamagai 1–2	458	126	179	66	61	890
Inolelo 1–3	422	123	162	283	52	1042
Kalitu	2	0	0	0	0	2
Ngofila 1–5	254	3	37	47	49	390
Beredi North	17	0	0	6	0	23
Beredi South 1–5	120	60	76	122	22	400
Mihama	2	0	0	0	0	2
Ipembe	8	33	0	1	0	42
Nyawa	33	5	7	34	3	82
Kininginila	12	0	6	25	43	86
Total all sites	3984	11,258	1650	9608	253	26,753

[a] Includes birds, invertebrates and their traces, plant remains and casts, and coprolites.

be subdivided into two separate collecting localities, namely, Tinde West and Tinde East (see Harrison and Mbago, this volume, Chapter 1). The faces of the two cliffs expose a series of subhorizontal beds, consisting of swelling clays alternating with hard calcareous bands. Fossils *in situ* are restricted to a light gray calcareous clay impregnated with a honeycomblike calcareous matrix, and light gray to white clays immediately above and below this layer. Just above the fossil horizon is a distinctive bright red clay layer, which becomes thinner and paler in color laterally, and eventually disappears within 100 m or so of the main exposures at Tinde. It is probably of some significance that fossils have only been located where this marker bed occurs, and that the density of fossils is greatest at the Tinde West promontory where the red bed is thickest and brightest in coloration. Even though the hard calcareous bed that contains the fossils at Tinde can be traced laterally for several kilometers, these lateral equivalents do not appear to be fossiliferous, in spite of exhaustive searches. As noted by Verniers (this volume, Chapter 2), it seems likely that the same diagenetic processes involved in the formation of this local red bed were responsible for conditions suitable for the preservation of the fossilized remains.

The lithologic evidence indicates that the fossil beds were laid down as fine calcareous clays in a shallow lake, and that soon thereafter the lake underwent a period of recession. Subaerial exposure of clays led to the formation of the red bed, the limited extent of which implies that the lake bed at Tinde was possibly slightly more elevated than those of the surrounding area. In addition, through percolation of surface water down through the sediments, or more likely through the action of capillarity up from the lowered water table, calcium carbonates were concentrated in a narrow band just below the red beds and slightly above the level of the new water table. The increased concentration of calcium carbonates led to the mineralization and preservation of the animal remains in this horizon, while those in the undifferentiated swelling clays above and below were largely destroyed (see Verniers, this volume, Chapter 2 for further details). There is no evidence that the fossils were deposited in a subaerial setting. In fact, such a suggestion is contradicted by the preservation of the fossils, which show no evidence of the kinds of damage that are typical of bones exposed on the surface of a paleosol (see below for further discussion of this topic). They were evidently deposited in an aquatic environment and then covered with fine sediments within a short time of decomposition of the soft tissues.

The geological evidence and the preponderance of aquatic and hydrophilic vertebrates, discussed below, clearly indicate a lake fringe setting. The fossil site appears to be situated on a more elevated portion of the lake floor in close proximity to a low island chain in the center of the lake (Harrison and Verniers, 1993; Harrison and Mbago, this volume, Chapter 1; Verniers, this volume, Chapter 2). It probably represents the remains of a shallow, swampy lake shelf, with seasonally emergent mud flats and levees.

Trial excavations conducted at Tinde, as well as observations based on material exposed at the surface, but still *in situ*, confirm the initial finding of Grace and Stockley (1931) that full-scale excavations at the site are not practical. The major problems are that (1) the matrix containing the fossils is extremely hard, making the extraction of complete bones a difficult and very time-consuming enterprise, and (2) the bones are disarticulated, isolated elements scattered randomly throughout the fossiliferous horizon, without the occurrence of dense concentrations or partial skeletons (see below). The best way to recover fossils at the site is to collect them from the surface after they have weathered out, or to excavate them from *in situ*, as they become exposed on the surface.

Due to the calcareous nature of the sediments, the bones are heavily mineralized and extremely brittle. Trial excavations have revealed that the bones are usually preserved *in situ* as whole, but disarticulated, elements, and that as they weather out the long-bone shafts and other delicate bones tend to fragment and splinter rather quickly. In fact, very few entire limb bones were recovered from the surface, typically only their more compact articular ends are preserved. By contrast, robustly constructed bones, such as podials, metapodials, and phalanges have a high rate of recovery (see Tables II–IV). Material recovered *in situ* is very well preserved with smooth external surfaces, and none of the specimens shows any indication of predepositional weathering, or abrasion and rolling due to transportation in a fluvial setting. In addition, there is no evidence of carnivore or crocodile bite marks or gnawing by rodents.

Table II. Recovery Rate of Bovid Skeletal Elements at Tinde

Element	NISP[a]	Frequency[b]	MNI[c]	Recovery rate[d]
Glenoid of scapula	29	2	15	13.2
Proximal humerus	4	2	2	1.8
Distal humerus	35	2	18	15.9
Proximal ulna	5	2	3	2.3
Proximal radius	16	2	8	7.2
Distal radius	6	2	3	2.7
Innominate fragments	12	2	6	5.5
Proximal femur	17	2	9	7.7
Distal femur	19	2	10	8.6
Proximal tibia	6	2	3	2.7
Distal tibia	25	2	13	11.4
Fibula	8	2	4	3.6
Patella	0	2	0	0.0
Astragalus	219	2	110	99.5
Calcaneus	79	2	40	35.9
Other podials	126	14	9	8.2
Metapodials	144	8	18	16.4
Phalanges	144	8	18	16.4
Vertebrae	77	30	3	2.3
Cheek teeth	100	24	5	4.5
Horn cores	100	2	50	45.5

[a] Number of individual specimens.

[b] The number of elements expected in a single individual.

[c] Minimum number of individuals.

[d] The recovery rate represents the actual number of recovered elements expressed as a percentage of the expected number of elements based on the maximum MNI for the species.

Table III. Recovery Rate of Hippopotamid Skeletal Elements at Tinde

Element	NISP[a]	Frequency[b]	MNI[c]	Recovery rate[d]
Glenoid of scapula	3	2	2	25.0
Proximal humerus	2	2	1	16.7
Distal humerus	6	2	3	50.0
Proximal ulna	0	2	0	0.0
Proximal radius	3	2	2	25.0
Distal radius	2	2	1	16.7
Innominate fragments	7	2	4	58.3
Proximal femur	0	2	0	0.0
Distal femur	0	2	0	0.0
Proximal tibia	1	2	1	8.3
Distal tibia	5	2	6	41.7
Fibula	0	2	0	0.0
Patella	2	2	1	16.7
Astragalus	12	2	6	100.0
Calcaneus	11	2	6	91.7
Other podials	50	22	3	37.9
Metapodials	45	16	3	46.9
Phalanges	69	48	2	24.0
Vertebra	24	30	2	13.3
Cheek teeth	56	28	2	33.3

[a] Number of individual specimens.

[b] The number of elements expected in a single individual.

[c] Minimum number of individuals.

[d] The recovery rate represents the actual number of recovered elements expressed as a percentage of the expected number of elements based on the maximum MNI for the species.

Table IV. A List of Bovid and Hippopotamid Skeletal Elements from Tinde Ranked According to Their Recovery Rate

Bovidae		Hippopotamidae	
Element	Recovery rate[a]	Element	Recovery rate[a]
Astragalus	99.5	Astragalus	100.0
Horn cores	45.5	Calcaneus	91.7
Calcaneus	35.9	Innominate fragments	58.3
Phalanges	16.4	Distal humerus	50.0
Metapodials	16.4	Metapodials	46.9
Distal humerus	15.9	Distal tibia	41.7
		Other podials	37.9
		Cheekteeth	33.3
		Glenoid of scapula	25.0
		Proximal radius	25.0
		Phalanges	24.0
		Distal radius	16.7
		Proximal humerus	16.7
		Patella	16.7

[a] The recovery rate represents the actual number of recovered elements expressed as a percentage of the expected number of elements for the highest minimum number of individuals (MNI). Only those elements with a recovery rate greater than 15% are included here. For a full listing see Tables II and III.

It is pertinent to note here that when the fossils are grouped according to their degree of susceptibility to fluvial transportation (Voorhies, 1969; Behrensmeyer, 1975), Group I skeletal elements (i.e., ribs, vertebrae, sacra, sterna, and sesamoid bones, including patellae), which have the highest tendency to be transported, are distinctly underrepresented in the Tinde collections (see Tables II and III). This could support the interpretation that winnowing by flowing water may have selectively removed these elements from the depositional context. However, the low incidence of these elements is more likely to be due to a collecting bias. Ribs and vertebrae, which make up the most significant component of Group I elements, when fragmentary, are likely to be left in the field as unidentifiable fossils. As noted above, an absence of fluvial transportation is also supported by the preservation of the bones, as well as by the lithological evidence (i.e., homogeneous and fine-grained clays, without evident bedding structure).

The sample of excavated materials is relatively small, but it is evident from these preliminary data that long bones tend to be positioned horizontally within the beds. A minority of bones was found to be steeply inclined, suggesting the possibility that large mammals wading in the shallow waters may have accidentally impacted them into the soft sediments at the bottom of the lake. In addition, the bones do not exhibit any distinct alignment of their long axis that would imply orientation by the action of currents. Although no articulated skeletons or partial skeletons have been recovered at Tinde, a number of well-preserved skulls of bovids have been found with postcranial elements of the same species in close association. These may constitute the remains of single individuals in which the skeleton has been disarticulated and jumbled together. In addition, on top of a low mound just to the south of the cliff at Tinde East a dense concentration of fragmentary and weathered bones composing the associated cranial and postcranial elements of a hippopotamid individual was recovered in 1994.

In an attempt to obtain quantitative data on the scatter and degree of breakage of the bones at the site, a program of controlled surface collection was carried out during the 1992 field season. A transect grid, made up of 56 squares, each measuring 10 × 10 m, was laid down to cover the southern portion of the main fossiliferous exposure at Tinde West and across the gap separating Tinde West from Tinde East (Fig. 2). Each transect square was searched intensively by three collectors in succession for a total period of up to 40 minutes. During this time every exposed fossil was collected. A total of 18,274 bones and bone fragments was recovered (Table V). The average density of bones in the transect area was 3.26/m^2, with densities ranging from 0.36/m^2 to 11.33/m^2. However, it is important to note that these numbers represent minimum densities, as it was not possible to collect all of the bone fragments in the time allotted, and the number of fragments would have increased dramatically if the surface debris had been screened. Nevertheless, the results do provide a crude, but reasonable, approximation of the density, distribution and patterns of fragmentation of fossil bones at Tinde.

The main findings of the controlled surface collection can be summarized as follows: (1) Mammalian bones make up 55.0% of all of the fossils collected, while fish and reptiles represent 41.2% and 3.7%, respectively (Table V); (2) the total number of bones recovered is greatest within 40 m of the cliff face at Tinde West,

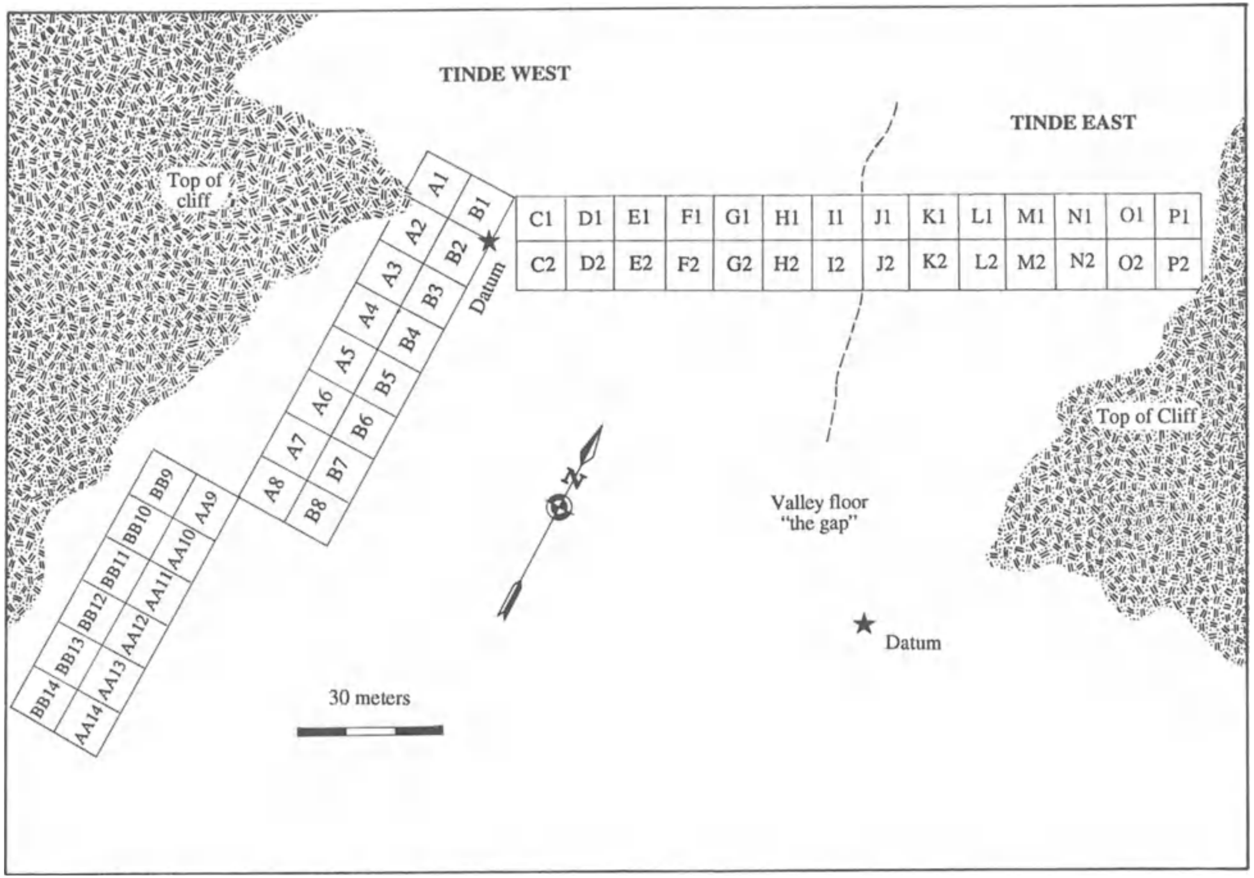

FIGURE 2. Schematic map showing the location of the transect grid used in the controlled surface collection at Tinde. The dividing line between Tinde East and Tinde West placed between squares I and J represents the lowest topographic level in the gap between the two bluffs.

Table V. Number of Bones Recovered from the Controlled Surface Collection at Tinde

	Fish	Reptiles			Mammals		
Square	Total	Turtle scutes	Croc. bones	Croc. teeth	Ident.	Indet.	Total
A1	231	1	2	0	18	45	63
A2	358	6	1	0	17	76	93
A3	263	4	0	2	7	82	89
A4	163	5	9	1	15	142	157
A5	134	7	2	2	7	123	130
A6	106	9	0	0	9	121	130
A7	187	15	0	0	10	205	215
A8	196	31	7	3	17	215	232
B1	327	5	1	1	10	141	151
B2	147	2	1	0	11	166	177
B3	116	1	0	0	2	124	126
B4	116	6	6	2	5	293	298
B5	36	7	2	0	10	335	345
B6	122	6	0	0	2	210	212
B7	578	18	0	4	17	516	533
B8	483	27	7	3	17	366	383
C1	12	10	0	0	9	294	303
C2	13	4	0	0	5	85	90
D1	28	4	0	0	13	453	466
D2	12	6	0	0	8	286	294
E1	18	0	0	0	6	134	140
E2	4	0	0	0	4	138	142
F1	20	1	0	0	6	204	210
F2	11	0	0	0	4	140	144
G1	15	0	0	0	3	40	43
G2	7	0	0	0	0	44	44
H1	14	2	0	0	0	68	68
H2	8	0	0	0	2	79	81
I1	16	0	0	0	1	59	60
I2	15	0	0	0	0	21	21
J1	18	0	0	0	0	58	58
J2	24	0	0	0	2	59	61
K1	57	0	0	0	2	63	65
K2	34	16	0	0	1	77	78
L1	73	0	0	0	0	64	64
L2	103	0	0	0	5	140	145
M1	37	1	1	0	0	78	78
M2	33	0	0	0	3	96	99
N1	69	6	3	0	4	96	100
N2	65	1	2	0	1	66	67
O1	40	11	0	0	2	64	66
O2	24	8	0	0	8	43	51
P1	43	17	0	0	0	45	45
P2	21	36	1	1	0	43	43

(*continued*)

Table V. (Continued)

	Fish	Reptiles			Mammals		
Square	Total	Turtle scutes	Croc. bones	Croc. teeth	Ident.	Indet.	Total
AA9	371	9	3	3	14	306	320
AA10	246	12	2	2	7	332	339
AA11	601	24	3	2	11	400	411
AA12	410	43	9	4	19	440	459
AA13	268	14	15	1	10	384	394
AA14	197	6	4	2	15	164	179
BB9	265	12	5	1	18	200	218
BB10	142	59	0	3	35	356	391
BB11	232	36	0	0	26	306	332
BB12	126	40	2	1	15	204	219
BB13	143	9	6	3	15	164	179
BB14	139	11	0	1	9	148	157
Total	7537	543	94	42	457	9601	10,058
% of Total bones and teeth	41.2	3.0	0.5	0.2	2.5	52.5	55.0

Abbreviations: Ident., identifiable bones; Indet., indeterminate bones; Croc., crocodile; Sq., transect square.

and the number declines sharply toward the center of the gap (Fig. 3); (3) Tinde East is much less productive than Tinde West, probably because (a) the cliff face is less steeply inclined, (b) the fossil horizon is located at a lower level on the cliff face, and (c) as a result, the fossil bed is covered with a thicker layer of detritus, which results in a much slower rate of erosion; (4) the bones from the middle of the gap exhibit a much higher degree of breakage than those recovered closer to the cliff face, and the proportion of more compact mammalian bones (i.e., podials, metapodials, phalanges, distal humeri, and bovid horn cores) increases significantly (Table VI); (5) the degree and type of breakage and abrasion suggest that the thin scatter of bones recovered from the middle of the gap has been transported primarily by the trampling effects of domestic cattle, although the action of heavy seasonal rains should not be discounted as an important factor in the redistribution of bones after they have eroded out of the fossil beds; (6) the data suggest that fossil fish remains are much more prone to fragmentation and are much less easily transported than many mammal bones because they are only found in high concentrations within 20 m of the cliff face (Fig. 3); and (7) differences in the densities of bones at Tinde West indicate that the bones may be eroding out of the fossil bed in different concentrations in different parts of the site.

We may conclude from these observations that the bones were not exposed to scavenging or weathering prior to deposition. It seems likely, therefore, that

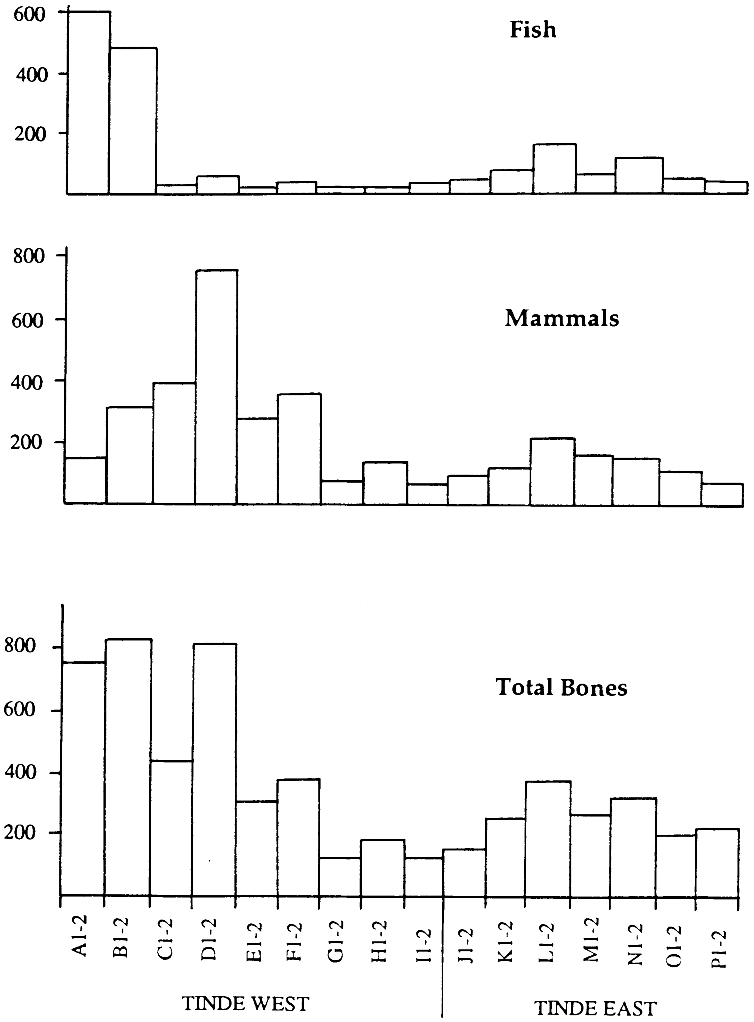

FIGURE 3. Histogram showing the frequency and distribution of bones across the gap at Tinde, based on the results of the controlled surface collection. The vertical axis represents the number of individual bones collected. The horizontal axis represents the transect squares depicted in Fig. 2.

the animals were introduced into the lake as whole carcasses. Disarticulation of the skeleton may have occurred as the soft tissue decomposed, or as the result of random drift of individual bones subsequent to decomposition. From the preservation and orientation of the individual bones it does not appear that fluvial currents were a major factor in distributing or concentrating the bones. As discussed above, a certain amount of postdepositional damage to surface material may be attributable to trampling by cattle, and large bones exposed on the surface for some time develop a heavy white patination, and exhibit a combination of splits, cracks, and heavy pitting caused by erosion and weathering

Table VI. Analysis of the Degree of Breakage of Bones across the Gap at Tinde

	Fish		Mammals			
Squares	Total	% of max.	Ident.	Indet.	Total	% Indet.
A1 & A2	488	100.0	35	121	156	77.6
B1 & B2	429	87.9	21	307	328	93.6
C1 & C2	25	5.2	14	379	393	96.4
D1 & D2	40	8.2	21	739	760	97.2
E1 & E2	22	4.5	10	272	282	96.5
F1 & F2	31	6.4	10	344	354	97.2
G1 & G2	22	4.5	3	84	87	96.6
H1 & H2	22	4.5	2	147	149	98.7
I1 & I2	31	6.4	1	80	81	98.8
J1 & J2	42	8.6	2	117	119	98.3
K1 & K2	91	18.6	3	140	143	97.9
L1 & L2	176	36.1	5	204	209	97.6
M1 & M2	70	14.3	3	174	177	98.3
N1 & N2	134	27.5	5	162	167	97.0
O1 & O2	64	13.1	10	107	117	91.5
P1 & P2	64	13.1	0	89	89	100.0

Abbreviations: max., squares with the highest total number of bones; Ident., identifiable bone; Indet., indeterminate bone. Totals represent number of individual bones recovered.

processes. In consequence, the best-preserved material is obtained from *in situ* or from the talar slope of the cliff face soon after it has eroded out of the fossil bed.

The large collections from Tinde include almost two thousand taxonomically identifiable mammal specimens. Yet, despite the relative abundance of fossils, the mammalian fauna is not particularly diverse. Only 11 species are represented (Fig. 4). Bovids are by far the most common group of mammals at the site (the three species represented constitute 70.0% of all mammals), followed in importance by hippopotamids (23.7%), proboscideans (2.5%), and suids (2.2%). Equids, giraffids, and carnivores are represented, but are relatively rare elements in the fauna (Table VII). One reason for such a low taxonomic diversity might stem from a taphonomic bias against the preservation of mammals of small size. The complete absence of micromammals from the entire Tinde Member, despite programs of intensive screening at several sites, and the fact that all of the mammals, with few exceptions, are taxa of large to medium size, would lend support to such an inference. In fact, at Tinde, the smallest mammal represented (with the exception of a small carnivore) is a medium-size bovid (with an average body weight of about 100 kg), referred to as *Kobus* aff. *subdolus* by Gentry (this volume, Chapter 5). This strong bias toward mammals of relatively large size might be due to factors inherent in the formation of the sediments, whereby small and fragile bones are differentially destroyed. In addition, the scenario proposed above, that whole carcasses were transported prior to disarticulation of the

- Mammalia
  - Artiodactyla
    - Bovidae
      - *Kobus* aff. *subdolus*
      - ?*Tragelaphus* sp.
      - *Damalacra* sp.
    - Giraffidae
      - *Giraffa* sp.
      - ?*Sivatherium* sp.
    - Suidae
      - *Nyanzachoerus kanamensis*
    - Hippopotamidae
      - *Hexaprotodon harvardi*
      - *Hexaprotodon*, small species
  - Perissodactyla
    - Equidae
      - *Eurygnathohippus* sp.
  - Proboscidea
    - Elephantidae
      - indet.
  - Carnivora
    - Viverridae
      - indet.
- Aves
  - indet.
- Reptilia
  - Chelonia
    - Trionychidae
      - indet.
    - Pelomedusidae
      - indet.
  - Crocodylia
    - Crocodylidae
      - *Crocodylus* sp.
- Osteichthyes
  - Siluriformes
    - Clariidae
      - *Clarias* sp.
  - Dipnoi
    - Protopteridae
      - *Protopterus* sp.

FIGURE 4. Faunal list from Tinde East and Tinde West (Tinde Member). Source: Chapters 5–13, this volume.

skeleton and incorporation of individual bones into the sediments, would certainly favor a taphonomic bias toward mammals of large body size.

However, at least one further line of evidence indicates that ecology, rather than taphonomy, may have been a key factor in contributing to the impoverished faunal diversity at Tinde. Among the large mammals, two species, *Kobus* aff. *subdolus* and *Hexaprotodon harvardi*, are remarkably common, and together they make up 82.2% of the mammalian fauna. Based on their modern counter-

Table VII. Frequency (%) of Specimens of Mammalian Taxa at the Main Locality Complexes in the Manonga Valley

	Tinde West, Tinde East	Kiloleli 1–4	Inolelo 1–3, Shoshamagai 2	Wembere–Manonga Formation (all sites)
Bovidae	70.0	22.5	22.0	45.8
Giraffidae	1.2	0.4	0.6	0.9
Suidae	2.2	2.8	24.1	9.2
Hippopotamidae	23.7	20.8	15.4	20.5
Equidae	0.3	16.5	3.0	4.2
Rhincerotidae	0.0	22.6	0.0	4.3
Proboscidea	2.5	13.1	29.8	13.1
Rodentia	0.0	0.0	3.9	1.2
Carnivora	0.1	1.1	1.3	0.6
Primates	0.0	0.1	0.0	0.1
Total %	100.0	99.9	100.1	99.9
Number of specimens	1929	691	852	3984

parts, these two species presumably shared a preference for lakeshore, riverine, and swampy habitats. Such a scenario fits perfectly with the reconstructed environment based on sedimentologic and geomorphological evidence. The depositional setting at Tinde can be inferred to be one of a shallow, permanently flooded lake shelf, located near small, low-lying islands in the center of the lake basin. This would have been accessible only to mammals that were strong swimmers, such as *Kobus* and *Hexaprotodon*. The occurrence of proboscideans and suids in reasonable numbers, and the extreme rarity of the more cursorial equids, rhinocerotids, and carnivores would be consistent with this paleoecological reconstruction.

Fossil fish are ubiquitous at Tinde, but despite their abundance they exhibit a remarkably low taxonomic diversity, with only two genera represented (Fig. 4; Stewart, this volume, Chapter 11). *Clarias*, a clariid catfish, dominates the ichthyofauna, and constitutes over 95% of all specimens collected. It is extremely common at the site, with cranial and postcranial elements well represented. In fact, dense concentrations of *Clarias* are found eroding out throughout the fossiliferous horizon, and at Tinde East resistant nodules of darkly stained calcareous clay preserve large numbers of almost complete skulls and other skeletal elements. Since such nodules are uncommon at Tinde West, a subtle difference in facies or diagenesis between Tinde East and Tinde West is implied. The only other genus of fish recorded at Tinde is *Protopterus*, the African lungfish. Although taphonomic factors might favor the preservation of large and robust fish elements at Tinde, the fact that intensive microscreening has failed to yield any trace of additional taxa suggests that the original fish fauna was taxonomically impoverished, possibly as a result of suboptimal environmental conditions. Stewart (this volume, Chapter 11) notes that *Clarias* and *Protopterus*, both air-breathers, are tolerant of deoxygenated and swampy conditions that could not otherwise support fish. Abundant remains of freshwater turtles and the occurrence of large crocodiles at Tinde similarly indicate a shallow-water lacustrine environment.

Interestingly, fossil mollusks and other invertebrate remains are entirely absent from Tinde. Several shell fragments of bivalve mollusks have been recovered by WMPE from the surface, and Stockley (1930) and Grace and Stockley (1931) report finding a broken internal cast of a freshwater gastropod, which they attribute to *Viviparus*. However, these specimens are almost certainly derived from late Pleistocene or Holocene deposits. Bivalves and gastropods, similar in preservation to those from Tinde, and with identical adhering matrix, occur quite commonly throughout the Manonga Valley, associated with superficial layers of mbuga clay (see Van Damme and Gautier, this volume, Chapter 12; Harrison and Baker, this volume, Chapter 13). The absence of mollusks at Tinde may be due to the same environmental circumstances that appear to have negatively impacted on the diversity of the fish fauna, namely, swampy, poorly oxygenated conditions. However, Van Damme and Gautier (this volume, Chapter 12) suggest an alternative possibility that during the diagenesis of the swelling clays differential destruction of mollusks may have occurred. This could well be an important contributing factor, but we do know that fossil mollusks are found at sites, such as Kininginila (see below), from similar horizons within the Tinde Member (Van Damme and Gautier, this volume, Chapter 12).

Other localities in the Manonga Valley with fossiliferous horizons that correlate with the Tinde Member are much less productive, and in general terms their faunas are consistent with those from Tinde. However, several sites, including Ipembe, Kininginila, and Nyawa, do present an interesting contrast, and provide further insight into the paleoecology and taphonomy of the Tinde Member. The main differences among the mammalian faunas are that equids occur more commonly at these sites than they do at Tinde, and there is a higher taxonomic diversity of bovid species represented. Even though the samples are small, these differences are striking enough to signify a difference in paleoecology. Unlike Tinde, Kininginila has also yielded a diverse fish and molluscan fauna that suggests a shallow, well-oxygenated open lake, with densely vegetated, swampy margins (Stewart, this volume, Chapter 11; Van Damme and Gautier, this volume, Chapter 12). The paleoecological evidence therefore suggests that Kininginila represents a similar shallow lake setting to that inferred for Tinde, but one that was less swampy and more permanent, and perhaps closer to the shoreline of an emergent land surface. No mollusks have been recovered from Nyawa, but the occurrence of cichlids supports similar open-water conditions (Stewart, this volume, Chapter 11).

Finally, it is worth mentioning the unusual occurrence of micromammals from the Tinde Member at Mwambiti 5. The site consists of a low eroded hillock that rises less than 5 m above the general floor of the Manonga Valley. The exposed Tinde Member beds consist of a series of swelling clays with alternating thin bands of hard calcareous clays that rest conformably on the red beds of the Ibole Member. In 1994 Bill Sanders (University of Michigan) discovered some well-preserved cranial and postcranial remains of at least two individuals of a species of small murid eroding out of the base of the hillock. Their good preservation, even of such fragile elements as vertebrae and ribs, and their close association indicates that they were only recently exposed on the surface, and that they had not been transported from their original site of deposition. The fossils were evidently derived from the swelling clays at the base of the Tinde Member, from an horizon only 1.7 m above the top of the Ibole Member. This layer is unusual in having a reddish tinge, which may imply that the fossil horizon had emerged subaerially soon after its deposition. At the time of the initial discovery no other bones were recovered, and screening of the sediments proved unsuccessful. During a second visit to the site a number of fragmentary fish bones were recovered, which were evidently derived from the Tinde Member. The rodent bones are heavily mineralized and light gray to bluish in coloration, with darkly stained teeth, typical of fossil mammals from the Tinde Member. This discovery is unique in a number of respects: (1) Micromammals are otherwise entirely unknown from the Tinde Member, (2) associated skeletal materials are extremely rare from the Manonga Valley, and (3) the rodent bones were the only mammals found at the site. These point to an unusual taphonomic occurrence, one that could best be explained as the preservation of entire rodent skeletons buried in a burrow, or perhaps the remains of one or more owl pellets.

4. Taphonomy and Paleoecology at Kiloleli (Kiloleli Member)

The complex of sites in the vicinity of the village of Kiloleli, designated as Kiloleli 1 to 4, are second in importance only to Tinde in terms of their paleontological productivity (Table I). The sites consist of a series of low cliffs and slopes that become increasingly shallow as they pass northward from the most elevated promontory at Kiloleli 4, which flanks the northern margin of the Precambrian base of Shoshamagai Hill, to the low and poorly exposed slopes at Kiloleli 1. The outcrops consist of a series of hard calcareous bands intercalated within a thick layer of light gray swelling clays. The uppermost hard clay band is dark gray to almost white in color, and appears to be unfossiliferous. Just below this is a similar, but slightly thicker, clay layer, densely packed with the fragmentary remains of fossil fish, turtles, and crocodiles. Bones of mammals are also preserved, but appear to be relatively uncommon. Below this is a series of hard bands, including a conglomerate, up to 50 cm in thickness, with poorly sorted pebbles up to several centimeters in diameter. These compose the primary fossiliferous beds at Kiloleli. In addition to bones and teeth of fish and aquatic reptiles, those of mammals are quite common and well preserved. In addition, at Kiloleli 1 the conglomerate contains small bivalves attributable to *Spathopsis wahlbergi*.

The sediments were deposited in a shallow but relatively stable lake. The occurrence of a coarse and poorly sorted conglomerate implies that the depositional setting was located close to the shoreline of the lake. Such littoral facies are absent from the center of the basin during deposition of the Tinde Member, and this may mean that Lake Manonga was relatively much smaller during Kiloleli times. Alternatively, the conglomerates may have been deposited along the shoreline of an island within the lake itself. The Precambrian rocks that form the base of Shoshamagai Hill, as well as of Kiloleli Hill just to the north, would certainly have been high enough to produce low-lying islands at a time when the lake was relatively shallow. However, the lithologic evidence from other sites of similar age supports the inference that the lake basin was shallower and more restricted during deposition of the Kiloleli Member. In the eastern portion of the basin, at the localities of Ngofila and Beredi South, the Kiloleli Member consists of a combination of shallow lake margin, deltaic and floodplain facies, as well as paleosols (Verniers, this volume, Chapter 2). At this time, it is conceivable that Lake Manonga covered an area of only 1500 km^2, less than one sixth of its maximal extent during deposition of the Tinde Member. This recession of the lake may have been due, at least in part, to silting up and infilling of the original lake basin, but probably also reflects changes in the local drainage patterns, possibly correlated with increased tectonic activity to the northeast (see Harrison and Mbago, this volume, Chapter 1).

As at Tinde, the bones are heavily mineralized and extremely brittle, and the best material has been recovered as surface finds after it has eroded out of the hard encasing matrix. More than six hundred identifiable mammals have been recovered, which constitute 17.3% of the entire mammalian fauna from the Manonga Valley (Table I). The fauna from Kiloleli is quite different from that recovered from Tinde (Table VII and Fig. 5). Differences in the species-level taxonomy of several of the major groups of mammals clearly reflects what appears to be a temporal difference between the Kiloleli and Tinde Members (see Harrison and Baker, this volume, Chapter 13). More important from a paleoecological perspective is that the faunas indicate differences in habitat structure between Tinde and Kiloleli. Compared with Tinde, where bovids and hippopotamids compose more than 90% of the fauna, at Kiloleli these two groups represent only 43.3% of the mammalian fauna. By contrast, perissodactyls and proboscideans, which are rare at Tinde (making up only 2.8% of the mammalian specimens), are much more abundant at Kiloleli (52.1%) (Table VIII). This suggests that the paleoecology at Kiloleli is representative of more open-country habitats. A further important distinction between the two site complexes is provided by the composition of the bovid community. The fauna from Kiloleli is dominated by alcelaphines (61.1% of all bovid specimens), while that at Tinde is predominantly composed of reduncines (83.6%). Comparisons of modern African faunas show that there is a relationship between the frequency of alcelaphines and reduncines and habitat types. Using census data from modern African wildlife preserves (Shipman and Harris, 1988), it is possible to calculate the relative frequency of these two groups in different habitats (the r/a index = reduncines × 100/reduncines + alcelaphines). An r/a index higher than 20 is found in habitats that are dominated by woodlands, while a lower index is typical of bushland and grassland habitats. An r/a index of only 15 for the bovid community at Kiloleli suggests that bushland and open country were the primary habitats available. By contrast, Tinde has an r/a index of 84, which clearly

Mammalia			
	Artiodactyla		
		Bovidae	
			Kobus aff. *subdolus* *Praedamalis* sp. *Damalacra* sp. Alcelaphini, larger species Alcelaphini, smaller species *Aepyceros* sp.
		Giraffidae	
			?Sivatherium sp.
		Suidae	
			Nyanzachoerus kanamensis
		Hippopotamidae	
			Hexaprotodon harvardi
	Perissodactyla		
		Equidae	
			Eurygnathohippus aff. *hasumense*
		Rhinocerotidae	
			Ceratotherium praecox.
	Proboscidea		
		Gomphotheriidae	
			Anancus sp.
		Elephantidae	
			Loxodonta cf. *exoptata* *Elephas ekorensis*
	Primates		
		Cercopithecidae	
			indet.
Reptilia			
	Chelonia		
		Trionychidae	
			indet.
		Pelomedusidae	
			indet.
	Crocodylia		
		Crocodylidae	
			Crocodylus sp.
Osteichthyes			
	Siluriformes		
		Clariidae	
			Clarias sp.
	Dipnoi		
		Protopteridae	
			Protopterus sp.
Mollusca			
	Bivalvia		
		Mutelidae	
			Spathopsis wahlbergi

FIGURE 5. Faunal list from Kiloleli 1–4 (Kiloleli Member). Source: Chapters 5–13, this volume.

confirms a woodland setting. Similar comparisons using data on modern bovid communities have been used to infer the paleoecology at Plio-Pleistocene sites in East and South Africa (Vrba, 1980, 1985; Shipman and Harris, 1988), but it is uncertain just how far back into the Neogene such analogies can usefully be applied. However, the fact that paleoecological inferences based on the fossil bovids at Kiloleli and Tinde are consistent with other lines of evidence indicates that at least some aspects of the habitat preferences of modern bovid tribes are applicable to these late Miocene communities.

In conclusion, the mammal fauna indicates that Kiloleli represents a drier, more open country habitat than that at Tinde. Even so, the occurrence at Kiloleli of reduncines, along with significant numbers of suids and hippopotamids with dentitions evidently adapted for browsing, implies that bushland–woodland habitats were still available. The evidence best fits a scenario of a relatively dry, densely vegetated bushland and woodland, with broad tracts of more humid woodlands fringing the lake basin and associated river systems. As discussed above, drier conditions during deposition of the Kiloleli Member may be a direct consequence of reduction in the size of the lake, which would have made it much more susceptible to periods of regression and to changes in the local hydrological system. Another possibility is that shrinkage of the lake and increasing aridity are both a consequence of wider climatic changes.

Evidence for paleoecological inference derived from nonmammalian taxa is rather limited. Fossil fish remains are extremely common at Kiloleli, but they are not taxonomically diverse (Stewart, this volume, Chapter 11). Just like the fauna at Tinde, Kiloleli is dominated by lungfish and clariid catfish, which suggests that the lake was relatively swampy and poorly oxygenated. A similar conclusion might be drawn from the fact that crocodiles appear to be relatively less common. At Kiloleli and Tinde, for example, the ratio of craniodental remains of crocodiles to mammalian remains is 8:100 and 3:100, respectively, while at Shoshamagai and Inolelo (Ibole Member), at which open-water conditions are inferred, crocodiles are much more abundant, with a ratio of 24:100.

As noted by Harrison (1991), the individual sites at Kiloleli appear to represent a south–north gradient of facies ranging from nearshore deposits at Kiloleli 4 to open lake deposits at Kiloleli 1. This inference is also supported by the differential distribution of fossil mollusks. At Kiloleli 1, large to medium-size bivalves belonging to the genus *Spathopsis* are relatively common, and their distribution and preservation clearly indicate an autochthonous assemblage. The occurrence of *Spathopsis* suggests open-water conditions in a shallow (less than 20 m in depth), well-oxygenated lake (Van Damme and Gautier, this volume, Chapter 12). By contrast, fossil mollusks are absent from the main exposures at Kiloleli 2–4, and this supports the evidence derived from the ichthyofauna that the shallow margin of the lake was swampy and poorly oxygenated.

Samples of fossils from the Kiloleli Member have also been obtained from other sites in the Manonga basin. The most important of these, at least from a paleoecological perspective, are Ngofila 2, Ngofila 4, and Beredi South 1. The mammal faunas at these sites are relatively small, but they appear to be identical in composition to those at Kiloleli. As at Kiloleli, rhinocerotids and equids are especially common. Beredi South 1 is of interest in that an almost complete cranium of *Eurygnathohippus* has been recovered from the site, in association with a partial forelimb (Bernor and Armour-Chelu, this volume, Chapter 8), probably derived from the same individual. Specimens recovered *in situ* at Kiloleli suggest that preservation at the site is similar to that at Tinde, in which bones are preserved broken or entire, but usually dissociated from other elements of the same individual. The equid material from Beredi South is unusually well preserved compared with that from Kiloleli, and it indicates a slightly different depositional setting and taphonomic history.

A somewhat different perspective on the paleoecology of the Kiloleli Member is provided by fossil evidence from Ngofila. In the upper part of the Kiloleli Member at Ngofila 2, there is a light brown-yellow clay horizon, less than 2 m in thickness, which is densely packed with fossil mollusks. The molluscan fauna from this site is quite diverse, a representative sample of which has been studied by Van Damme and Gautier (this volume, Chapter 12). Based on the habitat preferences of their modern counterparts, the gastropods indicate shallow, well-oxygenated, swampy conditions at the margin of the lake, with relatively dense plant growth. The fish fauna, however, is identical to that from Kiloleli in being impoverished, with only *Clarias* and *Protopterus* represented (Stewart, this volume, Chapter 11). Another interesting feature of the gastropod horizon at Ngofila 2 is that it provides clear evidence that soon after deposition of the lacustrine sediments, the lake underwent a period of recession, with subsequent paleosol formation. The common occurrence of root casts up to 10 mm in diameter indicates that the soft, fine-grained sediments provided an ideal substrate (presumably still located close to the water table) for the growth of large woody plants. It also provided a suitable matrix for nest-building Hymenoptera. Flask-shaped brood cells of solitary bees, similar to those described from the early Pliocene of Laetoli, northern Tanzania, are relatively common (Ritchie, 1987). All brood cells observed *in situ* are vertically aligned with their caps positioned superiorly, indicating that they have been preserved in their original life position. Similarly, at Nyawa (to the northwest of the main site) there is a thin horizon of hard calcareous clay in the upper part of the Kiloleli Member that preserves numerous vertical tunnels, presumably made by burrowing invertebrates. The nature of the sediments and the construction of the burrows suggest that they were made subaerially by insects, probably termites.

The main conclusion that we can draw from a synthesis of the geological and paleontological evidence from the Kiloleli Member is that the lake at this time was relatively small and quite shallow, with swampy, lake-margin facies located close to the center of the basin. Evidence of paleosols intercalated between lacustrine horizons demonstrates that the lake also underwent periods of regression. In conjunction with a reduction in the extent of the lake, the surrounding area appears to have become somewhat drier, with predominantly woodland habitats being succeeded by a woodland–bushland mosaic.

5. Taphonomy and Paleoecology at Shoshamagai and Inolelo (Ibole Member)

Shoshamagai 2 and Inolelo 1–3, making up a complex of sites on the northern side of the Manonga Valley, are the most productive fossil localities associated with the Ibole Member (Table I and Fig. 6; Harrison, 1993; Harrison and Mbago, this volume, Chapter 1). The fossils are all derived from a thick bed of ferruginous clays, exposed by erosion on the floor of the valley (Harrison and Mbago, this volume, Chapter 1; Verniers, this volume, Chapter 2). These are the oldest fossiliferous deposits so far discovered in the Manonga Valley. The four localities represent disjunct outcrops of the same fossiliferous horizon, and the material

- Mammalia
  - Artiodactyla
    - Bovidae
      - *?Tragelaphus* sp.
      - *Kobus* aff. *porrecticornis*
      - *Praedamalis* sp.
      - *Damalacra* sp.
      - Alcelaphini, smaller species
    - Suidae
      - *Nyanzachoerus kanamensis*
    - Hippopotamidae
      - *Hexaprotodon harvardi*
  - Perissodactyla
    - Equidae
      - *Eurygnathohippus turkanense*
      - *Eurygnathohippus* cf. "*sitifense*"
  - Proboscidea
    - Gomphotheriidae
      - *Anancus kenyensis*
    - Elephantidae
      - *Primelephas gomphotheroides*
      - *Stegotetrabelodon* sp.
  - Carnivora
    - Felidae
      - *Machairodus* sp.
  - Rodentia
    - Thryonomyidae
      - *Thryonomys* sp.
    - Muridae
      - *Saccostomus major*
      - *Tectonomys africanus*
      - *Saidomys parvus*

FIGURE 6. Faunal list from Shoshamagai and Inolelo 1–3 (Ibole Member). Source: Chapters 5–13, this volume.

- Aves
  - indet.
- Reptilia
  - Chelonia
    - Trionychidae
      - indet.
    - Pelomedusidae
      - indet.
  - Crocodylia
    - Crocodylidae
      - *Crocodylus* sp.
- Osteichthyes
  - Siluriformes
    - non-clariid indet.
    - Clariidae
      - *Clarias* spp.
  - Perciformes
    - Cichlidae
      - indet.
  - Characiformes
    - Characidae
      - *Hydrocynus* sp.
      - *Alestes* spp.
  - Dipnoi
    - Protopteridae
      - *Protopterus*
- Mollusca
  - Gastropoda
    - Viviparidae
      - *Bellamya* aff. *capillata*
    - Ampullariidae
      - *Pila ovata*
      - *Lanistes ovum*
    - Thiaridae
      - *Cleopatra* aff. *ferruginea*
  - Bivalvia
    - Mutelidae
      - *Spathopsis wahlbergi*
      - *Mutela dubia*

FIGURE 6. (Continued)

recovered can all be assumed to represent a single fauna (Fig. 6). Moreover, there are no indications from the taxonomic composition of the fauna or from differences in preservation of the material to indicate that different sedimentologic or taphonomic processes might have been operating at the different localities.

No detailed study of the taphonomy was carried out at Shoshamagai–Inolelo, but basic information on the preservation of fossils was recorded. Bones from Shoshamagai–Inolelo tend to be less brittle than those from Kiloleli and Tinde, so that a good number of almost complete jaws and limb bones, especially those of suids and proboscideans, has been recovered from the surface or removed from *in situ*. The fossils are generally found as disarticulated and isolated elements. However, in contrast to the taphonomic situation at Kiloleli or Tinde, where associated material is extremely rare, partial skeletons appear to be more common in the Ibole Member. At least two partial skeletons of proboscideans are known from Shoshamagai 2, and a partial axial skeleton of a huge proboscidean has been recovered from Beredi South 5. None of the fossils exhibits signs of rolling, abrasion, or weathering, and there are no indications of any carnivore activity (despite the fact that mammalian carnivores and crocodiles are common at Shoshamagai–Inolelo and at other Ibole Member localities). However, it is interesting to note that each of the partial skeletons in the Ibole Member is associated with concentrations of carnivore coprolites. It could be that the proboscideans were preyed on by sabre-toothed cats, the only large carnivores so far known from Shoshamagai–Inolelo, with minimal damage to the bone and skeleton.

The preservation of the fossils at Shoshamagai–Inolelo indicates an autochthonous assemblage, in which partial and complete carcasses or individual bones settled to the bottom of a shallow, still lake, and were subsequently covered by a layer of fine sediments. Preliminary data on the preferred orientation of *in situ* bones indicate that skeletal elements were not aligned by the action of water currents.

In addition to individual bones and associated skeletal elements being more completely preserved at Shoshamagai and Inolelo, there is also a much wider size spectrum of mammalian taxa, ranging from small rodents to proboscideans. Even so, large mammals (greater than 200 kg) represent the most common weight class. Micromammals are entirely lacking from the faunas at Kiloleli and Tinde, and even the remains of small to medium-size mammals in the 1–100 kg range are rare, suggesting that there may be a definite taphonomic bias against the preservation of smaller mammals. The most common weight class of mammals at Tinde is represented by medium-size bovids (100–200 kg), while at Kiloleli large mammals (greater than 200 kg) make up more than 70% of the fauna.

The composition of the mammalian fauna from the Ibole Member at Shoshamagai–Inolelo is quite different from that at either Tinde or Kiloleli (Fig. 6). The fauna is dominated by proboscideans (*Anancus kenyensis* and *Primelephas gomphotheroides*) and suids (*Nyanzachoerus kanamensis*), which compose 29.8% and 24.1% of the fauna, respectively. Based on the anatomy of their dentitions, these were large, browsing herbivores that would have exploited dense bushland and woodland habitats. Bishop (1994) has suggested that the postcranial morphology of *N. kanamensis* is consistent with a preference for intermediate or mixed open-country and closed habitats. She also notes that there are some postcranial similarities with the extant *Babarusa* that might indicate specialized adaptations for swampy environments. Hippopotamid remains are quite common, and this is consistent with other lines of evidence that indicate that Shoshamagai–Inolelo represents a shallow, lake-margin setting.

The bovids from Shoshamagai–Inolelo have been assigned to at least four different species (Gentry, this volume, Chapter 5), and they occur almost as commonly as suids (Table VII). As at Kiloleli, the bovid fauna is dominated by alcelaphines. Reduncines, hippotragines, and tragelaphines are rare. The r/a index for Shoshamagai–Inolelo is only 9, which is comparable to that for modern African habitats that are predominantly bushland and grassland. This result is somewhat surprising in light of the abundance of suids, proboscideans, and hippopotamids, which points to a swampy lake margin fringed by woodlands. There are two possible explanations. Either the fauna represents a mixed community derived from several different habitats, or, as cautioned above, the relative abundance of different bovid tribes is not sensitive or reliable enough to act as an indicator of habitat preference for late Neogene communities. Certainly there is no evidence from the preservation of the fossils to indicate that the assemblage has been transported prior to burial, and we can rule out the possibility that the fauna has been mixed as a consequence of taphonomic resorting. Nevertheless, a lakeside setting is a location where taxa with very different habitat preferences might congregate for access to water, and this could account for what appears to be a palimpsest of lake-margin, woodland, and open-country communities. The inference that open-country habitats may have existed at Shoshamagai–Inolelo is only partially supported by wider comparison of the fauna. Winkler (this volume, Chapter 10) notes that the rodent fauna is suggestive of savannas, but it would also be consistent with lake-margin habitats bordered by reed beds and moist grassy areas (Kingdon, 1974; Denys, 1987). However, unlike at Kiloleli, where perissodactyls dominate the fauna, equids are rare at Shoshamagai–Inolelo (representing only 3.0% of the mammalian fauna) and rhinocerotids are entirely absent (Table VII). This would tend to exclude a paleoecological setting that included extensive open-country habitats.

The fish fauna, which includes several pelagic species, indicates a shallow well-oxygenated lake, with open-water conditions (Stewart, this volume, Chapter 11). This is further supported by the high proportion of crocodiles (see above). Similarly, the composition of the molluscan fauna points to a shallow lake with large open stretches of well-oxygenated water, in association with swampy and densely vegetated lake margins (Van Damme and Gautier, this volume, Chapter 12).

The combined sedimentologic and paleontological evidence indicates that during the time of deposition of the Ibole Member a large shallow lake filled much of the Manonga basin. However, the lake does not appear to have been as extensive as it was during the time of formation of the Tinde Member, or as permanent. Several cycles of red bed formation in the Ibole Member indicate that the lake underwent periods of regression, during which the lake floor emerged subaerially. These periods of regression appear to have been of relatively short duration, since there is little or no evidence that the lake beds were substantially reworked. There are clear indications, however, of the development of paleosols. Root casts are common, and at Ngofila 1 numerous large ovoid termitaries (20–40 mm in diameter) have been recognized. The latter are most similar in shape and general construction to the fungus-comb chambers of

Odontotermes, a genus with a wide range of habitat preferences, ranging from dry savanna to moist woodlands (Sands, 1987).

6. Conclusions

This chapter presents a overview of the taphonomy and paleoecology of late Miocene and early Pliocene fossil localities in the Manonga Valley. It provides a preliminary description of the local paleoecological setting in the Manonga basin during the time of deposition of the Wembere–Manonga Formation, and it also contributes useful information that will eventually add to a more complete understanding of the diversity of habitats in East Africa during the later Neogene. Without this type of information, both from sites with fossil hominids and those without, we will be unable to make informed statements about the possible ecological factors underlying the differentiation of early hominids, and their subsequent habitat preferences.

The sedimentologic and paleontological evidence indicate that during the time of deposition of the Ibole Member the Manonga basin was occupied by a large, shallow lake. The lake apparently underwent periods of regression during which the lake floor emerged subaerially. Paleosols, commonly preserving rhizoliths and traces of insects, were produced during these dry phases. The periods of regression appear to have been of relatively short duration, since there is little evidence that the lake beds were eroded or reworked in the intervals between deposition of lake sediments. The aquatic fauna indicates that the lake had open stretches of well-oxygenated water, with swampy, densely vegetated margins. The mammalian fauna suggests that the habitats around the lake consisted predominantly of dense woodland, but that the general area supported a more diverse mix of habitats, including open grassland–bushland and woodland habitats.

During the formation of the Tinde Member, the paleolake appears to have been relatively stable, and this is when it reached its greatest extent. Evidence suggests, however, that the lake still underwent brief phases of regression, but that these were less frequent and probably more localized than those in the Ibole Member. Based on evidence from the aquatic fauna and from sedimentology, the center of the lake basin appears to have been occupied by a body of well-oxygenated, open water, similar to that inferred for the Ibole Member. Relatively swampy, anoxic conditions are generally more commonly found around the lake margins and islands, as well as on raised portions of the lake floor (such as at Tinde), probably as a result of increased rates of sedimentation.

The depositional setting at Tinde can be inferred to be one of a shallow, permanently flooded lake shelf, located near low-lying islands in the center of the lake basin. As a consequence of this, it is biased ecologically and taphonomically in favor of large-bodied hydrophilic forms. Unfortunately, the Tinde fauna is not very helpful in reconstructing the terrestrial paleoecology at this time. Better information is derived from other Tinde Member faunas that indicate a similar mosaic of habitats as that inferred for the Ibole Member, with woodlands predominating.

The paleolake was shallower and more restricted during deposition of the Kiloleli Member, probably as a result of the infilling of the basin by a thick series of lake sediments. Swampy, lake-margin facies are found close to the center of the lake basin, with evidence of extended periods of emersion and fluvial reworking of sediments. Regression of the lake, possibly in combination with major changes in the patterns of drainage of the basin associated with the initiation of rifting to the northeast, appears to correlate with a shift in the local paleoecology. The mammalian fauna from the Kiloleli Member, when compared with that from the Tinde Member, clearly indicates drier, more open-country conditions. It is not known, however, whether this ecological shift is a local phenomenon directly related to regression of the lake, or whether the two events are merely associated with wider changes in the regional or global climate.

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Chapter 5

Fossil Ruminants (Mammalia) from the Manonga Valley, Tanzania

ALAN W. GENTRY

1. Introduction

An account is given of the fossil Giraffidae and of the much more abundant fossil Bovidae collected in the Manonga Valley, Tanzania, by the Wembere–Manonga Paleontological Expedition in 1990 and 1992. The geology of the area and the history of its study are given in other chapters of this book. Several references are made to material collected by C. Grace in 1929 at Tinde and now in the Natural History Museum, London (Stockley, 1930).

Localities and deposits mentioned in the text other than those of the Manonga Valley are as follows:

> Baccinello, Italy, upper Miocene (Thomas, 1984a); Baringo deposits, Kenya, middle and upper Miocene and including the Ngorora Formation (Hill *et al.*, 1985); Dhok Pathan, Siwaliks, upper Miocene (Barry and Flynn, 1989); Djebel Krechem, Tunisia, upper Miocene (Geraads, 1989); Douaria, Tunisia, upper Miocene (Roman and Solignac, 1934); Hadar Formation, Ethiopia, Pliocene (Walter and Aronson, 1993); Hasnot, Siwaliks Group, Pakistan, upper Miocene (Barry and Flynn, 1989); Koobi Fora Formation, East Turkana, Kenya, Pliocene and lower Pleistocene (Harris, 1991); Laetoli,

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Neogene Paleontology of the Manonga Valley, Tanzania, Volume 14 of *Topics in Geobiology*, edited by T. Harrison, Plenum Press, New York, 1997.

Tanzania, Pliocene (Leakey and Harris, 1987); Langebaanweg, South Africa, earliest Pliocene (Gentry, 1980); Lothagam, Kenya, late Miocene (Behrensmeyer, 1976); Lukeino, Kenya, upper Miocene (Pickford, 1978); Maragheh, Iran, upper Miocene (Bernor, 1986); Mpesida, Kenya, upper Miocene (Bishop *et al.*, 1971); Nachukui Formation, West Turkana, Kenya, Pliocene and lower Pleistocene (Harris *et al.*, 1988); Nakali, Kenya, upper Miocene (Aguirre and Leakey, 1974); Ngorora Formation, Kenya, middle and upper Miocene (Hill *et al.*, 1985); Olduvai Gorge, Tanzania, Pliocene and lower Pleistocene (Hay, 1976); Pikermi, Greece, upper Miocene (Solounias, 1981); Piram (formerly Perim) Island, India, upper Miocene (Pilgrim, 1939); Rawe, Kenya, late Pliocene (Kent, 1942); Sahabi, Libya, late Miocene (Boaz *et al.*, 1987; Geraads, 1989); Shungura Formation, Omo, Ethiopia (Heinzelin, 1983); Siwaliks Group, Pakistan and India, Miocene to Pliocene (Barry and Flynn, 1989); Wadi Natrun, Egypt, upper Miocene (Andrews, 1902; Geraads, 1987:22).

Tooth cusp nomenclature follows Gentry (1992). A basal pillar may be found in the center of the lingual side of upper molars or the labial side of lower molars, completely or partly separate from the rest of the occlusal surface. It is the entostyle of the upper molars and the ectostylid of the lower molars. Tooth lengths and breadths were measured at occlusal level. Heights were measured on the mesostyles of upper molars, metastylids of lower molars, and protoconids of lower premolars. The paired measurements given for a horn core are their anteroposterior and transverse basal diameters, respectively. Paired measurements given for teeth are occlusal length and occlusal width, respectively, and all measurements are in millimeters. Ma, million years; WM, Wembere–Manonga; BMNH, Natural History Museum, London; KNM, Kenya National Museums, Nairobi; SAM, South African Museum, Cape Town; MNI, minimum number of individuals.

2. Fossil Giraffids

Only two specimens of fossil giraffids were seen, but others have been collected.

Family Giraffidae Gray, 1821
Genus *Giraffa* Brünnich, 1771
Type species *Giraffa camelopardalis* (Linnaeus, 1758)
Giraffa sp.

Material.

WM047/90	Back of left M_3 (Figs. 1A,B), late middle wear. Occlusal length of whole tooth would have been c. 43.0 mm.	Tinde West

This partial tooth is about the same size as in living *Giraffa camelopardalis.* The fossette between entoconid and hypoconid is closed at its rear end and almost certainly at its front end also. No fossette can be seen on the hypoconulid lobe (talonid) of the tooth and the lingual wall extends uninterrupted from the entoconid backward on to the talonid. A basal pillar is present on the labial side

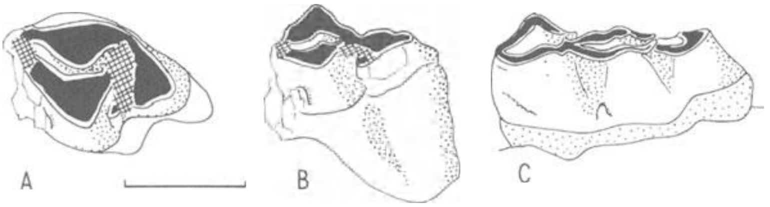

FIGURE 1. Teeth of fossil *Giraffa*. (A–B) Occlusal and labial views of distal (=posterior) portion of left M_3 (WM047/90) of *Giraffa* sp. from Tinde West. (C) Labial view of left M_3 (BMNH M13634) of *G. punjabiensis* from the Siwaliks. Cross-hatching = matrix. Anterior direction to the left. Scale = 20 mm.

in front of the hypoconid and a supplementary one is present between the hypoconid and the talonid. The enamel has a rugose surface.

Some postcranial bones at Tinde West have also been identified as giraffid (e.g., 035/90 right unciform, 051/90 right cuneiform, 413/90 right scaphoid, 272/92 left magnum, 1895/92 right fibula). They are similar to *Giraffa* but only about 60–70% of the size of the modern species (T. Harrison, pers. comm., 29 March 1993). The Grace collection from Tinde contains a partial left proximal ulna (BMNH M43799), a right astragalus (M43797), and a second phalanx (M43798), which all appear to be the same size or only slightly smaller than in the modern species.

Comparisons. Fossil *Giraffa* teeth and postcranials are difficult to assign at species level since size is in practice the only distinguishing criterion and since size probably increased over time in one or more lineages (Harris, 1991, p. 106). Giraffes of the East African Plio-Pleistocene are ascribed to three extinct species in addition to *Giraffa camelopardalis* itself, which may occur as far back as the top of the Nachukui Formation (Harris, 1976b, 1991):

1. *Giraffa jumae* Leakey, 1965. At least as large as *G. camelopardalis*. Its type locality is Rawe. Also from the Tulu Bor to Okote Members of the Koobi Fora Formation, Olduvai beds I to IV, the Hadar Formation, Laetoli, and probably the Shungura Formation.
2. *Giraffa stillei* (Dietrich, 1941).* Smaller than the last species and including *Giraffa gracilis* Arambourg, 1947. The type locality is Laetoli, and it is also known from the Tulu Bor to KBS Members of the Koobi Fora Formation, Olduvai beds I and lower II, Shungura Formation and Hadar Formation.
3. *Giraffa pygmaea* Harris, 1976b. The smallest species. The type locality is the KBS Member of the Koobi Fora Formation, and it is known through that Formation from the Lonyumun Member (Harris, 1991, p. 359) to the Okote Member. It is also in Bed I and upper Bed II at Olduvai and in the Shungura Formation.

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*This name is sometimes dated from Dietrich (1942), but the details given in Dietrich (1941, p. 220) are sufficient to make the name available from the earlier year.

These East African species are of unknown relationship to fossil giraffes elsewhere in Africa, some of which have names of their own. Harris (1976a) described a large giraffe from Langebaanweg as *Giraffa* (cf. *G. jumae*) and gave the length of an M_3 as 46.9 mm. A Langebaanweg giraffid lower dentition (SAM L31138; BMNH cast M36473) has an M_3 length of 39.3 mm.

Giraffa is only sketchily known in East Africa before Laetoli, as for instance at Lukeino (Pickford, 1978). Churcher (1979) identified a Lothagam upper molar as *Palaeotragus germaini* Arambourg, 1959, a north African Vallesian-equivalent species, but Geraads (1986, p. 474) thought the tooth was close to *Giraffa*. Hill *et al.* (1985, Fig. 4) showed a sedimentary and time gap in the Baringo deposits of East Africa between the last Palaeotraginae at about 10.0 Ma and the first Giraffinae at about 6.0 Ma. However, Aguirre and Leakey (1974) record giraffids from Nakali, a locality in the intermediate time interval (Hill, 1987, p. 592). The upper molar of Aguirre and Leakey (1974, Fig. 5) is c. 34.0 mm long and has a strong mesostyle and strong labial ribs, seemingly closer to *Giraffa* than to palaeotragines. In addition to the Nakali remains, a cast (BMNH M30125) of an upper molar (KNM BN1139) from the Ngorora Formation looks quite like a *Giraffa* with its bulky styles. It has a lingual cingulum around the protocone and an approach to a bifurcation at the rear of the protocone crest.

Fossil representatives of *Giraffa* are also found in southern Asia. *Giraffa punjabiensis* Pilgrim, 1911 comes from the Dhok Pathan (Colbert, 1935) in the time span 7.1–5.0 Ma (Barry *et al.*, 1991). British Museum (Natural History) material assigned to this name comes mostly from Hasnot (c. 7.0 Ma). The species is like *Palaeotragus coelophrys* of Maragheh in size (probably near to the size of *G. stillei* among African species) and P_4 crest morphology, although the premolars look wider and P_2 is relatively longer (compare Colbert, 1935, Fig. 193 with Mecquenem, 1924–25, Pl. 2 fig. 8). The lower molars also have basal pillars. Matthew (1929, pp. 541, 546) was inclined to link the species with the Pikermi *Bohlinia attica* (Gaudry and Lartet, 1856), the latter being perhaps an immigrant to Eurasia and related to *Giraffa*.

The two chief features of interest in the Tinde tooth are that it looks as if it was low crowned and as if the lingual wall of the entoconid is rather flat. These features, if correctly interpreted, would be different from lower molars of living and fossil *Giraffa*. It is of a size appropriate for *Giraffa jumae*. The right M_3 on the holotype mandible of *G. jumae* (BMNH M14957) is in a similar wear state and has an occlusal length close to 43.0 mm. The hypoconid lobe on the Tinde tooth has more of a narrow V-shape and the basal pillars are better marked. The flat entoconid wall of the Tinde M_3 is like Eurasian palaeotragines, but the brachyodonty is not. A cast of an upper dentition (BMNH M4066) of *Bohlinia attica* is more brachyodont than *Giraffa*, but it would be unconvincing to claim an African record for this genus on only a partial tooth. An illustrated lower dentition of *B. attica* (Wagner, 1861, Pl. 1 fig. 3) does not look particularly low-crowned.

The three giraffid postcranial bones in the Grace collection are of a size to be conspecific with the tooth. Compared with modern giraffe the articular surfaces on the trochlear notch of the ulna are narrower and the olecranon process was probably less reduced. The astragalus is narrower and the top half of the lateral edge in anterior view less offset against the lower half of the same edge, much as in *Bohlinia attica* (Geraads, 1979, p. 380, Pl. 2). The proximal articular facets on the second phalanx are less wide.

Genus *Sivatherium* Falconer and Cautley, 1836
Type Species *Sivatherium giganteum* Falconer and Cautley, 1836
?*Sivatherium* sp.

Material.

WM715/90	Left lower molar (Figs. 2A,B), early middle wear, c. 45.0 × c. 27.0 × c. 24.0 high.	Kiloleli 2

This somewhat damaged tooth has a small basal pillar, so it may be an M_1 in which such pillars are more frequent than in other lower molars.

A somewhat damaged distal metapodial in London (BMNH M43852) is large enough to belong to this species. It was collected by C. Grace in 1929 at Tinde.

Comparisons. Sivatherium is best known as *S. giganteum* of the Indian later Pliocene and *S. maurusium* (Pomel, 1892) of the African later Pliocene and Pleistocene. Harris (1976a) separated the Langebaanweg representative as *S. hendeyi*, differing from later *Sivatherium* in having no knobs, flanges, or palmate digitations on its ossicones and with longer metacarpals. (Supposed examples of its anterior ossicones were later accepted as having been misattributed [Harris,

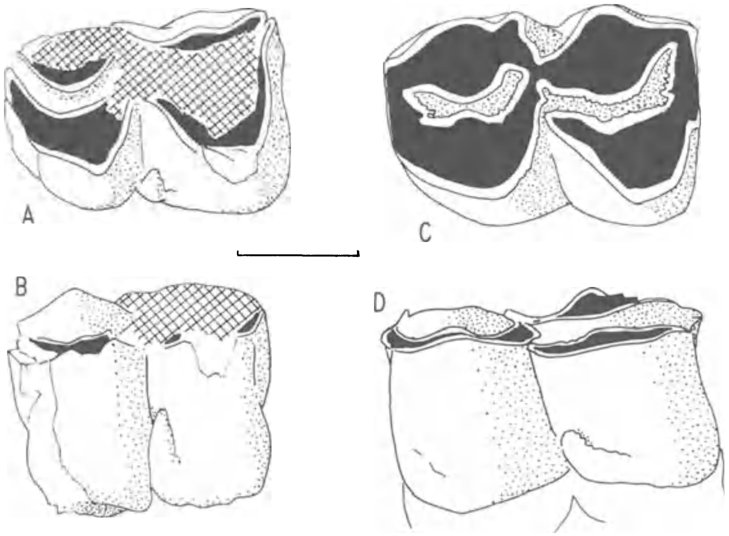

FIGURE 2. Teeth of *Sivatherium*. (A–B) Occlusal and labial views of left lower molar (WM715/90) of ?*Sivatherium* sp. from Kiloleli 2. (C–D) Occlusal and labial views of left M_1 in mandible (BMNH 40677) of *S. giganteum* from the Siwaliks. Cross-hatching = matrix. Anterior direction to the left. Scale = 20 mm.

1991, p. 108].) The teeth of *S. hendeyi* were said to be indistinguishable from those of *S. maurusium*. In Africa *Sivatherium* survived at least until late in the middle Pleistocene.

The Kiloleli lower molar is about as long as an M_1 or small M_2 of *S. giganteum* or *S. maurusium*. It differs from those species in the more narrowly pointed labial lobes (protoconid and hypoconid), less outbowing of lingual ribs, and in the robust basal pillar. The front central fossette is not transversely constricted across its center as can sometimes be seen in *S. giganteum*. These seemingly primitive characters give the tooth more resemblance to the upper Miocene sivatheres of Eurasia, for example, *Decennatherium pachecoi* of Crusafont Pairo (1952, Pls. 25–27), *Hydaspitherium megacephalum* and *H. magnum* (see Colbert, 1935, Fig. 181; also BMNH M13641), *Helladotherium duvernoyi* (BMNH cast M4067), and *Birgerbohlinia schaubi* (see Montoya and Morales, 1991). *Bramatherium*, based on *B. perimense* Falconer 1845 from Piram Island, may be the senior generic synonym for some or all these species except the last. Interestingly, Geraads (1985, pp. 317–318) considered that the then earliest known African sivathere (a fragmentary upper dentition from Douaria, now rivaled for antiquity by the Kiloleli tooth) could as well be related to its Eurasian contemporaries as to later African sivatheres.

The Kiloleli tooth will here be doubtfully referred to *Sivatherium* and not to *Bramatherium* or *Birgerbohlinia*. This course avoids for the present the complications surrounding the question of the morphology of horns in Miocene sivatheres. Where known, horns in the *Bramatherium* group are inserted close together above or just behind the orbits. There may also be a smaller posterior pair of horns. *Birgerbohlinia*, on the other hand, has a large posterior pair of horns and a smaller anterior pair, more like *Sivatherium*.

The distal metapodial is about the same size as examples of *Helladotherium duvernoyi* from Pikermi.

3. Fossil Bovids

Family Bovidae Gray, 1821

The following sequence of bovid tribes is used in this chapter, taken from Gentry (1992):

- Subfamily Bovinae
  - Tribes Tragelaphini, Boselaphini, Bovini, Cephalophini
- Subfamily Antilopinae
  - Tribes Neotragini, Antilopini
- Subfamily Hippotraginae
  - Tribes Reduncini, Hippotragini
- Subfamily Alcelaphinae
  - Tribes Aepycerotini, Alcelaphini
- Subfamily Caprinae
  - Tribes Ovibovini, Caprini, indeterminate

In this arrangement the first subfamily could be regarded as division Boodontia and the second, fourth, and fifth as division Aegodontia. Boodonts are somewhat more primitive and have "ox-like" teeth, while aegodonts are more advanced and have "goat-like" teeth. Thomas (1984b) discussed this dichotomy in bovids, recognition of which goes back to Schlosser (1911, pp. 499, 501). Given the primitive state of boodonts, the crucial proposition implied in the order of listing of the aegodont subfamilies is that Alcelaphinae and Caprinae are closely related as a crown group while Antilopinae occupy an intermediate position. The cladistic position of Reduncini and Hippotragini is uncertain, and Gatesy *et al.* (1992) warn that the diversification of bovid tribes remains difficult to resolve, even when based on mitochondrial ribosomal DNA.

As in other mammal families, teeth are important in bovid classification, even allowing for the additional help available from horn cores. Teeth of the tribe Bovini show the classical boodont features of large basal pillars on molars, transversely (labiolingually) wide upper molars, complex central fossettes and strong labial ribs between the styles on upper molars, and outbowed lingual walls on lower molars. Teeth of the tribe Caprini have no basal pillars and show transversely narrow upper molars, simpler central fossettes and more or less flat labial walls between the styles on upper molars, pointed lingual lobes on upper molars, and lower molars with flat lingual walls. These differences cannot be elevated to become boodont/aegodont differences because there is too much variation among the constituent tribes of each division. Thus, teeth of Alcelaphini differ from those of caprine tribes by having acquired much more rounded outlines of the labial and lingual lobes on the molars, although they still lack basal pillars. Also, the molars of Tragelaphini, although not very high crowned, have certain resemblances to caprines. Hence, when one comes to consider the classification of a problematic tribe, tooth characters are not straightforward aids for the task.

Tribe Tragelaphini
Genus *Tragelaphus* Blainville, 1816
Type species *Tragelaphus scriptus* (Pallas 1766)
Tragelaphus sp.

Material.

WM1742/92	Left M_2 (Figs. 3C,D), early middle wear, c. 19.0 × c. 9.2.	Shoshamagai 2 (Ibole Member)
WM1743/92	Front of a left lower molar (Fig. 3A), early middle wear.	Shoshamagai 2 (Ibole Member)
WM239/90	Back of left M_3 (Fig. 3B), early middle wear.	Tinde West

The front of the lower molar 1743/92 is not from the same individual as 1742/92. These teeth are about the size of the modern species *Tragelaphus spekei, angasi,* or *imberbis.*

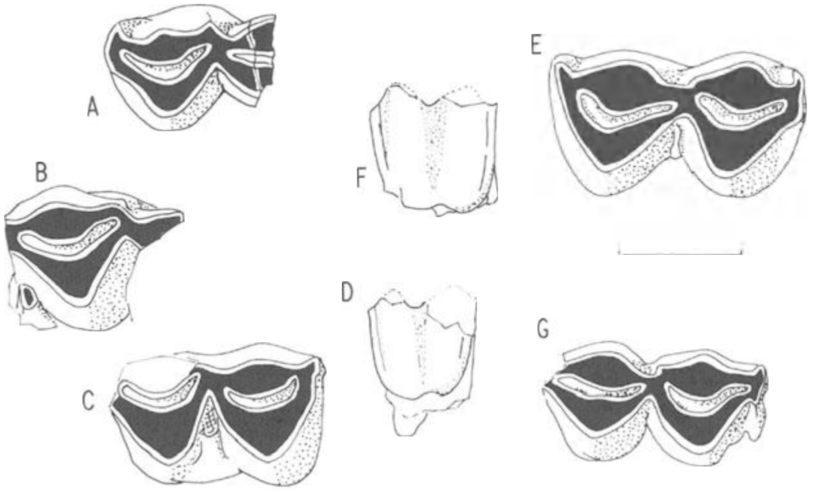

FIGURE 3. Teeth of *Tragelaphus* sp. (A–D) and *Praedamalis* sp. (E–G). (A) Occlusal view of front of a left lower molar (WM1743/92) from Shoshamagai 2. (B) Occlusal view of damaged distal portion of left M_3 (WM239/90) from Tinde West. (C–D) Occlusal and lingual views of left M_2 (WM1742/92) from Shoshamagai 2. (E–F) Occlusal and lingual views of right M_2 (WM831/92) from Kiloleli 2. (G) Occlusal view of right lower molar (WM1324/92) from Kiloleli 4. Anterior side to the right for D, E, and G; otherwise, to the left. Scale = 10 mm (A–C, E, G) or 20 mm (D, F).

Comparisons. Unlike Alcelaphini from the Manonga Valley sites, the M_2 1742/92 has a basal pillar, labial lobes that are rather long transversely, and the junction between its front and back halves placed too far lingually. Unlike Manonga Reduncini it lacks a goat fold and the lingual walls are flatter. The partial molar 1743/92 has no goat fold or basal pillar, and does have a metaconid rib on the lingual wall. The partial M_3 239/90 is unlike Alcelaphini in having a basal pillar and in the labial lobe being too narrow as it approaches its point; it is probably too large and with too flat a lingual wall to match reduncines. Compared with modern tragelaphines the points of the labial lobes may be less emphasized, but little real difference can be seen.

Thomas (1981, p. 358) accepted as boselaphine certain dentitions from *Hipparion* levels at Ngorora that Gentry (1978a) had thought could be tragelaphine. It can be agreed that early Tragelaphini are present at Mpesida, Lukeino, and Langebaanweg (Gentry, 1978a, 1980; Thomas, 1980), although both authors gave differing identifications of some individual specimens at Mpesida. The teeth of all these putative tragelaphines are the same size as those from the Manonga Valley.

Tragelaphine horn cores from Lothagam have been referred to a species *Tragelaphus kyaloae* Harris 1991, described from the Nachukui Formation and also present in low levels of the Koobi Fora Formation. Its horn cores are more compressed anteroposteriorly than at Lukeino or Langebaanweg, and thus are more like the later *T. nakuae* Arambourg 1941.

Tribe Reduncini
Genus *Kobus* A. Smith, 1840
Type species *Kobus ellipsiprymnus* (Ogilby, 1833)
Kobus aff. *subdolus*

Material from Tinde West.

WM298/90	Skull parts including horn core (index 37.1 × 33.8) plus distal left tibia, probably belonging with WM668/92
WM667/92	Cranium with left horn core
WM764/92	Skull parts, horn cores (index 38.7 × 33.5), and right mandible with P_3–M_3 (Figs. 6C,E) in middle wear. P_{2-4} c. 30.0, M_{1-3} c. 54.0; P_3 = 10.9 × 6.0, P_4 = 12.7 × 6.7, M_1 = 14.6 × 9.7, M_2 = 17.2 × 9.7, M_3 = 22.1 × 9.4

WM181/90 index 32.6 × 29.0, WM184/90, WM191/90, WM207/90 45.6 × 41.6, WM377/90, WM506/90 34.7 × 28.0, WM15/92 36.6 × c. 32.5, WM16/92 37.8 × 34.3, probably WM21/92 39.0 × 30.0, WM1840/92 32.2 × c. 28.7. Left horn cores

WM183/90 32.1 × 28.2, WM185/90, WM188/90 (Fig. 4) 36.5 × c. 34.0, WM189/90, WM256/90, WM318/90 36.3 × 33.6, probably WM342/90 39.8 × 32.0, probably WM497/90 39.0 × c. 32.0, WM499/90 34.2 × 28.9, WM574/92 48.8 × 40.6, WM1864/92 39.9 × 34.3. Right horn cores

WM376/90	Left mandible with broken teeth
WM668/92	Mandibles in matrix, probably belonging with 298/90
WM001/92	Left maxilla, perhaps palate, with P^3–M^3
WM002/92	Left M2/ and M3/, late middle wear. M^2 = 16.3 × 15.6, M^3 = 17.1 × 14.9

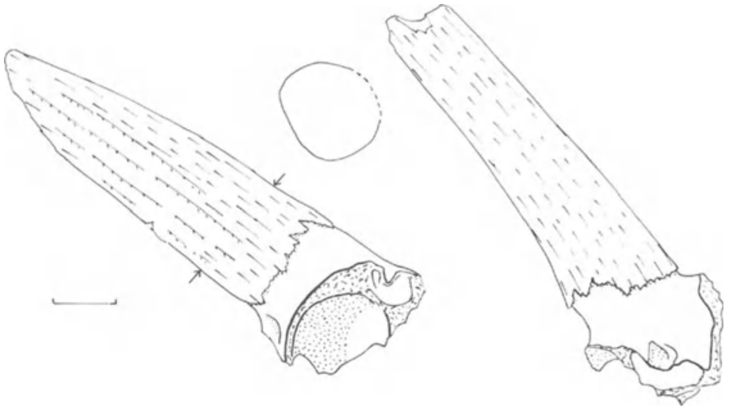

FIGURE 4. Right horn core of *Kobus* aff. *subdolus* (WM188/90) from Tinde West in lateral (left) and anterior (right) views. A cross section is also shown at the level indicated by the arrows; anterior direction to the base of the illustration, lateral side to the left. Scale = 20 mm.

Also 9 right upper molars, 4 left upper molars, right P^4, right deciduous P^4, left deciduous P^4, 8 right lower molars, 4 left lower molars. Among them the following can be measured:

WM168/90	Right M^3 (Figs. 5B,D), early wear, 17.9 × 10.4 × c. 21.5 high
WM238/90	Part right upper molar, early wear, c. 18.0 occlusal length
WM165/92	Part right upper molar, early middle wear, c. 17.5 long
WM204/92	Left upper molar, late wear, 12.0 × c. 14.0. By size an M^1
WM569/92	Much of right ?M^3, early middle wear, c. 17.0 long
WM653/92	Left upper molar, early wear, c. 18.0 × c. 12.0
WM654/92	Right M^2 or M^3, late middle wear, 16.8 × 16.6
WM749/92	Right M^3 (Fig. 5A), early wear, c. 19.0 × c. 10.0 × c. 19.5 high
WM1859/92	Left M^1 (Fig. 5C), early middle wear, 16.1 × 11.4
WM205/92	Right P^4 (Fig. 5E), late middle wear, 11.4 × 9.7
WM751/92	Left dP^4, early middle wear, 14.9 × c. 10.6
WM754/92	Right dP^4 (Figs. 5F,G), early wear, 14.8 × 10.5 × 9.7 high. A different individual from WM751/92
WM170/90	Most right M_3, early middle wear, c. 22.0 × 9.5
WM226/90	Right M_3 (Fig. 6A), early middle wear, c. 23.2 × 8.4
WM474/90	Right lower molar, prob. M_2, unworn, 17.6 × 5.4 × 21.6 high

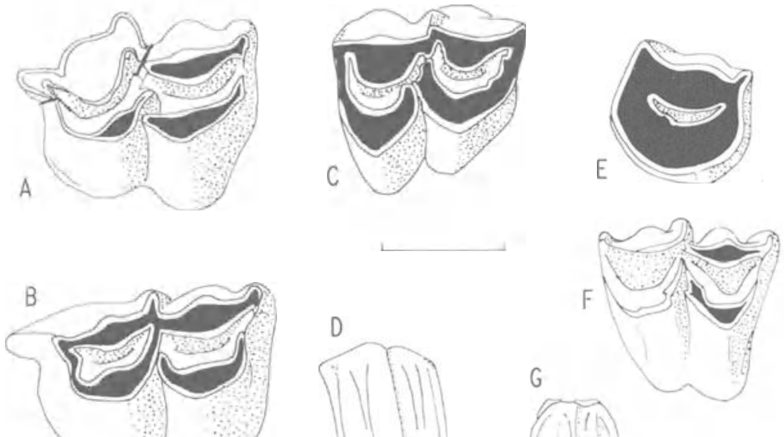

FIGURE 5. Upper teeth of *Kobus* aff. *subdolus* from Tinde West. (A) Occlusal view of right M^3 (WM749/92). (B) Occlusal view of right M^3 (WM168/90). (C) Occlusal view of left M^1 (WM1859/92). (D) Labial view of right M^3 (WM168/90). (E) Occlusal view of right P^4 (WM205/92). (F–G) Occlusal and labial views of right dP^4 (WM754/92). Anterior side to the right, except C. Scale = 10 mm (A–C, E–F) or 20 mm (D, G).

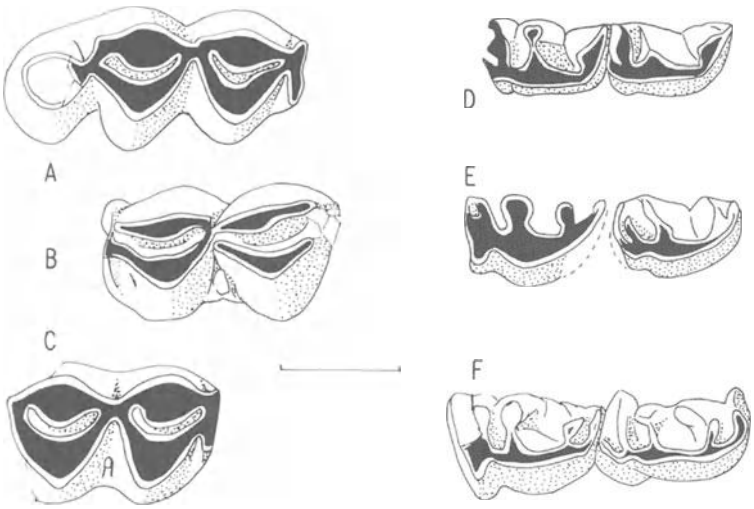

FIGURE 6. Occlusal views of lower teeth of *Kobus* aff. *subdolus* (A–C, E) and other fossil Reduncini. (A) Right M_3 (WM226/90) from Tinde West. (B) Broken left M_3 (WM464/92) from Tinde West. (C) Right M_2 (WM764/92) from Tinde West. (D) Right P_{3-4} cast (BMNH M34743) of premolar (SAM L32850) from Langebaanweg. (E) Right P_{3-4} (WM764/92) from Tinde West. (F) Right P_{3-4} cast (BMNH M34569) (also see Pilgrim 1939, Figs. 11b, 11b') from the Siwaliks of Hasnot, Pakistan. Anterior side to the right except for B. Scale = 10 mm.

WM138/92	Part left lower molar, probably M_2, early middle wear, 16.7 × c. 8.9
WM464/92	Left M_3 (Fig. 6B), early wear, c. 23.0 × 7.0 × c. 22.0 high
WM513/92	Right lower molar, probably M_2, early middle wear, c. 16.8 occlusal length
WM748/92	Left lower molar, ?M_2, late wear, 16.7 × 11.2
WM1858/92	Right lower molar, probably M_1, in mandible fragment, early wear, 16.1 × 6.7 × c. 18.5 high (unworn)

Material from Sites Other Than Tinde West.

WM1707/92	Right horn core, 44.0 × 38.6	Beredi South 4
WM730/90	Right P_4, late wear, 11.7 × 7.1	Kiloleli 2
WM647/90	Back right M_3, unworn, c. 20.0 long × 23.0 high	Kiloleli 4
WM1466/92	Left horn core, 35.2 × 30.3	Ngofila 4
WM1489/92	Left horn core, c. 37.9 × 34.2	Beredi North
WM1493/92	Fragment (?left) upper molar	Beredi North

Several horn cores and pieces thereof, a maxillary tooth row, and two isolated teeth collected by Grace in 1929 from Tinde can all be referred to this species.

The best preserved are a right horn core (BMNH M43795) and a left horn core (M43796).

The common reduncine horn cores vary quite a lot in size. They show little transverse compression, the lateral surface more flattened than the medial one, their widest mediolateral diameter lying rather anteriorly, a strong posterolateral angle, deep longitudinal grooving posteriorly, transverse ridges sometimes on their anterior surfaces, insertions above the backs of the orbits, insertions at a low angle in side view, much divergence, little backward curvature in their proximal parts, slight upward curvature distally, limited sinus development in the vicinity of the supraorbital pit but no sinuses in the pedicels, and deep postcornual fossae. The frontals are quite deep at the suture between the horn core bases, and the dorsal part of the orbital rim projects quite strongly.

The braincase is moderately long, the cranial roof is steeply inclined but not curved downward in its posterior part, the mastoids are moderately sized and face partly laterally, the ventral rim or edge just below the mastoid is weak and there is no dorsal rim (Gentry, 1985, Fig. 8), the nuchal crest is quite strong and forms the effective boundary of the occipital surface, the occipital edge is not rounded in the form of a semicircle, a median vertical ridge was present on the occipital, the temporal lines approach fairly closely, and the auditory bulla was probably large.

Reduncine teeth from the Manonga Valley sites are about the size of extant *Kobus leche*, but they are more primitive than in living reduncines.

Comparisons. The horn cores are very like those of the early reduncines *Kobus subdolus* Gentry, 1980 and *Kobus* sp. 2 at Langebaanweg, the *Redunca* aff. *darti* of Lehmann and Thomas (1987) at Sahabi, and *Kobus* sp. (right horn core cast BMNH M8200) at Wadi Natrun. Differences among them are minimal. The Manonga Valley specimens may have greater divergence and some show less backward curvature along the anterior edge of the proximal part of the horn cores in profile. The Sahabi specimens may have more inclined insertions and longer pedicels. The frontlet from Sahabi has a less flattened lateral surface, but this is not true of three further horn cores in the Rome collection. *Kobus subdolus* horn cores may be shorter. The *Kobus* sp. 2 at Langebaanweg is like the Manonga ones in its strong divergence but may have stronger backward curvature. The cranial characters are also like those described for the two Langebaanweg reduncines. Compared with later reduncines of the Shungura Formation (Gentry, 1985) the characters of the occipital and mastoid area are closest to those of *Kobus ancystrocera* (Arambourg, 1947), but the horn cores are much shorter.

The main tooth characters of living reduncines are: moderate hypsodonty; teeth rather small in relation to skull and mandible size; upper and lower molars with basal pillars; lingual lobes of upper molars and labial lobes of lowers constricted; upper molars with strong styles; localized ribs between the styles; central fossettes of upper molars with indentations (spurs) of their outlines and tending in later wear to have long, labially directed, transverse arms; lower molars with goat folds and front and rear outbowings of lingual walls; upper and lower P2s small; lower premolars with an appearance of anteroposterior compression; P_4s with a strongly projecting hypoconid and often a deep and narrow

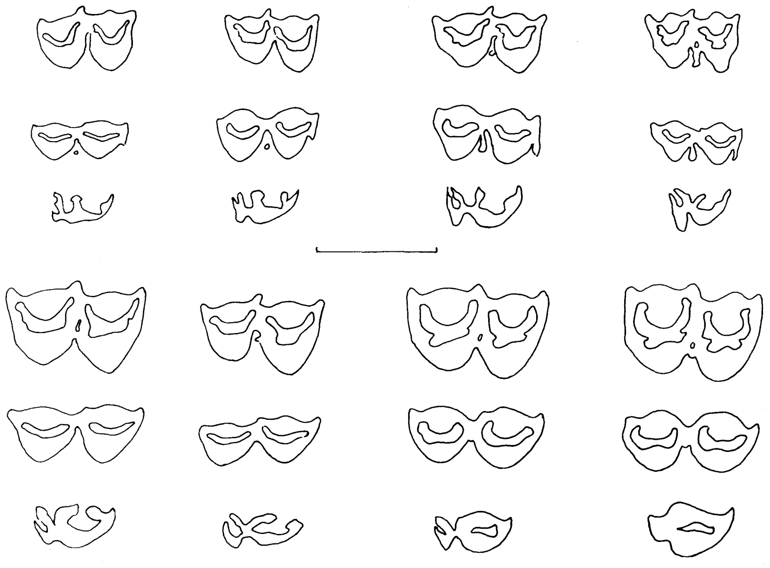

FIGURE 7. Occlusal views of cheek teeth to show morphological evolution. Top three rows: M^2s, M_2s, and P_4s of Reduncini. Bottom three rows: M^2s, M_2s, and P_4s of Alcelaphini. Columns, from the left: Langebaanweg, Manonga, Shungura Formation, and extant. All teeth are of the right side and with anterior sides to the right. Scale = 20 mm.

labial valley in front of it; P_4s usually without paraconid–metaconid fusion to form a complete lingual wall.

In general earlier reduncine teeth are less distinctive than later ones (Fig. 7) in having lower-crowned teeth, basal pillars smaller or even absent, less constricted lingual lobes of upper molars and labial lobes of lower molars, ribs on upper molars less localized, central fossettes of upper molars less complicated, smaller goat folds on lower molars, lingual walls of lower molars perhaps less strongly outbowed, longer premolar rows, and the entostylid more distinct from the entoconid on the back of P_4. Some of these features are detectable in teeth of the Manonga Valley collection, which are similar to reduncine teeth already recorded as *Kobus* aff. *porrecticornis* from Mpesida and Lukeino (Thomas, 1980, pp. 84,87, Fig. 1 nos. 6,7, Fig. 2 no. 6), and more primitive than those of the Shungura Formation. Upper molars are lower crowned than in modern reduncines, have weaker labial ribs (especially on the metacone), their lingual lobes are less constricted and with more of an angled point, a trace of a basal pillar can be seen only on the M^1 753/92 from Tinde West, and central fossettes are simpler than in extant *K. leche*. Lower molars have smaller goat folds, less constricted labial lobes, and basal pillars that are absent or weaker. The P_4 on 764/92 has no appearance of anteroposterior compression and its hypoconid does not project very strongly in a labial direction. Its paraconid and metaconid do not approach one another lingually.

Siwaliks reduncine lower molars of comparable antiquity are about the same size as the Manonga ones, but have stronger basal pillars, possibly less pointed labial lobes, and possibly a longer P_3 in relation to P_4.

The Manonga reduncines are, however, advanced on Langebaanweg teeth thought to be reduncine and previously discussed in Gentry (1980, pp. 255–260). This is evident in the stronger labial ribs and the more complex central fossettes on upper molars, and in the stronger basal pillars, goat folds, and outbowed lingual walls on the lower molars. It is probably also true for shortening of the premolar row and greater depth of the labial valley in front of the hypoconid on P_4. Hence, while the Manonga reduncine could be referred to *Kobus subdolus* on the basis of its horn core and cranial characters, its relatively advanced teeth seem to forbid this course.

Kobus aff. *porrecticornis* (Lydekker, 1878)

Material.

WM1107/92	Right horn core base, c. 33.9 × 25.2	Inolelo 1
WM966/92	Distal part left horn core	Inolelo 1
WM969/92	Right M^2, early middle wear, 17.9 × 14.9	Inolelo 1
WM975/92	Left M_2, early wear 19.0 × 7.7	Inolelo 1

The horn core 1107/92 has a damaged pedicel and is preserved to about 45.0 mm above the base. It is sufficient to show the presence of a second and rarer reduncine species in the collection. It differs from the common Tinde West reduncine by being more transversely compressed, having less of a flattened lateral surface, a less pronounced posterolateral angle and perhaps by having less strong longitudinal grooving posteriorly.

The second horn core is more tentatively assigned. Its divergence diminishes distally. The teeth are presumably conspecific with the horn cores but are not distinguishable from teeth of *Kobus* aff. *subdolus*.

Comparisons. The horn core 1107/92 is like the Siwaliks *Kobus porrecticornis* (Lydekker, 1878), which is most probably from the upper part of the Dhok Pathan stage. Thomas (1980, p. 84) noted that *K. porrecticornis* appears between sandstones 6 and 7 (loc. 97) at the base of the Kundvali unit in the type zone of the Dhok Pathan. In Africa the same or a similar species is known from Mpesida and Lukeino and from the Baard's Quarry lower assemblage at Langebaanweg. The Baard's Quarry lower assemblage was assessed as late Pliocene, around 2.0 Ma, by Hendey (1978) and as younger than the main Langebaanweg 'E' Quarry assemblage by Gentry (1980), despite the presence of this archaic *Kobus* and of a boselaphine. Better-preserved horn cores from these localities show additional differences from the main Tinde West reduncine in having stronger backward curvature and in the divergence not increasing distally (Lydekker, 1878, Pl. 25 fig. 4; 1886, Fig. 2; Pilgrim, 1939, Pl. 1 fig. 9 [cross section only]; Thomas, 1980, Fig. 1 no. 13, Fig. 5; Gentry, 1980, Fig. 63). Gentry (1980, p. 323) listed and discussed the characters of these horn cores and noted that the supraorbital pit in Baard's Quarry examples was smaller than at other localities. Thomas (1980, p. 87) reported internal sinuses in the vicinity of the supraorbital pit for the Lukeino species.

The teeth from Mpesida and Lukeino, which Thomas (1980, Fig. 1 nos. 6,7, Fig. 2 no. 6) took as *Kobus* aff. *porrecticornis*, are perhaps a little smaller than the Manonga Valley teeth of *Kobus* aff. *subdolus*.

Pilgrim had followed Lydekker in assigning *Kobus porrecticornis* to the Antilopini, and favored a relationship to *Aepyceros* on characters both of the horn core and of an assigned maxilla (Pilgrim, 1939, Fig. 3), but Gentry (1970, p. 317) suggested a reduncine affinity. Both Thomas (1980) and Gentry (1978a, 1980) treated the species as belonging to *Kobus*, whereas Pilgrim (1939, p. 44) had founded the genus *Dorcadoxa* for it. Horn cores of *Kobus* aff. *subdolus* may show an evolutionary advance over *K.* aff. *porrecticornis* in that they are more fully reduncine in characters such as a less compressed cross section, a more flattened lateral surface, a more posterolateral keel, and a diminished backward curvature basally. It is therefore interesting that the Inolelo 1 assemblage comes from the Ibole Member underlying the Tinde and Kiloleli Members with *Kobus* aff. *subdolus*.

Tribe *Hippotragini*
Genus *Praedamalis* Dietrich, 1950
Type species *Praedamalis deturi* Dietrich, 1950
Praedamalis sp.

Material.

WM1760/92	Horn core	Shoshamagai 2 (Ibole Member)
WM873/92	Horn core	Kiloleli 2
WM 831/92	Right M_2 (Figs. 3E,F) in middle wear, 21.2 × 10.1	Kiloleli 2
WM 1324/92	Right mandible with molar (Fig. 3G) in early wear, c. 18.8 × 8.5	Kiloleli 4

The second horn core is a basal part only, about 75 mm long and with the top of the pedicel also present. The maximum basal diameter is 30.3 and the maximum diameter at right angles to this is 27.9, but the orientation of these diameters in relation to the skull is not known. The thickest part of the smaller (?mediolateral) diameter lies close to the center point of the larger (?anteroposterior) diameter. The slight degree of compression probably increases above the base. There is no flattening of the surfaces of the horn core and no keels. The horn core is very slightly curved in one plane and has some sign of a sinus in its pedicel.

From what is preserved of it, this horn core matches *Praedamalis deturi* as described in Gentry (1987) but is quite a lot smaller. *Praedamalis deturi* is known from the Laetolil Beds at Laetoli and from the Denen Dora Member of the Hadar Formation (Gentry, 1981) where the horn cores appear to be less compressed mediolaterally. Illustrations of *Praedamalis* horn cores may be seen in Dietrich (1950, Pl. 2 fig. 23) and Gentry (1981, Pl. 2; 1987, Pl. 10.7).

The first horn core is more doubtfully assigned. It is just over 60 mm long and very slightly curved in one plane. It is not known from how far above the base it comes. The two diameters, measured as at the base of 873/92, are 25.7 and 21.9, giving it slightly more compression than the other horn core.

A horn core of *?Hippotragus* sp. has been described from Sahabi (Lehmann and Thomas, 1987, p. 328, Fig. 4A). Geraads (1989, p. 786, Pl. 2 Fig. 1) assigned to the Hippotragini a frontlet with horn core bases and two M_3s from the upper Miocene of Djebel Krechem, and the Mpesida horn core of Thomas (1980, Fig. 1 [12]) could also be a hippotragine.

The lower molar on 1324/92 is in early wear. It is not an M_3 and if the ventral ramus does indeed rise just behind it then the M_3 would have been unerupted. It has a prominent goat fold, and the front and back halves are insufficiently squashed anteroposteriorly to match Reduncini although the difference is not substantial. The mandibular horizontal ramus is not deep enough for Alcelaphini. It shows no basal pillar. The M_2 831/92 has some indication of a goat fold, and of a tiny basal pillar barely separated from the hypoconid.

These teeth are more primitive than in modern *Hippotragus* in the less prominent goat fold, less outbowed lingual lobes, no constrictions across the labial lobes, and much smaller basal pillars. The first character and often the last also differ from *Oryx*. The teeth could well belong to the same species as the *Praedamalis* horn cores.

Tribe *Alcelaphini*
Genus *Damalacra* Gentry, 1980
Type Species *Damalacra neanica* Gentry, 1980
Damalacra sp.

Material from Shoshamagai 2 (Ibole Member).

WM1042/92	Right M^3, early middle wear, 21.2 × 13.4. Possibly same individual as 1741/92.
WM1044/92	Right M/1, middle wear, c. 21.1 × c. 10.1
WM1094/92	Right P^4, middle wear, 12.0 × 11.5
WM1740/92	Right M_3 (Fig. 9A), early middle wear, 24.2 × 9.3
WM1741/92	Right M^2, early middle wear, 22.2 × 14.3
WM1745/92	Right P/3 (Fig. 9D), early wear, 11.3 × 6.1

Also 2 partial left upper molars from Shoshamagai 2

Material from Inolelo 1.

WM967/92	Left M^3 (Fig. 8A), early middle wear, c. 21.2 × c. 13.2
WM968/92	Left M$_3$, unworn, c. 28.0 × 9.3 × 31.4 high
WM970/92	Right M^2, middle wear, 22.4 occlusal length
WM971/92	Left M$_3$, early middle wear, c. 27.0 × c. 9.5
WM972/92	Right M$_1$, middle wear, 17.8 × 9.2
WM973/92	Right M^3, early middle wear, 20.1 × 11.7 × c. 28.0 (estimated unworn height)
WM974/92	Left M$_2$, middle wear, 21.9 × 11.3
WM980/92	Right maxilla with M$^{1-2}$ (Fig. 8B), early middle wear, M^1 = 19.8 × 14.4, M^2 = 22.3 × 13.2
WM988/92	Right P^4, early middle wear, 12.5 × 9.9
WM1005/92	Left upper molar, possibly M^3, late wear, 20.9 × 14.8
WM1108/92	Right M^3, late wear, 18.7 × 16.1
WM1109/92	Right M^2 (Fig. 8D), early middle wear, 19.9 × 14.6
WM1114/92	Left M^3, early wear, 21.0 × 13.3 × c. 31.0 high
WM1966/92	Right M$_1$, middle wear, with a basal pillar, 17.9 × 9.3

Also 2 right and 2 left upper molars from Inolelo 1 and a right and a left upper molar from Inolelo 3

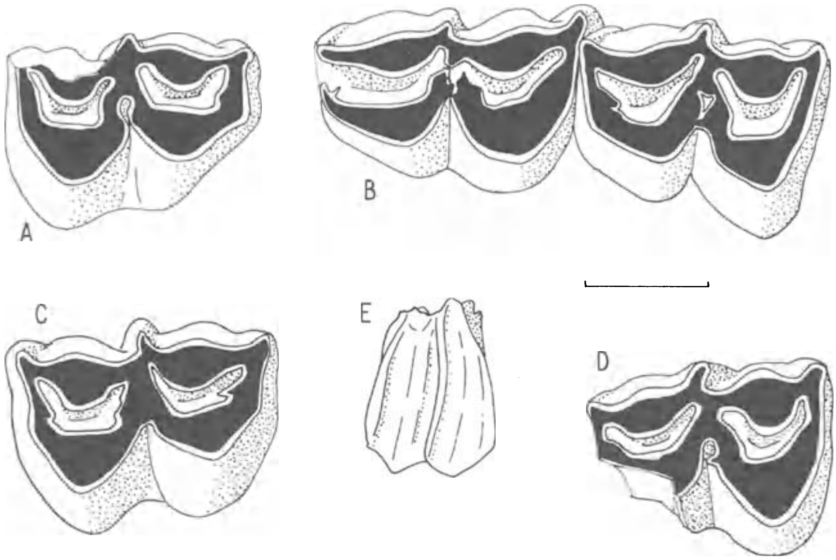

FIGURE 8. Upper molar teeth of *Damalacra* sp. (A) Occlusal view of left M^3 (WM967/92) from Inolelo 1. (B) Occlusal view of right M$^{1-2}$ (WM980/92) from Inolelo 1. (C) Occlusal view of left upper molar (WM169/90) from Tinde West. (D) Occlusal view of right M^2 (WM1109/92) from Inolelo 1. (E) Labial view of left M^1 (WM167/90) from Tinde West. Anterior side to the left for C and E; otherwise, to the right. Scale = 10 mm (A–D) or 20 mm (E).

Material from Tinde West.

WM167/90	Left M^1 (Fig. 8E), earliest wear, 21.3 × 12.7 × 23.5 high
WM169/90	Left upper molar (Fig. 8C), early middle wear, 20.9 × 13.4
WM169/92	Left upper molar, prob. M^2, early middle wear, 22.5 × c. 17.0
WM174/92	Left upper molar, perhaps M^1, late middle wear, c. 19.2 × c. 16.0
WM772/92	Right M^2, early middle wear, c. 18.8 long, much damaged
WM173/90	Right mandible with molars, prob. M_2 and broken M_3, late middle wear, M_2 = c. 16.7 × c. 11.7, M_3 = c. 25.0 × 12.1
WM1862/92	Right mandible with M_2 (Fig. 9B), early wear, 21.1 × 8.9 × c. 34.0
WM176/90	Right P_4 in early wear plus M_1 in middle wear (Fig. 9C)

Also 2 left lower molars from Tinde West

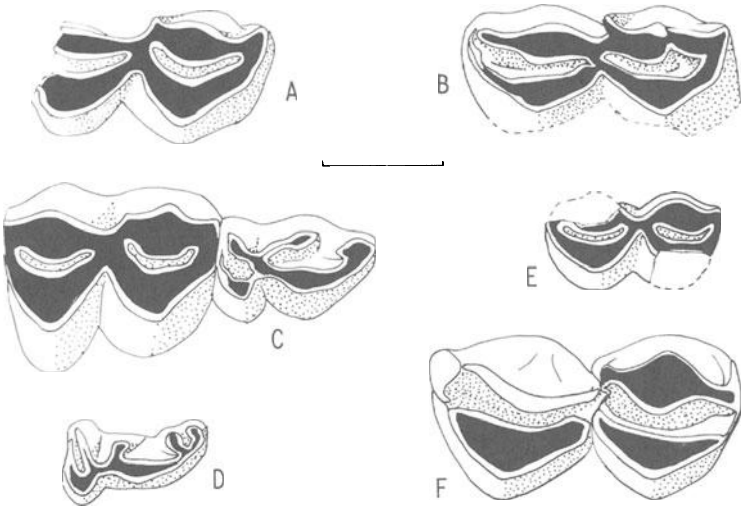

FIGURE 9. Occlusal views of lower cheek teeth of fossil Alcelaphini. (A) Partial right M_3 of *Damalacra* sp. (WM1740/92) from Shoshamagai 2. (B) Right M_2 of *Damalacra* sp. (WM1862/92) from Tinde West. (C) Right P_4–M_1 of *Damalacra* sp. (WM176/90) from Tinde West. (D) Right P_3 of *Damalacra* sp. (WM1745/92) from Shoshamagai 2. (E) Left lower molar of Alcelaphini, smaller sp. (WM1429/92) from Ngofila 2. (F) Right M_2 from mandible of Alcelaphini, larger sp. (WM1251/92) from Kiloleli 2. Anterior sides to the right except for E. Scale = 10 mm.

Material from Kiloleli 2.

WM599/90	(?Right) horn core base, 46.9 × 33.0
WM832/92	Left M_1, early middle wear, 18.8 × 8.8
WM837/92	Right M^3, early middle wear, c. 21.2 long
WM915/92	Partial right M_3, unworn or earliest wear, c. 26.0 long × 30.5 high
WM1252/92	Right M^3, early wear, c. 20.8 × 14.4 × c. 42.7 (first two measurements taken at lower level than damaged occlusal surface)

Material from Kiloleli 3.

WM833/92	Right M^1, early middle wear, c. 18.6 × 14.4
WM941/92	Partial left lower molar, early middle wear

Also a left upper molar from Kiloleli 2, and a left lower molar from Kiloleli 4

Also a left lower molar from Ngofila 5

Material from Beredi.

WM1503/92	Right mandible with dP_4–M_1, M_1 in early wear, dP_4 = c. 21.0, M_1 = 19.7 × 7.9	Beredi South 1
WM1492/92	Left lower molar, probably M_2, middle wear, 19.1 × c. 10.0	Beredi North

Also lower molar in block from Beredi South 1, 2 right upper molars and 2 pieces of left lower molars from Beredi North

A right horn core base (BMNH M43794), in the 1929 Grace collection from Tinde, belongs to this species. Its paired basal diameters are 38.7 × 31.9.

The piece of a possible *Damalacra* horn core at Kiloleli 2 is broken across its pedicel. It is about 80 mm long and shows mediolateral compression diminishing distally, flattening of the presumed lateral surface, an approach to a posterolateral keel basally, divergence increasing distally, and a large sinus in the pedicel. Its compression exceeds other *Damalacra* (Gentry, 1980, Fig. 39) and hence raises doubt about its specific identity.

Most of the alcelaphine teeth in the collection are very nearly as big as *Parmularius altidens* of Olduvai Gorge Bed I and about 10% smaller in occlusal lengths than the two *Damalacra* species at Langebaanweg. M^3s have less of a metastyle flange than in contemporaneous reduncines. Lower molars can be distinguished from those of the reduncines in the same collection by being larger, without goat folds, with flatter lingual walls, with wider labial lobes, stronger metastylids in earlier wear, and M_{2+3} without basal pillars. Hypsodonty probably exceeds that of the Manonga reduncines (Fig. 10).

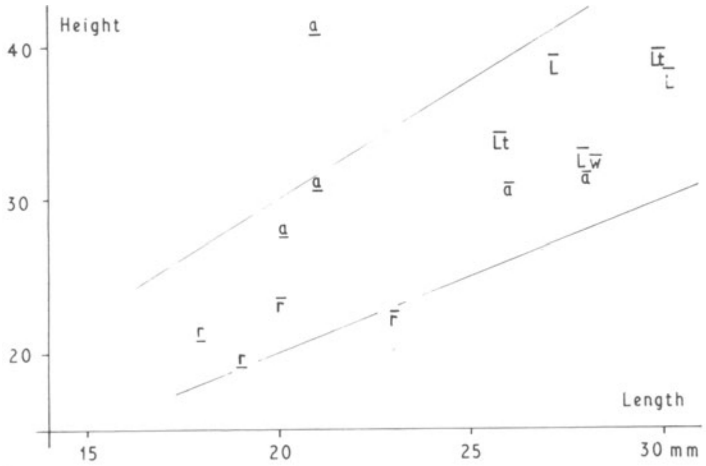

FIGURE 10. Dimensions of unworn or almost unworn M_3s and M^3s of Alcelaphini and Reduncini. a = Manonga Alcelaphini; r = Manonga Reduncini; L = Langebaanweg Alcelaphini; Lt = Laetoli Alcelaphini; w = Wadi Natrun Alcelaphini. M^3s with bars below the readings, M_3s with bars above. The upper diagonal line is that along which height is 150% of length; the lower line is that along which both dimensions are equal. Alcelaphine M_3s of Pleistocene and Holocene age (not shown) are nearly all above the 150% line.

Comparisons. The slight backward curvature, flattened lateral surface, and compression of the horn core 599/90 make it more like *Damalacra acalla* than *D. neanica* at Langebaanweg. The cast of a Wadi Natrun horn core (BMNH M8199) believed to belong to *Damalacra* (Gentry, 1980) has some flattening of its lateral surface, but is probably straighter.

The Manonga Valley teeth are slightly advanced on Langebaanweg alcelaphine teeth. Some of the following characters may be detectable: upper molars with a stronger paracone labial rib, more rounded lingual lobes, and more complicated central fossettes; lower molars more advanced in outbowing of lingual walls between stylids, with rounding of labial lobes, and more sign of transverse narrowing of middle part of central fossettes; the single P_4 (176/90) with a shorter and more posteriorly directed entoconid than at Langebaanweg, but with its paraconid and metaconid still separate. Survival of basal pillars (ectostylids) on M_1s agrees with Langebaanweg.

They are less advanced than Laetoli alcelaphine teeth (BMNH 1935 collection, which may not be exclusively from Laetolil Beds) in less rounded lingual lobes of upper molars, basal pillars on M_1s, and perhaps by less outbowing of lingual walls and less rounding of labial lobes of lower molars. Their degree of hypsodonty is lower than at Laetoli or later sites; interestingly, it may also be lower than at Langebaanweg so far as can be seen from only a few specimens (Fig. 10; also Gentry, 1980, Fig. 43).

Two Wadi Natrun teeth appear to be of Alcelaphini, close in morphology to the Manonga species. One is an upper molar (Stromer, 1907, p. 120, Pl. 20 fig. 1) and the other an incomplete and unworn M_3 (Andrews, 1902, p. 439, Pl. 21 fig. 9). A cast of the second is in London (BMNH M12361). Gentry (1980, p. 296) previously took both teeth as of *Damalacra*, close to the Langebaanweg species. The hypsodonty of the M_3 is close to that of the Manonga Valley and Langebaanweg alcelaphines.

If the age of the Manonga localities should be pre-Pliocene, these teeth would be important as the earliest unequivocal alcelaphine teeth in Africa. Thomas (1981) rejected at least some of the alcelaphine teeth claimed for the Baringo sites by Gentry (1978a), and Langebaanweg is customarily placed in the earliest Pliocene. The primitive aspect of Langebaanweg alcelaphine (and reduncine) teeth is, however, puzzling for its reputed age.

Alcelaphini, larger sp.

Material.

WM1251/92	Juvenile right mandible with damaged, newly erupted M_2 (Fig. 9F), c. 26.1 × 11.0	Kiloleli 2

Alcelaphini, smaller sp.

Material.

WM1921/92	Left M^3, early middle wear, 19.0 × c. 11.7 (× c. 28.0 high when unworn)	Shoshamagai 2 (Ibole Member)
WM1495/92	M_3 (?right), occlusal length c. 19.5	Beredi North
WM1429/92	Left lower molar (Fig. 9E), middle wear, occlusal length c. 15.7	Ngofila 2

There is evidence at more than one of the Manonga localities for a rarer smaller alcelaphine species and at Kiloleli 2 for a much larger one. The molar on the mandible 1251/92 of the larger species is very little worn, so if it were an M_1, it could not already have had an adult P_4 in front of it. The tooth in front, broken at the neck, was not a dP_4, therefore the molar cannot be an M_1. Its occlusal length is about a third larger than in the M_2s of the common alcelaphine.

The occlusal length of the M_3 1495/92 is about three quarters the size of M_3s in the common alcelaphine, and the occlusal length of the lower molar 1429/92 is about four fifths the size of M_1s and M_2s in the common species. The molar 1429/92 has its lingual wall too rounded for *Aepyceros*, and it does not possess a goat fold or basal pillar like a reduncine. The labial rib of the paracone on the M^3 1921/92 is insufficiently localized for the tooth to be of a reduncine and it is too hypsodont. It is rather large to be conspecific with the two lower molars attributed to a small alcelaphine.

Tribe Aepycerotini
Genus *Aepyceros* Sundevall, 1847
Type species *Aepyceros melampus* (Lichtenstein, 1812)
Aepyceros sp.

Material.

WM875/92	Part right horn core	Kiloleli 2
WM636/90	Part left horn core	Kiloleli 3

Little can be noted about these pieces of horn cores. The first is preserved for about 70 mm of its length and the second for about 50 mm. They are curved, not compressed in cross section, without any indication of torsion, and one surface is flattened. They match *Aepyceros* better than the *Prostrepsiceros libycus* Lehmann and Thomas, 1987 of Sahabi. Thomas (1980) recorded *Aepyceros* from Lukeino.

4. Summary of Manonga Ruminants

The Manonga ruminants are distributed stratigraphically as shown in Table I, which also gives a complete list of the species present. Table II shows their distribution among the localities.

Most of the bovid fossils in the collection can be satisfactorily identified as reduncine or alcelaphine. No boselaphines, bovines, neotragines, antilopines, or ovibovines have been noted. Reduncines predominate at Tinde West, but alcelaphines are the commoner tribe at Shoshamagai, Inolelo, and Kiloleli, hinting at possible differences in paleoecology between the localities. Absence of Antilopini could connote less open or dry habitats. Kiloleli 2 has the most varied species list. The possible primitiveness of *Kobus* aff. *porrecticornis* to *Kobus* aff. *subdolus* fits the concept that Inolelo is stratigraphically lower than localities with the latter species.

Table I. Stratigraphic Distribution of Ruminants in the Wembere–Manonga Formation

	Wembere–Manonga Formation		
	Ibole Member	Tinde Member	Kiloleli Member
Giraffa sp.		X	
?*Sivatherium* sp.		X	X
Tragelaphus sp.	X	X	
Kobus aff. *subdolus*		X	X
Kobus aff. *porrecticornis*	X		
Praedamalis sp.	X		X
Damalacra sp.	X	X	X
Alcelaphini, larger sp.			X
Alcelaphini, smaller sp.	X		X
Aepyceros sp.			X

Table II. Locality Distribution of Ruminants in the Wembere–Manonga Formation

Locality	Species	Specimens
Ibole Member		
SHOSHAMAGAI 2	*Tragelaphus* sp.	teeth
	Praedamalis sp.	horn core
	Damalacra sp.	teeth
	Alcelaphini smaller sp.	tooth
INOLELO 1	*Kobus* aff. *porrecticornis*	horn core, teeth
	Damalacra sp.[a]	teeth
INOLELO 3	*Damalacra* sp.	teeth
Tinde Member		
TINDE WEST	*Giraffa* sp.	tooth
	?*Sivatherium* sp.	metapodial (Grace collection)
	Tragelaphus sp.	tooth
	Kobus aff. *subdolus*[b]	horn cores, teeth
	Damalacra sp.[c]	teeth
Kiloleli Member		
KILOLELI 2	?*Sivatherium* sp.	tooth
	Praedamalis sp.	horn core, tooth
	Kobus aff. *subdolus*	tooth
	Damalacra sp.[d]	horn core, teeth
	Alcelaphini larger sp.	juvenile mandible
	Aepyceros sp.	horn core
KILOLELI 3	*Damalacra* sp.	teeth
	Aepyceros sp.	horn core
KILOLELI 4	*Praedamalis* sp.	tooth
	Kobus aff. *subdolus*	tooth
	Damalacra sp.	tooth
BEREDI SOUTH 1	*Damalacra* sp.	teeth
BEREDI SOUTH 4	*Kobus* aff. *subdolus*	horn core
BEREDI NORTH	*Kobus* aff. *subdolus*	horn core, ?tooth
	Damalacra sp.[e]	teeth
	Alcelaphini smaller sp.	tooth
NGOFILA 2	Alcelaphini smaller sp.	tooth
NGOFILA 4	*Kobus* aff. *subdolus*	horn core
NGOFILA 5	*Damalacra* sp.	tooth

[a] *Damalacra* sp. MNI = 4: right probable M^2s 970, 980, 987, and 1109.

[b] *Kobus* sp. MNI = 13: left horn cores; (MNI = 6 on right M_3s).

[c] *Damalacra* sp. MNI = 2: left upper molars, or on combination 173/90 (right M_{2+3}) + 176/90 (right P_4 + M_1) + 1862/92 (right M_2).

[d] *Damalacra* sp. MNI = 2: right M^3s 837 and 1252.

[e] *Damalacra* sp. MNI = 2: rear parts of 2 left lower molars (1491/92, neither being an M_3) plus left lower molar, probably M_2 (1492/92).

5. Reduncine Phylogeny

Gentry (1978b, p. 567) proposed that reduncines evolved from boselaphines, although Pilgrim (1939, p. 21) had been less definite about their boodont status. My 1978 view was based on the boodont aspect of the teeth of modern reduncines, the strong temporal ridges behind the horn bases of Siwaliks fossil reduncines, which resembled those of boselaphines, the fact that reduncines more primitive than those of the East African Plio-Pleistocene were to be found in the Siwaliks, and that Siwaliks horizons rich in boselaphines underlay those in which the reduncines appeared. However, when teeth of the early African reduncine *Kobus subdolus* were discovered in abundance at Langebaanweg (Gentry, 1980), they turned out to be unlike the classical boodont pattern.

The reduncine teeth in the Manonga area reemphasize the strangeness of the Langebaanweg ones. It is conceivable that the Langebaanweg teeth could be the pattern from which Reduncini evolved. They are nonboodont in the sense of being unlike boselaphines or early bovines, and in an African context they look rather like tragelaphines (Gentry, 1980, pp. 255–260). This line of thought would lead to a derivation of reduncines from an aegodont source, perhaps close to the ancestry of Antilopini. Yet the reduncine teeth of the Manonga sites could have descended from teeth like those in upper Miocene Boselaphini, and with fewer changes too. The question is unresolved, and Gentry's (1992) analysis of bovids failed to find a satisfactory place for Reduncini in the evolutionary sequence of bovid tribes.

It was noted earlier that *Kobus* aff. *subdolus* may have horn cores more advanced toward later reduncines than does *K.* aff. *porrecticornis*, which occurs lower in the Manonga basin stratigraphic sequence. If this should be true, then parallel evolution must have occurred either in the advanced horn cores of the Langebaanweg *Kobus subdolus* and Manonga *Kobus* aff. *subdolus* or in the advanced teeth of *K. porrecticornis* from various localities and *Kobus* aff. *subdolus*.

6. Faunal Correlations

The Manonga ruminants are later than the middle Miocene as shown by the presence of modern African tribes of bovids. They must date from before the middle of the Pliocene. This is shown with varying certainty by the brachyodonty of the *Giraffa* M_3; the characters by which the ?*Sivatherium* lower molar resembles upper Miocene rather than Plio-Pleistocene sivatheres; the similarity of the *Kobus* aff. *subdolus* horn cores to those of Langebaanweg, Sahabi, and Wadi Natrun; the reduncine teeth being more primitive than in the Shungura Formation and matching those of Mpesida and Lukeino; the occurrence of *Kobus* aff. *porrecticornis* at Mpesida and Lukeino; the primitiveness of the supposed *Praedamalis* teeth; and the alcelaphine teeth being more primitive than at Laetoli and not much advanced on those of Langebaanweg. Only the occurrence of *Praedamalis*, previously recorded from Laetoli and the Hadar Formation, would suggest an age as late as the middle of the Pliocene. The Manonga ruminants are thus relevant for assessing temporal correlations of Miocene or early Pliocene localities such as Langebaanweg, Lukeino, Mpesida, Sahabi, and Wadi Natrun.

The most interesting comparison is with Langebaanweg, usually accepted as of lowest Pliocene age, where early species of *Tragelaphus, Kobus*, and *Damalacra* are found, but where the reduncine teeth are notably more primitive and the alcelaphine teeth slightly more primitive than at the Manonga localities. The Langebaanweg ruminant fauna also contains a boselaphine, likely to be an end representative of the upper Miocene *Miotragocerus/Tragoportax* stock, a primitive bovine, and *Raphicerus* and *Gazella*, indicating that the tribe Antilopini was by now separate from its common ancestry with the Neotragini. The reduncine and alcelaphine teeth, but not the reduncine horn cores, suggest an earlier time level for Langebaanweg, and an earlier time level could entail moving Langebaanweg back to the Miocene. The puzzling European bovid *Maremmia hauptii* (Weithofer, 1888) from Baccinello and other localities in Tuscany is also worth mentioning in this connection. This species is a dentally precocious offshoot close to the ancestry of African Alcelaphini (Thomas, 1984a, Fig. 4). Along with the neotragine *Tyrrhenotragus gracillimus* it seems to represent a temporary irruption of African forms into a restricted part of southern Europe. Despite its upper Miocene age, its teeth are again more advanced than in the Langebaanweg Alcelaphini. In possible opposition to any deduction of a Miocene age for Langebaanweg, it should be noted that the *Sivatherium* from there shows minimal differences from later Plio-Pleistocene species according to Harris (1976a), whereas the sole sivathere tooth at Kiloleli 2 is only very questionably a *Sivatherium* and could as easily go into the Miocene genus *Bramatherium*. A final factor that hinders faunal comparisons with Langebaanweg is the possibility of late-surviving primitive characters in species living at the southern extremity of the African continent.

A resemblance of the Manonga ruminants to those of Mpesida and Lukeino is apparent in the shared occurrences of *Tragelaphus, Kobus* aff. *porrecticornis, Aepyceros*, and a possible hippotragine. It is also clear that reduncine teeth are at a similar level of evolutionary advance. However, no horn cores like those of the more common Manonga Valley *Kobus* aff. *subdolus* were found, so perhaps the Manonga sites other than Inolelo, with its possible *K.* aff. *porrecticornis*, are slightly later. No boselaphines were found, but an early bovine was present at Lukeino. The almost certain absence of Alcelaphini from Mpesida (Thomas, 1980, p. 84) and Lukeino points to a strong paleoecological difference from the Manonga sites other than Tinde West. Mpesida and Lukeino are generally reckoned to be of late Miocene age.

Little is yet known of the upper Miocene fauna of Lothagam 1. A giraffid and various antelopes including a boselaphine are present (Smart, 1976). It would be interesting to know whether the absence of boselaphines in the Manonga Valley is because none has yet been found, because the ecology was wrong for them, or because the sites postdate the African extinction of that tribe.

The tribes Reduncini and Alcelaphini, so common in the Manonga Valley, are represented by little-known species apparently at comparable evolutionary levels at Wadi Natrun. Sahabi has a *Kobus* like *Kobus* aff. *subdolus* of the Manonga Valley, as well as a *Hippotragus*. Sahabi also has a large *Miotragocerus/Tragoportax* different from the Langebaanweg one, a bovine, and a *Prostrepsiceros*, all unknown so far in the Manonga Valley. Geraads (1989, p. 791) has advocated a mixture of upper Miocene with Pliocene ruminants at Sahabi.

These comparisons of ruminant faunas suggest a late Miocene date for the Manonga Valley, close to Mpesida and Lukeino and possibly later than the supposedly Pliocene Langebaanweg. The North African faunas of Sahabi and Wadi Natrun are of more uncertain date.

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Chapter 6

The Anatomy, Paleobiology, and Phylogenetic Relationships of the Hippopotamidae (Mammalia, Artiodactyla) from the Manonga Valley, Tanzania

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1. Introduction

Hippopotamids are well represented in the Manonga Valley fauna, composing 23.4% of all large mammals, and they are second in importance only to bovids. Several species of hippopotamids are represented. The material from the Ibole and Tinde Members, with the exception of a single postcranial specimen, can be assigned to *Hexaprotodon harvardi*, a large hexaprotodont hippopotamid, which is relatively common at late Miocene and early Pliocene sites in East Africa (Harrison, 1993). The remaining specimen from the Tinde Member, an isolated phalanx, apparently belongs to a smaller species of *Hexaprotodon*. The taxonomic affinities of the hippopotamids from the overlying Kiloleli Member are more difficult to ascertain because so few specimens have been recovered. Even though they are most reasonably referred to *Hex. harvardi*, they differ in some minor details from the type material, and it is conceivable that they may represent a somewhat more progressive form. In addition to Neogene hippopotamids, several isolated teeth and some postcranial remains of *Hippopotamus* have been recovered from late Quaternary horizons. Apart from a brief discussion of their biochronological implications, these latter specimens are not included in the following analysis.

The aim of this chapter is to present a brief descriptive and comparative account of the hippopotamid material from Neogene sediments in the Manonga Valley. As the specimens are rather fragmentary, consisting primarily of isolated teeth and unassociated postcranials, they do not provide much new information about the anatomy of *Hex. harvardi*, which is otherwise well known from Lothagam and from sites in the Baringo basin. However, the Manonga Valley material is significant for two main reasons: (1) It serves to extend the geographic range of *Hex. harvardi* from southern Ethiopia, and northern and central Kenya, southward as far as northern Tanzania (the Baringo basin in Kenya, previously the southernmost locality with *Hex. harvardi*, is located almost 600 km northeast of the Manonga Valley), and (2) it provides a new focus for reassessing the paleobiology, taxonomy, and phylogenetic relationships of this species, which has received relatively little attention since it was initially described by Coryndon (1977).

2. Materials

Almost three hundred hippopotamid specimens are known from the Manonga Valley (Table I). There are no complete crania, and in fact, cranial and mandibular specimens are poorly represented. The collection comprises mostly isolated teeth (28%) and postcranials (67%). Hippopotamids have been recovered from all of the major stratigraphic units of the Wembere–Manonga Formation (see Harrison and Verniers, 1993; Verniers, this volume, Chapter 2, for a detailed discussion of the stratigraphy), although they occur much less frequently in the Ibole and Kiloleli Members than they do in the Tinde Member, which has yielded almost 70% of the material described here (Table I). Material

Table I. Number and Distribution of Hippopotamid Remains from the Manonga Valley

Unit	Localities	Cranial fragments	Mandibular fragments	Teeth	Post-cranials	Total
Kiloleli Member	Ngofila 4	0	0	0	3	3
	Beredi South 1 & 3	0	0	2	1	3
	Kiloleli 2–4	1	0	16	29	46
Tinde Member	Tinde (1929)	4	0	19	22	45
	Tinde East	0	1	6	33	40
	Tinde West	3	1	24	96	124
Ibole Member	Shoshamagai 2	2	0	9	1	12
	Inolelo 1–3	2	0	8	16	26
Total		12	2	84	201	299

from the Ibole and Tinde Members is clearly identifiable as *Hex. harvardi*, while the few specimens from the Kiloleli Member are provisionally assigned to the same species. An isolated phalanx from the Tinde Member apparently belongs to a smaller species of *Hexaprotodon*.

In addition, a small collection of hippopotamids from Kiloleli 2 was obtained from a yellow clay horizon at the top of the sequence. The bones are pale gray, with a yellowish tinge, and they are generally chalky and quite friable in nature. A similar assemblage has also been recorded from a horizon above the Kiloleli Member at Ngofila 2, where several of the bones exhibit signs of human activity in the form of cut marks. The material from Kiloleli 2 consists of some associated postcranial remains and several isolated teeth of a large hippopotamid. The stout metapodials, the broad unciform with a reduced styloid process, and the narrow, hypsodont lower molars are typical of *Hippopotamus*, and comparisons show that they are morphologically indistinguishable from modern *Hip. amphibius*. Although few other fossil mammals were recovered from this particular horizon at Kiloleli 2, several associated teeth have been identified as *Phacochoerus* sp. It is reasonable to assume that these bones are late Pleistocene or Holocene in age. The only other hippopotamid specimen recorded from the Manonga Valley is a fragment of a molar, probably of *Hip. amphibius*, from the mbuga clays at Kininginila. These clays are widely distributed throughout the Manonga Valley as superficial sediments, and they are estimated to be late Quaternary in age (see Harrison and Baker, this volume, Chapter 13).

The major portion of the hippopotamid material included in this study was collected between 1990 and 1994 by the Wembere–Manonga Paleontological Expedition (WMPE). This material is housed in the National Museums of Tanzania in Dar es Salaam. The remaining specimens were recovered in 1929 by Grace and Stockley at the site of Tinde, and this latter collection is housed in the Natural History Museum, London. Specimens from the National Museums of Tanzania are identified by their field numbers, which are prefixed by the letters WM (for Wembere–Manonga), while the London specimens are prefixed by the letter M. Comparisons with fossil hippos from other sites in Africa and Eurasia, as well as extant hippos, were made at the Natural History Museum, London, the Rijksmuseum van Natuurlijke Historie, Leiden, the Institut Paleontologic, Sabadell, the American Museum of Natural History, New York, and the National Museums of Kenya, Nairobi.

3. Temporal and Geographic Distribution of *Hexaprotodon harvardi*

Preliminary reports on the geology and paleontology of the Turkana and Baringo basins in Kenya made reference to the occurrence of a previously undescribed primitive hexaprotodont hippopotamid from late Miocene and early Pliocene sediments (Patterson, 1966; Patterson *et al.*, 1970; Coryndon, 1970; Bishop *et al.*, 1971; Coryndon and Coppens, 1973; Maglio, 1974). Patterson *et al.* (1970) identified this material as *Hippopotamus (Hexaprotodon)* sp. nov. A. A brief review of the fossil hippopotamids from the Turkana basin led Coryndon (1976) to identify a new species from Lothagam 1 and Kanapoi, which she provisionally referred to as sp. "D" nov. Later, Coryndon (1977) formally proposed the name *Hex. harvardi* for this species. Additional specimens were subsequently described from sites of similar age in the Baringo basin (Coryndon, 1978a,b). To date, only preliminary accounts of the morphology of *Hex. harvardi* have been published (Coryndon, 1977, 1978a,b), so the recovery of new material from the Manonga Valley provides an ideal opportunity to present a more comprehensive overview of the anatomy and taxonomic status of *Hex. harvardi.*

Hexaprotodon harvardi represents the earliest known member of the Hippopotaminae (see section 6 for a fuller discussion of its phylogenetic status). It is restricted to the late Miocene and early Pliocene of East Africa, known primarily from sites in the Turkana and Baringo basins of Kenya, dated at 7–4 Ma. The species is best known from the type site of Lothagam in northern Kenya, where an extensive series of well-preserved cranial and postcranial specimens has been recovered (Coryndon, 1977, 1978a). Based on faunal comparisons, the age of Lothagam is generally regarded as 5–7 Ma (Patterson *et al.*, 1970; Maglio, 1974; Smart, 1976; Behrensmeyer, 1976; Hill and Ward, 1988; Hill *et al.*, 1992, Hill, 1994). This has been confirmed by recent radiometric dates (Leakey *et al.*, 1996) which give an age of 4.72–6.24 Ma for the main fossil beds. Coryndon (1977), in her initial description of the species, also included material from Kanapoi, a site about 50 km south of Lothagam on the western side of Lake Turkana. The sediments are younger than those from Lothagam, and are estimated to be 3.9–4.2 Ma (Patterson, 1966, Maglio, 1974; Hill, 1994; Brown,1994; Leakey *et al.*, 1995). As noted by Coryndon (1977, 1978a), the sample from Kanapoi is somewhat more derived than the type material in several key craniodental characteristics (see section 6.2 for details). Leakey *et al.* (1995) recently identified the hippopotamid from Kanapoi as *Hex.* cf. *protamphibius*, but detailed comparisons of the cranial and dental morphology confirms its closer affinities with *Hex. harvardi.*

The species has also been recorded from Baringo (Coryndon, 1978a,b). The best sample comes from the Lukeino Formation, dated at 5.6–6.2 Ma (Hill *et al.*, 1985, 1986; Hill and Ward, 1988; Hill, 1994). These specimens are indistinguishable from those from Lothagam. A small, but important, collection is also known from the earlier Mpesida Beds, dated at 6.4–7.0 Ma (Hill *et al.*, 1985, 1992; Hill and Ward, 1988; Hill, 1994). These specimens are morphologically very similar to *Hex. harvardi* from Lothagam and Lukeino, but they are slightly larger in size (the cheek teeth have an occlusal area that is 16.6% larger, and several specimens exceed the 95% confidence limits for the combined sample from Lothagam and Lukeino). Coryndon (1978b) also noted a general similarity between the specimens from Lukeino and those from the Toluk and Aterir Beds, which date from about 4.5–5.0 Ma (Coryndon, 1978a; Hill, 1994), although the collections are too fragmentary to be able to attribute them with certainty to *Hex. harvardi*. It is also possible that *Hex. harvardi* may be represented in the lower Chemeron Formation, which is estimated to be 3.7–5.6 Ma (Coryndon, 1978b; Hill *et al.*, 1985; Hill, 1994). A few isolated teeth of a medium-size hippopotamid, almost certainly attributable to *Hex. harvardi*, have been reported from the Ngorora Formation, which is estimated to be 9.0–12.3 Ma (Bishop and Chapman, 1970; Maglio, 1974; Bishop and Pickford, 1975; Pickford, 1978a; Coryndon, 1978a,b; Hill *et al.*, 1985; Gèze, 1985; Hill and Ward, 1988; Hill, 1994). However, Pickford (1983) has argued that the provenience of these specimens is doubtful, and that they may be derived from the Mpesida Beds or the Lukeino Formation.

Further north, in Ethiopia, *Hex. harvardi* has been provisionally identified from the Adu Asa and Sagantole Formations of the Middle Awash Valley (Kalb *et al.*, 1982a,b,c). These sediments are estimated to be 6–4 Ma (Kalb *et al.*, 1982a,b,c; Kalb and Jolly, 1982; Kalb & Mebrate, 1993; Kalb, 1993), consistent in age with *Hex. harvardi* sites in northern Kenya.

4. Craniodental Material

Unfortunately, cranial and mandibular specimens are not well represented in the collections from the Manonga Valley, and most of the craniodental specimens consist of isolated teeth (see Table I). All of the permanent dentition, with the exception of P_1, is represented, however, and the collections also include examples of upper and lower deciduous premolars. A catalog of the craniodental specimens from the Manonga Valley is presented in Table II, and a list of standard measurements is given in Table III. A description of the new material from the Manonga Valley is presented in the following sections, along with a discussion of the general morphology, comparative anatomy, and taxonomy of *Hex. harvardi*.

4.1. Cranium and Mandible

Few cranial specimens have been recovered from the Manonga Valley. WM 056/90 comprises a left premaxilla of a juvenile individual in which the three

Table II. List of Hippopotamid Craniodental Specimens from the Manonga Valley[a]

Tinde[b]	
M 44683	Right maxilla of juvenile individual with canine erupting and roots of P^1 and dP^{2-4}, and the anterior alveolus for M^1
M 44684	Right M^1 or M^2 in maxilla fragment, heavily worn
M 44685	Right M_2, moderately worn
M 44686	Left M^3, lightly worn
M 44687	Left M^1
M 44688	Left dP_2, apex of main cusp lacking
M 44689	Right P^2, worn, distal margin missing
M 44690	Right maxillary fragment with distobuccal portion of M^1 and alveolus of M^2
M 44691	Left M_2, mesiolingual portion of the crown lacking
M 44692	Left maxillary fragment of juvenile individual with M^2 preserved in crypt
M 44693	Lower canine, fragment
M 44709	Upper canine, fragment
M 44710	Lower canine, tip of crown only
M 44711	Lower canine, fragment
M 44712	Lower canine, fragment
M 44713	Lower canine, fragment
M 44714	Lower canine, fragment
M 44715	Upper canine, fragment
M 44716	Lower incisor, fragment
M 44717	Lower incisor, fragment
M 44718a–b	Lower canine, two conjoining fragments
M 44719	Lower incisor, fragment
M 44712	Lower incisor, fragment
Tinde West	
WM 036/90	Right M^2, fragment
WM 056/90	Right premaxilla of subadult individual with the I^{1-3} just erupting
WM 245/90	Right mandibular fragment, edentulous with roots of M_{2-3}
WM 268/90	Right P^3, distolingual portion of crown only
WM 283/90	Lower canine, fragment
WM 469/90	Right M_3, distal portion of crown only, heavily worn
WM 470/90	Right M_1, missing distal one-third and mesiolingual corner of crown, moderately worn
WM 481/90	Right M^1 in maxillary fragment, moderately worn
WM 557/90	Lower molar fragment
WM 558/90	Right P_2 or P_3
WM 814/90	Lower incisor, worn
WM 087/92	Left P^3, lingual accessory cuspule and portion of main cusp only
WM 113/92	Left P^3, lingual heel of crown only, unworn
WM 222/92	Molar fragment
WM 421/92	Left dP^2, mesial portion of crown only, slightly worn
WM 521/92	Upper molar fragment, probably M^1
WM 547/92	Right P^4, unworn
WM 572/92	Right dP_4, distobuccal portion of crown only
WM 577/92	Upper canine, fragment
WM 621/92	Left M_3, distal portion of crown only, heavily worn
WM 763/92	Lower canine, fragment
WM 1899/92	Left P_2 or P_3, slightly damaged
WM 1905/92	Right dP^2, distal portion of crown only
WM 1906/92	Right lower incisor, possibly I_3, moderately worn
WM 105/94	Left P^3, slightly damaged mesially
WM 910/94	Left dP^2, distal portion of crown only, moderately worn
WM 918/94	Lower canine fragmen
WM 924/94	Left premaxilla of immature individual with I^{1-2} erupting, root of dP^3

(*continued*)

Table II. (Continued)

Tinde East	
WM 319/90	Left M_3, mesiobuccal corner of crown missing, moderately worn
WM 326/90	Lower canine, fragment
WM 442/90	Lower canine, 3 fragments
WM 445/90	Right upper canine, medial portion of apex only
WM 695/92	Right mandibular fragment, edentulous with the roots of M_{1-2}
WM 1854/92	Right M^2, missing mesiolingual corner of crown, heavily worn
WM 070/94	Lower canine, fragment
Kiloleli 2	
WM 594/92	Left P^3, lacking mesial portion of crown, moderately worn
WM 852/92	Right M_3, mesiobuccal corner missing, unworn
WM 853/92	Right M_1 or M_2, heavily worn
WM 855/92a	Right P^4, distobuccal fragment of crown only, unworn
WM 855/92b	Left P_2 or P_3, distal fragment of crown only
WM 855/92c	Right P_4, distobuccal portion of crown only
WM 855/92d	Right lower incisor, probably I_3, moderately worn
WM 1281/92	Upper molar fragment
WM 1283/92	Upper incisor, probably right I^2, tip of crown only
WM 394/94	Lower canine, fragment
WM 399/94	Tip of upper incisor and base of crown of lower incisor
Kiloleli 3	
WM 753/90	Left lower canine, fragment
WM 755/90	Right upper incisor, probably I^1
WM 761/90	Right M^2, distal two-thirds of crown only, unworn germ
WM 794/90	Right maxillary fragment, edentulous with the roots of M^{1-3}
Kiloleli 4	
WM 656/90	Left dP_3, distal portion of crown only, worn
WM 808/90	Left M_1 or M_2, moderately worn
Shoshamagai 2	
WM 1169/92	Upper canine, fragment
WM 1780/92	Left maxillary fragment with dP^3, roots of dP^4, alveoli of dP^2 and M^1, dentition moderately worn
WM 1810/92	Left M^2, moderately worn
WM 1811/92	Left M^2, distal moiety of crown only, moderately worn
WM 1813/92	I^3, heavily worn
WM 1815/92	Right dP_4, distal portion of crown only, moderately worn
WM 1818/92	Right dP^2, distal portion of crown only, tip of main cusp incomplete, unworn
WM 1932/92	Upper molar fragment
WM 198/94	Left M_3, moderately worn
WM 286/94	Left maxillary fragment with distal portion of dP^4, heavily worn, M^1, moderately worn, and the partially preserved crowns of P^4 and M^2 preserved in crypts
WM 299/94	Tip of upper incisor, probably left I^2
Inolelo 1	
WM 1000/92	Left M_2, moderately worn
WM 1001/92	Left upper canine, fragment
WM 1064/92	Left I^3, very worn
WM 1119/92	Left P^3, distal portion of crown only, slightly worn
WM 1121/92	Right P^1 in maxillary fragment, worn
WM 1150/92	Left M_2, mesial moiety of crown only, heavily worn
WM 1151/92	Molar fragment
WM 140/94	Lower canine, fragment

(continued)

Table II. (Continued)

Inolelo 3	
WM 664/94	Left maxillary fragment with base of erupting canine, roots of P^1, base of dP^2, and P^2 exposed in crypt
WM 669/94	Left P_2 or P_3
Beredi South 1	
WM 1514/92	Left lower incisor, possibly I_1, tip of crown missing, slightly worn
Beredi South 3	
WM 1670/92	Right upper canine, fragment

[a] Specimens from the Natural History Museum in London have accession numbers prefixed by M. Specimens from the National Museums of Tanzania in Dar es Salaam are unaccessioned, and are referred to here by their field numbers only (prefixed by WM for Wembere–Manonga).

[b] All of the specimens in the Natural History Museum in London were collected in 1929 by Grace and Stockley at the site of Tinde. The field notes of Grace and Stockley establish that they collected material from both Tinde West and Tinde East, but the two samples cannot be differentiated.

Table III. List of Dental Measurements of Hippopotamids from the Manonga Valley[a]

Upper dentition

		Max				
WM 056/90	I^1	13.0(–)				
	I^2	14.2				
WM 755/90	I	18.6				
WM 1064/92	I	15.4				
WM 1283/92	I	22.2				
		AP	TR			
WM 577/92	C^1	—	46.1(–)			
WM 1001/92	C^1	48.3(–)	54.8(–)			
WM 1670/92	C^1	36.4(–)	44.3(–)			
M 44709	C^1	33.8(–)	51.0(–)			
		MD	BL	BL Mes	BL Dist	HT
WM 421/92	dP^2	—	—	—	—	24.4
WM 1818/92	dP^2	—	16.4	—	16.4	—
WM 1905/92	dP^2	—	15.0	—	15.0	—
WM 1780/92	dP^3	35.2	21.3	—	21.3	—
WM 1121/92	P^1	22.6	15.3	—	—	—
M 44689	P^2	38.0	26.6	—	—	—
WM 594/90	P^3	—	—	—	30.5(–)	—
WM 1119/92	P^3	—	—	—	30.5(–)	—
WM 105/94	P^3	—	—	—	26.9	—
WM 547/92	P^4	29.3	36.7	—	—	—
WM 481/90	M^1	46.2	41.6	41.6	40.1	—
M 44687	M^1	44.0	38.1	37.6	38.1	—
M 44684	$M^{1/2}$	42.3	—	—	—	—
WM 761/90	M^2	—	—	—	47.2	46.0
WM 1810/92	M^2	48.2	—	—	42.0	37.5
WM 1811/92	M^2	—	—	—	37.7	—
WM 1854/92	M^2	53.0	—	—	47.3	—
M 44686	M^3	48.2	49.9	49.9	43.6	—

(*continued*)

Table III. (Continued)

Lower dentition

		Max				
WM 814/90	I	19.1				
WM 855/92	I	18.0				
WM 1514/92	I	18.0				
WM 1906/92	I	16.9				
M 44716	I	34.5				
M 44717	I	38.4				
M 44719	I	22.4				
M 44720	I	23.7				
		AP	TR			
WM 326/90	C_1	66.0(–)	35.2(–)			
WM 753/90	C_1	56.8(–)	30.1(–)			
WM 763/92	C_1	51.5(–)	—			
WM 070/94	C_1	60.6(–)	34.5(–)			
M 44693	C_1	61.3(–)	37.4(–)			
M 44710	C_1	50.0(–)	32.5(–)			
M 44711	C_1	—	34.6(–)			
M 44718	C_1	57.2(–)	34.9(–)			
		MD	BL	BL Mes	BL Dist	HT
M 44688	dP_2	29.1	14.7	14.7	13.0(–)	—
WM 656/90	dP_3	—	—	—	17.7	—
WM 558/90	$P_{2/3}$	37.2	23.3	21.2	23.3	37.8
WM 1899/92	$P_{2/3}$	37.0(–)	24.2	19.4	24.2	—
WM 470/92	M_1	—	—	30.0(–)	—	—
WM 808/90	$M_{1/2}$	51.5	34.1	34.1	33.0	—
WM 853/92	$M_{1/2}$	47.3	32.2	31.0	32.2	—
WM 1000/92	M_2	56.0	40.7	40.5	40.7	—
WM 1150/92	M_2	—	—	37.4	—	—
M 44685	M_2	50.4	34.9	34.9	33.2	31.3
M 44691	M_2	45.5	—	—	38.5	—
WM 319/90	M_3	66.6	—	—	34.1	41.2
WM 852/92	M_3	72.7	—	—	38.9	47.6
WM 198/94	M_3	69.2	40.0	—	—	41.5

Abbreviations: AP, maximum anteroposterior length; BL, maximum buccolingual breadth; BL Dist, buccolingual breadth of distal moiety of crown; BL Mes, buccolingual breadth of mesial moiety of crown; HT, maximum height of crown; M, accession number prefix for specimens housed in the Natural History Museum, London; Max, Maximum diameter; MD, maximum mesiodistal length; TR, maximum transverse width; WM, field number prefix for specimens housed in the National Museums of Tanzania; (–) minimum value.

permanent incisors are just beginning to erupt (Fig. 1). The premaxilla is weathered and slightly abraded, having been exposed on the surface for some time prior to collection. The specimen is morphologically very similar to the premaxilla in the type specimen of *Hex. harvardi* from Lothagam (KNM-LT 4). The Manonga Valley specimen is somewhat smaller and less robust than the latter, but this may be accounted for by their difference in age; the Lothagam specimen represents the skull of an adult with advanced dental wear.

The palatal portion of the premaxilla is relatively flat, and the two halves of the bone evidently met coronally in the midsagittal line at an obtuse angle. As

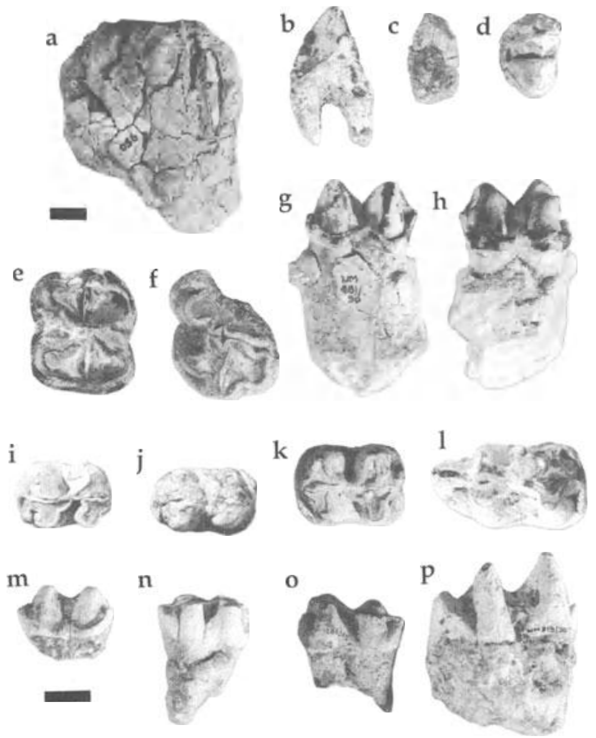

FIGURE 1. Craniodental specimens of *Hex. harvardi* from the Manonga Valley. (a) WM 056/90, left premaxilla with I^{1-3}, palatal view; (b) WM 558/90, right P2 or P3, ligual view; (c) WM 1121/92, right P^1, lingual view; (d) 547/92, right P^4, occlusal view; (e) WM 481/90, right M^1, occlusal view; (f) 1854/92, right M^2, occlusal view; (g) WM 481/90, right M^1, lateral view; (h) WM 481/90, right M^1, medial view; (i) WM 853/92, right $M_{1/2}$, occlusal view; (j) WM 808/90, left $M_{1/2}$, occlusal view; (k) WM 1000/92, left M_2, occlusal view; (l) WM 319/90, left M_3, occlusal view; (m) WM 853/92, right $M_{1/2}$, buccal view; (n) WM 808/90, left $M_{1/2}$, buccal view; (o) WM 1000/92, left M_2, buccal view; (p) WM 319/90, left M_3, buccal view. Scale bars = 10 mm. Top scale bar for a–h, bottom scale bar for i–p.

is typical of *Hexaprotodon* (and also *Choeropsis*), the premaxillae are fused along their entire length in the midsagittal line, and there is no separation anteriorly, as is commonly seen in *Hippopotamus* (Colbert, 1935; Coryndon, 1977; Steunes, 1989). Posteriorly, a remnant of the anterolateral margin of the incisive foramen is preserved. It is located close to the midline of the palate, just posterior to the central incisors. Lateral to the large opening for the incisive foramen is a distinct groove, presumably the anterior continuation of a smaller subsidiary incisive canal. The anterior margin of the premaxilla is broad and straight. It curves laterally around the root of I^3, and then is separated by a shallow concavity from the widely flaring maxilla, which is greatly expanded to accommodate a massive upper canine. The maximum breadth of the palate anteriorly can be estimated to have been 125 mm. The facial portion of the premaxilla is quite steep anteriorly and inferiorly, but it flattens out superiorly to produce a more gently sloping lateral margin to the nasal aperture. The nasal aperture has a broad

U-shaped margin inferiorly, and it approaches very close to the alveolar margin of the incisors (the height of the nasoalveolar clivus in the midline is only 15.5 mm).

A second premaxillary fragment (WM 924/94) from Tinde West confirms the hexaprotodont nature of the dentition. It is a left premaxilla of an immature individual preserving the roots of I^1 and dI^3, and the broken crown of I^2, which was just beginning to erupt. The two permanent incisors are situated side by side in the front of the jaw, while the dI^3 is positioned somewhat more posteriorly.

Five additional cranial specimens preserve portions of the maxilla. M 44683 consists of a right maxillary fragment of a juvenile preserving the tip of the canine, just beginning to erupt, and the roots of P^1 and dP^{2-4}; WM 794/90 is an edentulous right maxillary fragment with the roots of M^{1-3}; WM 1780/92 is a left maxilla of a juvenile with dP^3; WM 286/94 is a left maxilla with dP^4–M^1, and portions of the crowns of P^4 and M^2 retained in their crypts; and WM 664/94 is a left maxillary fragment of a juvenile individual preserving the base of the canine, the roots of P^1, the base of the crown of dP^2, and the unerupted crown of P^2 exposed in its crypt.

The palate appears to have been relatively deep and concave to V-shaped in section. The estimated breadth of the palate at the level of dP^3 in WM 1780/92 is 73 mm. In the juvenile specimens the facial aspect of the maxilla is steep and slightly concave above dP^{2-3}. The infraorbital foramen is located 45 mm above the alveolar margin of the maxilla, which indicates a relatively deep face when compared with *Hip. amphibius* of similar dental age, but similar to *C. liberiensis.* The maxilla is stoutly constructed, with a solid corpus of bone accommodating the roots of the cheek teeth. The anterior root of the zygomatic arch originates very low down on the face, close to the alveolar margin of the maxilla, as in *Choeropsis*. In *Hip. amphibius* the zygomatic arch originates higher on the face, in association with a deeper lower face and more elevated orbits.

Cranially, *Hex. harvardi* shares with *Choeropsis* a number of features that can reasonably be inferred to be plesiomorphic for the Hippopotaminae: (1) There is a tendency for the median suture of the premaxillae to be fused anteriorly; (2) the muzzle is relatively short in relation to the length of the neurocranium; (3) the orbits are placed laterally (not elevated superiorly as in *Hip. amphibius*) and located about midway along the length of the cranium; (4) the anterior root of the zygomatic arch is situated low on the face, at or below the level of the infraorbital foramen (in *Hip. amphibius* the infraorbital foramen is situated lower on the face relative to the root of the zygomatic arch); (4) the nasals are expanded posteriorly; (5) lacrimal and nasal bones are separated by a well-developed antorbital process of the frontal; and (6) the nuchal region does not rise superiorly much above the level of the frontal bone.

The mandible is known only from WM 695/92 and WM 245/90, but these are too incomplete to provide any detailed morphological information. The mandibular corpus appears to be relatively robust, and the anterior root of the ascending ramus originates opposite M_3.

4.2. Upper Dentition

4.2.1. Incisors

WM 056/90, a right premaxilla of a subadult individual, preserves the crowns of I^1–I^3, in an early stage of eruption (Fig. 1). The crowns are enamel-covered and unworn, but they are weathered and badly abraded, so details of their morphology cannot be determined. All three incisors appear to be subequal in size, evenly spaced, and arranged in a gently curving arc in the premaxilla. The crowns are relatively small in relation to the size of the premaxilla, but the incisors would presumably have increased in diameter with continued growth. I^1 is subcircular in cross section. I^2 is more elliptical, with the mesiodistal diameter greater than the buccolingual diameter. I^3 is still partially retained within the crypt, so its cross-sectional shape cannot be ascertained. A similar morphological pattern can be reconstructed from the anterior dentition in a juvenile premaxilla, WM 924/94.

WM 056/90 and WM 924/94 definitively establish that the Manonga Valley hippopotamid was hexaprotodont. In terms of their relative size, the upper incisors are similar to those of *Hex. harvardi* from Lothagam and Lukeino, in which all three incisors are subequal (see Table IV for comparative data on upper incisors). An almost complete skull of *Hex. harvardi* from Kanapoi (KNM-KP 8529), however, is more derived in having an I^1 that is distinctly larger than the other two incisors. Subequal upper incisors are also characteristic of *Hex. sivalensis* from the early Pliocene of the Siwalik Hills, but there is a tendency in this species for I^3 to be somewhat reduced. The only other hexaprotodont

Table IV. Comparison of Uppper Incisors in Fossil and Extant Hippopotamids

Species	Number of incisors	Relative proportions of incisors
Hexaprotodon harvardi		
Lothagam & Lukeino	Hexaprotodont	I^{1-3} subequal ($n = 1$, 80:100:84)[a]
Manonga Valley	Hexaprotodont	I^{1-3} subequal
Kanapoi	Hexaprotodont	I^1 larger,I^{2-3} subequal
Hexaprotodon sivalensis sivalensis	Hexaprotodont	I^{1-2} subequal, I^3 slightly smaller ($n = 1$, 89:100:77)
Trilobophorus afarensis	Hexaprotodont	1^{1-3} subequal
Hexaprotodon protamphibius turkanensis	Hexaprotodont	I^{1-3} subequal
Hexaprotodon aethiopicus	Tetraprotodont	I^{1-2} subequal ($n = 2$, 100:93)
Hexaprotodon karumensis		
Koobi Fora (Upper Burgi)	Tetraprotodont	I^1 much larger than I^2 ($n = 1$, 100:72)
Koobi Fora (Upper KBS)	Diprotodont	
Hippopotamus gorgops	Tetraprotodont	I^{1-2} subequal ($n = 1$, 88:100)
Hippopotamus amphibius	Tetraprotodont	I^{1-2} subequal ($n = 29$, 100:80)[b]
Choeropsis liberiensis	Tetraprotodont	I^{1-2} subequal ($n = 9$, 98:100)[b]

[a] Numbers in parentheses represent the relative size (maximum mesiodistal diameters) of the incisors. The largest incisor is equal to 100. They are average values arranged in sequence starting with I1. *n* is the sample size.

[b] Data from Pavlakis (1987).

hippopotamids from East Africa are *Hex. protamphibius turkanensis* from the lower part of the sequence in the Turkana basin, *Hex. coryndonae* and *Trilobophorus afarensis* from the Afar region of Ethiopia, and possibly also *Hex. imagunculus* from the Western Rift. I have no detailed information on the relative proportions of the upper incisors in these species, but they were apparently subequal, at least in *Hex. protamphibius turkanensis* and *Trilobophorus afarensis* (Gèze, 1985). Most other Plio-Pleistocene hippopotamids from East Africa are distinguished from *Hex. harvardi* in having a tetraprotrodont pattern with two subequal incisors (Gèze, 1985; Harris, 1991, Table IV). However, *Hex. karumensis* from the upper Burgi and lower KBS Members at Koobi Fora is further derived in having a tetraprotodont arrangement in which the lateral incisor is considerably smaller than the central incisor, and this subsequently gave rise to a diprotodont form in the upper KBS Member (Harris, 1991).

The Manonga Valley collections include several isolated upper incisors, but identification of their serial position in the jaw has proved problematic. WM 755/90 and WM 1283/92 are moderately worn, and probably represent I^1 and I^2, respectively. WM 1064/92 and WM 1813/92, both possibly attributable to I^3, are at a more advanced stage of wear. Only the apical portions of the incisors are preserved. The enamel, which is restricted to a continuous strip along the buccal face of the crown, is quite thick, and is marked by a series of faint longitudinal striae. The incisors exhibit a marked curvature toward the mesial and lingual aspects. In cross section, the crowns are rectangular to oval in shape, with the buccolingual diameter being slightly greater than the mesiodistal diameter. In intermediate stages, wear is restricted to the lingual or distolingual face of the crown. This produces a relatively flat or mesiodistally convex occlusal plane, bordered buccally by a raised enamel margin. This ensures that, with continued wear, a sharp incisive edge is maintained. As noted by Coryndon (1978a), this type of wear, produced by tip-to-tip occlusion with the lower incisors, is typical of *Hexaprotodon*. However, in more worn specimens, such as WM 1064/92 and WM 1813/92, in which the enamel surface has been entirely lost through attrition, the occlusal surface is biconvex or conical in shape.

Morphologically and metrically the upper incisors from the Manonga Valley are consistent with those of *Hex. harvardi* from Lothagam. They share the following characteristics: (1) hexaprotodonty, (2) subequality in size, and (3) tip-to-tip occlusion with the lower incisors.

4.2.2. Canine

Partially preserved upper canines have been recovered from Tinde West, Tinde East, Shoshamagai 2, Inolelo 1, and Beredi South 3 (see Table III). The morphology is typical of upper canines of *Hexaprotodon*. They bear a deep V-shaped groove posteriorly, bordered medially and laterally by angular margins. In cross section the upper canine is mediolaterally wider than long, with a flattened anterior face that is narrower than the posterior face. The canine has a convex medial margin, so that the crown curves outwards laterally when seen in ventral view. The enamel is distributed only on the posterior and lateral aspects of the tooth, and its surface is marked by fine striae, rather than the coarse ribs characteristic of *Hippopotamus*. The upper canines wear obliquely anteroposteriorly, at an angle of approximately 135° to the anterior plane, so that the anterior margin of the crown is less elevated above the alveolar plane than the posterior margin.

In comparison with *Hip. amphibius* the canines appear to be relatively large. However, given the high degree of variability (especially with canines that continue to grow throughout life) and sexual dimorphism in canine size in hippopotamids, this is a difficult feature to compare, especially with the small sample sizes available for fossil hippopotamids. Some indication of relative canine size, however, can be gained by relating maximum diameter of the base of the upper canine to the mesiodistal length of M^2. In a sample of 27 skulls of *Hip. amphibius*, the upper canine was found to be mesiodistally shorter than M^2 (with an index less than 100) in all individuals, except for a single specimen with an index of 107 (range = 55–107; mean = 76). By contrast, the modern pygmy hippo, *Choeropsis liberiensis*, has relatively larger upper canines, being usually somewhat mesiodistally longer than M^2 (n = 11; mean index = 110; range = 87–133). Comparative data for *Hex. harvardi* (n = 5; mean index = 108; range = 84–128) confirm that this species has relatively large upper canines. Although there are no upper canines directly associated with molars from the Manonga Valley, comparisons of isolated teeth suggest that the canines were relatively large, similar in size to those from Lothagam and Mpesida.

In sum, the upper canines from the Manonga Valley are identical to those of *Hex. harvardi* from Lothagam and Lukeino. They share the following characteristics that are typical of *Hexaprotodon* (and *Choeropsis*): (1) They are relatively large in size; (2) there is a deep groove along the posterior aspect of the crown; and (3) the enamel surface is finely striated.

4.2.3. Premolars

P^1 is represented by a single isolated specimen, WM 1121/92, from Inolelo 1 (Fig. 1). The crown is mesiodistally long and narrow, and it exhibits a slight degree of buccolingual waisting. It has a single main cusp, which, although worn, was evidently quite tall, with a slight lingual curvature toward its apex. The cingulum is narrow and ill-defined, but it surrounds most of the base of the crown.

This specimen is similar in morphology to those from Lothagam and Lukeino, although it is somewhat smaller. However, it is distinctly larger than the P^1 in later East African hippopotamids, which is very small, and tends to be shed with advancing age. Moreover, maxillary fragments from Tinde (M 44683) and Inolelo 3 (WM 664/94) preserve the roots of P^1, and judging from their size they would have accommodated a sizable tooth (at least 29 mm long in WM 664/94).

Coryndon (1977, 1978a,b) has suggested that *Hex. harvardi* is characterized by having a double-rooted P^1, a feature also seen in *Hex. sivalensis*, and in hippopotami from the Holocene of Madagascar (Steunes, 1981, 1989). Although the root of the tooth is still embedded in bone in WM 1121/92, from the contour of its cervix, as well as from its exposed tip, it appears that only a single root was present. M 44683 and WM 664/94, however, do preserve the roots of a double-rooted P^1. Similar variability in this feature can also be shown to occur in samples of *Hex harvardi* from other sites, such as Lothagam and Kanapoi.

P^2 is a long and narrow tooth, with a single main cusp. The cingulum is continuous around the base of the crown. Arising from the main cusp is a distal crest, which bears several prominent cuspules. P^3 is represented by a number of fragmentary specimens, which together allow a composite description of the tooth. The crown is triangular in shape, being broadest in its distal moiety, owing to the development of a prominent distolingual heel. There is a single main cusp, which is tall, lingually recurved, and triangular in cross section. Three crests descend from the apex of the main cusp. The mesial crest arcs basally to terminate at a well-developed cingular shelf. The two distal crests and the distal basin of the crown bear numerous accessory cuspules. A continuous cingulum passes around the base of the crown, but it is especially well developed along the lingual margin. P^4 is a bicuspid tooth, with a well-developed accessory cusp that is only slightly less elevated than the main cusp (Fig. 1). The crown is broader than long, and elliptical to triangular in shape. A strong cingulum completely surrounds the base of the crown. Accessory cuspules are variably developed. The occlusal area of P^4 falls within the 95% confidence limits of the combined samples from Lothagam and Lukeino (Table V). Although the upper premolars are variable in size, shape, and structure in fossil hippopotamids, the specimens from the Manonga Valley are similar to those from Lothagam and Lukeino in being large, robust, polycuspidate teeth.

As noted by Coryndon (1978a), the length of the upper premolar series is subequal to or exceeds that of the molar row in *Hex. harvardi*. However, as P^1 is commonly lacking in hippopotamids and because fossil material is rarely complete enough to obtain data on the lengths of the premolar and molar series, a

Table V. Size of the Cheek Teeth of *Hex. harvardi* from Lothagam, Lukeino, and Manonga Valley

	Occlusal area (mesiodistal length × buccolingual breadth)				
	Lothagam and Lukeino[a]				
	N	Mean	Range	S.D.	Manonga Valley[b]
P^3	10	1280	994–1560	183	
P^4	22	1233	985–1726	176	1075
M^1	13	1630	1318–1969	206	1676, 1921
M^2	16	2314	1688–3037	400	2024, 2507
M^3	18	2221	1353–2586	297	2405
P_3	4	1004	879–1151	104	867, 895(–)
P_4	14	1176	874–1738	219	
M_1	13	1341	1035–1673	179	
M_2	20	1828	1371–2286	189	1752, 1759, 2279
M_3	17	2319	1789–2785	239	2271(–), 2828(–), 2768

Abbreviations: *N*, sample size; S.D., standard deviation; (–) minimum value.

[a] Data from Lothagam and Lukeino is combined.

[b] Data from Manonga Valley represents individual specimens.

more practical measure of relative upper premolar size has been devised. The index is calculated as follows: The sum of the mean lengths of individual teeth for the P^{2-4} series is divided by the sum of the mean lengths of individual teeth in the M^{1-3} series, expressed as a percentage. In *Hex. harvardi*, this index is 81, which confirms that the premolar series is relatively long when compared with most other hippopotamids (*Hex. sivalensis* = 75; *Hex. karumensis* = 73; *Hex. aethiopicus* = 68; *Hip. gorgops* = 65; *Hip. major* = 69; *Hip. amphibius* = 68; *C. liberiensis* = 83). An alternative measure of the relative size of the premolars is given by the total occlusal area of the upper and lower P3 and P4 expressed as a percentage of the total occlusal area of the upper and lower molars. In *Hex. harvardi* the P3 and P4 have an occlusal area that is 40% of that of the molars, whereas in all other hippopotamids P3 and P4 are much smaller, with an area that is only 30 ± 5% of the molar occlusal area (Table VI).

In summary, the upper premolars from the Manonga Valley share the following characteristic features with *Hex. harvardi* from Lothagam: (1) They are relatively large in size and robust, with pustulate enamel; (2) P^1 is large, and commonly double-rooted; and (3) P^4 is bicuspid, with a well-developed accessory cusp.

4.2.4. Molars

The upper molars are broad and low-crowned, with a prominent cingulum that entirely encircles the base of the crown (Fig. 1). The four main cusps are low and conical in shape. In lightly worn molars, each cusp bears a triangular-shaped exposure of dentine, but as wear advances this becomes an open trefoil shape typical of *Hexaprotodon* (Coryndon, 1978a). The hypsodonty index (height of the crown × 100/buccolingual breadth of the crown) cannot be calculated for any of the complete upper molars from the Manonga Valley because of their advanced stage of wear. However, the height can be measured in two partially preserved unworn upper molars (WM761/90 and WM 1810/92), and in both of these specimen the hypsodonty index can be estimated to have been less than 90. These values are comparable to those seen in *Hex. harvardi*, and in other species of *Hexaprotodon* from East Africa, which have a general range of 70–100. *Choeropsis* is similar to *Hexaprotodon* in having brachyodont upper molars; the hypsodonty index rarely exceeds 100. By contrast, *Hip. amphibius* has upper molars that are distinctly more hypsodont, with an index that may exceed 120.

The upper molars from the Manonga Valley are comparable in overall size to those from Lothagam and Lukeino, and in terms of their occlusal areas (mesiodistal length × buccolingual breadth) they all fall within the 95% confidence limits for the combined sample from Lothagam and Lukeino (Table V). Compared with other hippopotamids, the upper molars are similar in size to *Hex. sivalensis*, slightly larger than *Hex. protamphibius*, and somewhat smaller than those of *Hex. karumensis*, *Hip. amphibius*, *Hip. major*, and *Hip. gorgops*. They are considerably larger than the dwarf forms *Hex. imagunculus* and *Hex. aethiopicus*, as well as the modern pygmy hippopotamus, *C. liberiensis* (Table VI).

Table VI. Size and Proportions of the Cheek Teeth in Fossil and Extant Hippopotamids[a]

	A	B	C	D	E
Hex. harvardi	4,693	11,653	100	100	40:100
Hex. sivalensis	3,398	12,062	72	104	28:100
Hex. protamphibius	3,029	9,620	65	83	31:100
Hex. karumensis	3,922	13,809	84	119	28:100
Hex. aethiopicus	1,916	7,112	41	61	27:100
Hex. imagunculus	2,235	6,860	48	59	33:100
Hip. gorgops	4,511	17,151	96	147	26:100
Hip. major	4,512	16,161	96	139	28:100
Hip. amphibius	4,209	13,444	90	115	31:100
C. liberiensis	1,101	3,510	23	30	31:100

[a] A, mean combined occlusal area (mesiodistal length × buccolingual breadth) of upper and lower P3 and P4 (mm^2). B, mean combined occlusal area of upper and lower molars (mm^2). C, mean combined occlusal area of upper and lower P3 and P4 expressed as a percentage of that in *Hex. harvardi*. D, mean combined occlusal area of upper and lower molars expressed as a percentage of that in *Hex. harvardi*. E, mean combined occlusal area of upper and lower P3 and P4 expressed as a ratio of combined occlusal area of upper and lower molars. Source of data: Harrison (unpublished), Pavlakis (1987), Harris (1991), Faure (1985).

Another interesting characteristic of *Hex. harvardi* is the moderate size differential between the upper molars. Their relative size (occlusal area), expressed as a ratio of the largest of the teeth, and arranged in sequence from M^1 to M^3, is 70:100:96. Comparative data for other hippopotamids are as follows: *Hex. sivalensis*, 66:96:100; *Hex. protamphibius*, 68:100:98; *Hex. karumensis*, 65:95:100; *Hex. aethiopicus*, 77:100:93; *Hex. imagunculus*, 50:91:100; *Hip. gorgops*, 50:83:100; *Hip. amphibius*, 73:100:97; *Choeropsis liberiensis*, 61:99:100. In this respect, *Hex. harvardi* is similar to *Hex. protamphibius* and *Hip. amphibius*, with most other hippopotamids having a somewhat more pronounced size differential between the upper molars.

In summary, the upper molars from the Manonga Valley are consistent in size and morphology with those of *Hex. harvardi* from Lothagam and Lukeino. They are distinguished from those of other species of *Hexaprotodon* from East Africa (but generally similar to *Hex. sivalensis* from Asia) by the following combination of features: (1) the upper molars are larger in size (although they tend to be slightly smaller than those of *Hex. karumensis*); (2) the crowns are more brachyodont; and (3) the size differential between the molars is less pronounced (except for *Hex. protamphibius*).

4.2.5. Deciduous Dentition

The dP^2 is represented by four fragmentary specimens (WM 421/92, WM 1818/92, WM 1905/92, and WM 910/94). The narrow, elongated crown has a distinct buccolingual waisting midway along its length. There is a single main cusp located in the midline of the crown, somewhat closer to the mesial than to the distal end of the tooth. Originating from the apex of the main cusp are sharp mesial and distal crests. The latter gives rise to a small, but prominent, accessory cusp, situated just to the buccal side of the midline. The basal cingulum is continuous around the distal, distobuccal, and lingual margins of the crown, but it is poorly developed on the mesiobuccal face. A well-preserved dP^3 is associated with the partial maxilla of a juvenile individual from Shoshamagai 2 (WM 1780/92). The crown is elongated and triangular in shape, being broadest distally and narrowing mesially. It is a molariform tooth, with three main cusps and a prominent mesial accessory cuspule. The protocone is a large, conical cusp situated in the midline of the crown, slightly toward the mesial end of the tooth. The two distal cusps are subequal and transversely aligned. They are lower and less voluminous than the protocone. The cingulum is well developed, forming a narrow ledge that almost entirely surrounds the base of the crown. A small tubercle is located on the cingular shelf between the distolingual cusp and the protocone. The dP^3 is very similar to those from Lothagam, although it is slightly smaller and relatively narrower.

4.3. Lower Dentition

4.3.1. Incisors

The lower incisors have low, stout, and conical crowns. The enamel covering is fairly thin, and is either smooth or finely crenulated. The base of the crown is bordered by an irregular but well-defined cingulum on its mesial, lingual, and distal aspects. The root is extremely long, and circular to elliptical in cross section. In early stages of wear a flat facet is cut obliquely down onto the lingual face of the crown, to produce a broad, chisel-shaped apical cutting edge. As wear progresses, and the incisor continues to grow, this facet gradually extends onto the root. In more aged individuals the enamel-covered portion of the crown is completely obliterated by wear, and all that remains is a stout cylinder of dentine with a smoothly polished, wedge-shaped tip. This continued growth also explains why the maximum diameter of the largest incisor from the Manonga Valley is over twice that of the smallest incisor. In *Hip. amphibius*, aged adults commonly have lower central incisors that are more than three times the diameter of those of subadult individuals.

The similarity in size of the individual lower incisors from the Manonga Valley in which some enamel is still retained suggests that they may have been of relatively uniform size in the mandible. Subequal incisors are also found in mandibular specimens from Lothagam and Lukeino. Among other hexaprotodont hippopotamids from East Africa, only *Trilobophorus afarensis* has subequal lower incisors (Gèze, 1985). Interestingly, a lower jaw of *Hex. harvardi* from Kanapoi (KNM-KP 1) is more specialized in this regard in having a central incisor that is quite a bit larger than the two lateral incisors. A similar tendency for a slight reduction of the lateral incisors is also seen in *Hex. sivalensis* and *Hex. imagunculus*, and is found to an even greater extent in *Hex. protamphibius turkanensis* and *Hex. coryndonae* (Table VII). The latter species is unusual, however, in having I_2 smaller than I_3. *Hexaprotodon karumensis* from the upper Burgi Member, *Hex. aethiopicus*, *Hip. gorgops*, and *Hip. amphibius* are further derived in having a tetraprotodont arrangement of the lower incisors, in which

Table VII. Comparison of Lower Incisors in Fossil and Extant Hippopotamids

Species	Number of incisors	Relative proportions of incisors
Hexaprotodon harvardi		
Lothagam & Lukeino	Hexaprotodont	I_{1-3} subequal
Manonga Valley	Hexaprotodont	I_{1-3} subequal?
Kanapoi	Hexaprotodont	I_1 larger, I_{2-3} subequal (*n* = 1, 100:64:77)[a]
Hexaprotodon sivalensis sivalensis	Hexaprotodont	I_1 slightly larger than I_3, I_2 smaller (*n* = 6, 100:73:88)[b]
Trilobophorus afarensis	Hexaprotodont	I_{1-3} subequal
Hexaprotodon imagunculus	Hexaprotodont	?I_1 slightly larger than I_2, I_3 smaller still (*n* = 3, 100:85:71)[c]
Hexaprotodon protamphibius turkanensis	Hexaprotodont	I_1 much larger, I_{2-3} subequal (*n* = 1, 100:50:51)
Hexaprotodon coryndonae	Hexaprotodont	I_1 much larger than I_3, I_2 smaller still
Hexaprotodon karumensis		
Koobi Fora (Upper Burgi)	Tetraprotodont	I_1 much larger than I_2 (*n* = 4, 100:64)
Hexaprotodon aethiopicus	Tetraprotodont	I_1 much larger than I_2 (*n* = 3, 100:66)
Hippopotamus gorgops	Tetraprotodont	I_1 much larger than I_2 (*n* = 2, 100:67)
Hippopotamus amphibius	Tetraprotodont	I_1 much larger than I_2 (*n* = 27, 100:63[d]; *n* = 28, 100:59[e])
Choeropsis liberiensis	Diprotodont	

[a] Numbers in parentheses represent the relative size (maximum mesiodistal diameters) of the incisors. The largest incisor is equal to 100. They are average values arranged in sequence starting with I1. *n* is the sample size.

[b] From measurements presented by Hooijer (1950) the following comparative data can be calculated for *Hex. sivalensis* subspp.—*sivalensis* (100:79:93), *namadicus* (93:69:100), *palaeindicus* (89:36:100), *sivajavanicus* (100:93:70), *koenigswaldi* (100:78:86), and *soloensis* (100:80:92).

[c] Data from Cooke and Coryndon (1970), Erdbrink and Krommenhoek (1975).

[d] Data from Hooijer (1950).

[e] Data from Pavlakis (1987).

the lateral incisor is only about two thirds of the diameter of the central incisor (Harris, 1991). Later samples of *Hex. karumensis* from the upper KBS Member are diprotodont (Harris, 1991), and in this respect they resemble the modern pygmy hippopotamus, *Choeropsis liberiensis.*

The lower incisors from the Manonga Valley are, therefore, similar to those of *Hex. harvardi* from Lothagam in their general morphology, and probably also in being subequal in size. In addition, they have the tip-to-tip wear pattern that is typical of *Hexaprotodon.*

4.3.2. Canines

The lower canine is bilaterally compressed and strongly backwardly recurved. It is D-shaped in cross section with a flattened or slightly concave medial face and a convex lateral face. The posterolateral surface of the crown is marked by a shallow longitudinal groove. Enamel is distributed evenly on the medial, anterior, and lateral sides, but is lacking from the posterior face. Apart from fine longitudinal striae, the enamel is perfectly smooth. Wear is concentrated on the enamel-free posterior portion of the tooth.

The canines from the Manonga Valley are strongly bilaterally compressed, with a mean breadth–length index of 59 (n = 6; range = 53–65). This is a distinctive feature that they share with the samples from Lothagam and Lukeino (n = 9; mean index = 63; range = 57–76). Although other species of hippopotamids, both fossil and extant, exhibit a wide range of variation, the canines tend to be less compressed than those of *Hex. harvardi*, with mean values for this index of 65–67.

As in the upper canines, an index of relative lower canine size (maximum canine diameter × 100/mesiodistal length of M_2) provides a useful basis for comparison. In the two extant species of hippopotami it is common for aged adults to have canines with a maximum diameter that exceeds that of the mesiodistal length of M_2. The highest indices recorded in *Hip. amphibius* and *C. liberiensis* were 143 and 133, respectively. Comparative data on *Hex. harvardi* and other fossil hippopotamids indicate that they had canines no larger than those of the modern species, with a maximum index less than 130 (i.e., *Hex. harvardi*, 110; *Hex. sivalensis*, 120; *Hex. karumensis*, 128).

The lower canines from the Manonga Valley are typical of *Hexaprotodon* in having a smooth or finely striated enamel surface. They are comparable to *Hex. harvardi* from Lothagam and Lukeino in their size, general structure, and degree of bilateral compression.

4.3.3. Premolars

P_1 is not represented in the collections from the Manonga Valley. P_2 and P_3 in *Hexaprotodon* are morphologically very similar, and apart from size, it is difficult to distinguish isolated teeth (Fig. 1). All four of the specimens that can be identified as either P_2 or P_3 probably represent P_3. The single main cusp is tall, and distally recurved. The crown is mesiodistally long and narrow, and buccolingually slightly waisted in the mesial moiety of the crown. The mesial, distal, and distolingual crests are pustulate. A narrow but well-developed cingulum forms an almost continuous rim around the base of the crown. Perched on the distolingual margin of the crown is a prominent accessory cusp. The tooth bears two short roots. P_4 is represented by a single fragmentary specimen (WM 855/92). It is a molariform tooth, with an elevated main cusp, a prominent shelflike cingulum, and a distinct talonid with weakly developed pustules. The lingual portion of the crown is not preserved, so the development of the accessory cuspule, which is usually prominent in *Hex. harvardi*, is not known.

The lower premolars from the Manonga Valley are similar to *Hex. harvardi* from Lothagam and Lukeino in being relatively large in size, with well-developed accessory cuspules, and a pustulate enamel surface. In terms of their occlusal areas (mesiodistal length × buccolingual breadth), the lower premolars all fall within the 95% confidence limits for the combined sample from Lothagam and Lukeino (Table V). As discussed above, the relatively large size of the premolars is a distinctive characteristic of *Hex. harvardi* (Table VI).

4.3.4. Molars

The lower molars are relatively long and narrow, with a slight waisting midway along the length of the crown (Fig. 1). The cusps are quite low and conical. As in the upper molars, each cusp has a sub-triangular-shaped exposure of dentine with slight wear, but this becomes a simple trefoil shape in later stages of wear. The mesial pair of cusps is larger and more elevated than the distal pair. The metaconid and hypoconid are linked by a low, rounded crest that passes obliquely across the talonid basin. Occasionally, a distinct metaconulid is present. On M_1 and M_2, a short crest originates from the hypoconid and passes distally, to give rise to a small hypoconulid on the cingular shelf. The hypoconulid on M_3 is low, but relatively large, and it is bordered buccally and lingually by well-developed accessory cuspules, the ectostylid and endostylid, respectively. The buccal and lingual cingula are absent, or are restricted to small conical tubercles or narrow shelves located at the base of the crown between the main cusps. The mesial and distal cingula are elevated and well developed. Morphologically, the lower molars from the Manonga Valley are indistinguishable from those of *Hex. harvardi* from Lothagam and Lukeino.

The hypsodonty index (height of the crown × 100/buccolingual breadth of the crown) for the only complete and relatively unworn lower molars (M 44685 and WM 198/94) is 90 and 104, respectively. These teeth are relatively brachyodont compared with the lower molars from Lothagam and Lukeino, which have a range for this index of 92–113, and they also fall at the lower end of the general range for other species of *Hexaprotodon* from East Africa (89–127). However, two partially preserved M_3s from the Manonga Valley are higher crowned, and their estimated hypsodonty index (111 and 113) coincides well with the upper limits for *Hex. harvardi*. In comparison with extant hippopotamids, the lower molars of *Hex. harvardi* are more similar to those of *Choeropsis*—with a maximum hypsodonty index of 116—than they are to the distinctly high-crowned teeth of *Hip. amphibius*, which have a maximum index of 139.

In *Hex. harvardi*, the lower molars increase in size (mesiodistal length × buccolingual breadth) posteriorly, corresponding to the following ratio: 58:79:100. Similar size differentials between the lower molars are found in *Hex. protamphibius* (59:82:100) and in *Hip. amphibius* (60:76:100). Other hippopotamids, however, exhibit a more marked increase in size from M_1 to M_3, as follows: *Hex. sivalensis* (43:66:100); *Hex. karumensis* (51:70:100); *Hex. aethiopicus* (54:74:100); *Hex. imagunculus* (58:66:100); *Hip. gorgops* (46:70:100); and *Choeropsis liberiensis* (53:83:100).

The lower molars from the Manonga Valley are comparable in size to those from Lothagam and Lukeino. In fact, based on their occlusal area (mesiodistal length × buccolingual breadth), all but one fall within the 95% confidence limits for the combined sample of lower molars from Lothagam and Lukeino (Table V). The exception is an M_3 from Kiloleli 2, which is only slightly larger than the largest specimen from Lothagam. In comparison, the molars of *Hex. harvardi* are similar in size to those of *Hex. sivalensis*; smaller than those of *Hex. karumensis*, *Hip. amphibius*, and especially *Hip. gorgops*; slightly larger than those of *Hex.*

protamphibius; and significantly larger than those of *Hex. imagunculus*, *Hex. aethiopicus*, and *Choeropsis liberiensis*.

In summary, the lower molars from the Manonga Valley are consistent in size and morphology with those of *Hex. harvardi* from Lothagam and Lukeino. They are distinguished from those of other species of *Hexaprotodon* from East Africa by the following combination of features: (1) larger size (except for those of *Hex. karumensis*, which tend to be larger still); (2) crowns more brachyodont and slightly narrower; and (3) less pronounced size differential between the molars (except for *Hex. protamphibius*).

4.3.5. Deciduous Dentition

The lower deciduous dentition is represented by four isolated teeth. The dP_2 (M44688) is a narrow, elongated tooth, with a slight buccolingual waisting midway along its length. The single main cusp is tall. Originating from its apex are a low and rounded mesial crest, that bifurcates toward its base, and a pustulate distal crest. Basally, there is a strong cingulum that entirely encircles the crown. The dP_3 is represented by a single incomplete and worn specimen (WM 656/90), which consists of the distal portion of the crown only. Mesially, the crown was relatively narrow, and it was dominated by a single tall cusp. The talonid basin has two well-developed cusps on its distal margin that are arranged in a transverse pair. A narrow but well-defined cingulum is continuous around the base of the distal moiety of the crown. The dP_4 is a low-crowned, molariform tooth, with a well-developed cingulum. The lower deciduous premolars are morphologically very similar to the corresponding teeth from Lothagam, but they tend to be slightly smaller in size.

5. Postcranial Material

In this section I present an account of the postcranial remains from the Manonga Valley. The intention is not to provide a comprehensive description of individual elements, but rather to highlight the structural differences that distinguish the postcranium of *Hex. harvardi* from those of extant hippopotamids. Several authors have previously drawn attention to the importance of postcranial characteristics for differentiating *Hexaprotodon* and *Choeropsis* from *Hippopotamus* (e.g., Hopwood, 1926; Arambourg, 1947; Cooke and Coryndon, 1970; Coryndon, 1977, 1978a,b; Gèze, 1985; Pavlakis, 1990; Harris, 1991). The aim of this present analysis is to define these differences more precisely, and to use them as a basis for making general inferences about the possible locomotor behavior and habitat preferences of *Hex. harvardi*.

5.1. Vertebrae

Five isolated vertebrae have been recovered from the Manonga Valley, all from Tinde West (Table VIII). WM 010/90 consists of the centrum and posterior portion of the neural arch of an axis vertebra. It is comparable in size to that of female

Table VIII. List of Hippopotamid Vertebrae and Limb Bones from the Manonga Valley

Tinde	
M 44697	Right distal humerus, lacking portion of distal articulation.
M 44698	Right distal tibia.
M 44699	Right patella, lacking inferior tubercle and medial margin.
M 44725	Distal radial epiphysis.
M 44727	Proximal radio-ulna, fragmentary.
Tinde West	
WM 001/90	Left distal tibia.
WM 002/90	Left distal tibia.
WM 010/90	Axis vertebra, centrum and caudal portion of neural arch.
WM 208/90	Right glenoid of scapula.
WM 222/90	Thoracic vertebra, almost complete.
WM 352/90	Caudal vertebra, probably caudal 3 or 4.
WM 475/90	Right patella, lacking inferior tubercle.
WM 574/90	Thoracic vertebra, portion of centrum and neural arch only.
WM 679/90	Right distal fibula.
WM 666/92	Lumbar vertebra, almost complete.
Tinde East	
WM 316/90 & 456/90	Left distal humerus, two conjoining pieces.
WM 317/90	Left distal tibia.
WM 321/90	Right proximal tibia, medial portion only.
WM 557/92	Left distal humerus, ulnar trochlear only.
WM 081/94	Caudal vertebra.
Kiloleli 2	
WM 1286/92	Right distal tibia.
WM 837/94	Left distal tibia.
Inolelo 1	
WM 140/94	Right distal tibia.
Inolelo 3	
WM 656/94	Left distal radio-ulna.
Beredi South 1	
WM 1517/92	Right distal tibia.
Ngofila 4	
WM 1475/92	Right humerus, shaft and distal end only.
WM 1476/92	Left distal femur.
WM 1477/92	Right proximal radio-ulna, fragmentary.

individuals of *Hip. amphibius*, and is generally similar in morphology. However, it differs in the following respects: the posterior articular facets are situated closer together, suggesting a narrower neural arch dorsally; the centrum is anteroposteriorly relatively shorter and dorsoventrally more compressed; and the dens is relatively more stout.

Two thoracic vertebrae are represented in the collections. WM 222/90 is an almost complete vertebra (lacking the transverse processes) from the posterior end of the thorax (probably T11–13). WM 574/90 is more fragmentary, consisting of a portion of the centrum and neural arch from a midthoracic vertebra (probably T8–10). Both vertebrae are similar in most respects to *Hip. amphibius*, but they differ in having a mediolaterally broader, anteroposteriorly shorter, and dorsoventrally shallower centrum, and a more cranially oriented anterior costal facet.

WM 666/92 and WM 684/94 are relatively complete lumbar vertebrae, although their transverse and spinous processes have been lost. As in the thoracic vertebrae, the centrum is anteroposteriorly relatively much shorter than it is in *Hip. amphibius*. The proportions of the thoracolumbar vertebrae indicate that *Hex. harvardi*, like *C. liberiensis*, may have had a relatively shorter trunk than *Hippopotamus*.

WM 352/90 consists of a weathered and abraded 3rd or 4th caudal vertebra. WM 081/94 is a more fragmentary caudal vertebra, consisting of the centrum only. Compared with the corresponding vertebrae in modern *Hippopotamus* the fossils have relatively stouter transverse processes and a shorter centrum.

5.2. Pectoral Girdle and Forelimb

The forelimb is represented by several partial scapulae and a number of fragmentary limb bones (Table VIII). In addition, a sizable sample of carpals, metacarpals, and manual phalanges is also known, and these are discussed in section 5.4. The majority of these specimens comes from Tinde, but smaller collections have also been recovered from Inolelo, Ngofila, and Kiloleli (Tables IX and XI).

5.2.1. Scapula

Three scapula fragments have been identified as hippopotamid. WM 208/90 and WM 251/94 represent the distal portion of the scapula preserving the glenoid fossa, the coracoid process, and the base of the spine. WM 374/90 is more fragmentary, consisting of a portion of the glenoid and scapular neck only. They are comparable in size to those of female *Hip. amphibius*, and they are generally similar in morphology. The fossils differ from *Hip. amphibius* and *C. liberiensis*, however, in several respects. The coracoid process is shorter and stouter (similar in this respect to *Choeropsis*), the base of the scapular spine is relatively more robust, with the latter extending distally as far as the lateral margin of the glenoid, and the neck of the scapula is somewhat thicker. The glenoid cavity is mediolaterally expanded, and much more nearly approaches a subcircular outline, rather than an oval. The breadth–length index of the glenoid articular surface in WM 208/90 (90.8) and WM 251/94 (86.5) corresponds with the upper limit of the range for extant hippopotamids (75.2–92.5).

5.2.2. Humerus

Only the shaft and the distal end of the humerus is known, being represented by three specimens from Tinde and a single specimen from Ngofila 4. They are all comparable in size to humeri of *Hip. amphibius*, but they differ in a number of respects. The distal articulation for the radio-ulna, for example, differs in being more strongly spooled, with a more pronounced median keel, and a more angular or raised lateral margin. The olecranon fossa is deep, proximodistally high, but mediolaterally quite narrow. The breadth–height index of the olecranon fossa in WM 1475/92 is 92.9. In *Hip. amphibius* the olecranon fossa tends to be relatively broader and more triangular in shape, rather than elliptical. The medial epicondyle in the fossils is more stoutly developed than in *Hip. amphibius*, presumably for the attachment of more powerful carpal and digital flexors. On the other hand, the lateral epicondyle and the lateral supracondylar ridge, to which the digital and carpal extensors attach, tend to be more weakly developed. In these respects the fossil humeri correspond more closely to the pattern seen in *C. liberiensis.*

5.2.3. Radius and Ulna

A right proximal radio-ulna, WM 1477/92 from Ngofila 4, consists of a portion of the shaft of the ulna, approximately 18 cm long, lacking most of the sigmoid notch and olecranon, as well as most of the proximal end of the radius. The radius is completely ankylosed to the ulna, except for a large, elliptical interosseus foramen that perforates between the two bones proximally for the passage of the posterior interosseus nerve and artery. The posteromedial aperture of the foramen opens into a broad groove distally that eventually blends in smoothly with the general surface of the shaft. Similarly, the anterolateral aperture also opens into a shallow groove for the anterior interosseus artery and nerve. A similar pattern is typically found in young adults of modern hippopotami, although with increasing age and continued bone deposition, the groove develops into a well-defined gutter or partially enclosed canal that runs the entire length of the shaft.

The proximal articular surface of the ulna has a more pronounced median keel than in *Hip. amphibius*, and this accords well with the strong degree of spooling of the trochlea seen in the distal humerus. An additional proximal ulna fragment of a subadult individual is known from Tinde (M 44727). It preserves the olecranon process, lacking the unfused epiphysis, and the proximal half of the sigmoid notch. The olecranon process is longer and more robust than in *Hip. amphibius*, and it is more strongly posteriorly tilted. The proximal portion of the sigmoid notch is more strongly convex mediolaterally than in *Hip. amphibius*, and this is consistent with the deep and relatively narrow olecranon tunnel in the fossil humeri. The distal radius is represented by an abraded and unfused epiphysis (M 44725) and a partial radio-ulna (WM 656/94). They are consistent in morphology with both *Hip. amphibius* and *C. liberiensis.*

5.3. Hindlimb

The hindlimb is represented by a distal femur from Ngofila 4, several distal tibiae, a distal fibula and two patellae from Tinde, and distal tibiae from Beredi South, Kiloleli, and Inolelo (Table VIII). The material is similar in overall size to the corresponding bones of extant *Hip. amphibius.*

5.3.1. Femur

The left distal femur from Ngofila 4 (WM 1476/92) is weathered and abraded. The main differences distinguishing the fossil from the femora of *Hip. amphibius* are that the patellar groove is deep, with more strongly keeled medial and lateral margins, the two condyles are anteroposteriorly longer and mediolaterally narrower, the intercondylar notch is relatively wider, and the scars for the collateral ligaments are more pronounced. These features, also characteristic of *C. liberiensis*, are functionally associated with increasing the stability at the knee joint during rapid movements in the parasagittal plane, and are presumably adaptations associated with fast-running, cursorial locomotion.

5.3.2. Patella

Two patellae are known from the Manonga Valley, but unfortunately, both specimens are incomplete. WM 475/90 lacks only the apex for attachment of the patellar ligament, whereas M44699 is more fragmentary, lacking the apex and medial wing of the patella. The fossils are comparable in size to the patellae of female *Hip. amphibius*, but they are distinctive in being much more robust. In WM 475/90 the anteroposterior thickness of the bone is 80.3% of the mediolateral breadth, which is much more similar to other species of *Hexaprotodon* and to *C. liberiensis* (68.1–77.2%) than to *Hip. amphibius* (51.9–62.2%). In addition, the fossil patellae are similar to those of *C. liberiensis*, and differ from those of *Hip. amphibius*, in having a shorter and less curved medial wing, a feature linked with a better-developed medial keel on the patellar groove of the distal femur.

5.3.3. Tibia

A portion of a right proximal tibia is known from Tinde (WM 321/90). Some differences in the configuration and proportions of the articular surfaces for the distal femur distinguish the fossil from *Hip. amphibius*, but these are relatively minor and probably do not reflect important functional differences. The distal tibia, on the other hand, has a suite of functionally significant traits, consistent with those seen in the astragalus (see below), that serve to distinguish *Hex. harvardi* from *Hip. amphibius*. These are as follows: the distal end of the tibia is mediolaterally broader and more rectangular in outline; the styloid process on the posteromedial margin is higher and more conical; the midline keel is more elevated, and it is bordered medially and laterally by deeper articular grooves; and the pit for the medial ligament is deep, but not so extensive. In all of these respects the fossils resemble *C. liberiensis*. The shape and configuration of the distal articular surface of the tibia in *Hex. harvardi* is functionally associated with increased stability at the astragalocrural joint, allowing more rapid movements of the ankle joint in flexion and extension.

5.3.4. Fibula

The fibula is represented by a single well-preserved specimen, WM 679/90. In comparison with the distal fibula of *Hip. amphibius* it is a relatively stout bone, and the articular surface for the astragalus is more extensive and more obliquely oriented (its long axis is oriented at an angle of 48° to the long axis of the shaft). It is, however, comparable in morphology to the fibula in *C. liberiensis*.

5.4. Manus and Pes

5.4.1. Carpals

Examples of all elements of the carpus, with the exception of the trapezium, are known from the Manonga Valley (Table IX). The carpals are comparable in general size to those of *Hip. amphibius* (Fig. 2).

Table IX. List of Hippopotamid Carpals and Tarsals from the Manonga Valley

Tinde	
Tarsals	
M 44694	Left astragalus.
M 44695	Left astragalus, lacking distal end.
M 44696	Right astragalus, missing proximolateral corner.
M 44700	Left navicular, fragmentary.
M 44726	Left calcaneum, proximal portion only.
Carpals	
M 44721	Right cuneiform.
M 44722	Right cuneiform.
M 44723	Pisiform.
M 44724	Left unciform.
Tinde West	
Tarsals	
WM 003/90	Left astragalus.
WM 004/90	Right astragalus.
WM 011/90	Left astragalus, slightly abraded, some superficial cracking.
WM 028/90	Right lateral cuneiform.
WM 204/90	Left calcaneum, proximal portion of bone only.
WM 205/90	Left astragalus.
WM 248/90	Left astragalus, lateral portion only.
WM 259/90	Left calcaneum, lacking distal end of bone.
WM 270/90	Calcaneum, heel process only.
WM 304/90	Right calcaneum, proximal portion only.
WM 426/90	Left astragalus.
WM 467/90	Left calcaneum, proximal end of heel process only.
WM 685/90	Left calcaneum, proximal portion only.
WM 092/92	Right cuboid.
WM 118/92	Right lateral cuneiform.
WM 119/92	Right navicular.
WM 121/92	Left navicular, fragmentary.
WM 272/92	Right lateral cuneiform.
WM 351/92	Right calcaneum, distal end only.
WM 544/92	Calcaneum, heel process only.
WM 615/92	Left navicular.
WM 689/92	Right navicular.
WM 707/92	Left astragalus.

(continued)

Table IX. (Continued)

Carpals	
WM 013/90	Left scaphoid.
WM 019/90	Left trapezoid.
WM 254/90	Left unciform.
WM 287/90	Left cuneiform.
WM 122/92	Left unciform.
WM 263/92	Right lunar.
WM 299/92	Left unciform.
WM 470/92	Left trapezoid.
WM 614/92	Left lunar.
WM 616/92	Right magnum.
WM 709/92	Left cuneiform.
Tinde East	
Tarsals	
WM 310/90	Left astragalus, lacking proximolateral margin.
WM 039/94	Left navicular.
Carpals	
WM 366/90	Left unciform.
WM 452/90	Right lunar, fragmentary.
WM 465/90	Right lunar, fragmentary.
WM 067/94	Right scaphoid.
WM 080/94	Right cuneiform, fragmentary.
Kiloleli 2	
Tarsals	
WM 857/92	Right astragalus.
WM 1242/92	Left cuboid.
WM 385/94	Right cuboid.
Carpals	
WM 727/90	Right cuneiform.
WM 383/94	Left unciform.
WM 384/94	Right magnum.
WM 386/94	Left lunar.
WM 387/94	Left magnum, fragmentary.

Two scaphoids are known. WM 067/94 is a complete and well-preserved right scaphoid. WM 013/90 is slightly damaged, with the trapezoid facet entirely lacking, and the articular surface for the magnum incompletely preserved. The bone is morphologically similar to that of *Hippopotamus*. However, it is dorsoventrally slightly more compressed. In addition, the articular surface for the radius is narrower, dorsoventrally more strongly concave, and mediolaterally less convex.

There are three almost complete and two partial lunars from the Manonga Valley (Fig. 2). The fossils are relatively more robust than those of modern *Hippopotamus*. The radial articular surface is similar in morphology to that in *Hippopotamus*. However, the articular surfaces for the unciform and magnum are relatively broader, being closer to a square in outline, rather than subrectangular, with distinct mediolateral waisting. In addition, the articular surface is

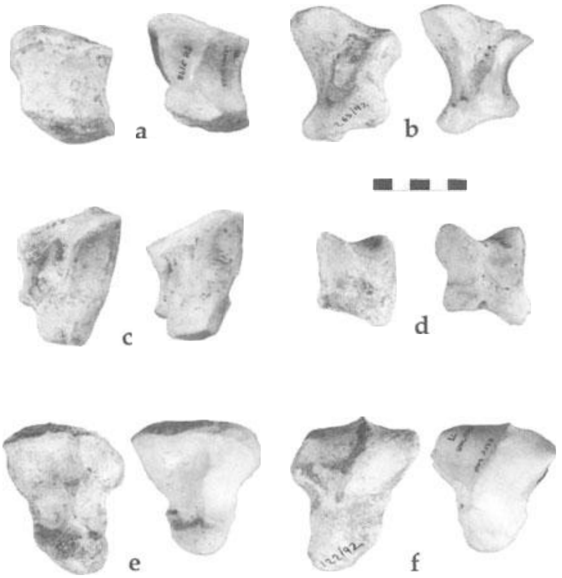

FIGURE 2. Comparison of carpals of *Hex. harvardi* (left) with those of *Hip. amphibius* (right). (a) WM 263/92, right lunar, distal view; (b) WM 263/92, right lunar, lateral view; (c) WM 263/92, right lunar, proximal view; (d) WM 287/90, left cuneiform, lateral view; (e) WM 122/92, left unciform, distal view; (f) WM 122/92, left unciform, proximal view. Scale bar = 50 mm.

smoothly convex in the mediolateral plane, and it lacks the distinct keel that separates the two facets seen in *Hip. amphibius*. Furthermore, the V-shaped beaks that occur on the dorsal and ventral margins of the distal lunar surface in *Hip. amphibius*, associated with this keel, are less distinct and more rounded in the fossils.

The six fossil cuneiforms from the Manonga Valley are similar in size to those of *Hip. amphibius*, and they conform closely in morphology (Fig. 2). The main differences appear to be that the fossils are proximodistally longer in relation to the dorsoventral height of the bone, and that the articular facet for the unciform is taller and somewhat narrower.

The pisiform, M 44723, is a stout, cylindrical bone that recurves medially toward its apex. In its general proportions it is comparable to the corresponding bones of extant hippopotamids. The articular facets for the ulna and cuneiform are most similar in their configuration to those in *C. liberiensis*. In *Hip. amphibius*, the cuneiform facet tends to be proximodistally narrower.

The unciform is represented by six specimens (Fig. 2). All are relatively complete, except for WM 366/90 and WM 383/94, which both lack the ventral process. They differ from the unciforms of *Hip. amphibius* and *C. liberiensis* in a number of respects: (1) the bone is dorsoventrally higher, mediolaterally narrower, and proximodistally thicker; (2) the styloid process is distinctly longer and more strongly distally recurved; (3) the facet for metacarpal III is relatively much larger, and is less clearly demarcated from the facet for the magnum; (4)

the facet for the magnum has a convex dorsal margin (in *Hip. amphibius* it is V-shaped, which interlocks with a corresponding depression in the magnum); (5) the facets for metacarpals IV and V are dorsoventrally higher and narrower; (6) the facets for metacarpal IV and V are separated inferiorly by a narrow interosseus sulcus, which terminates about one-third down from the dorsal margin at a deep ligamentous pit (in *Hip. amphibius* the two facets are contiguous, and a shallow ligamentous pit occurs more inferiorly); (7) the facet for metacarpal IV is generally dorsoventrally higher or subequal in height to the facet for metacarparpal V, whereas in *Hip. amphibius* the reverse is typically the case; (8) the facet for the semilunar is more distinctly sellar, being mediolaterally more concave, with a tighter arc of curvature dorsoventrally, and extending further onto the dorsal aspect of the bone; (9) the facet for the cuneiform also exhibits a more strongly developed saddle; and (10) the lateral wing of the bone is proximodistally thicker, and this leads to a wider separation between the facets for metacarpal V and the cuneiform (in *Hip. amphibius* the two facets almost touch).

Three partially preserved magnums are known (WM 616/92, WM 384/94, WM 387/94), each lacking the apex of the styloid process. As is generally the case in the other carpals, the magnum is mediolaterally relatively narrower than in *Hip. amphibius* and *C. liberiensis*. Medially, the dorsal facet for metacarpal II is smaller, and it has a narrower contact with the facet for the trapezoid. The articular surface for metacarpal III is mediolaterally narrower. The facet for the unciform is reniform, concave, and quite deeply excavated, but it lacks the V-shaped depression commonly seen in extant hippopotamids that allows the magnum and unciform to interlock.

The trapezoid is represented by two specimens. WM 019/90 is complete; WM 470/90 is somewhat weathered and abraded. They differ from those of *Hip. amphibius* in the following ways: (1) the bone is relatively mediolaterally narrower; (2) the facet for the scaphoid is narrower and mediolaterally more strongly concave; (3) the distal articular surface for metacarpal II is narrower, flatter, and more elliptical, rather than triangular in shape; and (4) there is no development of a beak on the dorsal aspect of the bone to interlock with the magnum.

The carpus of *Hex. harvardi*, therefore, differs in a number of respects from *Hip. amphibius*, and is much more similar to *C. liberiensis*. Perhaps the most striking difference, at least from a functional perspective, is that the wrist in *Hex. harvardi* is mediolaterally relatively narrower and more compact than in *Hippopotamus*, an adaptation in ungulates associated with a superior capability for fast running.

5.4.2. Tarsals

The astragali of *Hex. harvardi* are well represented in the collections from the Manonga Valley. They are similar in size or slightly smaller than those of *Hip. amphibius*, but they can be readily distinguished on the basis of a suite of morphological features (Fig. 3). These are as follows: (1) the fossil astragali are relatively narrower (Table X); (2) the saddle-shaped sustentacular facet for the

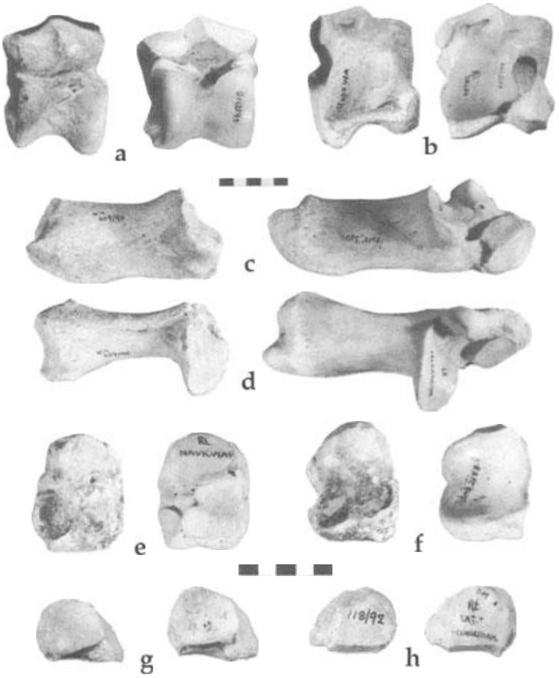

FIGURE 3. Comparison of tarsals of *Hex. harvardi* (left) with those of *Hip. amphibius* (right). (a) WM 004/90, right astragalus, superior view; (b) WM 004/90, right astragalus, inferior view; (c) WM 269/90, left calcaneum, medial view; (d) WM 269/90, left calcaneum, superior view; (e) WM 119/92, right navicular, distal view; (f) WM 119/92, right navicular, proximal view; (g) WM 118/92, right lateral cuneiform, distal view; (h) WM 118/92, right lateral cuneiform, proximal view. Scale bars = 50 mm. Top scale bar for a–d, bottom scale bar for e–h.

calcaneus is less strongly contoured; (3) the sustentacular facet is bordered distolaterally, medially, and proximomedially by deep and well-defined pits for the attachment of interosseus ligaments; similar depressions occur in the astragali of *Hip. amphibius*, but they tend to be even more strongly developed; (4) the naviculocuboid facet is similar in shape and proportions to that in modern *Hippopotamus*, except that the midline keel is more rounded in the fossil astragali, and the cuboid facet describes a tighter arc of curvature; (5) the trochlear surface for articulation with the distal tibia is relatively narrower, more deeply grooved, and with steeper medial and lateral walls; (6) the lateral margin of the tibial trochlea projects much further distally, and exhibits a smaller arc of curvature; (7) the medial margin of the tibial trochlea extends further round onto the inferior surface of the bone; (8) the naviculocuboid facet is much more widely separated from the lateral trochlear margin, and the roughened interosseus sulcus separating them is more deeply excavated; (9) the cuboid facet and the distal calcaneal facet meet at a sharper angle (the mean angle is 110° in the fossils and 123° in *Hip. amphibius*), and the cuboid facet is more laterally facing; (10) the fibula facet is more extensive and slightly convex; (11) the lateral calcaneal

Table X. Breadth–Length Index of Astragalus in Fossil and Extant Hippopotamids[a]

	N	Mean	Range
Hexaprotodon harvardi (Lothagam, Lukeino, Mpesida)	22	70.6	62.3–76.8
Hexaprotodon harvardi (Manonga Valley)	6	71.0	68.2–73.3
Hexaprotodon sivalensis	10	72.0	65.7–78.8
Hexaprotodon protamphibius	6	75.9	71.8–77.6
Hexaprotodon aethiopicus	6	73.6	65.5–78.1
Hexaprotodon karumensis	7	72.6	69.9–76.5
Kenyapotamus coryndonae	1	72.1	72.1
Hippopotamus gorgops	1	84.1	84.1
Hippopotamus amphibius	10	82.9	76.5–92.3
Choeropsis liberiensis	5	72.4	70.0–73.9

[a] $\text{Index} = \dfrac{\text{maximum length of astragalus} \times 100}{\text{maximum breadth of astragalus}}$

facet is represented by a small elliptical or triangular depression; in *Hip. amphibius* it is a large L-shaped facet (Fig. 3). In these respects, and in their general morphology, the fossil astragali are closely comparable to those of *C. liberiensis*. In comparison with *Hip. amphibius*, the proportions of the astragalus and the configuration of the articular facets for the tibia and fibula in *Hex. harvardi* imply that there was a greater range of flexion at the astragalotibial joint, especially in plantarflexed positions, and increased stability for speed of action in flexion and extension.

There are no complete calcanei from the Manonga Valley. Most specimens comprise the tuber calcis only, but several specimens preserve portions of the sustentaculum tali, the proximal and distal astragalar facets, and the cuboid facet (Fig. 3). Together these specimens permit a fairly complete composite description of the entire bone. The fossil calcanei are generally similar in size to female individuals of *Hip. amphibius*, but differ in a number of morphological details. For example, the heel process in the fossil calcanei is deeper and mediolaterally more slender. The proximal extremity of the heel process is more elliptical (rather than square) in outline, and it bears a deeper groove for a well-developed calcaneal tendon. Consistent with differences observed in the astagalus, the proximal calcaneal facet is flatter and more triangular in shape. The facet for the cuboid differs from that in modern *Hippopotamus* in being relatively shorter dorsoventrally, and in being mediolaterally slightly concave, rather than flat to slightly convex. In these respects the fossils conform closely to the morphological pattern in *C. liberiensis*.

Two cuboids (WM 092/92 and WM 385/94) are known from the Manonga Valley. The general construction of the bone is similar to that of both extant species of hippopotamus, but it differs from that of *Hip. amphibius* in being relative shorter in the proximodistal plane, in having a less strongly dorsoventrally concave astragalar facet, narrower articular facets for metatarsals IV and V, and deeper pits for ligamentous attachments to the astragalus.

Four fairly complete and two partially preserved naviculars are known. They are similar in morphology to those of *C. liberiensis*, but differ from *Hip. amphibius* in being mediolaterally narrower, having a narrower talar facet, with a wider arc of curvature and a more distinct dorsoventral keel, smaller and flatter articular surfaces for the cuneiforms, and a more extensive articular contact with the cuboid (Fig. 3).

Three almost complete lateral cuneiforms have been recovered from the Manonga Valley (Fig. 3). Apart from some minor differences in the shape of the navicular facet, the fossils are very similar in morphology to the lateral cuneiforms of *C. liberiensis* and *Hip. amphibius*. No middle and medial cuneiforms are known.

5.4.3. Metapodials

Metapodials are well represented in the collections from the Manonga Valley (see Table XI). They are readily distinguished from those of *Hippopotamus* in the following respects: (1) they are relatively longer and more slender; (2) the distal articular head is dorsoventrally shallower, with a more pronounced articular keel, and it tends to become increasingly narrower dorsally and does not extend as far onto the dorsal aspect of the bone; (3) on the dorsal surface of the shaft, just proximal to the distal articular surface, there is commonly a deep depression for the attachment of the capsule (this depression tends to be absent

Table XI. List of Hippopotamid Metapodials and Phalanges from the Manonga Valley

- Metacarpal II
  - Tinde East, WM 346/90 (proximal)
  - Kiloleli 3, WM 789/90
  - Inolelo 3, WM 657/94
- Metacarpal III
  - Tinde West, WM 005/90 (proximal)
  - Tinde East, WM 448/90 (proximal), WM 345/90 (proximal), WM 361/90
  - Inolelo 3, WM 658/94 (proximal)
- Metacarpal IV
  - Tinde West, WM 027/90 (proximal)
  - Tinde East, WM 348/90 (proximal)
  - Kiloleli 2, WM 840/92 (proximal)
  - Inolelo 3, WM 658/94 (proximal)
- Metacarpal V
  - Tinde West, WM 023/90 (proximal), WM 495/90, WM 576/92 (proximal)
  - Tinde East, WM 1843/92 (proximal)
- Metatarsal II
  - Tinde, M 44707 (proximal)
  - Kiloleli 2, WM 839/92
- Metatarsal III
  - Tinde, M 44708 (proximal)
  - Tinde West, WM 476/90
  - Kiloleli 2, WM 842/92 (proximal), WM 843/92

(*continued*)

Table XI. (Continued)

- Metatarsal IV
  - Inolelo 3, WM 659/94 (proximal)
- Metatarsal V
  - Tinde West, WM 249/90, WM 688/92, WM 563/92 (distal)
- Miscellaneous metapodials
  - Tinde, M 44703 (distal), M 44705 (distal), M 44706 (proximal), M 44709 (distal)
  - Tinde West, WM 275/90 (distal), WM 482/90 (distal), WM 606/92 (distal), WM 543/92 (distal), WM 018/94 (distal), WM 913/94 (distal)
  - Tinde East, WM 333/90 (distal), WM 460/90 (distal), WM 686/90 (distal)
  - Kiloleli 2, WM 708/92 (distal), WM 844/92 (distal), WM 388/94 (distal), WM 389/94 (distal)
- Proximal phalanges
  - Tinde, M 47701, M 47702 (distal)
  - Tinde West, WM 014/90 (fragment), WM 016/90, WM 037/90 (proximal), WM 041/90 (fragment), WM 421/90, WM 424/90 (fragment), WM 425/90, WM 477/90, WM 488/90, WM 491/92 (proximal), WM 609/92 (proximal), WM 610/92 (proximal), WM 677/92 (fragment), WM 710/92a (fragment), WM 146/92, WM 520/92, WM 019/94, WM 103/94, WM 916/94
  - Tinde East, WM 341/90, WM 353/90 (fragment), WM 371/90, WM 453/90, WM 1844/92, WM 1845/92 (fragment), WM 1848/92 (proximal epiphysis)
  - Kiloleli 2, WM 849/92, WM 1285/92 (distal)
  - Kiloleli 3, WM 746/90, WM 788/90, WM 791/90
  - Kiloleli 4, WM 524/94 (proximal)
  - Shoshamagai 2, WM 1942/92
  - Inolelo 1, WM 1031/92 (proximal), WM 1117/92
  - Inolelo 3, WM 686/94 (proximal)
- Middle phalanges
  - Tinde West, WM 050/90; WM 286/90, WM 468/90, WM 116/92 (proximal), WM 206/92, WM 400/92 (proximal), WM 607/92 (proximal), WM 608/92 (proximal), WM 710/92b (proximal), WM 611/92 (lacking proximal end), WM 612/92, WM 613/92, WM 774/92 (immature, lacking proximal epiphysis), WM 1896/92 (distal), WM 1999/92 (proximal), WM 123/94, WM 917/94
  - Tinde East, M 329/90, WM 462/90, WM 1846/92, WM 040/94 (proximal), WM 060/94
  - Kiloleli 2, WM 848/92, WM 1284/92 (proximal), WM 391/94a, WM 391/94b
  - Kiloleli 3, WM 946/92
  - Inolelo 1, WM 161/94
- Distal phalanges
  - Tinde West, WM 102/94
  - Kiloleli 2, WM 1287/92 (distal end missing)
  - Inolelo 2, WM 634/94

or very shallow in *Hip. amphibius*); and (4) the proximal articular surface tends to be narrower, but dorsoventrally deeper (Fig. 4). In most of these respects, the fossils correspond closely to metapodials of *Choeropsis*.

The most obvious feature that distinguishes the metapodials of *Hex. harvardi* from those of *Hip. amphibius* and *C. liberiensis* is that they are longer and more gracile. Comparative data on their relative robusticity show that *Hex. harvardi* has metapodials that are on average 16.5% less robust than *Hip. amphibius* and 15.9% less robust than *C. liberiensis*. However, relatively long and slender metapodials appears to be a general characteristic of *Hexaprotodon* (Table XII).

Another characteristic that purportedly distinguishes *Hexaprotodon* and *Choeropsis* from *Hippopotamus* is the occurrence of relatively shorter lateral

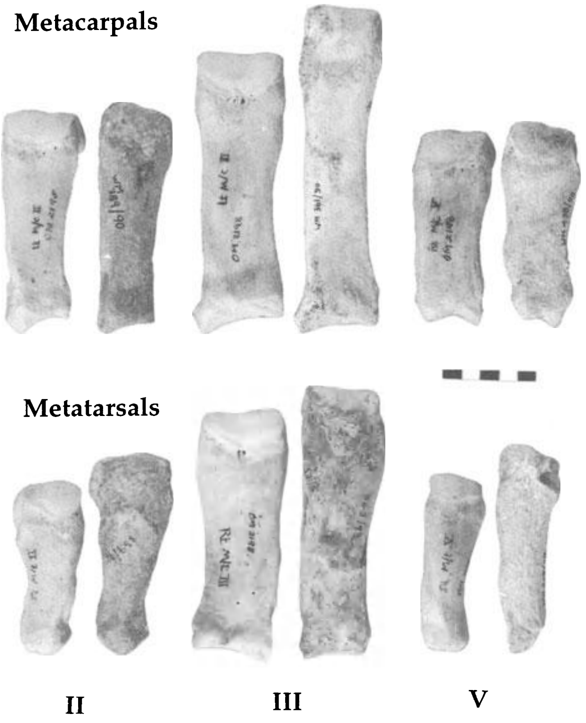

FIGURE 4. Comparison of metapodials of *Hex. harvardi* (right) with those of *Hip. amphibius* (left). Top row - MC II, WM 789/90; MC III, WM 361/90; MC V, WM 495/90. Bottom row - MT II, 839/92; MT III, 843/92; MT V, 249/90. Scale bar = 50 mm. Note the greater length and slenderness of the fossil metapodials.

Table XII. Mean Robusticity of Metapodials in Fossil and Extant Hippopotamids[a]

	Metacarpals				Metatarsals				
	II	III	IV	V	II	III	IV	V	Mean
Hex. harvardi	19.3	17.0	—	24.9	24.1	19.8	18.4	21.3	20.7
Hex. karumensis	20.7	18.5	17.7	25.1	26.8	20.2	20.7	25.1	21.9
Hip. gorgops	22.9	—	23.1	31.8	26.8	24.8	25.0	28.9	26.2
Hip. major[b]	26.1	24.9	28.7	35.5	32.4	28.9	28.9	33.5	29.9
Hip. amphibius (n = 14)	23.1	20.0	23.0	29.6	28.7	22.8	23.1	28.0	24.8
C. liberiensis (n = 3)	25.7	19.4	25.3	25.2	28.3	24.2	23.0	26.0	24.6

[a] Robusticity of metapodials $= \frac{\sqrt{\text{cross-sectional area of metapodial}}}{\text{total length of metapodial}}$

[b] Calculated from data published by Faure (1985).

digits in comparison with the median digits (Coryndon, 1977; Gèze, 1985; Harris, 1991). This observation is confirmed for the extant hippopotamids. Owing to the lack of associated pedal and manual material for most extinct species, it is not possible to calculate their relative ray length. Nevertheless, a good indication of relative size of the lateral rays can be obtained using data from the metapodials alone. In extant hippopotamids, for example, *Choeropsis* has much shorter lateral metapodials in relation to the length of the median metapodials than does *Hip. amphibius* (Table XIII). However, contrary to previous reports, comparative data for the fossil hippopotamids indicate that *Hexaprotodon* was more like *Hip. amphibius*, rather than *Choeropsis*, in having relatively long lateral rays. The isolated metapodials from the Manonga Valley provide additional confirmation that the lateral rays of *Hex. harvardi* were relatively long (Table XIII).

As noted above, a number of features of the distal metapodial serve to distinguish *Hex. harvardi* and *C. liberiensis* from *Hip. amphibius*. These differences presumably relate to increasing the stability of the metapodial–phalangeal joint during flexion and extension, especially important in ungulates with relatively elongated digits. The narrowing of the head dorsally, and its limited extension onto the dorsal aspect of the bone, suggests that stability was optimized during flexed postures, and that the potential for hyperextension at the joint was rather limited in comparison with *Hip. amphibius*. As Yalden (1971) has noted, the effectiveness of the flexion hinge of the manus is improved by limiting the range of hyperextension that is possible at these joints. A number of sesamoid bones have been recovered from Tinde and Kiloleli, and these are identical to the paired sesamoids associated with the distal metapodials in extant hippopotamids.

Metacarpal II is represented by complete, but slightly weathered, specimens from Kiloleli 3 (WM 789/90) and Inolelo 3 (WM 657/94), as well as a partial specimen from Tinde East (WM 346/90). The proximal articular surfaces differ

Table XIII. Relative Ray Length in Hippopotamids

	Relative length of lateral rays[a]		Relative length of lateral metapodials[b]	
	Manus	Pes	Manus	Pes
C. liberiensis (*n* = 4)	75.3	77.4	67.6	66.4
Hip. amphibius (*n* = 4)	84.3	75.3	79.8	69.6
Hex. harvardi	—	—	—	72.8
Hex. karumensis	—	—	77.6	72.0
Hex. aethiopicus	—	—	74.7	69.5
Hip. gorgops	—	—	—	74.0
Hip. major[c]	—	—	80.1	76.0

[a] Relative length of lateral rays = $\frac{\text{mean length of lateral rays (II and V)} \times 100}{\text{mean length of median rays (III and IV)}}$

[b] Relative length of lateral metapodials = $\frac{\text{mean length of lateral metapodials (II and V)} \times 100}{\text{mean length of median metapodials (III and IV)}}$

[c] Data from Faure (1985).

from those in *Hip. amphibius* in that the facet for the trapezoid is narrower and less markedly concave mediolaterally, the facet for the magnum is narrower, and that for metacarpal III is more extensive. A complete metacarpal III is known from Tinde East (WM 361/90), and a proximal metacarpal III, preserving much of the shaft, is known from Inolelo 3 (WM 658/94). The articular surface for the unciform is relatively smaller and more triangular in shape by comparison with that in *Hip. amphibius*, and the facet for the magnum tends to be dorsoventrally deeper. Metacarpal IV is represented by four incomplete specimens, preserving the proximal portion of the bone only. The unciform facet is narrower and dorsoventrally deeper, and the facet for metacarpal III is more closely applied to the medial side of the bone than is typically seen in *Hip. amphibius*. Metacarpal V, known from a single complete specimen (WM 495/90) and several fragmentary specimens from Tinde, differs from *Hip. amphibius* in having a narrow proximal articular surface, a less prominent saddling of the unciform facet, a less distinct styloid process, and a relatively smaller facet for metacarpal IV.

From the pes, metatarsal II and III are represented by complete specimens, metatarsal IV is known from a proximal fragment only, and metatarsal V is represented by several fragmentary specimens. Apart from the general characteristics of the metapodials described above, the main difference that distinguishes the metatarsals from those of *Hip. amphibius* is that the main proximal articular surfaces are mediolaterally narrower. This is consistent with the evidence from the tarsals that the pes of *Hex. harvardi* was relatively narrow.

5.4.4. Phalanges

A reasonable sample of isolated phalanges has been recovered from the Manonga Valley, but unfortunately, it has proved extremely difficult to sort them to their specific ray, or even whether they belong to pedal or manual digits. Nevertheless, it is possible to arrange them according to whether they belong to median or lateral digits (Table XI). Morphologically, they are closely similar to those of *Choeropsis*, but they differ in a number of respects from those of *Hip. amphibius*.

The proximal phalanges are relatively longer and more slender than those of *Hip. amphibius*. The index of robusticity of the proximal phalanges is significantly lower in *Hex. harvardi* than in either of the extant species, especially in *Hip. amphibius* (Table XIV). When combined with evidence from the metapodials, it is clear that *Hex. harvardi* had relatively elongated cheiridia, much more suited to fast-moving cursoriality. The distal articular surface of the proximal phalanges is dorsoventrally deeper, and it narrows dorsally more markedly than in *Hip. amphibius*. This arrangement serves to maximize the stability of the interphalangeal joint during flexion and extension, with greatest support being given when the middle phalanx is in a semiflexed position. By contrast, the broader articular surface in *Hip. amphibius*, especially on the dorsal aspect of the joint, permits greater stability when the middle phalanx is fully extended or even hyperextended. The proximal articular surface for the metapodial tends to be relatively narrower and more concave mediolaterally, the sagittal articular groove is deeper, and the medial, dorsal, and lateral margins are more sharply

Table XIV. Relative Robusticity of the Phalanges in *Hexaprotodon harvardi* and Extant Hippopotamids[a]

	Hex. harvardi			*Hip. amphibius*			*C. liberiensis*		
	N	Mean	Range	*N*	Mean	Range	*N*	Mean	Range
Proximal phalanges, lateral digits (II & V)	5	35.5	32.7–38.3	9	45.2	43.3–47.9	6	40.5	38.6–44.2
Proximal phalanges, median digits (III & IV)	8	37.7	33.9–40.6	9	42.3	40.7–44.4	7	40.2	37.7–41.9
Middle phalanges, lateral digits (II & V)	9	60.0	51.4–71.6	8	61.4	58.4–65.8	6	62.1	60.2–64.1
Middle phalanges, median digits (III & IV)	4	68.1	57.8–76.8	8	60.7	56.9–65.6	6	59.3	57.8–62.2

[a] $\text{Index} = \dfrac{\sqrt{\text{cross-sectional area of midshaft of phalanx}}}{\text{total length of phalanx}}$

defined, with a much better defined dorsal beak. These differences are functionally associated with improved stability at the metapodial–phalangeal joint, especially during rapid flexion and extension. Similarly, the middle phalanges can be distinguished from those of *Hip. amphibius* in being slightly less robust, with a proximal articular surface that shows adaptations for increased stability during parasagittal movements at the interphalangeal joint (i.e., the facet is mediolaterally narrower, the midsagittal keel is more pronounced, and the dorsal and ventral beaks are more projecting). Terminal phalanges have only been recovered from Kiloleli 2 and Inolelo 2. They are comparable in size, proportions, and morphology to those from the median manual digits of *Hip. amphibius*.

An isolated phalanx from Tinde West (WM 520/92) is noticeably much smaller than all of the other phalanges from the Manonga Valley. The specimen is a complete proximal phalanx from a lateral ray, probably from the pes. As both epiphyses are intact and fully fused, it is clearly from an adult individual. In its linear dimensions (the length of the phalanx is 42.1 mm) it is on average only 66% the size of the next smallest proximal lateral phalanx (which, incidentally, is about the same order of magnitude as that between phalanges of *Hip. amphibius* and *C. liberiensis*). Apart from its small size, however, the phalanx is similar in morphology and proportions to the other phalanges from Tinde. The diminutive size of WM 520/92 precludes it from assignment to *Hex. harvardi*, and it establishes the presence in the Manonga Valley of a much rarer pygmy species of *Hexaprotodon*. In terms of its size, it is quite a bit smaller than phalanges attributed to *Hex. aethiopicus*, a pygmy hippopotamus from the Turkana basin (Harris *et al.*, 1988; Harris, 1991). It is pertinent here to note that a small species of *Hexaprotodon*, of uncertain taxonomic status, also appears to have coexisted with *Hex. harvardi* at Lothagam and Lukeino (Coryndon, 1978b; M. G. Leakey, pers. comm.; Harrison, unpublished). Based on craniodental evidence, however, it appears that this latter species was a little larger than *Hex. aethiopicus*, but was comparable in size to *Hex. imagunculus* from the Western Rift.

5.5. Functional and Behavioral Implications of the Postcranium

The morphology of the forelimb of *Hex. harvardi*, especially the elbow joint, differs in a number of important respects from that of *Hip. amphibius*, and more closely resembles the pattern observed in *C. liberiensis*. In contrast to *Hip. amphibius*, the distal humeri of *Hex. harvardi* and *C. liberiensis* have a more strongly spooled trochlea, better development of the median keel, and a relatively deep and narrow olecranon fossa. These features are adaptations for increasing the stability of the elbow joint during rapid flexion and extension of the forearm. In addition, indications that the carpal and digital flexors may have been more strongly developed in *Hex. harvardi* are consistent with this functional interpretation. In ungulates the wrist joint acts as a "flexion hinge" in which the manus is folded during protraction of the forelimb to avoid dragging the digits (Yalden, 1971). Therefore, *Hex. harvardi*, with its combination of adaptations for rapid parasagittal movements of the forearm and its relatively long digits, would require well-developed digital and carpal flexors. Similar indications of adaptation for greater stability and an increased range of motion in the parasagittal plane are also found in the knee and astragalocrural joints. These adaptations, together with the more lightly built postcranial skeleton, longer and more slender limb bones, narrower and more close-packed carpus and tarsus, and longer metapodials and phalanges, suggest that *Hexaprotodon* was a more digitigrade, fast-moving animal, somewhat less specialized than *Hippopotamus* for an amphibious habit. The postcranium of *Hex. harvardi* is, however, very similar to that of *C. liberiensis*, remarkably so given the considerable difference in estimated body size between the two species (i.e., 250–275 kg for *C. liberiensis* and ~1000–2000 kg for *Hex. harvardi*).

6. Taxonomy and Phylogenetic Relationships

A comparison with other early hippopotamids is necessary to place the Manonga Valley material in its appropriate taxonomic, phylogenetic, and biochronological context. Following a review of its relationships at the generic level, a more detailed comparison of the material with early hippopotamids from East Africa, North Africa, and Eurasia is presented. Most of the observations discussed below are based on studies of original materials, but in a few cases, where noted, my comments refer to published descriptions, illustrations, and measurements.

6.1. Generic Affinities of the Manonga Valley Hippopotamid

6.1.1. Hexaprotodon

It is evident from the preceding descriptions of the craniodental and postcranial material that the large species of hippopotamid from the Manonga Valley can be referred to the genus *Hexaprotodon*. A number of primitive traits serve to distinguish *Hexaprotodon* from *Hippopotamus*. These include: upper and lower incisors with tip-to-tip occlusion and relatively flat apical wear; upper incisors set in a shallow parabolic series; upper canines with a deep posterior groove; upper and lower canines with finely striated enamel; premolars relatively large; molars brachyodont with well-developed cingula, tapered lobes, and a triangular enamel wear pattern; a short muzzle and elongated neurocranium; orbits situated laterally, approximately midway along the length of the cranium; a tendency for the median suture of the premaxillae to be fused anteriorly; lacrimals small and separated from the nasal bones by a well-developed antorbital process of the frontal bone; nasals expanded posteriorly; limb bones with joint surfaces that maximize stability for parasagittal movements; and elongated metapodials and phalanges (Coryndon, 1978a; Gèze, 1985; Harris, 1991).

6.1.2. Trilobophorus

In addition to *Hexaprotodon* and *Hippopotamus,* Gèze (1985) recognized a third genus of Plio-Pleistocene hippopotamid from East Africa, which he formally named *Trilobophorus.* The taxon is known only from the late Pliocene sites of Geraru and Hadar (Hadar Formation) in the Awash Valley (Gèze, 1985; Kalb & Mebrate, 1993). I have not had the opportunity to study the original material from Ethiopia, but the diagnosis presented by Gèze (1985), which mainly includes features of the skull and dentition typical of *Hexaprotodon*, provides insufficient grounds for the recognition of a separate genus. Based on the few unique characteristics listed by Gèze (1985), the material is tentatively retained as *Hex. afarensis*, although further comparisons are needed in order to determine its distinctiveness from *Hex. protamphibius turkanensis.*

6.1.3. Kenyapotamus

The earliest hippopotamids are known from the middle and late Miocene of East Africa. Pickford (1983) has described two species—*Kenyapotamus ternani*, from the middle Miocene of Fort Ternan and Maboko Island (12–15 Ma), and *Kenyapotamus coryndonae*, from the late Miocene of Ngeringerowa, Ngorora Formation, Nakali, and Namarungule Formation (7–10 Ma)—that he includes in a separate subfamily of the Hippopotamidae, the Kenyapotaminae. In addition, Pickford (1990b) has described the remains of *Kenyapotamus* from the Beglia Formation in Tunisia, dated at 9–10 Ma, which are close in morphology to those of *K. coryndonae*. There is good evidence to support the inference that *Kenyapotamus* represents the sister taxon of all later hippopotamids (hippopotamids of "modern aspect"), which are grouped together in the Hippopotaminae. Kenyapotamines are distinguished from hippopotamines primarily by the retention of more primitive traits. *Kenyapotamus*, for example, is much smaller than *Hex. harvardi* (the occlusal areas of the cheek teeth of *K. ternani* and *K. coryndonae* are only 24% and 38%, respectively, of those of *Hex. harvardi*), and it has simpler, more bunodont cheek teeth, with occlusal details closer to the ancestral suiform morphotype (Pickford, 1983). It would seem that the kenyapotamines, which replaced the anthracotheres as the dominant group of large amphibious mammals at the end of the early Miocene, at least in the local East African setting, were themselves superceded by the hippopotamines during the late Miocene

(6–7 Ma) (Coryndon, 1978a; Pickford, 1983). As the time interval between the last kenyapotamines and the appearance of the earliest hippopotamines is relatively slender (probably about 1 m.y.), and since the extent of the morphological differences between the two groups it striking, it seems likely that *Hexaprotodon* was an immigrant into East Africa during the late Miocene. Pickford (1983) has put forward the intriguing suggestion that increased tectonic activity in the Rift Valley system during this period may have impeded rivers and led to the development of a mosaic of lakes and lakeside environments, which established, possibly for the first time, suitable niches for the hippopotamines to expand their geographic range into East Africa.

6.1.4. Choeropsis

Further support for the hypothesis that hippopotamines may have originated outside of East Africa comes from the biogeography and phylogenetic affinities of the living hippopotamids. The extant pygmy hippopotamus, *Choeropsis liberiensis*, from West Africa, appears to be the sister taxon of all other hippopotamines, both living and fossil. Apart from a few autapomorphies of the dentition and postcranium, *C. liberiensis* conforms closely to the inferred ancestral morphotype of the Hippopotaminae, and in the structure of the face and neurocranium it would seem to be more primitive even than *Hex. harvardi*. I agree with Coryndon (1978a) and Pickford (1983), therefore, that the lineage leading to the modern pygmy hippopotamus diverged early, being derived from a common ancestor that was more conservative than any known fossil representative (except for *Kenyapotamus*) (see Fig. 5). This implies that the divergence of the Hippopotaminae occurred prior to their initial appearance in the fossil record in East Africa, and that, since the most primitive member of the subfamily, the extant pygmy hippopotamus, has a West African distribution, there is at least circumstantial evidence that the hippopotamines may have originated outside of East Africa.

Moreover, the inferred relationship between the living pygmy hippopotamus and the other hippopotamids discussed above has some important ramifications for the taxonomy of the group. Coryndon (1977) argued that *Choeropsis liberiensis* should be included in the genus *Hexaprotodon*, and this viewpoint has generally been adopted by subsequent workers. However, the marked similarities between *Hexaprotodon* and *Choeropsis* are undoubtedly a consequence of the retention of primitive hippopotamine traits, and do not provide evidence of a particularly close phylogenetic relationship. The current evidence would favor, in fact, the interpretation that the modern pygmy hippopotamus is a somewhat specialized derivative of the sister taxon of all other hippopotamines. In this case a separate generic designation seems appropriate.

6.1.5. Hippopotamus

A number of derived characteristics of the dentition, skull, and postcranium serve to distinguish *Hippopotamus* from all other hippopotamines. These include: tetraprotodont upper and lower incisors, with scissorlike occlusion; upper canines with a shallow posterior groove; upper and lower canines with

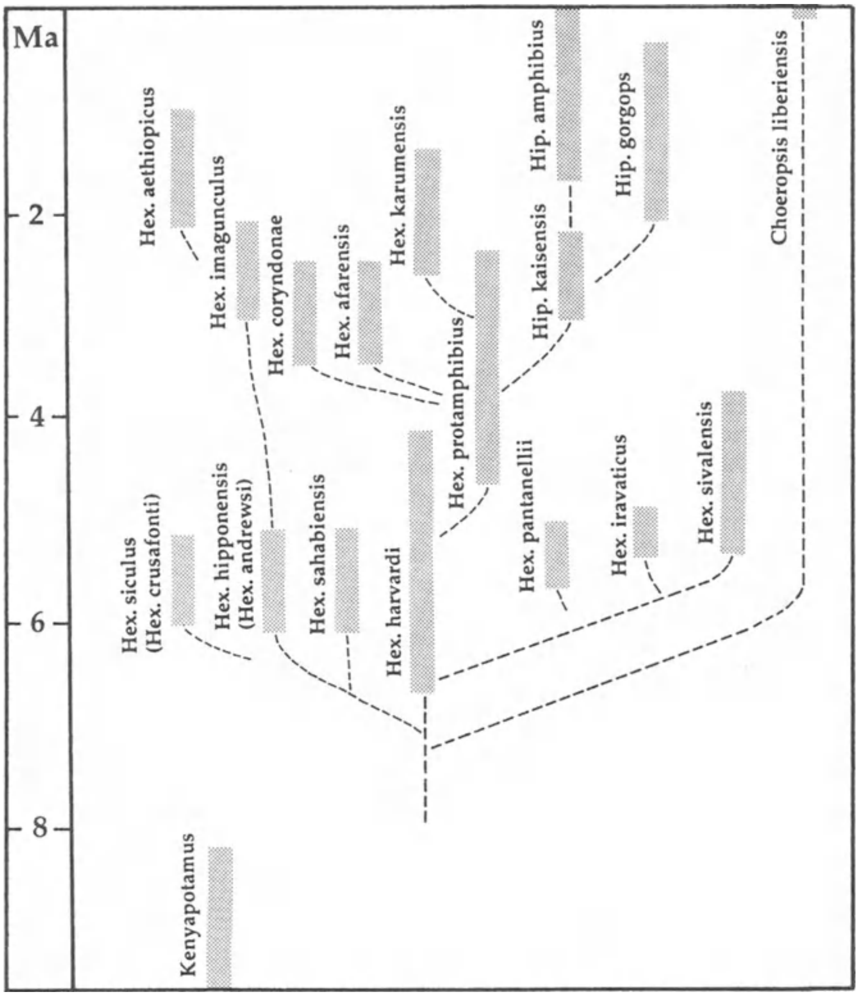

FIGURE 5. Phylogenetic relationships of African and Eurasian hippopotamids. The scheme is a provisional one, including only those taxa discussed in the text.

heavily grooved enamel; premolars small; molars elongated and more hypsodont, with poorly developed cingula, and a trefoliate enamel wear pattern; a long muzzle and an abbreviated neurocranium; orbits tend to be elevated superiorly; the median suture of the premaxillae remains unfused anteriorly; lacrimal large, making contact with the nasal bones; nasals expanded posteriorly; limb bones, metapodials, and phalanges short and robust, and adapted for a more amphibious habit (Coryndon, 1978a; Gèze, 1985; Harris, 1991).

These synapomorphies link *Hip. amphibius* with several fossil species from the Plio-Pleistocene of Africa (i.e., *Hip. kaisensis* and *Hip. gorgops*), and define them as a clade distinct from all other hippopotamines. *Hippopotamus* was presumably derived from an advanced member of the *Hexaprotodon* lineage, probably some time during the later part of the Pliocene (see Fig. 5). However, if *Hippopotamus* does indeed share a more recent common ancestor with one of the more derived species of *Hexaprotodon* than it does to primitive hippopotamines (such as *Hex. harvardi*), then we are forced to concede that the genus *Hexaprotodon*, as currently construed, represents a paraphyletic taxon. *Hexaprotodon* may be easy to diagnose on the basis of an extensive suite of characters (see description above), but these features appear to be entirely symplesiomorphic. In this case, the taxon has no integrity as a clade; it merely represents a cluster of stem species of hippopotamines that lack certain derived features characteristic of *Hippopotamus*. Clearly, a more detailed assessment of the phylogenetic relationships is required before the taxonomy of hippopotamines adequately reflects their cladistic affinities. It may be that Pickford's usage of *Hippopotamus* to encompass *Hexaprotodon*, while retaining *Choeropsis* as a distinct genus, may represent a suitable compromise to avoid the unnecessary proliferation of new names (Pickford, 1983). However, until such time as a detailed phylogenetic analysis has been undertaken, I continue to employ *Hexaprotodon* (*sensu lato*), with the explicit understanding that it almost certainly represents a paraphyletic grouping of unrelated stem hippopotamines.

6.2. East Africa

6.2.1. Lothagam, Kanapoi, and the Baringo Basin

As discussed above, the majority of specimens from the Manonga Valley can be assigned to *Hex. harvardi*. The Manonga Valley material retains a series of primitive traits of the dentition that are characteristic of *Hex. harvardi*, but in combination are lost or modified in all other species of *Hexaprotodon*. These include the retention of six upper and lower incisors of subequal size, strongly bilaterally compressed lower canines, a high incidence of double-rooted upper and lower P1s, large premolars with well-developed accessory cusps and pustulate crests, a premolar row that is subequal in length to the molar row, brachyodont molars, and a less pronounced size differential in the molar series.

It is important to take into account that *Hex. harvardi* is derived from sites that span a considerable time range (ca. 7–4 Ma). Although the samples from different time periods and geographic areas are limited, the evidence suggests that *Hex. harvardi* represents part of an evolving lineage that underwent morphological change through time. The oldest specimens attributed to *Hex. harvardi*, from the Mpesida Beds (6.4–7.0 Ma) in the Baringo basin, are morphologically very similar to the type material from Lothagam, but the teeth (and the postcranials) tend to be somewhat larger (the occlusal area of the cheek teeth is 16.6% larger on average, and more than one quarter of the teeth fall outside the 95% confidence limits of the sample from Lothagam). The younger material from Lukeino, which is apparently roughly contemporary with that from Lothagam (4.72–6.24 Ma), is morphologically and metrically indistinguishable from the latter. Most significant in this regard, perhaps, is the collection from the site of Kanapoi, which is younger than that from Lothagam and Lukeino, with an estimated age of 3.9–4.2 Ma (Leakey *et al.*, 1995). The Kanapoi material displays a suite of more derived characteristics of the skull and dentition: the orbits are raised slightly above the dorsal surface of the neurocranium; the upper and lower central incisors are noticeably larger than the lateral pair of incisors; P^1 is single-rooted; P^4 is relatively small, with a poorly developed lingual cuspule; and the premolars are smaller in relation to the size of the molars. Detailed comparisons of the material from the Manonga Valley show that the dental samples from the Ibole and Tinde Members are metrically and morphologically identical to those of *Hex. harvardi* from Lothagam and Lukeino, and that they are more conservative than the material from Kanapoi. This suggests that the *Hex. harvardi* samples from the lower beds of the Manonga Valley sequence are more comparable in age to Lothagam and Lukeino, at 5–6 Ma, than they are to the younger Kanapoi sample. There is some indication, however, that the isolated teeth and postcranials from the overlying Kiloleli Member are slightly larger and the molars more hypsodont that those from Tinde, and this may indicate the occurrence of a slightly more progressive form of *Hex. harvardi* in the Manonga Valley sequence. However, the differences are minor, and the samples too small to confirm this preliminary observation.

6.2.2. Turkana Basin

The Plio-Pleistocene hippopotamids from the Turkana basin have been reviewed in some detail by Gèze (1985) and Harris (1991). The lower part of the sequence in the Omo Valley (Shungura Members A and B) and Koobi Fora (lower Tulu Bor, Lokochot, Moiti, and Lonyumun Members of the Koobi Fora Formation), which dates from at least 4.35 Ma to younger than 3 Ma (Harris *et al.*, 1988; Harris, 1991; Brown, 1994), has yielded abundant remains of a hexaprotodont hippopotamid, *Hex. protamphibius* (Arambourg, 1944a). Gèze (1985) referred this material to a separate subspecies, *Hex. protamphibius turkanensis*, in order to differentiate it from the younger tetraprotodont material belonging to *Hex. protamphibius protamphibius* (Arambourg, 1947). In addition, Gèze identified at least one other species of *Hexaprotodon* from the lower part of the Omo sequence, *Hex. shungurensis*. However, I am inclined to agree with Harris (1991) that this latter species is possibly a junior synonym of *Hex. protamphibius*.

Hexaprotodon protamphibius turkanensis, which represents the earliest hippopotamid to occur in the Turkana basin, is more derived than *Hex. harvardi* in the following respects: the sagittal crest and nuchal crest are raised above the level of the muzzle; the orbits are slightly more elevated, and are positioned further posteriorly (located along the length of the cranium about 60–70% from the tip of the snout); the central lower incisor is larger than the lateral pair, rather than subequal; the premolars are smaller in relation to the size of the molars, and although variable, they have less of a tendency to develop accessory cuspules and pustulations; and the cheek teeth are smaller in overall size (they are on average less than 80% of the occlusal area of those in *Hex. harvardi*), and the lower molars are slightly more elongated (Harris *et al.*, 1988; Harris, 1991). Since many of the differences seen in *Hex. protamphibius* represent a continuation of the evolutionary transformation seen in time-successive samples of *Hex. harvardi*, it is reasonable to infer a direct ancestral–descendant relationship between them (Fig. 5).

6.2.3. Hadar

In addition to *Trilobophorus afarensis* discussed above, Gèze (1985) recognized a second species of hexaprotodont hippopotamid from the Hadar Formation, *Hex. coryndonae*. Although poorly known, it appears to be more derived than *Hex. harvardi*, as well as other East African hippopotamids, in having I_2 smaller than I_3 (see Table VII).

6.2.4. Western Rift

A sizable collection of hippopotamids has been recovered from sites in Uganda and Zaire in the Western Rift, associated with the Lake Albert and Lake Edward basins (Hopwood, 1926; Cooke and Coryndon, 1970; Erdbrink and Krommenhoek, 1975; Pavlakis, 1987, 1990; Yasui *et al.*, 1992; Faure, 1994). At least two species are represented: a pygmy hexaprotodont, *Hex. imagunculus* (Hopwood, 1926), and a larger, more advanced hippopotamid, *Hippopotamus kaisensis* (Hopwood, 1926). Previous workers have recognized additional species. Cooke and Coryndon (1970), for instance, distinguished several isolated cranial and mandibular specimens, which they referred to *Hippopotamus* sp. Pavlakis (1987), following Gèze (1980), tentatively referred these specimens to ?*Hex. shungurensis*. However, given the lack of adequate material for comparison, there seems little justification for distinguishing these specimens from *Hex. imagunculus*. Similarly, Erdbrink and Krommenhoek (1975) identified a new species, *Hippopotamus (Choeropsis) archechoeropsis*, supposedly somewhat smaller than *Hex. imagunculus*. However, as the task of correctly identifying the serial positions of cheek teeth is exceedingly difficult when using only isolated molars and jaw fragments of immature individuals, the metrical distinctiveness of these specimens may not be easy to verify. It seems equally plausible that these specimens can be attributed to *Hex. imagunculus* (see also Faure, 1994). In addition, Pickford (1990a) has recorded (without further explanation) additional species: *Hippopotamus* sp. from the late Miocene Oluka Formation, *Hip.* cf. *aethiopicus* from late Pliocene–early Pleistocene localities, and *Hip. amphibius* from the late Pleistocene Rwebishengo Beds. Also, Faure (1994) has recognized *Hip. gorgops* from the early Pleistocene Nyabusosi Formation (~1.8 Ma), and an undescribed species of *Hippopotamus* from the early Pliocene Nkondo Formation (~4.5–5.0 Ma).

Much of the taxonomic confusion stems from the fact that until recently the hippopotamid material from Uganda and Zaire was very fragmentary, and that limited samples were available from sites of unknown age or of dubious stratigraphic association (Pickford, 1990a; Pickford *et al.*, 1988, 1991, 1992). The recent recovery of a sizable new collection of fossil hippotamids from the Western Rift (Faure, 1994), along with a substantially revised biostratigraphic scheme (Pickford *et al.* 1992, 1993), may help alleviate some of these difficulties.

Based on published material, there are two well-established species of hippopotamids from late Miocene and early Pliocene localities in the Western Rift, *Hex. imagunculus* and *Hip. kaisensis*. According to Faure (1994), both species occur in sediments ranging in age from about 5 Ma to 1.8 Ma. The possible occurrence of additional species, however, requires confirmation.

Hippopotamus kaisensis was originally proposed by Hopwood (1926) as a subspecies of *Hip. amphibius*, and although this designation has been followed by a number of workers (Hooijer, 1950; Erdbrink and Krommenhoek, 1975; Pavlakis, 1987, 1990), there are some distinctive morphological differences that merit the recognition of a separate species (Hopwood, 1939; Cooke and Coryndon, 1970; Coryndon, 1978a; Gèze, 1985; Faure, 1994). It is quite clear that this species is closely related to *Hip. amphibius*, and it probably represents the conservative sister taxon of both *Hip. amphibius* and *Hip. gorgops* (Fig. 5).

Hexaprotodon imagunculus can be distinguished from *Hex. harvardi* by the following specialized features: (1) it is considerably smaller in size (the combined area of the cheek teeth is only 56% that of *Hex. harvardi*); (2) the lower incisors are apparently hexaprotodont, but the two lateral incisors, especially I_3, are smaller than I_1, not subequal; (3) the premolars are relatively small in comparison with the molars; (4) P1 is usually a single-rooted tooth; (5) the posterior premolars tend be less complex, with less prominent accessory cuspules; (6) the molars are slightly more hypsodont; and (7) the frontal does not make contact with the maxilla, due to the extension of the lacrimal medially (at least based on the Kazinga Channel partial cranium). *Hex. imagunculus* is more derived than *Hex. harvardi*, and it can readily be distinguished on the basis of size and morphology from the material from the Manonga Valley. However, as Erdbrink and Krommenhoek (1975) have noted, there may be some justification for synonymizing *Hex. imagunculus* with *Hex. hipponensis* from North Africa.

6.3. North Africa

Several species of hippopotamid have been described from the late Miocene and early Pliocene of North Africa. Gaudry (1876a,b) described some isolated teeth of a small hippopotamid from Bône, Algeria, as a distinct species, *Hippopotamus (Hexaprotodon) hipponensis*. There has been considerable discussion over whether or not the isolated incisors from the site indicate a hexaprotodont condition, but most workers have favored the original interpretation by Gaudry, that *Hex. hipponensis* had six lower incisors (Gaudry, 1876a,b; Pomel, 1890, 1896; Joleaud, 1920; Depéret, 1921; Arambourg, 1944b; Hooijer, 1950). Arambourg's (1944b) metrical data provide a ratio of relative incisor size of 100:79:76, in which I_1 is somewhat larger than the lateral incisors, comparable to the condition in *Hex. imagunculus*. Similar material from Wadi Natrun in Egypt (which is probably similar in age to Bône, and correlated to MN 13), described by Andrews (1902) and Stromer (1914), has been referred to the same species, but the incisors, which are apparently associated, imply a tetraprotodont rather than hexaprotodont pattern. Based on this inferred difference, Arambourg (1947) argued that the material should be referred to *Hex. protamphibius*, although he distinguished it as a separate subspecies, *andrewsi*. Subsequent workers have generally considered the two samples to belong to a single species, *Hex. hipponensis*, although it may eventually prove necessary to recognize the species distinctiveness of *Hex. andrewsi*. Furthermore, as noted above, the cheek teeth from Bône and Wadi Natrun are morphologically and metrically very similar to *Hex. imagunculus* from the Western Rift. They are, however, distinct from *Hex. harvardi* in their smaller size and more specialized dentition.

In 1987, Gaziry described a new species of medium-size hexaprotodont hippopotamid, *Hex. sahabiensis*, from the early Pliocene locality of Sahabi in Libya (~5 Ma). Gaziry (1987) listed a number of features that purportedly distinguish *Hex. sahabiensis* from *Hex. harvardi*. However, his comparisons were based entirely on Coryndon's published descriptions and drawings of *Hex. harvardi*, and this led him to misrepresent the morphological differences between the two species. For example, his claim that the development of accessory cusps, cingula, and enamel patterns on the molars and premolars is distinctive is of doubtful significance given the range of variability of these features in *Hex. harvardi*. Moreover, one of the major characteristics emphasized by Gaziry (1987) is the relatively much larger incisors and canines of *Hex. sahabiensis*. However, a closer inspection of Gaziry's data shows that he mistakenly compared Coryndon's mesiodistal crown lengths of the incisors and canines of *Hex. harvardi* with the apicobasal lengths of *Hex. sahabiensis*. It is hardly surprising, therefore, that he found the anterior teeth of his new species to be almost four times larger than the East African species! Nevertheless, *Hex. sahabiensis* is smaller (being more similar in size to *Hex. aethiopicus* and *Hex. imagunculus*) and more specialized than *Hex. harvardi* in having more reduced premolars and a greater size differential between the molars. These differences are probably adequate to distinguish *Hex. sahabiensis* from *Hex. harvardi* at the species level. However, the taxonomic distinctiveness of *Hex. sahabiensis* in relation to the contemporary North African species, *Hex. hipponensis* and *Hex. andrewsi*, which are closely comparable in size and morphology, as well as *Hex. crusafonti* and *Hex. primaevus* from Spain, needs further investigation. Also pertinent here may be an undescribed *Hexaprotodon* from the Baynunah Formation of Abu Dhabi on the Arabian peninsula, which is probably of similar age (Hill *et al.*, 1990; Whybrow *et al.*, 1990).

6.4. Europe and Asia

Toward the end of the Miocene, during the late Messinian, at sites correlated with MN 13, *Hexaprotodon* appears for the first time in the fossil record of Eurasia. It is part of a limited exchange of large mammals between Africa and Eurasia at this time, which also included the arrival from Africa of macaques and reduncine bovids. *Hexaprotodon* appears to have established a wide geographic range—extending from Spain in western Europe to Myanmar in Asia—within a very short period of time after its initial arrival. This may simply reflect the availability in tropical and subtropical Eurasia of a previously unoccupied niche for large semiaquatic herbivores, although the timing and pattern of dispersion into Eurasia is consistent with a model in which the rapid geographic expansion and diversification of *Hexaprotodon* in Africa just prior to its arrival in Eurasia was merely extended beyond the geographic limits of Africa.

The best known species from the late Miocene or early Pliocene of Eurasia is *Hexaprotodon sivalensis* from the Siwalik Hills of India and Pakistan (Falconer and Cautley, 1836; Lydekker, 1884; Colbert, 1935; Hooijer, 1950). Barry and Flynn (1989) record the earliest occurrence of this species in the Siwaliks at the Mio-Pliocene boundary, at 5.3 Ma. It is comparable in size and morphology to *Hex. harvardi*, and, in fact, in many respects, it appears to be much more similar to *Hex. harvardi* than are contemporary species in North Africa. However, it is more derived in a number of features: the orbits are more elevated; the lateral incisors tend to be slightly reduced relative to the size of the central incisor; the premolars are relatively small in relation to the size of the molars, and not as pustulate; and the lower molars exhibit a greater size differential as they progress posteriorly. In addition, it is worth noting that the cheek teeth of *Hex. sivalensis* show a remarkable degree of wear, even in quite young individuals, when compared with *Hex. harvardi*, and this may further imply an important ecobehavioral distinction between the two species. A second Asian species, *Hex. iravaticus* (Falconer and Cautley, 1847), slightly smaller, and possibly less derived than *Hex. sivalensis*, has been recovered from the early Pliocene Upper Irrawaddy Beds in Myanmar (Falconer and Cautley, 1836; Lyddeker, 1884; Colbert, 1938, 1943; Hooijer, 1950). However, it is poorly known, making it difficult to assess its taxonomic and phylogenetic relationships.

In Europe, species of *Hexaprotodon* have been recovered from several late Miocene (MN 13) sites in Italy, Spain, and France. Pantanelli (1879) described some fragmentary remains of a small hexaprotodont hippopotamid from Casino in Italy, which he referred to *Hip. hipponensis*. Later, Joleaud (1920) erected a new species, *Hip. pantanellii*. The material is similar in size and is consistent in morphology with the contemporary *Hex. iravaticus* from Asia and *Hex. hipponensis* from North Africa, although most authors have tended to maintain its distinctiveness (Joleaud, 1920; Depéret, 1921; Hooijer, 1946, 1950; Erdbrink and Krommenhoek, 1975; Coryndon, 1978a). A hippopotamid similar in size to *Hex. pantanellii* has also been described from Gravitelli in Sicily (Seguenza, 1902, 1907). Although the original specimens were destroyed in the Messina earthquake of 1908, Hooijer (1946) used Seguenza's published descriptions and figures to assign the material to a separate species, *Hip. siculus*.

In Spain, fragmentary remains of a medium-size species of hippopotamid have been recovered from a number of localities correlated with MN 13 (Morales, 1981; Mein, 1989; Moyà-Solà and Agustí, 1989). Aguirre (1963) described a new species, *Hip. crusafonti*, on the basis of material from Arenas del Rey, and Morales (1981) has assigned additional material from La Portera. In addition, comparable material of similar age, and probably referrable to the same species, has also been recovered from Arquillo and Venta del Moro in Spain (Crusafont *et al.*, 1963, 1964; Morales, 1981) and Mosson in France (Faure and Méon, 1984;

Faure, 1985). Crusafont *et al.* (1963), however, have given the name *Hip. (Hex.) primaevus* to the Arquillo specimens, but since no holotype was identified, it is considered a *nomen nudum*. Although poorly known, *Hex. crusafonti* is a relatively specialized hippopotamid, with only four incisors in the mandible (it is, in fact, the earliest known tetraprotodont), relatively small, simple premolars, and narrow, hypsodont molars. It is probably derived from a form such as *Hex. hipponensis*, and appears to have close affinities with *Hex. siculus* from Sicily, with which it may eventually prove to be synonymous (Fig. 5).

7. Summary and Conclusions

Based on detailed comparisons of the Manonga Valley material with fossil hippopotamids from other Miocene and Plio-Pleistocene sites in Africa and Eurasia, the following conclusions can be reached: (1) most of the specimens from the Manonga Valley can be referred to *Hex. harvardi*; the material retains a series of primitive traits of the dentition and cranium that are characteristic of *Hex. harvardi*, but in combination are lost or modified in all other species of hippopotamines; (2) the specimens from the Ibole and Tinde Members are morphologically and metrically indistinguishable from *Hex. harvardi* from Lothagam (the type site) and the Lukeino Formation, thereby implying a biostratigraphic age of 5–6 Ma; (3) the specimens from the Kilolei Member are referred to *Hex. harvardi*, but comparisons suggest the possibility that they may represent a slightly more progressive form than that from the Tinde and Ibole Members; (4) a single isolated phalanx appears to indicate the occurrence of a second, smaller species of hexaprotodont hippopotamid in the Manonga Valley; (5) *Hex. harvardi* is apparently restricted to late Miocene and early Pliocene sites in East Africa, dated to between 7.0 and 4.0 Ma; (6) the Manonga Valley material serves to extend the geographic range of the species from southern Ethiopia and northern Kenya (principally the Turkana and Baringo basins) southward as far as northern Tanzania; (7) the postcranial skeleton of *Hex. harvardi* is lightly built, with relatively long and slender limb bones and cheirida, suggesting a more digitigrade, fast-running, cursorial habit, in contrast to that of the more amphibiously adapted *Hippopotamus*; (8) *Hex. harvardi* is the earliest known member of the Hippopotaminae, and, based on its conservative craniodental morphology, the species appears to represent the primitive sister taxon of all other hippopotamines (with the possible exception of *Choeropsis liberiensis*); (9) the genus *Hexaprotodon*, as currently perceived, is a paraphyletic clustering of stem hippopotamines that lacks derived features of *Hippopotamus*, a taxonomic issue that can only be resolved with more detailed comparative analyses; and (10) the living pygmy hippopotamus, *Choeropsis liberiensis*, appears to be more primitive still than *Hex. harvardi* and should be retained in a separate genus (*contra* Coryndon 1977, 1978a).

NOTE ADDED IN PROOF. In 1996 WMPE recovered additional hippopotamids from Tinde, including several specimens that contribute pertinent new information on the anatomy and taxonomic placement of *Hexaprotodon harvardi* from the Manonga Valley. The most important specimens are as follows:

WM 696/96, from Tinde East, consists of a right premaxilla fragment with I^1–I^3. The specimen confirms the general morphology of the anterior lower face and the hexaprotodont nature of the incisors, as seen in 056/90. The three incisors are subequal in size, with relative proportions of 98 : 100 : 91 (see Table IV), and they are arranged in a gently curving arc. The estimated breadth of the palate across the premaxilla is 120 mm. This specimen provides further confirmation of the close similarity of the Tinde hippopotamid to *Hexaprotodon harvardi* from Lothagam.

WM 1100/96 consists of a partial cranium of a juvenile, which represents the most complete specimen of a hippopotamid so far recovered from the Manonga Valley. It was discovered at Tinde West by Dr. Avelin Malyango. The specimen preserves much of the maxilla, portions of the frontal, nasal, lacrimal and temporal bones on the right side, a fragment of the occiput, as well as left C, P^1, dP^3, M^{1-3} and right C, dP^{2-3}, M^{1-2}. The following combination of primitive features confirms its assignment to *Hex. harvardi*: (1) the muzzle is short in relation to the length of the neurocranium; (2) the orbits are situated low on the face, and they do not extend superiorly above the roof of the muzzle; (3) the anterior root of the zygomatic arch is stout, widely flaring in relation to the canine flanges, and situated very low on the face; (4) the nasal and lacrimal bones are separated by a well-developed antorbital process of the frontal; and (5) the P^1 is a large, single-cusped tooth with a bilobate or bifid root.

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Chapter 7

Fossil Suids from the Manonga Valley, Tanzania

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1. Introduction

This contribution discusses suid specimens from the Manonga Valley, Tanzania. The 1990, 1992, and 1994 expeditions to the Wembere–Manonga Valley recovered 65 suid specimens from ten sites (Table I). Fossils suids derive from horizons throughout the Wembere–Manonga Formation, although the majority were recovered from the Ibole Member (Harrison 1991, 1993, 1994; Harrison and Verniers, 1993; Harrison *et al.*, 1993; Haileab and Harrison, 1993; Mbago *et al.*, 1993; Verniers, this volume, Chapter 2). There were no differences between specimens from the different members so they are treated together here. All suid remains can be attributed to the Pliocene species *Nyanzachoerus kanamensis.*

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Table I. List of Fossil Suidae from the Manonga Valley[a]

Inolelo 1 (Ibole Member)	
WM 1060/92	Left M_3 fragment
WM 1061/92	Lower canine fragment
WM 1062/92	M3 fragment
WM 1122/92	Left P^4 fragment
WM 1147/92	Right M^3 fragment
WM 1148/92	Left M^1 fragment
WM 1149/92	Canine fragment
WM 1410/92	Nearly complete mandible, with right P_2–M_3, left P_2–M_2, and left I_2 preserved
WM 129/94	Right P^3
WM 130/94	Left P_2
WM 163/94	Right M^2
WM 632/94	Left M_1
Inolelo 3 (Ibole Member)	
WM 1231/92	Right maxillary fragment, with P^3–P^4 and mesial portion M^1
Kiloleli 2 (Kiloleli Member)	
WM 858/92	C_fragment
Kiloleli 4 (Kiloleli Member)	
WM 657/90	Right M^2
Mwambiti 3 (Ibole Member)	
WM 796/92	M^- fragment
Ngofila 3 (Kiloleli Member)	
WM 1452/92	M_ fragment
Ngofila 4 (Tinde Member)	
WM 802/94	Right M^3 fragment
Shoshamagai 1 (Tinde Member)	
WM 1732/92	Right I^2 fragment
Shoshamagai 2 (Ibole Member)	
WM 1052/92	Right maxillary fragment with P^2–M^3
WM 1053/92	Left mandibular fragment with M_3 fragment
WM 1054/92	Left M_3 fragment
WM 1071/92	Left and right maxillae with left P^3–M^3 and right P^4–M^3
WM 1077/92	Canine fragment
WM 1078/92	Right mandible fragment with M_3 fragment
WM 1079/92	Right P_4
WM 1080/92	Molar fragment
WM 1081/92	C fragment
WM 1083/92	C fragment
WM 1085/92	Right C^- fragment
WM 1086/92	P^2
WM 1087/92	Left edentulous premaxilla fragment
WM 1088/92	C fragment
WM 1163/92	Right M^2
WM 1165/92	Left I^1 fragment
WM 1770/92	C fragment
WM 1771/92	Right maxilla fragment with M^2 and M^3 fragment
WM 1774/92	Right M_1 fragment
WM 1776/92	M fragment
WM 1777/92	Right I_

(continued)

Table I. (Continued)

WM 1778/92	Right M_2 fragment
WM 1780/92	Left M^3
WM 1780/92	Postcanine tooth fragment
WM 1780/92	Right mandible fragment with M_2 roots and M_3 (unerupted)
WM 1782/92	Right I^2 fragment
WM 1783/92	Left I^3 fragment
WM 1785/92	Left P^4 fragment
WM 1788/92	P_2
WM 1808/92	C^- fragment
WM 1809/92	C^- fragment
WM 1816/92	C^- fragment
WM 1824/92	C fragment
WM 1922/92	C fragment
WM 1923/92	C fragment
WM 1924/92	Left I^2
WM 1928/92	I_ fragment
WM 1929/92	Right I^1 and associated tooth fragments
WM 199/94	Right P^3
WM 200/94	Right M^1
WM 293/94	Right I_2
WM 300/94	Left mandible fragment with erupting M_3
Tinde West (Tinde Member)	
WM 21/90	C fragment
WM 81/90	M3 fragment
WM 237/92	Left P^3 fragment
WM 545/90	Left M_2 germ fragment

[a] Organized by site, with stratigraphic provenance after Verniers (Chapter 2, this volume).

Preservation of the recovered specimens is in most cases excellent and indicates great promise for further collection. The sample currently under study does not include complete crania.

2. Descriptions

Order Artiodactyla Owen, 1848
Infraorder Suina Gray, 1868
Family Suidae Gray, 1821
Subfamily Tetraconodontinae Simpson, 1945
Genus *Nyanzachoerus* Leakey, 1958
Species *Nyanzachoerus kanamensis* Leakey, 1958

2.1. Maxillae

WM 1071/92* from Shoshamagai 2 is two nearly complete maxillae and the palate of a subadult individual (Fig. 1; see Table II for measurements). The

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*This field catalogue number includes specimens originally designated WM 1072/92 and WM 1076/92, which conjoin with WM 1071/92.

FIGURE 1. *Nyanzachoerus kanamensis* maxillae and palate, WM 1071/92, WM 1072/92, and WM 1076/92. Occlusal view.

fragments conjoin on the median palatine suture between P^4 and M^3. The body of the left maxilla is broken through the infraorbital foramen, superior to P^4. The base of the left zygoma is partially preserved, and appears to be enlarged and pneumatized. The palate is relatively narrow, and the erupted tooth rows diverge distally. The left maxilla (WM 1076/92) has P^3–M^3 and is broken anterior to P^3, the mesial root of which is exposed. The left M^2 is broken. The right maxillary fragments preserve P^4–M^3 and the distal root socket of P^3. The teeth are only slightly worn, and the enamel is in perfect condition. The crowns of the erupting M^3 germs are fully formed and visible in their crypts. To facilitate study, the surrounding bone on the right maxilla was removed intact by preparators at the National Museums of Kenya. Although *Nyanzachoerus kanamensis* is a dimorphic species, this specimen is a juvenile and thus has no definite indication of its sex.

Table II. Measurements (in mm) of Manonga Valley Suid Maxillae, with Measurements from Other Specimens of *Ny. kanamensis* from Other Localities Included for Comparison[a]

	L22188 male	L14429 female	L14430 male	L20552 male	KNM KP 264	KNM KP 239	WM 1071/92	WM 1052/92
Palate breadth P^2	63.7	58.5	60^d	58^d	73	53		
Palate breadth M^3					33	40		
Length P^2–P^4	54.0	52.5	55.5	59.0	68.0	51.9		56^d
Length P^3–P^4	41.2^b	37.7^b	42.1^b	41.8^b		39.9^c	44.3	42^d
Length M^1–M^3	110.5	104.8	109.5		99.1	95.2	109^d	102^d
Length P^2–M^3	164.5	158.0	165.5		161.6	147.0		157^d
Length P^3–M^3	152^b	143^b	152^b			135^c	151^d	143^d

[a] Accession numbers denote specimens from the following localities: L, Langebaanweg; KP, Kanapoi; WM, Manonga Valley.

[b] Calculated using measurements in Cooke and Ewer (1972) and unpublished data summaries of which are found in Harris and White (1979) and Bishop (1994).

[c] Calculated using unpublished data (Harris and White, 1979).

[d] Estimated value.

The right maxillary fragment WM 1052/92 from Shoshamagai 2 is badly damaged (Fig. 2). P^2 through M^3 are preserved, although the tooth crowns are in some cases displaced labially from their roots. M^3 was erupting at the time of death, and its crown had not reached the occlusal level. The enamel is fragmentary and has been lost in some areas. Nevertheless, some description and measurements are possible (see below). There is also evidence of distortion along

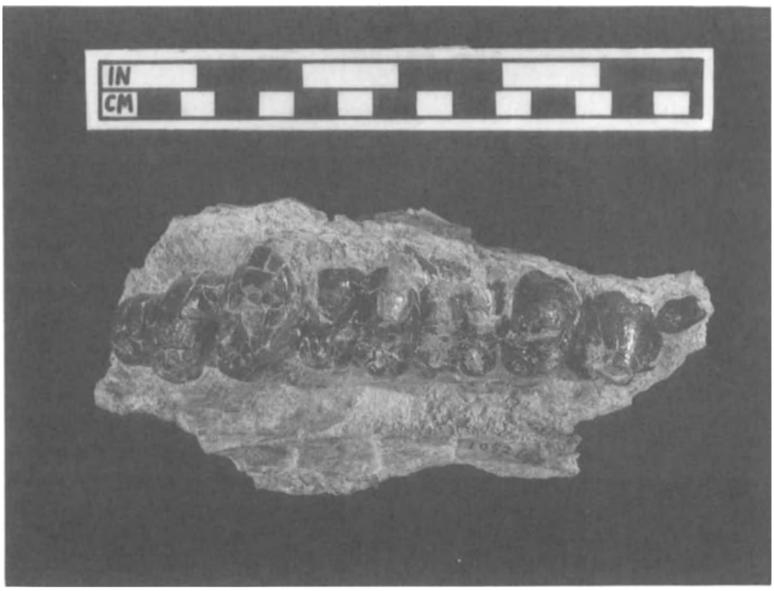

FIGURE 2. *Nyanzachoerus kanamensis* maxilla, WM 1052/92. Occlusal view.

the mesiodistal axis. The bone of the maxilla is comminuted along the lateral surface, and the otherwise undamaged palate has been displaced cranially 45° from its anatomical position. P^2 has also been rotated out of its anatomical position in the alveolus during diagenesis. No anatomical features of the maxilla are discernible.

WM 1231/92, from Inolelo 3, is an anterior fragment of a right maxilla containing P^3, P^4, and a mesial fragment of M^1. The anterior border of the fragment is an oblique break through the lateral surface of the maxilla in the middle of the P^4 root, diagonal through to the lingual surface at the level of the middle of M^1. Only the alveolar border of the palate is preserved. The fragment is broken superior to the tooth roots. The enamel preservation varies, with pitting on the occlusal surface and sides of the teeth. In contrast, the enamel closer to the cervix of the teeth is in excellent condition. The breakage anteriorly resulted in a conchoidal fracture, suggesting that this specimen has been damaged since being re-exposed on the surface prior to its recovery. Its condition is markedly worse than that of other suid specimens from the Manonga Valley, suggesting a different taphonomic history.

From Shoshamagai 2, WM 1771/92 is a right maxilla fragment bearing an extremely worn and damaged M^2 and the anterior cingulum and mesial trigone of M^3. The mesial roots of M^2 are exposed in the anterior break and the posterior aspect of the mesial M^3 roots is exposed in the posterior break. Cranially, the fragment is broken at the level of the tip of the M^3 roots. There is little anatomical detail preserved in the surviving maxillary bone fragment. However, the overall bone is massive, and the tooth roots are very deep. This overall impression of great size is strengthened by the appearance of the teeth themselves. The large M^2 is worn to the cervix and concave. All internal cusp morphology has been obliterated through wear so that there is a single dentine lake. Postmortem damage has removed the enamel from the sides of the tooth. The fragmentary M^3 is also well worn, although not to the extent of the M^2. The cusps are large with crenulated enamel. Wear has reduced the M^3 well below the level of the anterior cingulum. Although obliteration of the M^1 occlusal morphology is very common in *Nyanzachoerus kanamensis*, the obliteration of M^2 is less so, leading to the conclusion that this specimen represents a very old individual.

2.2. Premaxilla

An edentulous left premaxilla fragment has been recovered at Shoshamagai 2. It is broad proximally. The premaxilla preserves the sockets for three incisors, the primitively retained full complement, which diminish in size from I^1 to I^3. The sizes of the alveoli indicate that I^1 and I^2 were both relatively large and robust teeth, while I^3 was smaller. This is in agreement with the isolated incisors recovered. The specimen is broken lateral to the midpalatine line. The lateral, ascending portion of the premaxilla indicates a large nasal aperture.

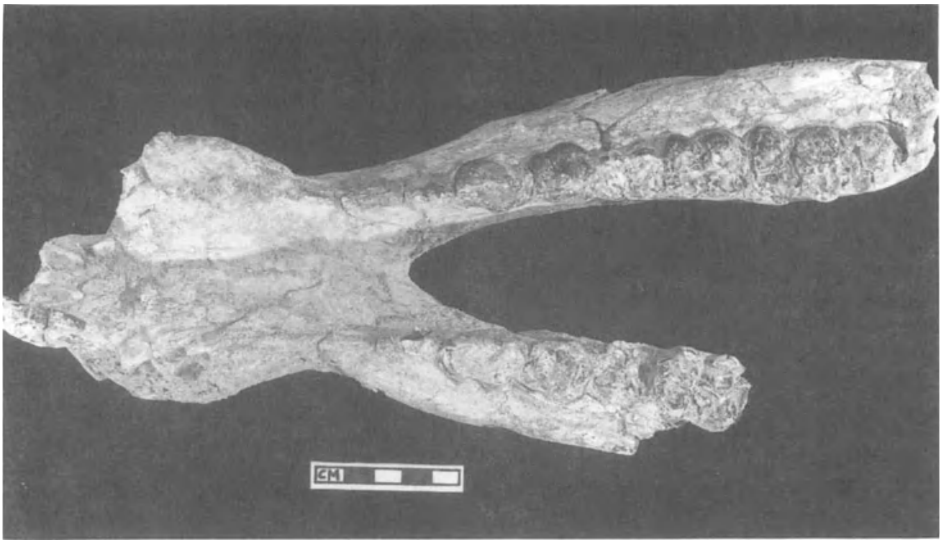

FIGURE 3. *Nyanzachoerus kanamensis* mandible, WM 1410/92. Occlusal view.

2.3. Mandible

A nearly complete mandible (WM 1410/92)* derives from the Ibole Member at Inolelo 1 (Fig. 3; see Table III for measurements). It was found in association with numerous bone fragments, some of which conjoin with the mandible. The angles and ascending rami are fragmentary. One large mandibular condyle has no point of attachment with the corpus and alveoli and therefore cannot be attributed to the specimen with confidence. The inferior corpus has weathered away on both sides of the mandible from the level of P_2, exposing the roots of the posterior cheek teeth. The right corpus is relatively undamaged and preserves P_3–M_3. The preservation of dental enamel is good, although some chemical changes during diagenesis, such as attack by acids, appear to have caused enamel pitting. The left M_3 is missing. The premolar series is well preserved, but the two preserved molars are damaged on their lingual aspect.

The symphyseal region is damaged on the right, with the alveolar margin missing from I_1–I_3. On the left, only I_2 is preserved, with the other incisors broken off at the cervix. Unfortunately, the sole surviving incisor has been broken and deformed during fossilization. It appears to be longer than those from Langebaanweg (Cooke and Hendey, 1992), but this is probably due to factors without taxonomic value, such as stage of wear. Both canines are missing, having been broken off at the alveolus. The anterior limit of the canine is not ascertainable due to damage of the alveolus. The deep symphysis is separated from the main

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*WM 1410/92 includes field catalogue numbers WM 1730/92 and WM 1731/92, which are bone fragments associated with WM 1410/92.

Table III. Measurements (in mm) of the Manonga Valley Suid Mandible, with Measurements of *Ny. kanamensis* Specimens from Other Localities Included for Comparison

	L20552 male	L20490 male	KNM KP 219 male	KNM KP 239 female	WM 1410/92
Length: tip to back of ramus	395	447	381	352	375[a]
Length of symphysis	133.5	162.5	145[a]	115	132
Breadth I_3–I_3	74.3	88.5		60	70[a]
Breadth across canine flanges	104.8	141.5		74	90
Breadth at constriction	84.5	90		61	65
Diastema I_3–P_2	94.5	106	89	72	94
Diastema C_–P_2	59.9	71.0	50[a]	48	60
Width between centers of P_2s	61	80	81	57	50
Thickness of corpus: P_4/M_1	53.7	49.5	51	37.5	39[a]
Height of corpus: P_4/M_1	69.7	79.5	77	59.5	70[a]
Length P_2–P_4	70.0	67.5	62.7	56.4	65
Length M_1–M_3	119.5	119.7	102.5	94.2	110
Length P_2–M_3	189.5	191.2	165.2	150.6	175

[a] Approximate measurement.

mandibular corpus by a marked postcanine constriction. Although the corpus is damaged inferiorly, it is possible to estimate its maximum mediolateral and dorsoventral dimensions (see Table III) along with several other measurements. The corpus does not appear to be as robust or inflated as the Langebaanweg specimens. It is more similar in these aspects to material from Kanapoi (Cooke and Ewer, 1972). The mediolateral distortion of the specimen may falsely contribute to this impression. It is most likely the mandible of a female individual, given the gracile nature of this specimen relative to the larger Kanapoi and Langebaanweg specimens and the small canine alveolus.

2.4. Upper Dentition

2.4.1. Incisors

The upper incisors are preserved only as isolated teeth. They do not differ significantly from previously published descriptions of *Nyanzachoerus kanamensis* (Cooke and Ewer, 1972; Cooke and Hendey, 1992). Two isolated I^1s, WM 1165/92 and WM 1929/92, show typical *Ny. kanamensis* morphology, with a strong main cusp joined posterolaterally to an additional small cusp. The lingual surface of I^1 shows an indentation at the border of the two cusps. WM 1929/92 is heavily worn, showing a deep, sinuous dentine lake. I^2, represented in the Manonga Valley sample by WM 1782/92 and WM 1924/92, also has a main anterior cusp with a smaller lateral one. There is a shallow indentation on the lingual side delineated by a series of small enamel ridges. Two specimens of I^3, WM 1732/92 and WM 1783/92, are subconical with slight ridging on the distolateral portion of the tooth. The alveoli preserved in the edentulous pre-

Table IV. Measurements (in mm) of Manonga Valley Suid Upper Incisors[a]

	I^1	I^2	I^3
WM 1165/92	21.47 9.67		
WM 1929/92	21.30 12.25		
WM 1782/92		14.62 6.42	
WM 1924/92		16.05 7.15	
WM 1732/92			11.39 7.69
WM 1783/92			12.28 9.14

[a] Teeth are measured at the cervix. Top measurement mesiodistal, bottom measurement buccolingual dimensions.

maxilla, WM 1087/92, described above, also indicate comparable tooth size and position to those previously described for *Nyanzachoerus kanamensis* (Cooke and Ewer, 1972; Cooke and Hendey, 1992; see Table IV for measurements).

2.4.2. Canines

There are no specimens from the Manonga Valley that preserve the orientation, implantation, or wear facets of the upper canine. The canine material is very fragmentary. In cross section, the available specimens have the appearance of a round-cornered square. From the preserved fragments it does not appear that enamel covered the entire surface of the tooth (Cooke and Ewer, 1972, *contra* Harris and White, 1979). Rather, verrucose enamel is in a wide band concentrated on the ventral aspect of the canine. The dorsal aspect is exposed dentine. The nature of sexual dimorphism in canine flanges cannot be evaluated for the Manonga Valley sample. The recovered specimens WM 1085/92, WM 1808/92, and WM 1809/92 are all very large and robust, and quite probably belonged to males. Another specimen, WM 1816/92, is much smaller and may represent a female or immature individual.

2.4.3. Premolars

The Manonga Valley sample includes no P^1. This portion of the maxilla did not survive in any of the recovered maxillae and there are no isolated specimens. P^2 is a relatively small tooth that is longest in the mesiodistal direction. It has two roots and is low crowned relative to the rest of the dentition. The main cone is joined by a small hypocone. The expanded anterior and posterior cingula coalesce to encircle the crown of the tooth. This morphology is more clear in the unerupted specimen WM 1086/92, than in WM 1052/92 which is a smaller specimen. The large and high-crowned P^3 has one enlarged main cusp. The tooth has a well-developed cingulum around the main cone, except on the labial surface. In some cases, for example WM 237/92, the development of the posterior cingulum is particularly pronounced. This presents a well-developed distolingual conule that is not as high as the main cusp of the tooth. P^4 (WM 1122/92, WM 1785/92) is similar in overall size and height to P^3. It has a single main lingual cusp and two labial cusps, all of equal height. The labial cusps fuse early in wear. The anterior and posterior cingula are well developed, but do not connect to encircle the tooth. P^4s sometimes appear mesiodistally compressed (see Table V for measurements).

2.4.4. Molars

The molars of *Nyanzachoerus kanamensis* are more hypsodont than those of *Nyanzachoerus syrticus* (= *tulotus*) (Cooke and Ewer, 1972; Leonardi, 1952), and those from the Manonga Valley are no exception. The molars increase in size from M^1 to M^3. The cusps, or major pillars of the teeth, are isolated and columnar rather than compact. The cingula are well-developed on the anterior and posterior aspects of M^1 (WM 1148/92) and M^2 (WM 657/90, WM 1163/92) and on the anterior aspect of M^3. The cingula do not encircle the tooth. The enamel is relatively thick. Enamel thickness appears to increase in posterior cheek teeth, so that it is thicker in M^3 than in M^1. This may be a function of wear stage, however, since anterior molars come into occlusion earlier, and are more worn. As the molars wear, the dentine lakes formed within the enamel pillars take on a characteristic star shape. In M^1 and M^2, the four main pillars are arranged as anterior and posterior pairs surrounding a single median pillar. The pillar pairs are often joined by shallow, cuspule-lined basins on the buccal and lingual aspects of the tooth. M^3 (WM 1147/92, WM 1780/92) consists of a trigone that resembles, but is larger than, that of M^2. Instead of a posterior cingulum, M^3 has a relatively elaborate talon with a variable number of major and minor pillars. The talon is well-developed and reaches the occlusal level of the trigone (see Table V for measurements).

2.5. Lower Dentition

2.5.1. Incisors

The preserved lower incisors (WM 1730/92 mandible, WM 1777/92 and WM 1928/92) all exhibit morphology similar to that previously described for *Ny. kanamensis* (Cooke and Ewer, 1972; Harris and White, 1979; Cooke and Hendey, 1992). Emplacement on the single preserved mandibular symphysis is in the form of a wide V (Harris and White, 1979). The lower incisors are broad and thick buccolingually. All possess a well-defined ridge on the lingual surface.

2.5.2. Canines

The lower canine is represented in the Manonga Valley sample by fragmentary specimens only. One lower canine is complete through its cross section (WM 1077/92), which is roughly triangular with an indentation on the posterior

Table V. Measurements (in mm) of Manonga Valley Suid Upper Dentition[a]

	P^2	P^3	P^4	M^1	M^2	M^3
WM 1071/92 L		21.57	20.43	19.32	33.12	
		22.48	26.32	19.18	33.53	
WM 1072/92 + WM 1076/92 R			20.49	19.58	32.38	57.79
			24.32	19.96	30.82	37.68
WM 1052/92	13.32	24.59				55.92
	9.20	24.06				38.35
WM 1231/92		26.70	20.53			
		23.26	25.57			
WM 1771/92					37.64	—
					32.65	42.20
WM 1086/92	14.96					
	9.61					
WM 237/92		25.09				
		25.24				
WM 129/94		23.90				
		23.20				
WM 199/94		21.80				
		22.53				
WM 1122/92			18.26			
			—			
WM 1785/92			19.26			
			23.75			
WM 1148/92				20.97		
				22.27		
WM 200/94				21.66		
				21.61		
WM 657/90					29.12	
					27.79	
WM 1163/92					29.06	
					27.40	
WM 163/94					32.57	
					25.00	
WM 1147/92						54.93
						33.19
WM 1780/92						55.84
						31.69

[a] Teeth are measured at the cervix. Top measurement mesiodistal, bottom measurement buccolingual.

surface. Smooth enamel covers the ventral and dorsal aspects of the canine. No conclusions can be drawn as to placement, wear facets, or curvature of the lower canines. The majority of fragments appear to be from large, robust teeth, but one (WM 21/90) may be from an immature or female individual.

Table VI. Measurements (in mm) of Manonga Valley Suid Lower Dentition[a]

	P_2	P_3	P_4	M_1	M_2	M_3
WM 1410/92 R	15.47 8.31	21.36 20.15	21.56 21.19	20.98 17.16	29.56 22.74	57.98 28.09
WM 1788/92	10.78 6.43					
WM 1079/92			26.93 23.39			
WM 1774/92				22.83 —		
WM 1054/92						— 26.85
WM 1780/92						60.78 28.22

[a] Teeth are measured at the cervix. Top measurement mesiodistal, bottom measurement buccolingual.

2.5.3. Premolars

The single specimen that preserves the anterior mandibular corpus shows no indication that P_1 had ever been present. P_2 is a small, low-crowned tooth that is longest mesiodistally. P_2 is directly adjacent to the P_3. A main cusp is positioned centrally, with a small additional cusp distal to it. There appears to be a pronounced posterior cingulum and a rather slight anterior one. P_3 is a broad, robust tooth. It is relatively high-crowned and has one main cusp. The anterior cingulum is present but slight, while the posterior cingulum is particularly well developed. P_4 is also large, and also has a single main cusp (WM 1079/92). Anterior cingulum development is more marked than in P_3. The posterior cingulum is also larger and higher than in P_3. It borders the posterior accessory cusp, which reaches almost to the unworn height of the tooth (see Table VI for measurements).

2.5.4. Molars

Although lower molars appear buccolingually compressed, they are otherwise like upper molars in their appearance (see above). The narrowness of the lower molars serves to make the pillar pairs seem even more columnar and isolated than in the uppers. Talonid development in M_3 is generally more obviously pronounced than in M^3, with a median pillar on the trigonid/talonid junction. The talonid consists of multiple additional pillars, usually with at least two major pillars (see Table VI for measurements).

3. Discussion

Fossils from the Manonga Valley are of interest to hominid paleontologists for biogeographic, biostratigraphic, and paleoecological reasons. From the perspective of dating African paleontological sites, it has long been known that suid fossils can provide significant biostratigraphic resolution (e.g., Cooke and Maglio, 1972; Harris and White, 1979). Biogeographically, the location of the Manonga Valley sites is intermediate between those of Kenya and Ethiopia in northeastern Africa and the South African sites. The nearest site of comparable age is that of Laetoli, which appears to sample a completely different environment (Harris, 1987). Since both "robust" and "gracile" hominid remains from southern and eastern Africa have been assigned to different species in South and East (see e.g. Wood, 1992), examination of the relationships between their associated endemic faunas may lead to a better understanding of the biogeography of Pliocene Africa and the origin of the Hominidae (Schrenk *et al.*, 1993). From an ecological standpoint, as large-bodied omnivores, suids have the potential to inform us about the habitats and dietary resources available to Pliocene hominids.

3.1 Biostratigraphy and Correlation

The radiometrically documented time span of *Nyanzachoerus kanamensis* in eastern Africa is from 4.5 to 2.85 Ma (Table VII) (Bishop, 1994). Although its radiometrically dated range is confined to the Pliocene, some occurrences from undated sites may predate the radiometrically determined first appearance of the species. In Kenya, *Ny. kanamensis* has been reported from Kanam West (Leakey, 1958), Kanapoi (Cooke and Ewer, 1972), Lothagam (Cooke and Ewer, 1972; Hill *et al.*, 1992), the Chemeron Formation (Hill *et al.*, 1986), the Koobi Fora Formation (Harris, 1983), and the Nachukui Formation (Harris *et al.*, 1988). Plummer (1991) suggests that a reported occurrence of the taxon at Kanjera, Kenya, was most probably due to an error in provenance. The taxon is known in Ethiopia from the Usno and Shungura Formations of the Omo Group (Cooke, 1976) and from Awash Group sediments in the Middle Awash (Kalb *et al.*, 1982; Kalb, 1993) and at Hadar (Cooke, 1978). The Kaiso Formation of Uganda has yielded *Ny. kanamenis* (Harris and White, 1979; Cooke, 1985; Cooke and Coryndon, 1970), as has the Nkondo Formation in Uganda (Pickford *et al.*, 1988, 1991). Boaz (1994) differs in his interpretation of the molluscan biostratigraphy of the Nkondo Formation, allying it to the Upper Kaiso, so either the attributed presence of *Ny. kanamensis* or faunal correlation is likely incorrect.

Table VII. Temporal Ranges for *Nyanzachoerus kanamensis* from Radiometrically Dated Contexts in East Africa

Omo, Ethiopia	4.17–2.85 Ma
Hadar, Ethiopia	3.30–2.85 Ma
Koobi Fora, Kenya	3.89–3.0 Ma
West Turkana, Kenya	3.45–3.43 Ma
Tugen Hills, Kenya	4.50–2.9 Ma
Known temporal range: 4.5–2.85 Ma	

Outside eastern Africa, *Ny. kanamensis* occurs in Sahabi, Libya (Cooke, 1987), Wadi Natrun, Egypt (Tobien, 1936; Cooke, 1985), and Chad (Coppens, 1967; Cooke, 1985). Langebaanweg, South Africa, is currently the southernmost limit of the taxon (Cooke and Hendey, 1993). Faunal correlations between undated sites and radiometrically dated East African localities provide biostratigraphic evidence that the temporal range of *Ny. kanamensis* is consistent through its geographic distribution. Although the species is widespread, the Manonga Valley specimens are the first known from Tanzania.

From a biostratigraphic perspective the Manonga Valley suids are not as useful as they might be, since all are attributable to *Nyanzachoerus kanamensis*, a morphologically variable species with a wide distribution in time and space. Although it is tempting to use dental metrics as an indicator of geological age, it can be demonstrated that third-molar dimensions and relative proportions in *Nyanzachoerus kanamensis* do not vary predictably with the geological age of the specimen (Table VIII, Figs. 4, 5) (Harris and White, 1979; Bishop, 1994). Although there are few teeth that have good radiometric dates (sample sizes 21–32), most raw dental metrics demonstrate a decrease in size through time. None of the regressions are statistically significant, however. No tooth dimension or ratio provided a correlation with geological age that was good enough to use for predictive purposes, i.e., to extrapolate the geological age of the site where the tooth was found. The samples from undated localities (e.g., Lothagam, Langabaanweg, and the Manonga Valley) cannot be used in this analysis, and

Table VIII. Statistics for Regressions between Absolute Measurements (in mm) and Dental Proportions of *Nyanzachoerus kanamensis* Third Molars and Geological Age[a]

Tooth	Measurement	Slope	Standard error of slope	Intercept	n	R^2	$p <$	Standard error of estimate
M^3	Basal length	−0.027	0.022	4.854	27	.02	.218	0.427
M_3	Basal length	+0.020	0.019	2.205	32	.00	.313	0.361
M^3	Breadth	−0.045	0.035	4.842	25	.03	.218	0.424
M_3	Breadth	+0.051	0.052	2.065	32	.00	.337	0.362
M^3	Trigone length	+0.034	0.054	2.496	21	.00	.531	0.482
M_3	Trigonid length	+0.080	0.048	0.743	22	.08	.114	0.381
Ratios:								
M^3	$\frac{\text{Basal length}}{\text{Trigone length}}$	−1.622	0.955	6.065	20	.09	.107	0.439
M_3	$\frac{\text{Basal length}}{\text{Trigonid length}}$	+0.237	1.358	2.971	21	.00	.863	0.416
M^3	$\frac{\text{Basal length}}{\text{Breadth}}$	−0.284	0.922	3.919	24	.00	.761	0.443
M_3	$\frac{\text{Basal length}}{\text{Breadth}}$	+0.160	0.502	2.948	29	.00	.753	0.349

[a] Slopes are with geological age, and therefore negative slopes indicate a relative increase in size with time. See also Figs. 4 and 5.

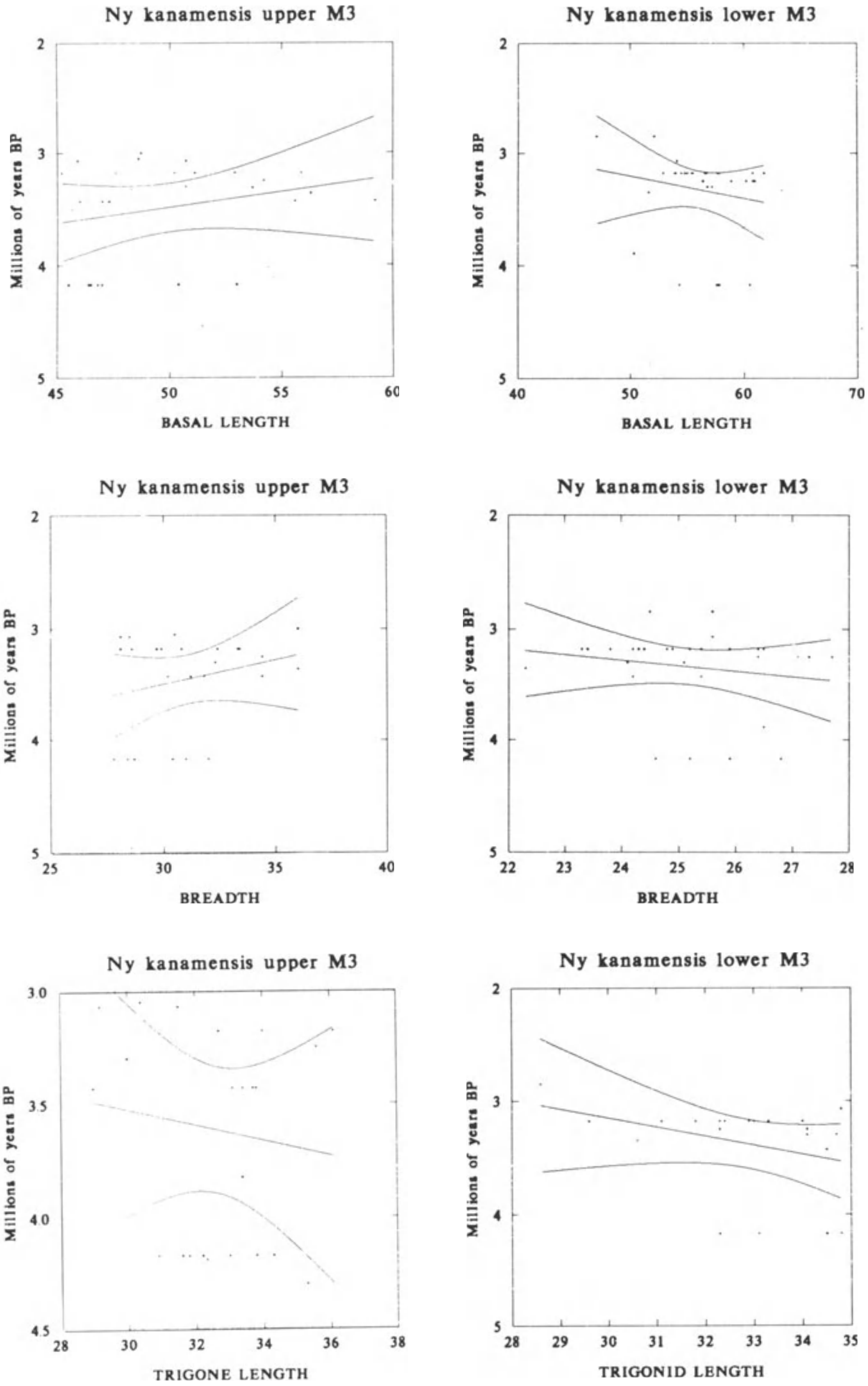

FIGURE 4. Plots with regression data and 95% confidence intervals for raw measurements (in mm) on dated *Nyanzachoerus kanamensis* third molars.

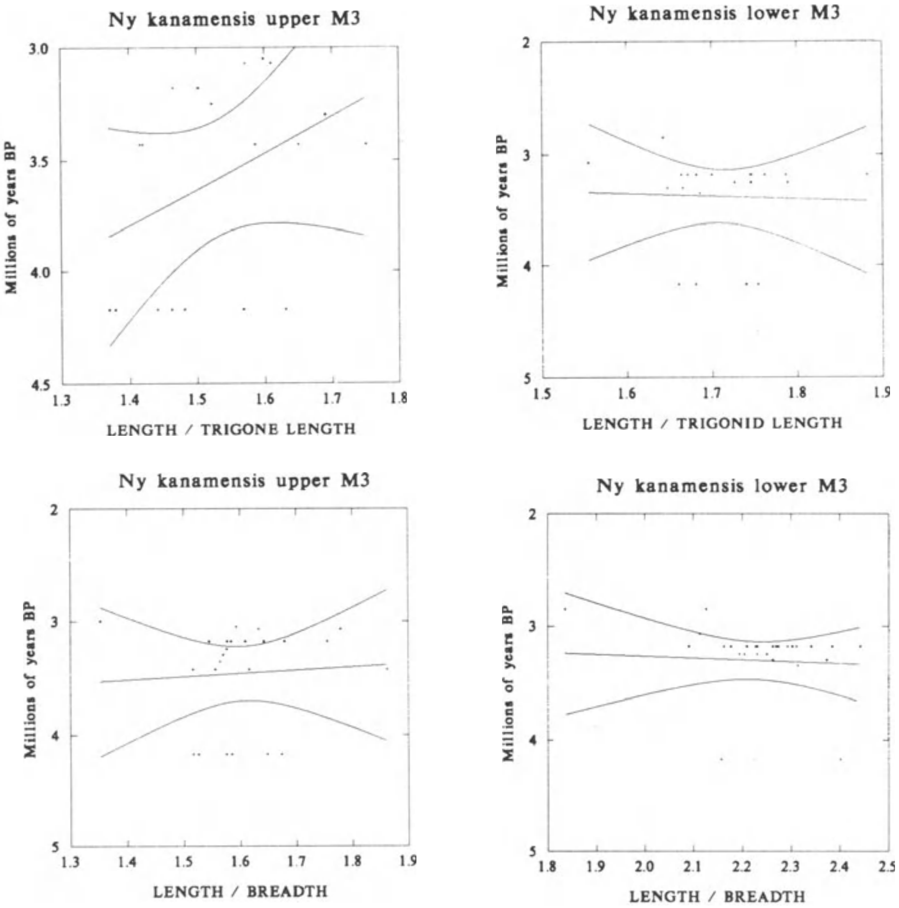

FIGURE 5. Plots with regression data and 95% confidence intervals for third molar proportions on dated *Nyanzachoerus kanamensis* third molars.

this might also bias the results since these localities may be somewhat older than the others in this analysis.

A further paradox related to sample size adds difficulty to attempts to extrapolate the geological age of a specimen from its size. Species are variable; when we have a large sample size for a species deriving from a particular time period, variation in dental dimensions are present in the contemporaneous population. It appears that these variations in populations are largely responsible for the difficulty in correlating dental dimensions with geological age, for within-species size ranges confound many of the observable correlations. The larger a sample from any particular time slice, the more likely the contemporaneous sample is to exhibit the full range of variation in size for the taxon throughout its temporal range. These results suggest that variation in tooth size might be related to overall body-size differences or sampling within populations rather than any temporal trend. In other words, the perceived increases in hypsodonty through time may represent allometric change rather than an adaptive or ecological shift (see also Turner and Wood, 1993). Furthermore, localized or temporary responses to varying environmental stimuli cannot be ruled out as an explanation for phenomena previously viewed as being progressive through time.

These results suggest that it is potentially misleading to rely on the size or "advanced" appearance of specimens encountered at a new or undatable locality to ascertain its geological age. Resultant regressions are not robust enough to use as anything but a gross estimate of sample age. As these poor correlations all occur in a relatively small geographic range for which radiometric dates are available, temporal correlations over large distances would involve even greater potential for error. The more reasonable method to estimate geological age of a site with a range of suid taxa would be to pinpoint the temporal overlap of all species represented there. The temporal ranges of some suid taxa are quite brief. Other, more enduring pig taxa overlap only briefly with others. This method should more accurately suggest geological ages for undatable localities. It is, however, equally subject to biases and inaccuracies due to sampling error and long-distance correlation. The fact that the samples of *Ny. kanamensis* from individual sites are highly variable undoubtedly contributes to this finding.

One suid specimen may aid in a more constrained biostratigraphic placement of the Manonga Valley sites. As mentioned in the description above, the dentition of WM 1771/92 is relatively massive. In fact, the overall size of this specimen is remarkable, not just for *Ny. kanamensis*, but for suids in general. Although its length is not preserved, the M^3 breadth slightly exceeds that of the broadest previously known suid upper third molar, KNM BC 1391, collected by Pickford from the Chemeron Formation of the Tugen Hills, near Lake Baringo, Kenya. The exact stratigraphic provenance of that specimen is unknown, but its site designation (2/201) indicates that it derives from the northern extension sites of the Chemeron Formation (Pickford *et al.*, 1983; Hill *et al.*, 1986, and pers. comm.). The Baringo specimen had been attributed to *Nyanzachoerus jaegeri* Coppens, 1971, the daughter species of *Ny. kanamensis* (Harris and White, 1979), but it is possible in light of the new evidence from the Manonga Valley that the Baringo specimen represents a morphological extreme of *Ny. kanamensis*. In neither the Baringo nor the Manonga Valley specimen is there any evidence of the great increase in hypsodonty or pillar complexity normally associated with more advanced *Ny. jaegeri*. Hypsodonty is somewhat increased in KNM BC 1391, particularly in the talon, but the specimen preserves no premolars so their reduction cannot be assessed. Unfortunately, the preserved portion of WM 1771/92 does not include the M^3 talon, which would be the most relevant area for a determination of its hypsodonty.

There is a chance that specimens such as WM 1771/92 and KNM BC 1391 differ substantially enough from other material to be considered as a separate subspecies. There is not adequate evidence either to prove or to dismiss this hypothesis, and there is the distinct likelihood that, with the discovery of additional material, the apparent division between the two morphotypes will be eradicated. In any case, KNM BC 1391 and WM 1771/92 are closely allied with the most primitive members of *Ny. jaegeri*, a taxon with a well-dated stratigraphic range that is extremely limited, with its first radiometrically dated appearance approximately 4.5 Ma (Bishop, 1994). Some occurrences of *Ny. kanamensis* and of *Ny. jaegeri* have been given older dates supported by biostratigraphic correlations based on other taxa (Hill *et al.*, 1992; White, 1995).

The time period that presumably encompasses the origin of *Ny. kanamensis* and the transition between *Ny. kanamensis* and *Ny. jaegeri*, 6 Ma to 4.5 Ma, is not well represented in the fossil record (Hill and Ward, 1988). An early Pliocene date for this sample is supported by the fact that no other suid species have been recovered from the Manonga Valley. Prior to approximately 5.6 Ma, the dominant suid is *Nyanzachoerus syrticus* (= *tulotus*) (Hill *et al.*, 1992). At sites younger than 3.89 Ma, *Notochoerus euilus* and, somewhat later, *Kolpochoerus afarensis* are commonly recovered from Pliocene faunas. However, biogeographic and ecological considerations cannot be eliminated as a cause of the absence of these later taxa from the Manonga Valley fauna. Nevertheless, the present evidence supports the conclusion that the Manonga Valley sample is from the latest Miocene or early Pliocene, 5.5–4.0 Ma.

3.2. Biogeography and Geographic Subspecies

Morphological and dental metric variation in *Ny. kanamensis* may be caused by factors other than geological age. For example, the recognition of the subspecies *Ny. kanamensis australis* Cooke and Hendey, 1992 from specimens from Langebaanweg, South Africa, suggests that the variation in *Ny. kanamensis* may have a predictable component related to its geographic range. The Langebaanweg sample of *Ny. kanamensis* consistently differs from described East African material in ways that are apparently unique (Table IX). No temporal significance or limitations are indicated for this subspecies. The most southerly of the Pliocene East African hominid sites, Laetoli, has no representatives of *Ny. kanamensis* (Harris, 1987). This absence is attributed to the unusual environmental and depositional conditions at Laetoli (Harris, 1985, 1987). Analysis of the affinities of the Manonga Valley suids with eastern or southern forms may provide meaningful information about the biogeography of Pliocene faunas.

Table IX. Defining Characteristics of the Subspecies *Nyanzachoerus kanamensis australis*[a]

Primitive
- Consistent retention of P^1 (in a slightly longer diastema).

Derived
- Larger and more robust cheek teeth.
- Low hump on the nasals at the level of the canine flange in males.
- Slightly longer diastema.

---

[a] From Cooke and Hendey (1992).

Table X. Summary Statistics for Manonga Valley Suids[a]

	P_2	P_3	P_4	M_1	M_2	M_3	P^2	P^3	P^4	M^1	M^2	M^3
n	2	1	2	1	1	2	2	4	4	3	5	4
Minimum	10.78	21.36	21.56	20.98	29.56	57.98	13.32	21.57	19.26	19.32	29.06	54.9
	6.43	20.15	21.19	17.16	22.74	28.09	9.20	22.48	23.75	19.18	27.29	31.7
Maximum	15.47	21.36	26.93	20.98	29.56	60.78	14.96	26.70	20.53	20.97	37.640	57.8
	8.31	20.15	23.39	17.16	22.74	28.22	9.61	25.25	26.32	22.27	32.65	38.4
Mean	13.12	21.36	24.24	20.98	29.56	59.38	14.14	24.49	20.18	19.96	32.26	56.10
	7.37	20.15	22.29	17.16	22.74	28.15	9.40	23.76	24.99	20.47	30.70	35.25
S.D.	3.14	—	3.80	—	—	1.98	1.16	2.14	0.61	0.89	3.53	1.22
	1.33	—	1.56	—	—	0.09	0.29	1.18	1.17	1.61	2.08	3.30

[a] Measurements (in mm) of complete teeth. Top measurement mesiodistal, bottom measurement buccolingual.

The suid remains from the Manonga Valley are fragmentary. No crania are yet known, so comparison to the derived cranial features of the new subspecies *Nyanzachoerus kanamensis australis* is not possible. Furthermore, none of the recovered upper dentition is preserved anterior to P^2. Harris and White (1979) redefined *Ny. kanamensis* as having a variably present P^1. This is a primitive character in the Suidae, the retention of which is characteristic of the Langebaanweg subspecies. It cannot be resolved whether the Manonga Valley sample possessed P^1s. Also, the extent of sexual dimorphism in the Manonga Valley sample cannot be assessed fully. *Ny. kanamensis* is a highly dimorphic species (Cooke and Ewer, 1972; Harris and White, 1979), but with the exception of canine robusticity, dimorphism is cranial rather than dental. The Manonga Valley sample does preserve upper and lower canines, some of which are massive and others more gracile. Sex determinations have been given in the descriptions for certain specimens where appropriate.

The summary statistics for the dentition of the Manonga Valley suids is presented in Table X. Available data for *Nyanzachoerus kanamensis* teeth from other sites are summarized in Table XI, to give an indication of the known metric variation in the teeth of this taxon. This information is presented in graphic form in Figs. 6 and 7. For each tooth, the Manonga Valley specimens conform well with the size distributions for the previously recovered *Ny. kanamensis* hypodigm. This is also the case for the recovered maxillae and mandible (see Tables II and III). Furthermore, inspection of Figs. 6 and 7 suggest that there is a geographic cline represented in the dental dimension, with larger specimens concentrated in the south, and smaller specimens in the north, of the geographic range of the species.

It should be noted, however, that the distribution of the dental metrics for the Langebaanweg sample also overlaps significantly with the ranges for *Ny. kanamensis* from other localities. Many of the sample sizes are small, however. The largest samples, the upper and lower third molars, were used in a statistical test to determine whether the differences in means were significant. In order to use a measurement that would remain unaffected by relative body size and instead

Table XI. Summary Statistics for *Nyanzachoerus kanamensis* from Localities Other Than the Manonga Valley[a]

	P_2[b]	P_3	P_4	M_1	M_2	M_3	P^2[b]	P^3	P^4	M^1	M2	M^3
N	11	32	36	12	33	60	14	22	26	12	22	47
Minimum length	10	19.2	18.0	18.1	21.7	47.0	12.7	19.4	17.0	14.9	23.0	44.0
Minimum breadth	7.4	14.3	15.6	14.2	16.4	21.1	7.7	18.4	21.0	17.7	22.7	26.3
Maximum length	15.9	30.1	27.6	24.9	34.5	65.5	17.4	28.1	21.6	25.4	34.3	61.4
Maximum breath	9.1	23.8	25.2	21.3	28.8	33.5	9.7	24.2	28.8	23.2	33.6	38.7
Mean	13.19	24.57	21.71	21.05	27.97	56.53	14.12	22.24	19.64	20.48	28.13	51.12
	8.17	19.70	20.16	13.49	21.45	25.84	8.39	21.14	23.67	20.53	27.66	32.00
S.D.	1.45	2.27	2.10	2.34	3.02	4.45	1.41	1.97	1.22	2.85	3.07	4.35
	0.51	2.55	2.53	2.14	2.37	2.59	0.58	1.83	2.02	1.76	2.85	2.85

[a] Dental measurements (in mm) for postcanine teeth follow the methods of Harris and White (1979). Although measurements from other sources have been used, they are for illustration only and are not necessarily strictly comparable. Cooke and Ewer (1972, pp. 166–167), for example, employ a slightly different measurement technique. Top measurement mesiodistal, bottom measurement buccolingual.

[b] Possession of a P2 is not a variable trait in *Ny. kanamensis*, but data were available from Langebaanweg only.

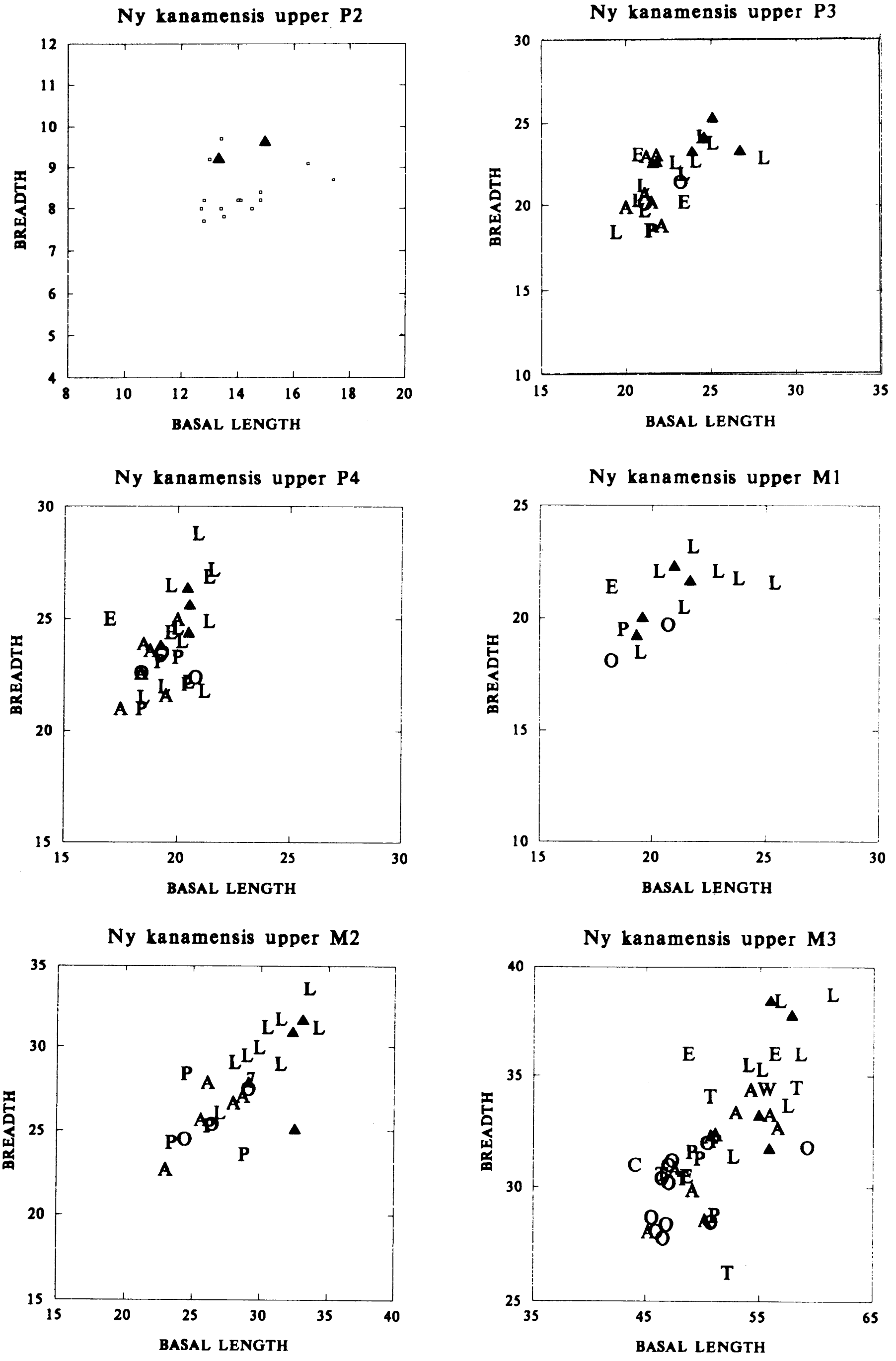

FIGURE 6. Plots summarizing metric data for *Nyanzachoerus kanamensis* upper dentition (in mm), by tooth. Key to localities: ▲, Manonga Valley; 7, Lothagam; A, Afar; C, Tchad; E, East Turkana; K, Kanam West; L, Langebaanweg; O, Omo; P, Kanapoi; T, Tugen Hills, Chemeron; U, Kaiso; W, West Turkana. Data for P^2 from Langebaanweg only.

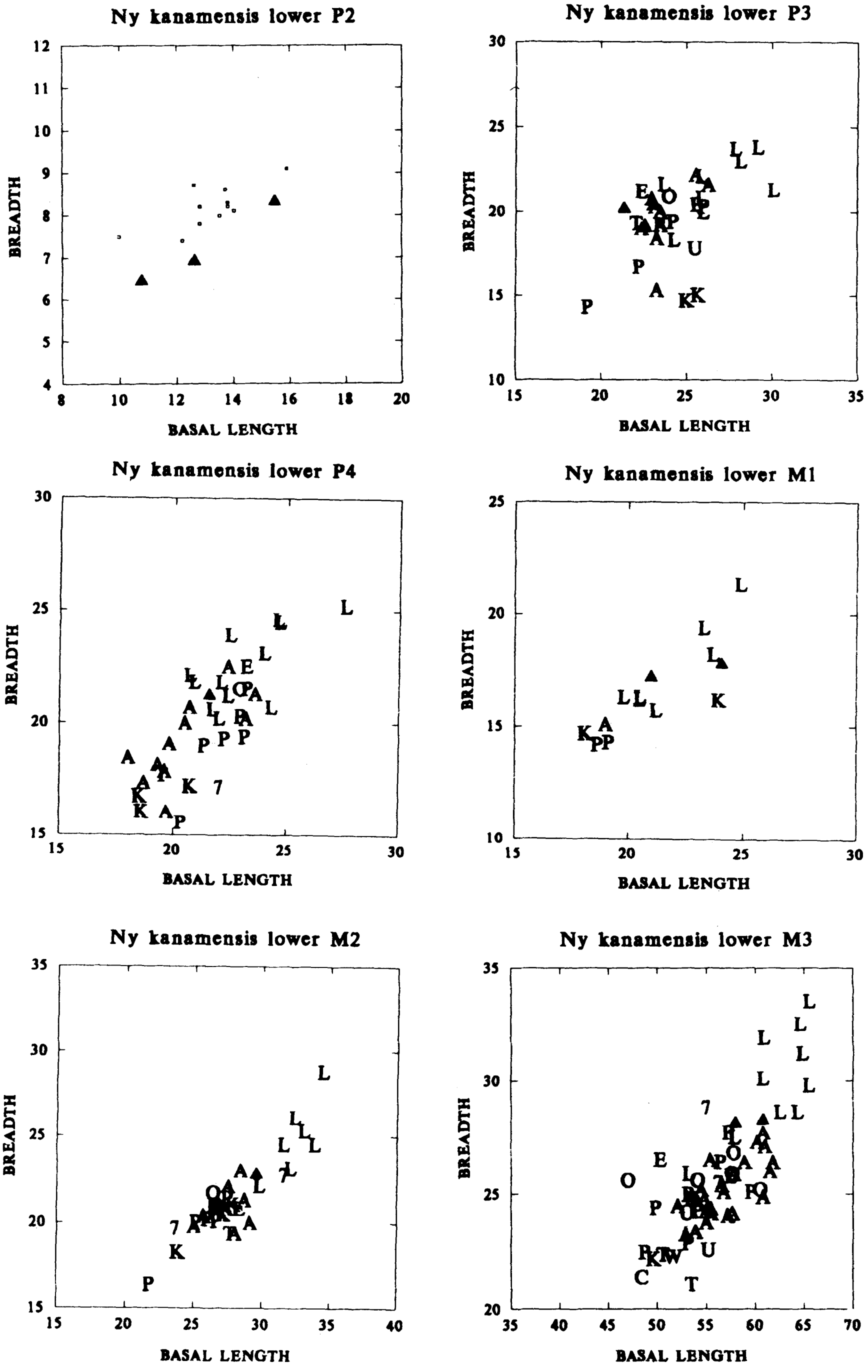

FIGURE 7. Plot summarizing metric data for *Nyanzachoerus kanamensis* lower dentition (in mm). Key to figures as in caption to Fig. 6. Data for P_2 from Langebaanweg only.

be taxonomically valent, the ratios of M3 length versus breadth were computed. Ratios from nine Pliocene localities were used. These were subjected to a Tukey HSD test and a Bartlett chi-square test for the homogeneity of group variances between all localities, including Langebaanweg and the Manonga Valley suids (Tables XII and XIII). The statistical software package SYSTAT was used for this analysis (Wilkinson, 1990).

For M^3, there was no significant difference between the means of any two localities of the 21 pairwise comparisons. There was also no significant difference between or within groups (chi square $p = .281$). Since there is no statistical difference between means, it cannot be shown that they were drawn from different samples. Examination of M_3 length–breadth ratios provided a similar result. In the 36 pairwise comparisons of Pliocene localities, the majority of the samples showed no significant differences (chi square $p = .358$). However, two pairwise comparisons of group means, of the Langebaanweg sample with those from the Afar and the Tugen Hills, did yield a statistically significant difference ($p = .007$ and $p = .035$, respectively). These regions are at extremes of the geographic range of *Ny. kanamensis* represented in the test. However, since M_3 samples from the Omo and Koobi Fora demonstrate no statistical separations from the Langebaanweg sample, geographic distance cannot be considered a complete explanation for metric variability in the *Ny. kanamensis* hypodigm.

Results of this analysis support the hypothesis that variation in *Ny. kanamensis* is geographical in nature. The strongest evidence for this hypothesis is that

Table XII. Results of Tukey Pairwise Comparisons for M^3 Length–Breadth Ratio[a]

Matrix of pairwise absolute mean differences

	n	Afar	Koobi Fora	Kanapoi	Langebaanweg	Omo	Tugen Hills	Manonga Valley
Afar	10	0.000						
Koobi Fora	4	0.123	0.000					
Kanapoi	4	0.001	0.122	0.000				
Langebaanweg	7	0.032	0.091	0.031	0.000			
Omo	13	0.002	0.121	0.001	0.030	0.000		
Tugen Hills	7	0.025	0.148	0.026	0.057	0.027	0.000	
Manonga Valley	4	0.026	0.097	0.025	0.006	0.024	0.051	0.000

Matrix of pairwise comparison probabilities

	Afar	Koobi Fora	Kanapoi	Langebaanweg	Omo	Tugen Hills	Manonga Valley
Afar	1.000						
Koobi Fora	0.669	1.000					
Kanapoi	1.000	0.807	1.000				
Langebaanweg	0.998	0.909	1.000	1.000			
Omo	1.000	0.676	1.000	0.998	1.000		
Tugen Hills	1.000	0.584	1.000	0.979	0.999	1.000	
Manonga Valley	1.000	0.923	1.000	1.000	1.000	0.994	1.000

[a] The matrix of pairwise comparison probabilities shows no significant differences between any two regional samples.

Table XIII. Results of Tukey Pairwise Comparisons for M_3 Length–Breadth Ratio

Matrix of pairwise absolute mean differences

	n	Afar	Kaiso	Kanapoi	Kanam West	Langebaanweg	Lothagam	Omo	Tugen Hills	Manonga Valley
Afar	26	0.000								
Kaiso	2	0.056	0.000							
Kanapoi	10	0.080	0.135	0.000						
Kanam West	2	0.065	0.121	0.015	0.000					
Langebaanweg	12	0.173	0.228	0.093	0.108	0.000				
Lothagam	2	0.204	0.259	0.124	0.139	0.031	0.000			
Omo	6	0.114	0.170	0.035	0.050	0.058	0.089	0.000		
Tugen Hills	2	0.137	0.081	0.216	0.201	0.309	0.340	0.251	0.000	
Manonga Valley	2	0.151	0.206	0.071	0.086	0.022	0.053	0.036	0.287	0.000

Matrix of pairwise comparison probabilities

	Afar	Kaiso	Kanapoi	Kanam West	Langebaanweg	Lothagam	Omo	Tugen Hills	Manonga Valley
Afar	1.000								
Kaiso	0.999	1.000							
Kanapoi	0.780	0.875	1.000						
Kanam West	0.998	0.983	1.000	1.000					
Langebaanweg	0.007[a]	0.258	0.755	0.957	1.000				
Lothagam	0.347	0.432	0.920	0.959	1.000	1.000			
Omo	0.582	0.737	1.000	1.000	0.992	0.992	1.000		
Tugen Hills	0.821	0.999	0.360	0.746	0.035[a]	0.124	0.246	1.000	
Manonga Valley	0.732	0.722	0.998	0.998	1.000	1.000	1.000	0.299	1.000

[a] Statistically significant difference between two regional samples.

third-molar dental metrics in the species, including the subspecies *Ny. kanamensis australis*, are consistent for the entire species and do not differ greatly from those in the subspecies *Ny. kanamensis australis*. The biogeographic implication is that the eastern and southern examples of *Ny. kanamensis* are members of a single species that cannot be separated statistically, at least on the basis of relative dental proportions. The cranial characteristics specific to *Ny. kanamensis australis* must be preserved in order to make definite attribution to that subspecies.

4. Conclusions

Suids from the Manonga Valley can be attributed to the species *Nyanzachoerus kanamensis*. The specimens cannot be assigned to the subspecies *Ny. kanamensis australis* (Cooke and Hendey, 1992), because (1) cranial material preserving regions in which subspecific characters occur has not been recovered and (2) dental metrics do not differentiate the subspecies from the other members of the species. *Nyanzachoerus kanamensis* has a documented temporal distribution that spans most of the Pliocene epoch. Although *Ny. kanamensis* does not exhibit any particular pattern of variability through time, three factors suggest that the suid fossils from the Manonga Valley date from the earlier part of the Pliocene. First, *Ny. syrticus*, the dominant late Miocene suid in East Africa, is not represented in the Manonga Valley fauna. Second, a specimen sharing some characteristics of the early Pliocene species *Ny. jaegeri*, thought to be a daughter species of *Ny. kanamensis*, suggests an age near to the divergence of those two taxa. Third, the absence of more derived suid species that are common later in the Pliocene suggest a latest Miocene or early Pliocene age for the fauna, of between 5.5 Ma and 4 Ma.

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Chapter 8

Later Neogene Hipparions from the Manonga Valley, Tanzania

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1. Introduction

The Manonga Valley basin in northern Tanzania comprises an extensive series of lacustrine and fluvial sediments deposited during the late Miocene and Pliocene (Harrison, 1991, 1993; Harrison *et al.*, 1993; Harrison and Verniers, 1993; Verniers, this volume, Chapter 2; Harrison and Baker, this volume, Chapter 13). Fossil mammals were first recorded in the Manonga Valley during the 1920s and 1930s (Stockley, 1929; Grace and Stockley, 1930; Williams and Eades, 1938) but substantial collections were not made until the Wembere–Manonga Paleontological Expedition (WMPE) first visited the area in 1990 (Harrison and Mbago, this volume, Chapter 1).

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Table I. Hipparion Remains from the Manonga Valley

Member	Locality	Number teeth	Number bones	NISP[a]	MNI[b]	Sedimentary context
Kiloleli	Kiloleli 2	32	2	34	3	Fluvial
	Kiloleli 3	2	1	3	1	Fluvial
	Kiloleli 4		1	1	1	Fluvial
	Beredi South 1	1	2	3	2	Fluvial
	Beredi South 2	2	4	6	2	Fluvial
	Beredi South 3	6	5	11	1	Fluvial
	Ngofila 2	1		1	1	Fluvial
	Ngofila 3	1		1	1	Fluvial
	Ngofila 4	5		5	1	Fluvial
Tinde	Tinde West	2		2	1	Lacustrine
	Ngofila 5	1		1	1	Lacustrine
Ibole	Inolelo 1	3		3	1	Lacustrine
	Shoshamagi 2	5		5	2	Lacustrine
	Ngofila 2L	1		1	1	Lacustrine
Total		62	15	77	19	

[a] NISP, number of identified specimens (excludes two specimens lacking locality data).
[b] MNI, minimum number of individuals.

The fossiliferous sediments, comprising the Wembere–Manonga Formation have been subdivided into three lithostratigraphic units: the Ibole Member, the Tinde Member and the Kiloleli Member (Verniers, this volume, Chapter 2). The Ibole Member (which now includes the "Mwambiti Member," previously recognized by Harrison and Verniers [1993] as a distinct member) consists of a series of fine laterized clays and probably formed when the lake was relatively restricted in its extent, and subject to periodic regression. The overlying Tinde Member consists of a thick series of swelling clays intercalated with hard calcareous bands. This represents a period of deposition when the lake was deeper, more extensive, and stable in its level. The Tinde Member has yielded the major portion of the fossil mammals recovered from the Manonga Valley. The uppermost member of the Wembere–Manonga Formation is the Kiloleli Member, which consists mainly of fluvial sediments that were deposited subsequent to the drainage of the lake basin. According to Harrison and Baker (this volume, Chapter 13), the Ibole and Tinde Members appear to best correlate with a latest Miocene–earliest Pliocene age (ca. 5.5–4.5 Ma), while the Kiloleli Member is believed to be somewhat younger, possibly middle Pliocene age (ca. 4–3 Ma). The younger age estimates for the Kiloleli Member follow, in part, early work on hipparion correlations by the authors.

Hipparionine remains have been identified from 14 localities within the Manonga Valley, from sediments that belong to each of the major stratigraphic units of the Wembere–Manonga Formation (see Table I). Equids appear to represent a relatively rare component of the fauna recovered from the Manonga Valley during the late Miocene-early Pliocene and are not well represented skeletally. A major increase in hipparion relative abundance is evident during the temporal span of the Kiloleli Member. This presumably corresponds to a time during which inferred ecological changes, associated with drainage of the lake basin, may have produced habitats more suitable for horses and other mammals adapted for open country habitats (Harrison, this volume, Chapter 4). Additionally, fossil equids, referable to *Equus burchelli*, are known from late Quaternary (Holocene) sediments at several localities in the Manonga Valley. These are discussed in Chapter 13 by Harrison and Baker (this volume).

2. Abbreviations and Definitions

Institutions. AL indicates Afar Locality, Ethiopia, and in this chapter includes only samples from the Hadar Formation (ca. 3.4–2.9 Ma); Ho indicates samples from Höwenegg, Germany (ca. 10.3 Ma; Swisher, 1996); KNM-LT indicates Kenya National Museums—Lothagam (Kenya; ca. 7–4.5 Ma); KNM-NA is Nakali (Kenya; ca. ?8.5 Ma); KNM-LU is Lukeino (Kenya; ca. 6 Ma); KNM-MP is Mpesida (Kenya; ca. 6.5 Ma); KL is Adudora (Ethiopia; ca. 6.0 Ma); WEEVP is Wee-ee (Ethiopia; ca. 4.0 Ma); MAKVP is Maka (Ethiopia; ca. 3.5 Ma); MAT is Matabaietu (Ethiopia; ca. 2.7 Ma). Age determinations of East African localities are currently in revision and these preliminary estimates have been kindly provided by Meave Leakey (Lothagam, Kenya), Andrew Hill (Baringo Basin, Kenya) and Timothy White (Middle Awash, Ethiopia).

Definitions. The taxon *Hipparion* has been used in a variety of ways by different authors.

Hipparionine or hipparion: horses with an isolated protocone on maxillary premolar and molar teeth and, as far as known, tridactyl feet, including species of the following genera: *Hipparion, Neohipparion, Nannippus, Cormohipparion, Hippotherium, "Proboscidipparion," "Plesiohipparion," "Sivalhippus," Pseudhipparion, "Eurygnathohippus"* (=senior synonym of *"Stylohipparion"*) and *Cremohipparion*. Characterizations of these taxa can be found in MacFadden (1984), Bernor and Hussain (1985), Webb and Hulbert (1986), Hulbert (1987), Qiu *et al.* (1987), Bernor *et al.* (1988, 1989), Woodburne (1989), and Hulbert and MacFadden (1991), Bernor *et al.* (1997).

Hipparion s.s.: The name is restricted to a specific lineage of horses with the facial fossa positioned high on the face (MacFadden, 1980, 1984; Woodburne and Bernor, 1980; Woodburne *et al.*, 1981; MacFadden and Woodburne, 1982; Bernor and Hussain, 1985; Bernor, 1985; Bernor *et al.*, 1987 and Fig. 4; Bernor *et al.*, 1989; Woodburne, 1989). The posterior pocket becomes reduced and eventually lost, and confluent with the adjacent facial surface (includes Group 3 of Woodburne and Bernor, 1980). We differ from some of the previous authors in that we do not recognize North American species of *Hipparion* s.s. Bernor (1985, and Bernor *et al.*, 1989) does not recognize any North American taxon as belonging to *Hipparion* s.s.; any morphological similarity is argued by Bernor to be homoplasious.

"Hipparion": several distinct and separate lineages of Old World hipparionine horses once considered to be referable to the genus *Hipparion* (Woodburne

and Bernor, 1980; Bernor *et al.*, 1980; MacFadden and Woodburne, 1982; Bernor and Hussain, 1985; Bernor, 1985; Bernor *et al.*, 1988; Bernor *et al.*, 1989).

Measurements. mm, millimeters (all measurements as defined by Eisenmann *et al.* (1988), and us here for teeth, and rounded to 0.1 mm).

Skeletal Designations. MP III, metapodial III; MC III, metacarpal III; MT III, metatarsal III; POB, preorbital bar; POF, preorbital fossa; DAW, distal articular width; var, measured variable.

M1–M39. indicate measurement numbers as published by Eisenmann *et al.* (1988) and by Bernor *et al.* (1997).

3. Materials and Methods

The hipparion skeletal assemblage reported upon here was collected by the Wembere–Manonga research program during the 1990, 1992, and 1994 field seasons. Preparation of the more delicate material was undertaken by Dr. William Sanders, University of Michigan, Department of Paleontology. Most of the remaining postcranial and dental material was prepared in the Laboratory of Paleobiology, Howard University, using dental tools and an airscribe.

Our analysis of the material includes the evaluation of both discrete character states and continuous variables in identifying hipparionine species and assessing their evolutionary relationships. Definition and use of discrete characters that we have adopted for the skull and mandible has developed, and been progressively refined, by Woodburne and Bernor (1980), Bernor and Hussain (1985), Bernor (1985), Bernor *et al.* (1988, 1989, 1993a, b) and Bernor and Lipscomb (1991, 1995). Investigations of postcranial anatomy and functional morphology follow Tobien (1959), Sondaar (1968) and Hussain (1971) and Bernor *et al.* (1997). Measurements follow those prescribed by the American Museum of Natural History International Hipparion Conference, 1981, and are defined in Eisenmann *et al.* (1988) and Bernor *et al.* (1997).

Data were entered, and sorted, using dBase IV and statistically compared to the Höwenegg sample of "*Hippotherium*" *primigenium* stage III (*sensu* Bernor *et al.*, 1993a, b, 1996, 1997; Bernor and Franzen, 1997) and other selected late Miocene–Pliocene hipparion locality samples currently under study by Bernor. The Höwenegg assemblage serves as a valuable comparative sample, because it is a relatively large population (14 partial to complete skeletons, including one embryo) accumulated over a very short duration, and as such represents as good a paleontological "population" as can be expected (Tobien, 1986; Swisher, 1996; Woodburne *et al.*, 1996a, b; Bernor *et al.*, 1997). For most of the bivariate plots we have been able to calculate 95% confidence ellipses of the Höwenegg sample of *Hippotherium primigenium* stage III (Bernor *et al.*, 1993a, b, 1997). We use this population as a standard for depicting the expected range of variability for any pair of variables analyzed. This allows a visual presentation of expected variation in a single population of hipparionine horses (see Bernor *et al.*, 1989, for further examples and results applying this methodology to other Old World hipparionine horses). In Tables II, III, and IV we categorize our specimens by size when identifiable as being larger (Eu. [for *Eurygnathohippus* lg. [for large]) or smaller (Eu. sm. [for small]).

Dbase IV and Systat 5.03 are licensed to Bernor through the Smithsonian Institutions, Department of Paleobiology, Washington D.C. 20560.

4. Description of the Material

The Manonga Valley hipparion material is described by geological interval (see Table I). All material was identified to element and side where possible, (Table II), and compared to the East African late Miocene–middle Pleistocene hipparion sequence. Since we are engaged in the early phases of this study of African hipparion evolution, observations rendered here cannot yet yield the systematic depth that is currently enjoyed for the group's Eurasian record. However, sufficient comparative material has been studied from the late Miocene and early Pliocene to make reasonably accurate taxonomic comparisons. We proceed by geological unit (oldest to youngest) below, and refer the reader to Table II for revelant measurements and to Tables III and IV for maxillary and mandibular character states.

4.1. Ibole Member

The Ibole Member comprises a thick marker bed of laterite and lies directly below the Tinde Member. Fossils have been collected from Shoshamagai 2 and Inolelo 1-3 localities and these are considered to represent a single fauna dating to the late Miocene or early Pliocene (Harrison, 1992, 1993).

There are nine hipparionine specimens derived from the Ibole Member, including three from Inolelo 1 and five from Shoshamagai 2. The Inolelo 1 specimens are: WM 159/94, a right M^2; WM 999/92, a maxillary cheek tooth fragment; WM 997/92, a left M_2. The first and last specimens are complete enough to suggest that they are referable to a smaller-size hipparionine species. The Shoshamagai 2 specimens are: WM 283/94, a right P^2 (large form); WM 1073/92, a left M^2 (small form); WM 1738/92, a left anterior portion of a maxillary cheek tooth (not a P^2); WM 284/94, a right M_1 (small form); WM 1161/92, a left M_2 (large form). There is one Ngofila 2 specimen from the Ibole Member (hereafter referred to as Ngofila 2L, "L" meaning lower stratigraphic horizon): WM 727/94, a left M^1 (small form).

WM 159/94 is a specimen of a smaller hipparion, in early third wear stage with the following morphological features: parastyle and mesostyle long and thin; crown height 49.2 mm and would most likely have achieved a crown height of ca. ≤ 60 mm; curvature in lateral view moderate to slight (distinctly not straight); plication frequency complex on posterior surface of prefossette, more moderate on other fossette surfaces; posterior wall of postfossette distinct; pli caballin single; hypoglyph deeply incised; protocone compressed-ovate with irregular contour to both its labial and lingual walls; protoconal spur is absent; protocone lingually placed with respect to hypocone. The size of this specimen

Table II. Measurements on the Teeth of Manonga Valley Hipparions

Spec ID	Specshort	Site	Tooth	Side	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
WM1161/92	Eu. lg.	1	tmM2	2	24.5	21.6	13.7	5.8	8.8	11.5	13.0	10.3	10.8	43.6	43.5	6.0	0.0	0.0
WM283/94	Eu. lg.	1	txP2	1	32.8	32.0	22.5	22.6	21.4	5.0	4.0	7.0	1.0	8.1	3.8	0.0	0.0	0.0
WM1073/92	Eu. sm.	1	txM2	2	22.2	20.0	0.0	0.0	30.0	3.0	6.0	4.0	5.0	0.0	0.0	0.0	0.0	0.0
WM159/94	Eu. sm.	1	txM2	1	21.2	20.7	22.1	21.2	49.2	2.0	8.0	4.0	1.0	9.4	2.2	0.0	0.0	0.0
WM284/94	Eu. sm.	1	tmP4	1	23.4	0.0	11.2	7.8	12.4	10.0	0.0	6.7	8.9	0.0	0.0	0.0	0.0	0.0
WM727/94	Eu. sm.	1	txM1	2	26.1	21.1	0.0	0.0	49.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM997/92	Eu. sm.	1	tmM2	2	0.0	0.0	12.2	5.8	8.0	8.1	9.7	9.5	9.8	27.3	26.9	26.4	0.0	0.0
WM1738/92	indet.	1	tx?	2	0.0	0.0	0.0	0.0	41.1	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM999/92	indet.	1	tx?	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM830/94	Eu. lg.	2	tmM1	1	26.6	23.7	17.0	8.0	8.5	14.5	15.6	14.3	13.3	37.2	39.0	40.8	1.8	0.0
WM703/92	Eu. sm.	2	txM3	2	22.0	20.6	16.4	14.0	45.0	0.0	0.0	0.0	0.0	11.0	5.0	0.0	0.0	0.0
WM277/92	indet.	2	tx	2	0.0	0.0	0.0	0.0	0.0	0.0	6.0	0.0	0.0	7.1	4.0	0.0	0.0	0.0
WM1470/92	Eu. lg.	3	tmI2	1	21.1	15.4	0.0	0.0	0.0	11.4	12.6	0.0	0.0	31.2	0.0	0.0	0.0	0.0
WM1473/92	Eu. lg.	3	txM	2	0.0	0.0	0.0	0.0	0.0	5.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM1512/92	Eu. lg.	3	txM1	2	28.9	21.5	23.9	21.6	65.2	0.0	0.0	0.0	0.0	10.0	0.0	0.0	0.0	0.0
WM1528/92	Eu. lg.	3	txP4	1	27.0	0.0	27.1	0.0	0.0	0.0	0.0	0.0	0.0	7.0	4.5	0.0	0.0	0.0
WM1528/92	Eu. lg.	3	txP3	1	26.3	0.0	27.9	0.0	43.0	0.0	0.0	0.0	0.0	8.9	4.7	0.0	0.0	0.0
WM1528/92	Eu. lg.	3	txP2	1	35.0	0.0	26.0	0.0	42.0	4.0	6.0	3.0	1.0	8.2	3.9	0.0	0.0	0.0
WM1528/92	Eu. lg.	3	txM3	1	25.8	0.0	21.6	0.0	49.1	0.0	0.0	0.0	0.0	9.4	2.6	0.0	0.0	0.0
WM1528/92	Eu. lg.	3	txM2	1	24.1	0.0	24.6	0.0	53.0	0.0	0.0	0.0	0.0	10.2	3.9	0.0	0.0	0.0
WM1528/92	Eu. lg.	3	txM1	1	25.0	0.0	26.1	0.0	0.0	0.0	0.0	0.0	0.0	9.3	4.2	0.0	0.0	0.0
WM1528/92	Eu. lg.	3	txI3	1	18.4	16.5	8.1	0.0	26.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM1528/92	Eu. lg.	3	txI2	1	18.0	15.5	10.4	0.0	39.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM1528/92	Eu. lg.	3	skull	1	153.5	0.0	0.0	0.0	0.0	0.0	89.5	76.7	163.4	0.0	0.0	0.0	71.2	42.9
WM1635/92	Eu. lg.	3	mciii	2	240.9	235.6	27.8	25.0	41.7	29.6	36.7	11.0	6.3	38.2	37.4	33.8	28.3	28.9

WM1652/92	Eu. lg.	3	tmP34	2	0.0	0.0	0.0	9.3	0.0	0.0	0.0	12.6	0.0	29.8	0.0	0.0	0.0	0.0
WM1656/92	Eu. lg.	3	txP3	2	28.0	24.6	27.9	25.5	50.7	1.0	6.0	5.0	1.0	7.9	4.5	0.0	0.0	0.0
WM1657/92	Eu. lg.	3	txM1	2	24.0	21.4	24.2	23.9	36.7	3.0	6.0	7.0	3.0	8.4	2.9	0.0	0.0	0.0
WM1659/92a	Eu. lg.	3	txP2	2	35.5	32.5	25.3	22.5	37.7	0.0	0.0	0.0	0.0	8.2	4.5	0.0	0.0	0.0
WM1661/92	Eu. lg.	3	tmM2	1	26.0	22.5	12.4	7.5	11.6	11.1	12.1	8.0	8.7	49.7	40.5	35.8	0.0	0.0
WM1668/92	Eu. lg.	3	ast	1	0.0	0.0	28.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM1669/92	Eu. lg.	3	mciii	2	240.4	232.6	29.6	25.4	46.4	32.2	37.9	14.3	9.9	40.2	39.5	34.5	29.4	29.7
WM368/94	Eu. lg.	3	radii	2	311.1	296.3	39.9	28.9	65.3	36.1	68.9	55.2	34.3	63.7	22.9	11.6	0.0	0.0
WM368/94	Eu. lg.	3	humer	2	0.0	0.0	30.3	38.7	0.0	0.0	69.9	70.5	47.1	34.5	42.1	0.0	0.0	0.0
WM407/94	Eu. lg.	3	tmP4	1	28.3	26.6	16.4	9.2	14.6	16.5	15.5	0.0	14.3	52.5	0.0	52.6	0.0	0.0
WM411/94	Eu. lg.	3	txI2	2	18.1	13.1	11.3	12.3	29.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM413/94	Eu. lg.	3	tmP4	2	0.0	0.0	15.6	7.7	11.5	16.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM414/94	Eu. lg.	3	tmP4	2	0.0	0.0	0.0	0.0	14.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM415/94	Eu. lg.	3	tmPx	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM735/90	Eu. lg.	3	tmP4	1	0.0	0.0	0.0	0.0	12.4	0.0	0.0	0.0	12.0	32.2	7.0	32.4	7.0	3.2
WM769/90	Eu. lg.	3	tmP3	2	0.0	0.0	15.3	0.0	12.5	18.2	17.7	14.5	15.3	20.1	21.9	0.0	0.0	0.0
WM800/90	Eu. lg.	3	txM1	2	28.1	23.0	0.0	0.0	47.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM823/92	Eu. lg.	3	mtiii	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	45.2	43.1	37.4	33.5	33.3
WM825/92	Eu. lg.	3	tmP4	1	28.0	25.8	0.0	0.0	0.0	14.8	14.9	0.0	0.0	60.6	50.1	48.2	0.0	0.0
WM826/92	Eu. lg.	3	tmP2	1	32.8	30.5	12.1	10.7	15.8	15.0	14.6	12.3	13.5	40.0	0.0	14.0	0.0	0.0
WM829/92	Eu. lg.	3	txI2	2	18.1	15.5	12.8	12.6	28.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM830/92b	Eu. lg.	3	txM3	2	0.0	0.0	0.0	0.0	0.0	0.0	5.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0
WM830/92c	Eu. lg.	3	tx?	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0
WM830/92d	Eu. lg.	3	tmP1	1	0.0	0.0	0.0	10.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM841/92	Eu. lg.	3	ast	1	64.5	60.2	33.5	65.0	50.0	35.3	46.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM934/92	Eu. lg.	3	ast	1	57.4	58.6	29.0	60.7	48.5	30.2	54.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM1268/92	Eu. sm.	3	tmM2	1	0.0	0.0	13.3	0.0	9.1	12.5	12.5	11.5	10.6	11.1	10.6	0.0	0.0	0.0
WM357/94	Eu. sm.	3	txM3	1	20.1	22.9	18.6	17.9	42.0	1.0	5.0	5.0	2.0	8.2	2.9	0.0	0.0	0.0
WM1264/92	indet.	3	tmM2	1	0.0	0.0	11.8	7.5	0.0	0.0	0.0	0.0	0.0	33.7	0.0	0.0	0.0	0.0

(continued)

Table II. (Continued)

Spec ID	Specshort	Site	Tooth	Side	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
WM1328/92	indet.	3	Ph.II	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM1436/92	indet.	3	tx	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM1455/92	indet.	3	tx	1	0.0	0.0	0.0	0.0	0.0	0.0	6.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0
WM1658/92	indet.	3	txP4	2	0.0	0.0	0.0	0.0	49.7	0.0	6.0	4.0	2.0	0.0	0.0	0.0	0.0	0.0
WM1659/92b	indet.	3	txM3	1	0.0	0.0	0.0	0.0	0.0	2.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM1673/92	indet.	3	mand.	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM1697/92a	indet.	3	Ph.II	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM1697/92b	indet.	3	Ph.II	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM260/94	indet.	3	txM3	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM261/94a	indet.	3	tm	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM261/94b	indet.	3	tx	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM368/94	indet.	3	ulna	2	374.7	64.9	34.0	50.9	58.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM416/94	indet.	3	txtm	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM416/94	indet.	3	tx	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM827/92	indet.	3	tm	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM830/92e	indet.	3	tx?	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM830/92f	indet.	3	tx?	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM830/92g	indet.	3	tm	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM830/92h	indet.	3	tx?	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM830/92i,j,k	indet.	3	txtm	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM643/94	indet.	4	tmM1	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WM746/94	indet.	4	tx	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

See Appendixes 1 and 2 for explanation of abbreviations and measurements.

Table III. Character State Distribution of Manonga Valley Hipparionine Maxillary Cheek Teeth

Spec ID	Specshort	Site	Tooth	C17	C18	C19	C20	C21	C22	C23	C24	C25	C26	C27	C28	C29	C30	C31
WM999/92	indet.	1	tx?					A										
WM1738/92	indet.	1	tx?			A												
WM1073/92	Eu. sp.	1	txM2			AB	A											
WM703/92	Eu. sp.	2	txM3		C	D	A	D	D–	I	?A	C	B					
WM277/92	indet.	2	tx			A		B		C	B	C						
WM800/90	Eu. lg.	3	txM1		C													
WM829/92	Eu. lg.	3	txI2													B	B	
WM830/92b	Eu. lg.	3	txM3			A			A									
WM830/92c	Eu. lg.	3	tx?			A												
WM1659/92	indet.	3	txP2		?C		B	A	C	D	B	C	B		A			
WM1512/92	Eu. lg.	3	txM1		D													
WM1658/92	indet.	3	txP4			A	B											
WM1657/92	Eu. lg.	3	txM1		?D	A	B	A	C	F	B	C		B				
WM1656/92	Eu. lg.	3	txP3		C	B	B–	B+	C	C	B	C	B					
WM1659/92	Eu. lg.	3	txM3			B												
WM1473/92	Eu. lg.	3	txM			B												
WM1436/92	indet.	3	tx			B		B										
WM1455/92	indet.	3	tx			B												
WM1528/92	Eu. lg.	3	txI2													B	A	
WM1528/92	Eu. lg.	3	txI3													B	A	B
WM1528/92	Eu. lg.	3	txP2			B	A	B	D	F	B	C	B					
WM1528/92	Eu. lg.	3	txP3			B	A	B	D	F	B	C	B					
WM1528/92	Eu. lg.	3	txP4			B	A	B	C	F	B	C	B					
WM1528/92	Eu. lg.	3	txM1			B	B	B	D	F	B	C	B					
WM1528/92	Eu. lg.	3	txM2			B	B	B	D	F	B	C	B					
WM1528/92	Eu. lg.	3	txM3			B	B	B	D	F	B	C	B					
WM159/94	Eu. sm.	1	txM3	C	?D	AB	B	B	B	F	B	C		B				
WM283/94	Eu. lg.	1	txP2	C		A	B	B	C	D	B	C						
WM411/94	Eu. lg.	3	txI2													B	A	
WM357/94	Eu. sm.	3	txM3	C	C	B	B	A	A	F	B	C		B				
WM261/94b	indet.	3	tx					B		D	B	C						

See Appendixes 2 and 3 for description of character state attributions and abbreviations.

Table IV. Character State Distribution of Manonga Valley Hipparionine Mandibular Cheek Teeth

Spec ID	Specshort	Site	Tooth	C28	C29	C30	C31	C32	C33	C34	C35	C36	C37	C38	C39	C40	C41	C42	C43	C44	C45	C46	C47	C48	C49
WM997/92	Eu. sm.	1	tmM2						AB			CE	B		B	C			A		D	A	A	A	A
WM1161/92	Eu. lg.	1	tmM2						AB			C	B		B	C	F	C	A		B	A	A	A	A
WM826/92	Eu. lg.	3	tmP2					B		A	B			A		C			A	C		A	A	A	A
WM735/90	Eu. lg.	3	tmP4													B			A				A	A	
WM825/92	Eu. lg.	3	tmP4																A						
WM1268/92	Eu. sm.	3	tmM2						AC			C	B		B	C	F	D			D	B	A	A	
WM769/90	Eu. lg.	3	tmP3					A		C	B			A		C			B	B		A	A	B	AB
WM827/92	indet.	3	tm																						
WM1264/92	indet.	3	tmM2						AB			CE	B		B						D			A	
WM830/92d	indet.	3	tmP																			A			
WM1652/92	Eu. lg.	3	tmP34					A						A		B	F	D	A	BC		B	B	A	B
WM1661/92	Eu. lg.	3	tmM2						CE			C	B		B	B	F	D	A		CD	B	B	A	B
WM1470/92	Eu. lg.	3	tmI2		B	A																			
WM284/94	Eu. sm.	1	tmP4					D		E	A			A		B	F	D	A–	E		C	C	A	B
WM284a/94	Eu. sm.	1	tmP4					A		C	B			A		B				D		A	A		A
WM830/94	Eu. lg.	2	tmM1						D			C	B		B	B	F	D	A		E	A	A	A	A
WM413/94	Eu. lg.	3	tmP4					AC		C	B			A		B	B			E		A	A	A	
WM414/94	Eu. lg.	3	tmP4							C													A		
WM407/94	Eu. lg.	3	tmP4					C		C	B			A					A	E		A	A	A	
WM415/94	Eu. lg.	3	tmPx					A		C	B			A					A						

See Appendixes 2 and 3 for description of character state attributions and abbreviations.

is rather small and is similar to material referred to *Eurygnathohippus* cf. "*sitifense*" from Lothagam (Bernor, in progress).

WM 999/92 is quite worn, includes a double pli caballin and the lingual border of the pre- and postfossettes.

WM 997/92 (fig. lg, h) is approximately in a middle stage of wear (maximum crown height is 29.5 mm) and includes a number of significant morphological features: metaconid round/elongate; metastylid square with angular anterior surface; metastylid spur absent; molar ectoflexid separates metaconid and metastylid; pli caballinid absent; linguaflexid a deep, broad U-shape; pre- and postflexids simple; anterior postflexid does not bend sharply lingually; protoconid band primitively rounded. The most prominent morphological feature however is the distinct occurrence of a diminutive ectostylid, rising 28.2 mm on the tooth's buccal wall. The ectostylid has a broken external wall and can be seen macroscopically to have had an increasingly attenuated interior inferosuperior cavity (filled with cement), until in the last 5.5 mm of its height, the cavity was closed. The ectostylid's apex is small and pointed, suggesting that this measurement records its maximum height. Recent work by Bernor (in progress) on Kenyan hipparions suggests that ectostylids first occur in both large and small late Miocene East African hipparions, and are variable in their expression at that time. The morphological features exhibited here are reminiscent of those in the smaller horse from the late Miocene Nawata Member of Lothagam, Kenya, and are therefore referred to *Eurygnathohippus* cf. "*sitifense.*"

WM 283/94 is a medium to large hipparion P^2 in a late stage of wear (mesostyle height = 21.4 mm). Salient morphological characters include: broad and posteriorly reflected mesostyle; distinctly curved mediolaterally, not straight; fossettes complex, particularly for this late stage of wear; posterior wall of postfossette narrowly distinct; pli caballin single; hypoglyph moderately deeply incised; protocone elongate-oval, isolated from protoloph, without spur and lingually placed compared to hypocone. The posteriorly reflected mesostyle recalls *Eurygnathohippus turkanense* and *Eurygnathohippus afarense*, while the crown curvature is more like the former (more primitive) than the latter taxon.

WM 1073/92 includes the lateral half of the tooth. The tooth was broken postdepositionally so that the remaining crown height (including the tooth's base) is 30 mm. The fossettes are complex to moderately complex (anterior surface of prefossette, 3 plis; posterior surface of prefossette, 6 plis; anterior surface of postfossette, 4 plis; posterior surface of postfossette, 5 plis; formulated hereafter 3.6.4.5) and the posterior wall of the postfossette is not clearly distinct. The tooth is relatively small and has a pointed parastyle similar to late Miocene East African *Eurygnathohippus* cf. "*sitifense*" (Bernor, in progress).

WM 1738/92 is the anterolateral portion of a maxillary cheek tooth preserving the anterior and medial portion of the prefossette. The prefossette is complexly plicated and comparable in morphology to early members of the *Eurygnathohippus* lineage.

WM 284/94 is an early wear–stage tooth. Only the superior 23 mm of the crown is preserved, but the tooth is broken in such a way as to have exposed the enamel pattern details on its inferior (rootward) surface. The tooth is that of a smaller hipparion and is morphologically characterized by: metaconid irregularly bilobed on occlusal surface, becoming rounded on inferior exposed surface; metastylid square occlusally, becoming angular inferiorly; metastylid spur very slightly developed occlusally, absent inferiorly; ectoflexid does not separate metaconid/metastylid either occlusally or inferiorly; pli caballinid single in both, but longer occlusally; protostylid a small pointed feature, vertically placed, lying lateral to protoconid band and not reaching the occlusal surface (i.e., courses superiorly within 12 mm of occlusal surface); ectostylid a poorly formed, unencircled elongate structure projecting from the anterolabial surface of the hypoconid enamel band; linguaflexid a deep broad U-shape, broader occlusally than inferiorly; preflexid and postflexid both with very complex margins occlusally, simple inferiorly; postflexid does not invade metaconid/metastylid; protoconid enamel band flattened occlusally (i.e., in early wear), rounded inferiorly (note that Table IV lists WM 284A/94, which actually is the morphology expressed on the rootward surface of the tooth). This specimen is remarkable in that in the early wear stage it retains a number of symplesiomorphic characters recalling the *Hippotherium primigenium* s.s. lineage (Bernor *et al.*, 1993a, b, 1997; Bernor and Franzen, 1997): irregularly shaped metaconid; square metastylid; presence of metastylid spur; great complexity of preflexid and postflexid. These characters are shown in this specimen to be lost after early wear. The size and morphology of this specimen recalls the Lothagam form *Eurygnathohippus* cf. "*sitifense*" (Bernor, in progress).

WM 1161/92 (fig. 1e, f) is approaching its middle third stage of wear (M10 = 43.6 mm) and shows a number of features typical for early members of the *Eurygnathohippus* lineage: metaconid rounded-elongate; metastylid anteroposteriorly compressed with an angular anterior surface; metastylid spur absent; ectoflexid separates metaconid/metastylid; pli caballinid virtually absent, being represented by only a slight fold in the hypoconid enamel band; protostylid a small, pointed projection continuous with the buccal wall and vertically placed, lying flush with the buccal wall; ectostylid present as a miniscule tubercle, rising no more than 6 mm from the basal cingulum; linguaflexid a deep V-shape; preflexid and postflexid with simple margins; postflexid anteroposteriorly oriented; protoconid enamel band rounded, showing no flattening. The size and morphology of this specimen is most conformable with that of *Eurygnathohippus* cf. *turkanense.*

WM 727/94 is a specimen from a smaller hipparionine in a middle stage of wear. The specimen is heavily weathered and encrusted with a hard matrix. The only morphological features retained in this specimen beyond its small size are the very thin parastyle and mesostyle. All three of these characters are hallmarks of the smaller Lothagam species (Bernor, in progress).

4.2. Tinde Member

The fauna from localities within the Tinde Member are thought by Harrison (1992, 1993) to be late Miocene age (ca. 6–5 Ma) and broadly contemporaneous with those at Lothagam (Harrison and Verniers, 1993). However, Bishop (this volume, Chapter 7) advocates an early Pliocene age based on suid stage of evolution.

The Tinde Member has yielded three hipparionine elements, WM 703/92, (Tinde West), an anomalous left M^3; WM 277/92, (Tinde West), a left maxillary cheek tooth fragment. From Ngofila 5, also within the Tinde Member, there is a right M_1, WM 830/94 (large form).

WM 703/92 has a crown height of 45 mm and is anomalous in having a mesostyle that is fissured vertically along its midline, pre- and postfossettes that are incompletely formed and irregularly shaped, and a protocone that is irregularly shaped and incompletely closed anteromedially (as seen in *Equus*). This tooth has a shape and curvature very much like a hipparion M^3. The pre- and postfossettes have no plis (probably due to early wear and the anomalous development of the fossettes); pli caballin(s) not well formed; hypoglyph not formed, protocone triangular-elongate and may have been connected to the protoloph; protoconal spur absent. Anomalously formed hipparionine cheek teeth are rare in the fossil record, but do occur.

WM 277/92 is a fragmentary left maxillary cheek tooth, with a considerable amount of morphology preserved: posterior border of prefossette complex; pli caballin distinctly short and single; protocone oval-shaped, isolated, and lacking a spur.

WM 830/94 is a larger hipparion tooth in a middle stage of wear. The occlusal pattern is well preserved and exhibits the following morphological characters: metaconid an irregular, trilobed shape; metastylid with angular anterior surface; metastylid spur absent; ectoflexid broad and separating metaconid/metastylid; pli caballinid present and single; protostylid a diminutive, vertically placed, pointed projection lying immediately lateral to the protoconid enamel band; ectostylid present, moderately broad at its base and becoming a very small pointed structure at its summit (40.8 mm, height), just short of the occlusal surface; linguaflexid a very broad, deep U-shape; pre- and postflexids with simple margins; postflexid not angular anteriorly; protoconid band rounded. This specimen approximates the size of *Eurygnathohippus hasumense/Eurygnathohippus afarense*, and the stage of evolution of ectostylid development would more closely approximate the former of these two taxa.

4.3. Kiloleli Member

This member includes sites at Kilolei 2, 3, and 4, Beredi South 1–3 and Ngofila 2U–4 and contains the majority of hipparion specimens known from the Wembere–Manonga Formation. The localities within the Kiloleli Member are believed to be younger than the Ibole and Tinde Members (Verniers, this volume, Chapter 2). Preliminary analyses of the fauna from Tinde and Kiloleli would suggest that significant paleoecological differences are also represented in these facies (Harrison and Verniers, 1993). The Beredi localities include a series of fluvial sediments that rest unconformably on the fossil lake deposits at Tinde.

Verniers (this volume, Chapter 2) now considers all Kiloleli Member localities to represent virtually synchronous deposition.

The Kiloleli localities include a number of hipparionine skeletal elements. Kiloleli 2 has the greatest abundance of hipparionines, including: WM 829/92, a left I^2 (?large form); WM 411/94, a left I^2 (large form); WM 826/92, a right P_2 (large form); WM 735/90, a right P_4 (large form); WM 825/92, a right P_4 (large form); WM 413/94, a left P_4 fragment (large form); WM 414/92, a left P_4 fragment (large form); WM 407/94, a right P_4 (large form); WM 415/94, a right mandibular premolar; WM 1268/92, a right M_2 (small form); WM 827/92, a mandibular cheek tooth fragment (indeterminate); WM 1264/92, a right M_2 (indeterminate); WM 830/92, several maxillary and mandibular cheek tooth elements, (indeterminate), including (a) a right mandibular P?, (b) a left M^3, (c) a left maxillary cheek tooth, (d) a right mandibular P?, (e) a right maxillary cheek tooth fragment, (f) a right maxillary cheek tooth fragment, (g) a left mandibular cheek tooth fragment, (h) a maxillary cheek tooth fragment, (i), (j), and (k) fragments; WM 416/94, 11 maxillary and mandibular cheek tooth fragments (indeterminate); WM 823/92, a left metatarsal III (large form); WM 841/92, a right astragalus (large form). Kiloleli 3 hipparionines include: WM 800/90, a left M^1 (large form); WM 769/90, a left P_3 (large form); WM 934/92, a right astragalus (large form). Kiloleli 4 has a single ?hipparionine specimen, WM 1328/92, a distal (3rd) phalanx II or IV (indeterminate).

WM 829/92 is a left ?I^2 in an apparent middle stage of wear. This tooth is somewhat like an I^1 in its semirhomboidal shape. Remarkable morphological features include: deep single grooves on the labial and lingual surfaces; presence of a single mesiolingual pillar; presence of a short flat lingual surface; slight restriction of the distolingual surface. All these features herald the morphology seen in Hadar Formation representatives of *Eurygnathohippus hasumense.*

WM 411/94 is a well-worn left I^2 with two distinct, labially-placed infundibula, marked lingual grooving and an irregular triangular shape. WM 411/94 shows a closer affinity with AL340-8 from the Denen Dora Member, Hadar, which we believe is plausibly referable to *Eurygnathohippus hasumense.*

WM 826/92 (Fig. 1a, b) is a large right P_2 from Kiloleli 2. Salient morphological features include: metaconid elongate; metastylid rounded; metastylid spur absent; premolar ectoflexid short and does not separate metaconid/metastylid; pli caballinid absent; ectostylid present but small, rising only 14.0 mm from its base; linguaflexid a shallow U-shape; pre- and postflexids have simple margins; postflexid anteroposteriorly oriented; protoconid enamel band rounded, showing no flattening. The size and morphology of this specimen conforms with a larger species of *Eurygnathohippus.*

WM 735/90 is a fragmentary right P_4 essentially including its posterior half. Salient morphological features include: presence of a large, single pli caballinid; ectostylid present and large (height = 32.4 mm, length = 7.0 mm, width = 3.2 mm); postflexid with a simple enamel margin and anteroposteriorly oriented. This specimen's well-developed ectostylid morphology is indicative of a more advanced stage of evolution than apparent in the Ibole Member hipparions reported here, and is referable by its stage of evolution to *Eurygnathohippus* aff. *hasumense* (*sensu lato*).

WM 825/92 (Fig. 1c) is a fully formed, but unerupted, right P_4 with a crown height of 60.6 mm, which would have been the maximum for this individual. Due to the lack of wear, the only apparent morphological feature is the presence of a well developed ectostylid, which ascends the lateral wall of the crown to 48.2 mm. Both the size of the tooth and degree of ectostylid development suggest a stage of evolution comparable to hipparions from the lower portion of the Hadar Formation.

WM 413/94 is a fragmentary left P_4 whose base and labial surface are missing. Approximately 80% of the anteriormost occlusal surface is complete. Salient morphological features include: metaconid rounded-elongate; metastylid angular on the anterior surface; metastylid spur absent; ectoflexid not separating metaconid/metastylid; pli caballinid single; protostylid absent; linguaflexid a very broad and deep U-shape; pre- and postflexids with simple margins; postflexid with straight anterior aspect; protoconid band rounded. The area of the tooth where the ectostylid would be found is missing.

WM 414/94 is a fragmentary left P_4 with only the metastylid and postflexid apparent. The metastylid in this specimen has an angular proximal surface and the postflexid has a simple margin.

WM 407/94 is a right P_4 that is complete except for the anterolabial wall (protoconid enamel band). This specimen is within the first third of wear (crown height = 52.5 mm) and the occlusal enamel pattern is well established. Salient morphological features include: metaconid angular on its posterior surface; metastylid angular on the facing anterior surface; metastylid spur absent; ectoflexid not separating metaconid/metastylid; ectostylid present, rising on labial wall (52.6 mm, height) and terminating apically as a small irregular-shaped circle at the crown's occlusal surface; linguaflexid a very broad, deep U-shape; pre- and postflexids with simple margins; postflexid anteroposteriorly oriented.

WM 415/94 is an unerupted right mandibular premolar. The tooth is broken in such a way as to expose some morphological details on the inferior (rootward) surface: metaconid rounded; metastylid strongly angular on anterior surface; metastylid spur absent; ectoflexid not separating metaconid/metastylid; ectostylid's inner (=lingualward) aspect present, exhibiting a prominent development within 36.9 mm of the unworn occlusal surface.

WM 1268/92 is a right M_2 in a very advanced stage of wear (crown height = 11.1 mm). A number of morphological features are apparent in this specimen, including; a rounded metaconid with an angular posterior surface; metastylid angular on its anterior surface; metastylid spur absent; ectoflexid with a broad U-shape and clearly separating metaconid/metastylid; pli caballinid absent; protostylid a small pointed projection continuous with the buccal cingulum; vertically placed and lying lateral to the protoconid band; no ectostylid apparent, but this is probably due to erosion of the tooth's lateral surface; linguaflexid a deep, broad U-shape; preflexid with complex margins while postflexid has simple margins and an anteroposterior orientation. Species attribution of this tooth is made difficult by its advanced stage of wear, but would appear referable to a smaller species of hipparion.

WM 827/92 is an unerupted juvenile mandibular cheek tooth fragment that is too poorly preserved to make cogent observations.

WM 1264/92 is a right fragmentary M_2 with a crown height of 33.7 mm. This specimen preserves a few salient features including: metaconid rounded-elongate; metastylid square-shaped with a distinctly angular mesial surface; metaconid spur absent; ectoflexid separates metaconid/metastylid; linguaflexid deep, having a broad U-shape; postflexid anteroposteriorly oriented. This specimen does not preserve an ectostylid but has a morphology consistent with other Kiloleli specimens.

Kiloleli 3 includes WM 830/92, a group of 11 fragmentary maxillary and mandibular cheek tooth elements preserving limited morphological information other than the observation that they are hipparionine. Of these specimens, the following contain some morphological information: WM 830/92b, a left M^3 with hypoglyph deeply incised (virtually encircled) and the posterior surface of the prefossette complex with five plis and the anterior surface of the postfossette with four plis; WM 830/92c, a fragmentary maxillary cheek tooth with complex plications of the anterior surface of the postfossette; WM 830/92d preserves a simple preflexid border. None of the features exhibited are inconsistent with the morphology of the other Kiloleli hipparions.

WM 416/94 includes 11 maxillary and mandibular cheek tooth fragments in too poor a state of preservation to describe. However, within this group of specimens there is a mandibular cheek tooth fragment that exhibits a well-developed, large ectostylid that is clearly evolutionarily advanced.

Finally, Kiloleli 2 has also yielded a virtually complete hipparionine left metatarsal III, WM 823/92.

WM 800/90 is a fragmentary M^1 in an early stage of wear with a crown height of 47.1 mm. The maximum crown height of this specimen would not have greatly exceeded this figure and therefore is somewhat low compared to the Hadar hipparions, *Eurygnathohippus hasumense* and *Eurygnathohippus afarense*.

WM 769/90 is a left P_3 in an advanced stage of wear (crown height = 20.1 mm). This specimen is distinguished by the following: metaconid rounded; metastylid angular on its proximal surface; metastylid spur absent; ectoflexid shallow and not separating metaconid and metastylid; pli caballinid absent; ectostylid absent; linguaflexid a deep, broad V-shape; pre- and postflexid with simple margins; postflexid anteroposteriorly oriented; protoconid band semiflattened. The lack of an ectostylid excludes the possibility of this specimen being a more advanced member of *Eurygnathohippus*, but is not entirely atypical for a stage of evolution comparable to *Eurygnathohippus hasumense* from the lower portion of the Hadar Formation.

WM 934/92 is a right astragalus of moderate size. Its affinities will be analyzed in section 4.4 below.

Kiloleli 4 has a single questionable hipparionine specimen, WM 1328/92, a distal (3rd) phalanx II or IV. In comparison with the early Vallesian (10.3 Ma) hipparions from Höwenegg Germany, this specimen has a generally similar appearance, but differs in a number of salient morphological features: the element is overall broader and shorter; the volar nutrient foramen is larger and not recessed within the hoof; the proximal articular facet is mediolaterally broader and dorsoventrally shorter, lacking a dorsoventral keel; overall, the hoof is shorter and less pointed.

Harrison *et al.* (1993), Harrison and Verniers (1993) and Verniers (this volume, Chapter 2) include the Beredi localities within the Kiloleli Member. The Beredi localities have yielded a moderate-size assemblage of hipparionine dental and postcranial remains. Beredi South 1 includes the following fossil material: WM 1528/92, a partial skull with dentition (large form); WM 1512/92, a left M^1 (large form); WM 357/94, a right M^3 (small form); WM 368/94, an associated distal humerus, radius, and ulna (large form): WM 1635/92, a left metacarpal III (large form). Beredi South 2 has yielded: WM 1652/92, a left $P_{3 \text{ or } 4}$ (large form); Beredi South 3 has yielded the greatest number of hipparion skeletal remains: WM 1659/92, a left P^2 (large form); WM 1656/92, a left P^3 (large form); WM 1658/92, a left P^4 (indeterminate); WM 1657/92, a left M^1 (large form); WM 1659/92a, a left P^2 (large form), and WM 1659/92b, a right M^3; WM 1661/92, a right M_2 (large form); WM 1673/92, an edentulous mandible (indeterminate); WM 1668/92, a right astragalus (large form); WM 1669/92, a left metacarpal III (large form); WM 1697/92a, a first phalanx II/IV, and WM 1697/92b, a second phalanx II/IV (both indeterminate).

The most complete specimen from this assemblage, and indeed the Wembere–Manonga Valley collection as a whole, is WM 1528/92, a maxillary–premaxillary specimen with I^2–I^3 and P^2–M^3 (fig. 2a, b and 3a). While broken in the region of the buccinator fossa, Dr. William Sanders (University of Michigan) managed to establish contacts along the nasal margin and palate between the premaxillary and more posterior maxillary portions. This specimen exhibits a very long snout (M1 = 153.5 mm; re: Eisenmann *et al.*, 1988) that has a broad muzzle breadth between the I^3's (M15 = 59.2), tapering sharply to its minimum breadth (M14 = 42.9 mm) approximately 71 mm distally. There is a faint trace of the anterior portion of the preorbital fossa (POF) dorsally high on this specimen at the juncture of P^3–P^4; the POF would have been vestigial, most probably unpocketed posteriorly, of shallow medial depth, lacking internal pits, lacking a discernable peripheral outline (with the possibility of a dorsal outline). The anterior rim and inferior orbital foramen are absent. The buccinator and canine fossae are confluent, the buccinator fossa was probably unpocketed and the malar fossa is absent. The nasal notch is not preserved. There are two very small alveoli for the canines, and there is no evidence that there was a dP^1 remaining after the permanent dentition erupted. Skull character state distributions are: C2 = C; C4 = I; C5 = ?D; C6 = D; C7 = A; C8 = DE; C9 = B; C10 = B; C11 = A; C12 = A; C13 = A; C14 = A; C15 = ?; C16 = B; C17 = C; C18 = ?D (explained in Legend for Tables IV and V).

The cheek teeth are of a large hipparionine species: P^2–P^4 (M7) = 89.5 mm; M^1–M^3 = 76.7 mm; P^2–M^3 = 163.4 mm. The incisors are large, curved, and have multiple grooves on both the buccal and lingual surfaces. I^3 is very elongate and transversely constricted. The cheek teeth are worn, and although the maximum crown height is found to be 53 mm in the M^2, the expected maximum crown height would be greater than 60 mm. Fossette ornamentation is moderate on all cheek teeth with the opposing borders of the pre- and postfossette having considerably more plis than the nonopposing borders. The posterior enamel border of the postfossette invades and apparently replaces the posterior border of P^2–P^4 (i.e., is indistinct), but not so on M^1–M^3, where it is clearly separate. Pli caballins are single on all cheek teeth. Hypoglyphs are mostly shallow, being moderately deep only on P^4. The protocone is isolated and has an elongate compressed-oval shape on all cheek teeth, with compression being most marked on M^2–M^3. The protoconal spur is absent and the protocone is more lingually placed than the hypocone on all cheek teeth. The P^2 anterostyle is elongate.

Compositely, WM 1528/92 compares quite closely with hipparionine skull material from Hadar, Ethiopia described by Eisenmann (1976). The snout proportions appear to be strikingly similar to AL 340-8 from the Denen Dora Member (DD-2, ca. 3.2 Ma, R. Walter, pers. comm.; Gray, 1980), however Eisenmann does not provide measurement 1 of Eisenmann *et al.* (1988) in this publication. Eisenmann (1976) does provide measurement 15 (her measurement 17 of Table 1 in her 1976 publication), which is comparable (57 mm) to WM 1528/92 (59.2 mm). Other details of cheek tooth size and character state attributions also compare closely with AL 340-8, as well as with the more complete specimen AL 363-18 (Eisenmann, 1976: Pl. 2.1, A–C, and Pl. 2.2, A–C; Pl. 4.1, A, and Pl. 4.2, A).

Eisenmann refers AL 340-8 to "Hipparion" sp., which she elects to distinguish provisionally at the species rank from another Hadar hipparion, "*Hipparion*" *afarense* (AL 363-118 from KH3, ca. 2.9 Ma), which is represented by a partial skull, lacking only the snout, and an associated complete mandible. The Hadar hipparions are currently under study by Bernor, and in the absence of a complete character state and statistical analysis it would be imprudent to validate or deny the possible specific distinctions that Eisenmann (1976) has provisionally recognized. However, it seems plausible that these two species are phylogenetically closely related, and may prove to be time-successive species of a single evolving lineage. They would appear to be closely related evolutionarily and most likely temporally to WM 1528/92. According to our brief review of East African hipparionine evolution below, the Hadar hipparions would best be referable to *Eurygnathohippus hasumense* (Denen Dora population, ca. 3.2–3.1 Ma) and *Eurygnathohippus afarense* (ca. 2.9 Ma).

WM 1512/92 is an unerupted left M^1 from Beredi South 1. Its size and crown height at mesostyle (M^5 = 65.2 mm, which would represent its maximum) make it closely comparable with Hadar Formation hipparions. It compares closely with WM 1528/92's P^3 in overall size, but the absence of any wear disallows morphological comparisons.

WM 357/94 is a right M^3 of a smaller hipparion retaining good occlusal detail. Morphological features include: very thin, bladelike parastyle and mesostyle; tooth distinctly curved; crown height 42.0 mm with maximum unworn height estimated to have been $\leq$60 mm (based on stage of wear likely being in early third; plications moderately complex with the two lingualmost plis of the posterior surface of prefossette being isolated, as enclosed enamel circles; posterior wall of postfossette distinct; pli caballin double; hypoglyph very deeply incised, virtually enclosing hypocone; protocone compressed-ovate, distinctly isolated from protoloph, lacking spur and ligually placed compared to hypocone). The size and morphology of this specimen recalls the Lothagam form *Eurygnathohippus* cf. "*sitifense*" (Bernor, in progress).

WM 368/94 is an associated left distal humerus, radius and ulna and a right proximal MC III. The radius is further discussed in section 4.4 below.

The left MC III, WM 1635/92, will be described below with the Beredi South 3 MC III, WM 1669/92.

Beredi South 2 has yielded a fragmentary left P_3 or P_4 (WM 1652/92) including the preflexid and the anterior portion of the postflexid. This specimen is in a middle stage of wear, having a crown height of 29.8 mm. Salient morphological features include: metaconid rounded; ectoflexid does not separate metaconid and metastylid; pli caballinid long and single; protostylid a small, vertically placed, pointed projection continuous with the buccal cingulum; ectostylid present (but largely broken away); linguaflexid a shallow U-shape; preflexid and postflexid with simple margins; postflexid anteroposteriorly oriented; protoconid enamel band with distinct flattening. This suite of characters compares favorably with *Eurygnathohippus hasumense* (Bernor, in progress).

WM 1659/92a (fig. 3f, g) is a left P^2 from Beredi South 3. It is in a middle stage of wear (crown height = 37.7 mm), exhibiting the following morphological features: postfossette posterior wall distinct; pli caballin double; hypoglyph moderately deeply incised; protocone elongate-oval, isolated from the protoloph; protoconal spur absent and lingually placed compared to the hypocone; anterostyle elongate. This tooth compares very closely with WM 1528/92's P^2.

WM 1656/92 (fig. 3d, e) is a left P^3 from Beredi South 3. This specimen is in an early stage of wear and has a crown height of only 50.7 mm. Salient morphological features include: a maximum crown height most likely less than 60 mm; moderately complex pre- and postfossette plications; posterior wall of the postfossette barely distinct; pli caballin double, with more anterior pli being sharply diminutive; hypoglyph moderately deeply incised; protocone oval shaped, lacking a spur and lingually placed compared to the hypocone. This specimen compares well with other P^3s from this assemblage, but has a maximum crown height somewhat less than the Hadar hipparions (Bernor, in progress).

WM 1658/92 is a fragmentary left P^4 from Beredi South 3, and includes the posterior portion of the prefossette and postfossette. The crown height of this specimen is 49.7 mm and the postfossette exhibits complex plications of the interfacing margins.

WM 1657/92 (fig. 3b, c) is a complete left M^1 from Beredi South 3. This specimen is in a middle stage of wear and has a crown height of 36.7 mm. Morphological features include: complex plications of the pre- and postfossettes; posterior wall of postfossette not distinct; pli caballin double; hypoglyph moderately deeply incised; protocone lingually placed compared to hypocone, with a compressed-ovate shape and lacking a spur. This specimen compares closely with WM 1528/92.

WM 1659/92b is a right M^3 fragment from Beredi South 3, and includes only the prefossette and anterolabial walls of the tooth. The only morphological feature exhibited on this specimen is the moderate complexity of the prefossette.

WM 1673/92 is an edentulous hipparionine mandibular symphysis from Beredi South 3. There is insufficient morphology preserved in this specimen to make comparisons with other hipparionines.

WM 1661/92 is a right M_2 from Beredi South 3. This specimen is in the first third of wear, having a crown height of 49.7 mm. Morphologically it is characterized by: metaconid square-shaped with an angular distal surface; metastylid with an angular anterior surface; metastylid spur absent; ectoflexid separates metaconid/metastylid; pli caballinid strongly developed and single; protostylid a small, vertically placed and pointed projection continuous with the buccal cingulum; ectostylid present, rising a minimum 35.8 mm high on the buccal crown surface; linguaflexid a deep V- to U-shape; pre- and postflexids with complex margins; postflexid anteroposteriorly oriented; protoconid band flattened. This specimen compares closely with AL 363-18 from the Denen Dora Member of Hadar.

There are two phalanges from Beredi South 3: WM 1697/92a, a first phalanx II/IV, and WM 1697/92b, an associated second phalanx II/IV. In all respects, these elements compare closely with the Höwenegg skeletons of *Hippotherium primigenium* (Bernor *et al.*, 1997). There are two left metacarpal IIIs from the Beredi localities; WM 1635/92 (fig. 4c, d) from Beredi South 1, and WM 1669/92 (fig. 4a, b) from Beredi South 3. These specimens are discussed further in section 4.4.

The Kiloleli Member Ngofila assemblage comprises six specimens. From Ngofila 2U (upper stratigraphic horizon) there is a left maxillary cheek tooth, WM 1436/92 (indeterminate). From Ngofila 3, there is a right maxillary cheek tooth, WM 1455/92 (indeterminate). Ngofila 4 has yielded a left M^3, WM 260/94, a maxillary cheek tooth fragment (indeterminate), WM 261/94a and WM 261/94b, are a mandibular cheek tooth and a left maxillary ?molar (indeterminate), WM 1473/92 (indeterminate) and a right I_2, WM 1470/92 (large). WM 1436/92, WM 1455/92, and WM 1473/92 preserve only the central portions of the respective cheek teeth, and all have moderately complex interfacing fossette borders; WM 1436/92 preserves a single pli caballin.

WM 260/94 is an unerupted left M^3 whose base is broken above the roots. Moreover, both the lingual and posterior surfaces of the tooth are absent, disallowing any morphological evaluation.

WM 261/94a and WM 261/94b are a lower and an upper cheek tooth fragment, respectively. The lower cheek tooth is too fragmentary to be determined. The upper cheek tooth is even more fragmentary and preserves only a portion of the protocone, which exhibits an elongate-oval shape, isolated from the protoloph, and lacks a spur. The pli caballin is single.

A right I_2, WM 1470/92 (fig. 1i, j), is in a middle stage of wear (height = 31.2 mm). This specimen compares closely with Hadar *Eurygnathohippus afarense* in the presence of multiple buccal and lingual grooves on the enamel surface and elongate-oval mesial-distal contour. However, the incisor does appear to be somewhat more curved than the Hadar horse, and may be indicative of a less-derived stage of evolution.

Finally, there are two specimens of indeterminate stratigraphic position: WM 643/94, a fragmentary M_1 found as surface float from Inolelo 2, and WM 746/94, six fragmentary upper and lower cheek tooth fragments found on the surface of Ngofila Hill (Ngofila 1). Neither of these specimens warrants description here.

4.4. Statistical Comparisons

Thus far we have recognized two sizes of hipparion in the Wembere–Manonga collection. This size differentiation is most evident in late Miocene and early Pliocene East African assemblages. In order to make suitable comparisons with other populations of East African hipparions currently under study, we have elected to present a series of bivariate plots overlain with 95% ellipses of the Höwenegg, Germany (10.3 Ma; Tobien, 1986; Bernor *et al.*, 1996; Swisher, 1996; Woodburne *et al.*, 1996), sample: P^2, radius, astragalus, metacarpal III and metatarsal III.

Maxillary P^2 was selected because, of all cheek teeth, it exhibits a minimal amount of variability in length and width measurements as the crown wears, and thus is the most suitable of the cheek teeth for size comparisons. Figure 5 includes two bivariate plots: (a) M3 (occlusal width) versus M1 (occlusal length);

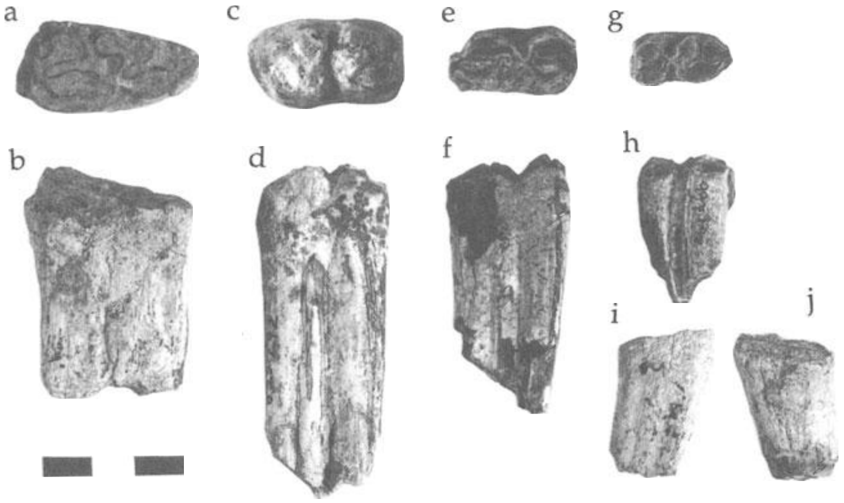

FIGURE 1. Lower dentition of *Eurygnathohippus* from the Wembere–Manonga Valley: (a) WM 826/92, P_2, occlusal view; (b) WM 826/92, P_2, buccal view; (c) WM 825/92, P_4, occlusal view; (d) WM 825/92, P_4, buccal view; (e) WM 1161/92, M_2, occlusal view; (f) WM 1161/92, M_2, lingual view; (g) WM 997/92, M_2, occlusal view; (h) WM 997/92, M_2, buccal view; (i) WM 1470/92, I_2, labial view; (j) WM 1470/92, I_2, lingual view. Scale = 30 mm.

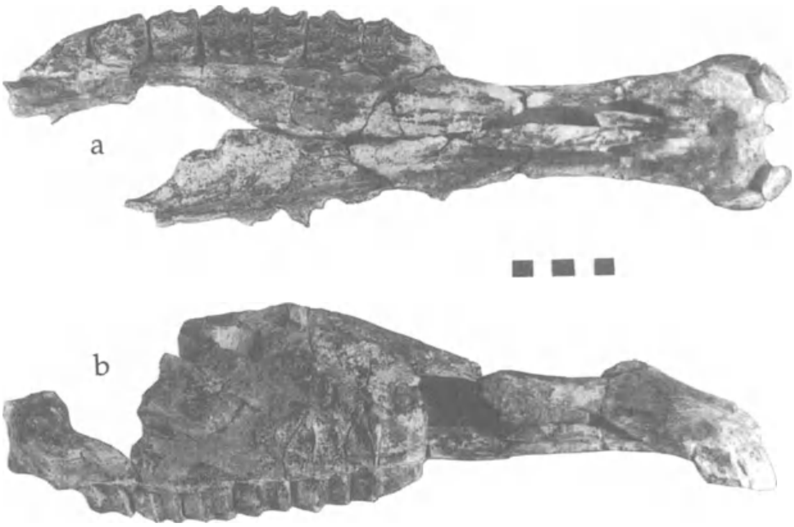

FIGURE 2. WM 1528/92, partial skull of *Eurygnathohippus* aff. *hasumense* from Beredi South: (a) palatal view; (b) right lateral view. Scale = 50 mm.

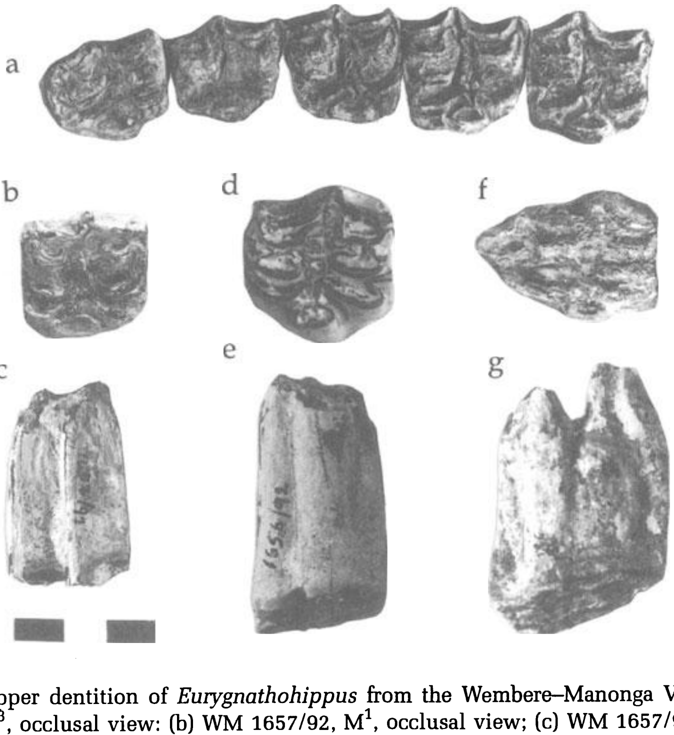

FIGURE 3. Upper dentition of *Eurygnathohippus* from the Wembere–Manonga Valley: (a) WM 1528/92, P^3-M^3, occlusal view: (b) WM 1657/92, M^1, occlusal view; (c) WM 1657/92, M^1, buccal view; (d) WM 1656/92, P^3, occlusal view; (e) WM 1656/92, P^3, lingual view; (f) WM 1659/92a, P^2, occlusal view; (g) WM 1659/92a, P^2, lingual view. Scale = 30 mm.

FIGURE 4. Third metacarpals of *Eurygnathohippus* from the Manonga Valley: (a) WM 1669/92, cranial view; (b) WM 1669/92 caudal view; (c) WM 1635/92, cranial view; (d) WM1635/92, caudal view.

(b) M4 (basal width) versus M2 (basal length). Comparison of the two plots verifies a minimal difference in the distribution of points, and as exhibited in Fig. 5a, the Höwenegg 95% ellipse does not show an inordinately great range of variability (note that since the Höwenegg hipparion P^2s are all within skulls, there is no possibility to measure basal crown dimensions). Figure 5a positions the Kiloleli Member P^2s on the upper right periphery of the Höwenegg ellipse and essentially in the center of the Hadar (ca. 3.4–2.9 Ma) sample. Also within the broad Hadar hipparion cluster is found the Upper Nawata (Lothagam; ca. 6.0 Ma), Wee-ee (ca. 4.0 Ma), Maka (ca. 3.5 Ma) and Matabaietu (ca. 2.7 Ma) samples. In the lower portion, and immediately peripheral to the Höwenegg ellipse, are consistently found the Lower Nawata (ca. 7 Ma) samples, as well as specimens derived from the Ibole Member, Adudora (ca. 6 Ma) and Wee-ee. Figure 5b exhibits some departures from this pattern that may be taken as being due to individual size variation. The Kiloleli Member hipparion represented here again falls essentially in the lower central portion of Hadar's extensive length range. For the most part, the Lothagam Lower Nawata sample clusters very closely together and tends to have a relatively low basal length versus basal width dimension (i.e., relatively short teeth). Adudora again clusters with the Lothagam Lower Nawata series, while Wee-ee and Maka range within the Hadar sample.

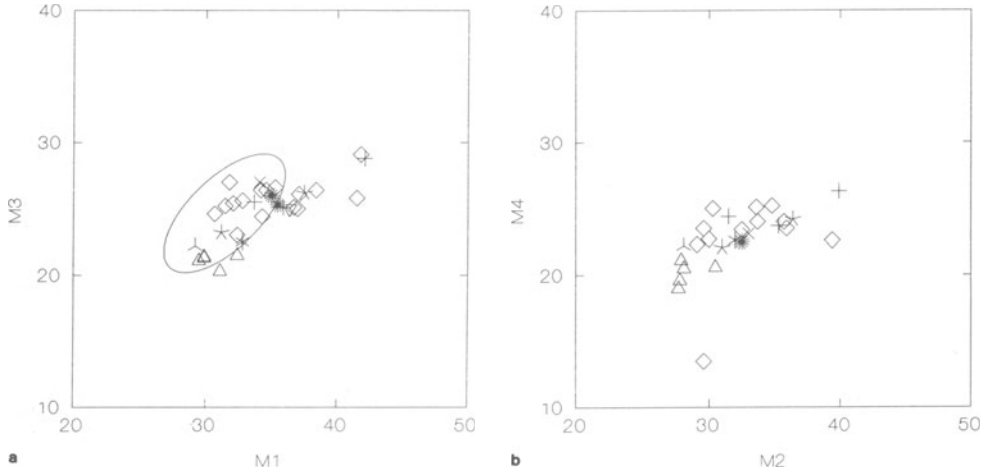

FIGURE 5. P^2 - (a) M3 (occlusal width) versus M1 (occlusal length); (b) M4 (basal width) versus M2 (basal length). Locality symbols (first digit = country code, second digit = locality code in Bernor's data base): Mpesida (Kenya; 19/11) ○; Lothagam (Kenya), Lower Nawata (19/1) △, Upper Nawata (19/2) ▽, Apak (19/3) ◁; Nakali (Kenya; 19/13) □; Hadar (Ethiopia; 18/1) ◇; Lukeino (Kenya; 19/12) ☆; Adudora (Ethiopia; 18/13) ⅄ ; Maka (Ethiopia; 18/2) +; Matabaietu (Ethiopia; 18/7) ×; Wee-ee (Ethiopia; 18/3) ✶ ; Ibole Member (Tanzania; 20/1) ✳ (simple); Kiloleli Member (Tanzania; 20/3) ✺ (complex).

Hadar has a very small individual that may represent a sampling or measuring anomaly.

Our preliminary results from the late Miocene and early Pliocene assemblages support the existence of at least two size classes of hipparion in these late Miocene–middle Pliocene hipparions. These bivariate plots attest to a smaller hipparion represented by P^2s from the Ibole Member, Adudora, and Lothagam's Lower Nawata Member. The "larger hipparion" exhibited in this plot is quite variable, and since the localities included here range over 4.5 m.y., this interval most probably includes distinct species of "larger" hipparions.

In 1994 WMPE recovered a beautiful associated partial forelimb from the Kiloleli Member, WM 368/94, including a distal humerus and a complete radio-ulna. The Höwenegg sample includes 23 radii, of which 11 are complete. Figure 6 includes bivariate comparisons of four different pairs of dimensions: (a) M1 (maximum length) versus M10 (distal maximum breadth); (b) M1 (maximum length) versus M3 (minimal shaft breadth); (c) M5 (proximal articular breadth) versus M6 (proximal articular depth); (d) M9 (distal articular breadth) versus M8 (distal articular depth).

Figure 6a reveals that the Kiloleli Member hipparion falls just outside the upper range of variability of the Höwenegg sample (311.1 mm versus 310 mm for the left side and 305 mm for the right side). The Hadar sample has greater length dimensions, but also some individuals with much greater maximum breadth. In Figure 6b, the minimal shaft breadth for the Kiloleli Member hip-

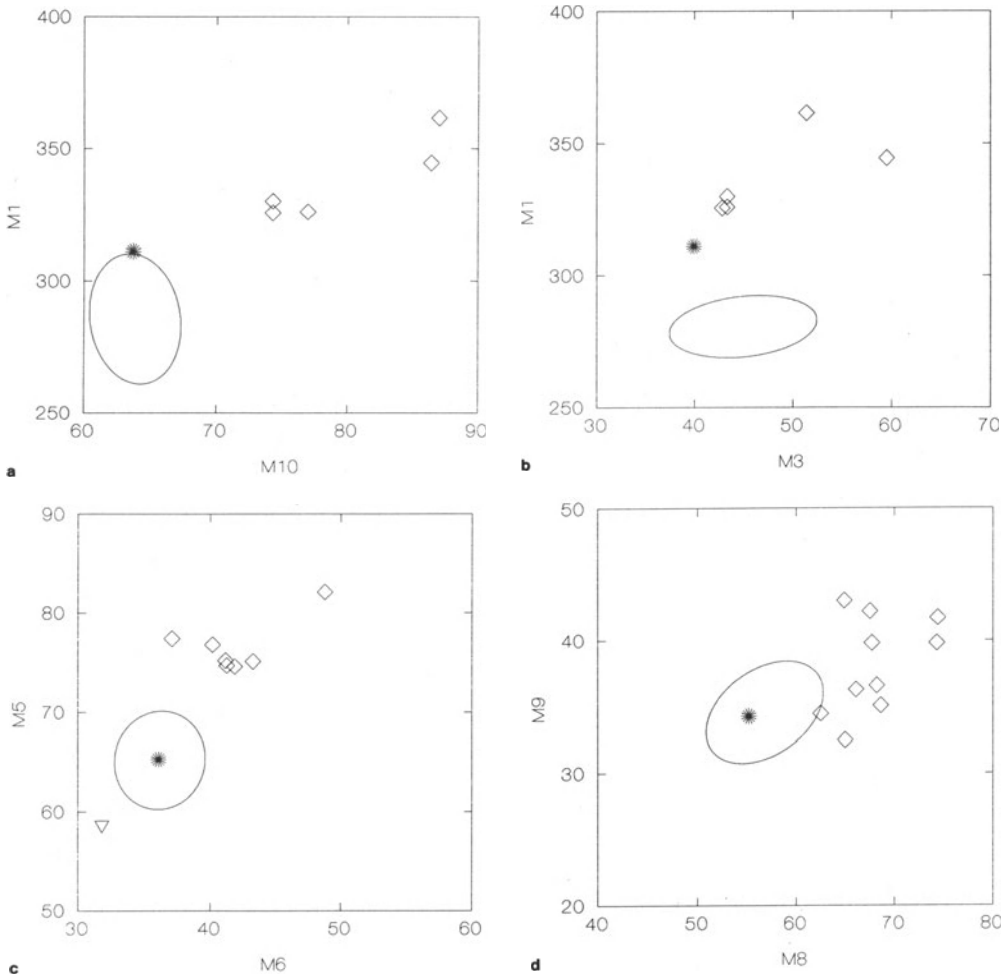

FIGURE 6. Radii - (a) M1 (maximal length) versus M10 (distal maximal breadth); (b) M1 (maximal length) versus M3 (minimal shaft breadth); (c) M5 (proximal articular breadth) versus M6 (proximal articular depth); (d) M9 (distal articular breadth) versus M8 (distal articular depth).

parion is at the lower portion of the Höwenegg range, while expected length is elevated (note that the Hö A54 radii had sufficiently damaged midshafts to render accurate measurement impossible; these specimens are not included in this plot). The Hadar hipparions exhibit a strikingly similar broad distribution of points as seen in Figure 6a, with some comparing closely with the Kiloleli Member horse and others having much elevated length and particularly elevated shaft breadth measurements. Figure 6c places the Kiloleli Member hipparion directly within the center of the Höwenegg 95% confidence ellipse for proximal articular breadth (M5) versus proximal articular depth (M6). One individual represented from the Upper Nawata Member has lower measurements for both dimensions and is certainly referable to the smaller hipparion from that locality. The Hadar hipparions again are quite variable, having elevated dimensions for both M5 and M6. Figure 6d again places the Kiloleli Member hipparion within the Höwenegg ellipse, while the Hadar hipparions have virtually all dimensions elevated for maximum articular breadth (M8), and partially overlapping and partially elevated for distal articular depth (M9).

The plots depicted in Fig. 6 provide us with some important information about the Kiloleli Member hipparion. First, the length and width dimensions reveal that it has relatively elongate limbs compared to the late Miocene Höwenegg hipparion, and that it is shorter limbed than most of the Hadar sample, but also more gracile in its build. Second, the small hipparion from Lothagam essentially exhibits the proportions of the Kiloleli Member hipparion in proximal dimensions (M5 versus M6) but is distinctly smaller. Also, the Hadar hipparions show a greater dispersion of measurements than is likely in a single species. This observation supports earlier ones made by Eisenmann (1983), and corroborated by the present authors here, that there is more than one species represented in the Hadar sample.

Astragali are amongst the best represented skeletal elements in Old World hipparion assemblages because their intrinsic anatomical structure best assures their survival for fossilization. Figure 7 exhibits three sets of bivariate plots: (a) M1 (maximum length) versus M3 (minimum breadth); (b) M7 (proximal maximum breadth) versus M2 (median length); (c) M5 (proximal articular breadth) versus M6 (proximal articular depth).

Figure 7a depicts one Kiloleli Member hipparion's measurements falling within the Höwenegg ellipse and the other just outside with elevated length (M1) and breadth (M3) measurements. The differences in these would not appear to be greater than expected in a single population if one compares the 95% ellipse of the Höwenegg sample, and they could conceivably be due either to real adult size differences or different ontogenetic stages being represented. Again, the Hadar hipparions exhibit generally elevated dimensions compared to the Höwenegg hipparions and one Kiloleli Member hipparion falls within the lower portion of the Hadar range for M1 and the center portion of M3's range. Falling distinctly below the Höwenegg, Beredi, and Hadar horses are samples from the Lower Nawata, Upper Nawata, and Lukeino; this provides further evidence for a smaller hipparion from these localities (it not being likely that all of these are juvenile individuals).

Figure 7b exhibits a generally similar pattern, with the Lothagam and Lukeino sample including individuals at the lower extreme of bivariate measurements, the Kiloleli Member hipparions falling within and outside the Höwenegg ellipse, and Hadar hipparions being at the upper extreme and outside the Höwenegg ellipse. This figure also depicts that there is one individual from the Lower Nawata Member positioned at the upper extent of the Höwenegg ellipse and within the Hadar cluster. Of further interest is a specimen from Nakali (ca. 8.5 Ma; Hill, pers. comm.) thought to be a direct derivative of Old World *Hippotherium primigenium*, and referred by them to *Hipparion africanum* (Aguirre and Alberdi, 1974), falling within the Höwenegg ellipse. Figure 7c again reveals that

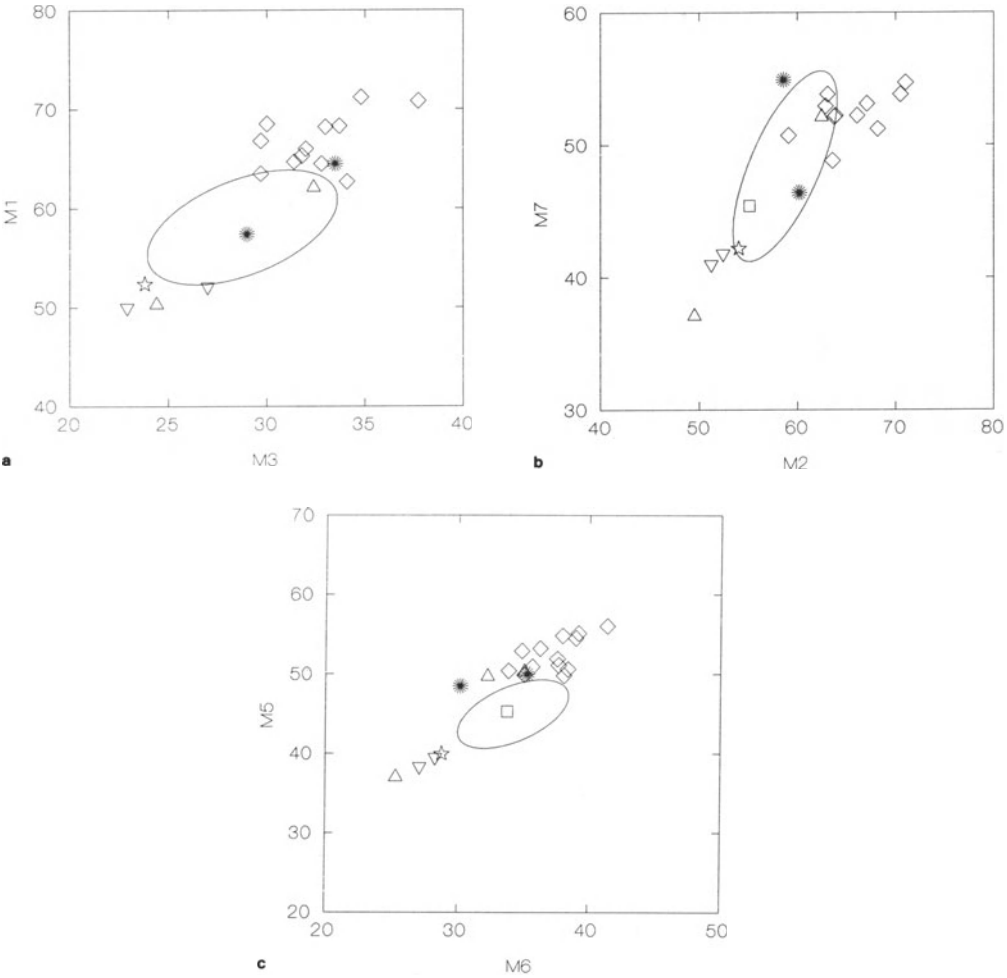

FIGURE 7. Astragali - (a) M1 (maximal length) versus M3 (minimal breadth); (b) M7 (proximal maximal breadth) versus M2 (median length); (c) M5 (proximal articular breadth) versus M6 (proximal articular depth).

the Nakali individual falls directly within the Höwenegg ellipse, while the Kiloleli Member, a single Lower Nawata specimen, and Hadar hipparions all fall above the Höwenegg ellipse for M5, but overlap in their M6 measurements. Also, there are Lower Nawata, Upper Nawata, and Lukeino individuals that fall distinctly below the Höwenegg ellipse as well as the other measurements.

The three astragali plots provide the following interpretation. First, the Kiloleli Member hipparions overlap in some of their dimensions with the more primitive species *Hippotherium primigenium* from Central Europe, as well as Kenya; these may plausibly indicate a similar body size. Second, Lothagam and Lukeino are late Miocene localities having a distinctly smaller hipparion. Third, Hadar once again exhibits a greater distribution of points than one would necessarily expect in a single species of hipparion, and that distribution overlaps in part with the Kiloleli hipparion.

Metacarpal IIIs and metatarsal IIIs have long been used by hipparion workers for species discrimination and interpretations of locomotor behavior. Figure 8 depicts three bivariate dimensions for our sample: (a) M1 (maximum length) versus M11 (distal articular breadth); (b) M6 (proximal articular depth) versus M5 (proximal articular breadth); (c) M12 (distal maximal depth of keel) versus M11 (distal maximal articular breadth).

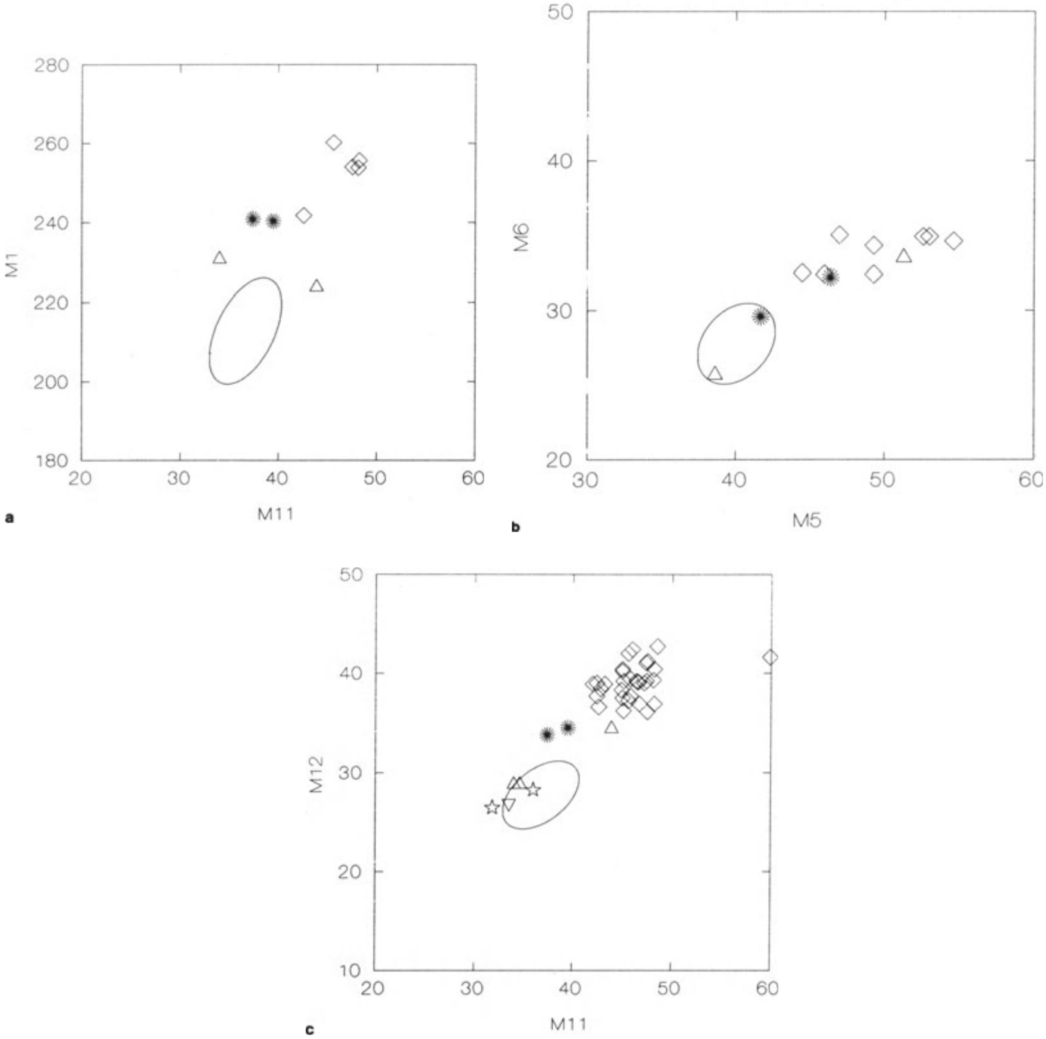

FIGURE 8. MC III's - (a) M1 (maximal length) versus M11 (distal articular breadth); (b) M6 (proximal articular depth) versus M5 (proximal articular breadth); (c) M12 (distal maximal depth of keel) versus M11 (distal maximal articular breadth).

Figure 8a reveals that all East African hipparions sampled here have elevated maximum length measurements except for one Lower Nawata specimen referable to *Eurygnathohippus turkanense*, which falls at the maximum length range but has highly elevated distal width measurements (Bernor, in progress). Another Lower Nawata specimen has clearly different proportions that are absolutely both longer and narrower. The Kiloleli Member specimens have much elevated length measurements compared to the Höwenegg sample, but retain relatively similar distal articular width measurements. Moreover, while having absolutely elevated M1 and M11 measurements compared to the smaller Lower Nawata specimen, their proportions are similar. The Hadar hipparions vary from being closely similar to the Kiloleli Member hipparion to being both absolutely longer and wider than that hipparion.

Figure 8b shows that one Kiloleli specimen and one Lower Nawata specimen falls within the Höwenegg ellipse for M6 versus M5, while the other has elevated values for both dimensions. Note once again that the differences between the two Kiloleli Member specimens are not evidently greater than expected for a single species when compared to the Höwenegg 95% ellipse, but because of the small sample size, a *t* test cannot be made. The larger Kiloleli Member specimen falls within the lower portion of Hadar's range for M6 and M5. Of further interest is that the larger Lower Nawata form falls within the upper part of the Hadar horses' range for M6 and M5 and was certainly a more heavily built form than the other Lower Nawata hipparion, and for that matter the Kiloleli Member hipparion. Figure 8c provides the following distinct clusterings: (1) the Höwenegg ellipse with a number of small East African hipparions closely approximating their size: Lower Nawata, Upper Nawata, and Lukeino; (2) a cluster of Hadar forms and the larger Lower Nawata hipparion; (3) the Kiloleli Member hipparions that are intermediate in their dimensions between clusters (1) and (2); (4) a very large Hadar hipparion outlier.

The three MC III plots provide the following data. First, the Kiloleli Member hipparions are relatively gracile in their length versus width dimensions: they have proportions similar to the smaller, more gracile taxon *Eurygnathohippus* cf. "*sitifense*" from Lothagam's Lower Nawata Member. Second, there may well be at least five different taxa represented in our pooled MC III sample: (1) the Kiloleli Member hipparion and a limited sample from Hadar; (2) the Höwenegg hipparion (relevant for comparison here); (3) the smaller Lothagam and Lukeino form, *Eurygnathohippus* cf. "*sitifense*"; (4) the larger Lothagam form, *Eurygnathohippus turkanense*; (5) a larger Hadar hipparion. This diversity of hipparion taxa is not surprising given the four million year temporal range represented by this sample (excluding Höwenegg of course).

Figure 9 depicts three bivariate dimensions for our MT III sample: (a) M1 (maximum length) versus M11 (distal articular breadth); (b) M6 (proximal articular depth) versus M5 (proximal articular breadth); (c) M12 (distal maximal depth of keel) versus M11 (distal maximal articular breadth).

Figure 9a does not include any specimens from the Manonga Valley, but is given here for the sake of completeness. Again, the Upper Nawata has a metatarsal, referable to *Eurygnathohippus turkanense*, that overlaps with the high range of variability in maximum length, but exceeds the distal articular breadth of the Höwenegg hipparion. The one Hadar hipparion has much elevated length and width measurements but would appear to be proportional to the Höwenegg hipparion.

Figure 9b again includes no Manonga Valley forms but reveals that there is a smaller Lothagam form (within the Höwenegg ellipse) and a larger Lothagam form within the upper range of the Hadar sample. Again Hadar exhibits a variability that suggests that more than one species is represented in that sample. The Manonga Valley hipparion sample does include a distal MT III fragment from the Kiloleli Member. This specimen as well as those from Lothagam are

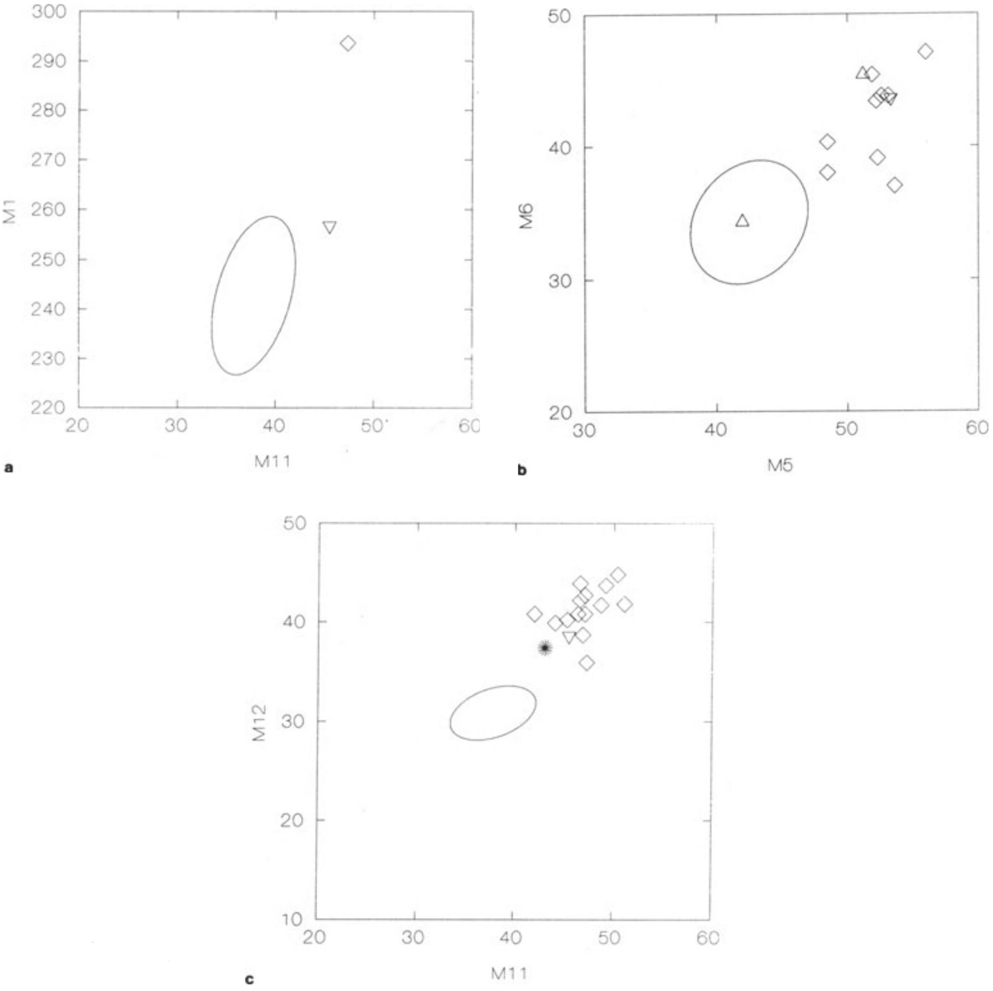

FIGURE 9. MT III's - (a) M1 (maximal length) versus M11 (distal articular breadth); (b) M6 (proximal articular depth) versus M5 (proximal articular breadth); (c) M12 (distal maximal depth of keel) versus M11 (distal maximal articular breadth).

found to be distinctly larger than the Höwenegg hipparion, and fall in the lower portion of Hadar's range of variation.

The information derived from MT III comparisons is quite minimal: (1) the Kiloleli hipparion sample conforms in size with the lower portion of the Hadar range of variability and *Eurygnathohippus turkanense* from Lothagam; (2) a smaller and larger form can be distinguished from Lothagam's Lower Nawata and Upper Nawata members.

5. Discussion

The Manonga Valley hipparions constitute a small assemblage that is critical from a number of standpoints: (1) They span a relatively long period of time, most probably the older horizons are latest Miocene or earliest Pliocene while the younger horizons are medial Pliocene; (2) they apparently represent multiple evolutionary stages; (3) they may represent more than a single species-lineage of the *Eurygnathohippus* clade; and (4) they may, especially, with further collection, document evolutionary changes in this poorly known period of the *Eurygnathohippus* clade's evolution.

East African hipparionine Miocene to mid-Pleistocene evolution has been studied piecemeal over the last 20 years or so. Methodologies have been variously morphologically based or metrically based, and not truly integrated; such an integrated evolutionary reconstruction is long overdue. With this qualification, we present a brief outline of East African hipparionine evolution as we currently understand it. We further qualify that the evolutionary scheme given here recognizes a limited number of cladogenetic events, and the apparent anagenetic record will almost certainly dissipate with more detailed site-by-site analysis.

Through a series of studies on East African hipparions, Hooijer (1975a, b, 1987; Hooijer and Maglio, 1974; Hooijer and Churcher, 1985) recognized a number of hipparion species. Hooijer (1975a, b) reported the early occurrence of *"Hipparion" primigenium* from Members D and E in the Ngorora Formation, Kenya (Bishop and Pickford, 1975; see Hill, 1995 for an updated chronology). This has been corroborated by Bernor (personal observation). Hooijer and Maglio (1973) ascribed the skull (KNM LT-136) from Lothagam's Upper Nawata Member to "*Hipparion*" *turkanense* and noted that this taxon was also present in the Mpesida Beds which have been dated to 6.5 Ma (Hill, 1995). Hooijer and Maglio (1974) also recognized a smaller-bodied hipparion in the Lothagam–Kanapoi–Ekora collection, which they referred to "*Hipparion*" cf. *sitifense.* Hooijer (1975a) classified the East African advanced "*Hipparion*" from Olduvai, BK II, as "*Hipparion*" cf. *ethiopicum* and noted that the lower dentitions of "*Hipparion*" *libycum* and "*Hipparion*" *steytleri* were indistinguishable from this taxon.

Eisenmann (1976, 1983) also identified a number of East African hipparionine taxa. "*Hipparion*" *afarense* was first described from the Denen Dora (DD-2, ca. 3.2 Ma) and Kada Hadar (KH3, ca. 2.9 Ma) members, in the Hadar Formation, Ethiopia (Eisenmann, 1976). Eisenmann (1983) referred an associated lower tooth row (P_4–M_2) from the Kubi Algi Formation, East Turkana, to "*Hipparion*" *hasumense* and suggested that the holotype (KNM-ER 2776) had close affinities to teeth previously ascribed to "*Hipparion*" sp. from the Denen Dora (Eisenmann, 1976) and some of the lower cheek teeth (e.g., KNM-BC 1157) from the Chemeron Formation, Kenya. Further hipparionine remains from the Koobi Fora Formation were attributed to "*Hipparion*" cf. *ethiopicum* and to "*Hipparion*" *ethiopicum* (Eisenmann, 1976), but Eisenmann later assigned the immature cranium, originally referred to "*Hipparion*" cf. *ethiopicum* (KNM-ER 3539), to "*Hipparion*" *cornelianum* (Eisenmann, 1983; but see Bernor and Armour-Chelu, in press for an alternative interpretation).

Churcher and Richardson (1978) summarized all previous work on African hipparionines and followed Hooijer (1975a) and Hooijer and Maglio (1973, 1974) in recognizing "*Hipparion*" *primigenium* as the earliest recorded hipparionine from early late Miocene deposits in North and East Africa, a species that was succeeded by the appearance of "*Hipparion*" *turkanense* and "*Hipparion*" cf. *sitifense* in East Africa during the late Miocene. Churcher and Richardson (1978) considered "*Hipparion*" *libycum* as the advanced Pleistocene hipparion of North, East, and South Africa and they synonymized this taxon with *Libyhipparion ethiopicum* from East Africa and *Stylohipparion steytleri* from South Africa.

Based on preliminary studies of the Ethiopian and Kenyan late Miocene–Pliocene sequences, and a review of the relevant literature (re: Bernor and Armour-Chelu, in press), we generally find the following evolutionary pattern. Hipparionine horses first appeared in East Africa as the product of a rapid migration across Eurasia, North Africa, and East Africa, the so-called Hipparion Datum (Berggren and Van Couvering, 1974; Bernor *et al.*, 1980, 1988; 1989, 1996; Swisher, 1996; Woodburne *et al.*, 1996). The oldest East African hipparions would appear to be represented by a limited sample from Chorora, Ethiopia (ca. 10.5–10.0 Ma), and are referable to *Hippotherium primigenium*. The first recorded occurrence in Kenya is from later age horizons, ca. 9.5 Ma, in the Baringo Basin, (Hill, 1995).

The *Hippotherium primigenium* clade persists as the only identified hipparion in the Kenyan–Ethiopian fossil record until ca. 8–7 Ma when two species of hipparionine occur in the Samburu Hills (Nakaya *et al.*, 1984; Bernor, personal observation). Bernor believes that the specimens from the Samburu Hills belong to the largely Asian–African "*Sivalhippus* complex" and, more specifically, the exclusively African *Eurygnathohippus* lineage. This early occurrence confirms observations reported by Bernor and Lipscomb (1991, 1995) that the *Eurygnathohippus* lineage diverged from Asian "*Sivalhippus*" *perimense* in the medial late Miocene. The likely presence of ectostylids (albeit rare) in the Samburu Hills hipparions permanent mandibular dentition, along with a suite of derived cranial and postcranial morphological features, is likely to confirm the existence of a large and a small lineage referable to the genus *Eurygnathohippus* as early as the 8–7 Ma time range.

The Lothagam sequence (Leakey *et al.*, 1996), likely ranging between 7 and 4.5 Ma (M. G. Leakey, pers. comm.; C. Feibel, pers. comm.) contains two members of the *Eurygnathohippus* lineage, *E. turkanense* and *E. "sitifense,"* both with the variable occurrence of poorly formed ectostylids in the permanent dentition. These two species are distinguished by their marked size differences, particularly in the postcranium. Lothagam also records a rare occurrence of another hipparion, perhaps not dissimilar from earlier members of the *Hippotherium primigenium* lineage (Bernor, in progress).

There is nothing reported or understood about East African hipparion evolution across the Mio-Pliocene border (ca. 5.3 Ma; Steininger *et al.*, 1996). The Lothagam sequence crosses this boundary, but the hipparion record on either side of this boundary is too limited to make any evolutionary generalization. The Middle Awash sequence also crosses the Mio-Pliocene boundary (White, pers. comm.), and the hipparions from here will prove important for documenting evolutionary changes in the *Eurygnathohippus* lineage (Bernor and White, in progress).

The Pliocene East African hipparion record is more extensive and somewhat better understood than the late Miocene one. The Omo sequence (ca. 4.5–2? Ma), Turkana sequence (?3–?1 Ma), Hadar sequence (3.4–2.9 Ma; Walter, pers. comm.), Laetoli sequence (3.8–3.6 Ma; Hay, 1987; Drake and Curtis, 1987; Hooijer, 1987) and Olduvai sequence (1.8–0.6 Ma) comprise an important assemblage in need of further study.

Hooijer (1975a) reported that specimens assigned to *"Hipparion"* sp. in the Shungura Formation (Members B to E) showed increasing crown height and ectostylid expansion, suggesting that they were derived from an evolving population (Hooijer and Churcher, 1985).

The Hadar sequence appears to have a hipparionine of more than one size, and there may have been some evolutionary change through the sequence. Eisenmann (1976) has reported at least two species of hipparion at Hadar. The older, characterized from the Denen Dora (DD) assemblage, was initially identified by a skull (AL 340-8; DD-2) and referred to *"Hipparion"* sp. Later, based on a postcranial skeleton associated with a mandibular dentition (AL 155-6; DD-2), Eisenmann referred the Denen Dora assemblage to *"Hipparion" hasumense*. We provisionally refer the Denen Dora assemblage to a single species, *Eurygnathohippus hasumense*, in the evolving large lineage of the genus *Eurygnathohippus*. The younger species, characterized by a skull and associated mandible from AL 363 (Kada Hadar 3; = KH3; ca. 2.9 Ma.) includes Eisenmann's type specimen of *Hipparion afarense* (= *Eurygnathohippus afarense*; a skull, AL 363-18). The *Eurygnathohippus hasumense - Eurygnathohippus afarense* evolutionary lineage would appear to be the sole, or at least most prevalent, one recorded from the Hadar sequence. It plausibly presages later larger hipparionine forms such as *Eurygnathohippus "ethiopicus"* and *Eurygnathohippus cornelianus* (Bernor and Armour-Chelu, in press).

Hooijer's (1975a) report of evolutionary changes in the Omo sequence records a significant evolutionary change ca. 2.4 Ma (Shungura Member F), wherein crown height increases and incisor morphology shifts. In Shungura Member C (ca. 2.8 Ma) lower cheek tooth specimens attributed to *"Hipparion"* sp. are at least 60 mm high. In the more advanced *"Hipparion" ethiopicum* present from

Member F, ectostylid height is at least 70 mm and crown heights measured over 80 mm (Hooijer and Churcher, 1985). While Hooijer (1975a) synonymized "*H.*" *ethiopicum* with the South African Pleistocene form "*H.*" *cornelianum*, we recognize "*H.*" *cornelianum* as a distinct species, highly derived in its mandibular symphysial and hypertrophied canine morphology. We question the extent of Eisenmann's hypodigm for *Eurygnathohippus cornelianus* and await further study of critical assemblages before a formal reassignment of specimens to this taxon (Bernor and Armour-Chelu, in press). Nevertheless, what emerges from Hooijer's (1975a, 1987), Eisenmann's (1983) and Bernor and Armour-Chelu's (in press) work is that the large *Eurygnathohippus* lineage evolved higher crowned teeth, more massive and pervasive ectostylids, and a highly autapomorphic incisor morphology, whereby in the later stages of evolution, all incisors become uncurved, high-crowned and procumbent, I^{1-2}/I_{1-2} become extremely hypertrophied, grooved and contain a strongly developed lingual pillar, and I_3 becomes atrophied and positioned immediately posterior to I_2. The most derived stages of evolution, referable to *E. cornelianus* s.s. are recorded from Olduvai and Cornelia, Orange Free State, South Africa (Hooijer, 1975a; Bernor and Lipscomb, 1995).

The evolutionary fate of the smaller, slender-limbed *Eurygnathohippus* "*sitifense*" clade is as yet unknown. This lineage is enigmatic from its beginning, in that the type assemblage of *H. sitifense*, from St. Arnaud Cemetery, Algeria, is poorly known and of uncertain chronologic age. The referral of the type species "*H.*" *sitifense* to East African populations is based on roughly similar size and apparent postcranial proportional similarities; critical morphological comparisons with the teeth are lacking (i.e., metaconid/metastylid morphology, presence/absence of ectostylids) and do not allow the certain attribution of this taxon to the *Eurygnathohippus* clade. However, the smaller East African *Eurygnathohippus* "*sitifense*" clade becomes rare in the Pliocene although one very small, new species of hipparion, and potentially a member of this clade, is found from the Middle Awash, in horizons dating to ca 1.0 Ma (White, pers. comm.; Bernor and White, in progress). The last occurrence of hipparions in East Africa appears to be at Olorgesaile, dated ca. 1.0 Ma (Deino and Potts, 1990).

The Manonga Valley hipparionine assemblage includes specimens that exhibit a suite of morphological characters that allow some tentative biochronological correlations. We discuss these relationships sequentially.

The Ibole Member Inolelo 1 locality has a small hipparionine that exhibits a number of characters consistent with the Lothagam small hipparion *Eurygnathohippus* cf. "*sitifense*": upper cheek teeth with thin, blade-like parastyles and mesostyles; crown height primitively ≤ 60 mm and mediolaterally curved; pli caballins single; hypoglyphs with deep incisions. Likewise, the lower cheek teeth of this small form share a number of characters with the Lothagam small hipparion: metaconids rounded; metastylids angular; linguaflexids a deep, broad U-shape; ectostylids poorly developed and diminutive. Shoshamagai 2 has both a larger and a smaller hipparion. The larger form has a broader mesostyle which is posteriorly reflected; cheek teeth also curved; pli caballins single; hypoglyph moderately complex; fossettes more complex than smaller form. The two Ibole

Member hipparion taxa most closely compare with the Lothagam Lower and Upper Nawata hipparions, *Eurygnathohippus turkanense* and *Eurygnathohippus* cf. "*sitifense*," and support a latest Miocene age for this portion of the Manonga Valley assemblage.

The Tinde hipparion assemblage is meager. The only specimen suitable for evolutionary/chronological comparisons is WM 830/94, a mandibular M_1. This specimen exhibits a better-developed ectostylid than seen in the one pertinent larger Ibole Member form, and on this basis alone may indicate a somewhat younger age.

The hipparions from the Kiloleli Member localities exhibit a significant morphological shift and are suggestive of a younger age. The most significant specimen is the cranial fragment, WM 1528/92. The maxilla of this specimen has a snout, incisor, and cheek tooth morphology most similar to AL340-8 from DD-2 at Hadar (ca. 3.2 Ma; Walter, pers. comm.), referred by Eisenmann (1976:580; Fig. 1, p. 592) to "*Hipparion*" sp., but provisionally by the present authors to *Eurygnathohippus hasumense*. The Kiloleli Member dentitions include incisors that most closely compare with those from the Sidi Hakoma and Denen Dora members at Hadar. Likewise, cheek tooth crown height and lower cheek tooth ectostylid development also most closely compare with hipparions from those Hadar members. The Kiloleli Member hipparion P^2s (Figs. 2, 5) are within the middle Hadar size range for length and width. The Kiloleli Member postcrania alternatively compare closely with or differ from the Hadar hipparions in a number of bivariate dimensions. First, the Kiloleli Member radius (Fig. 6) falls well below the Hadar range in length and width measurements, as well as proximal and distal articular breadth and depth measurements. Second, the various astragali measurements (Fig. 7) fall below or within the lower portion of the Hadar range. Third, the MC III (Fig. 8) measurements for length versus distal articular width fall below the Hadar range; for proximal articular depth versus breadth they fall below or in the lower part of the range for Hadar hipparions; for distal maximum depth of keel versus maximum articular breadth they fall distinctly below the Hadar series. The one MT III comparison (Fig. 9c) is consistent with the relevent MC III comparision.

If the Kiloleli and Beredi localities are of closely similar age as interpreted by Verniers (Chapter 2, this volume), then we can conclude that the predominately large hipparion from the Kiloleli Member achieved a skull evolutionary stage equivalent to the Denen Dora hipparion, *Eurygnathohippus hasumense* (in our sense); a lower cheek tooth morphology equivalent to, or slightly more primitive than, the Sidi Hakoma/Denen Dora hipparions and an appendicular skeleton that was less elongate and slightly more gracile in its build. The lack of good, well analyzed hipparion assemblages in the 5–3.4 m.y. age range can only lead us to conclude that the Kiloleli Member hipparions are best correlated with the Hadar Sidi Hakoma–Denen Dora assemblages, ca. 3.4–3.1 Ma, but had shorter and more gracile limbs. This result finds agreement with the Wembere–Manonga Valley paleomagnetic reversal stratigraphy recently completed by John Kappelman.

6. Conclusions

The Wembere–Manonga Valley hipparionine assemblage is a critical one in that it appears to sample evolution of the *Eurygnathohippus* group in the 5+ to 3 m.y. age range. There would appear to be two lineages of this group represented in the sample, a smaller *Eurygnathohippus* cf. "*sitifense*" found in the Ibole Member (and perhaps very limited in the Kiloleli Member), and a larger *Eurygnathohippus* lineage. The hipparions from the Ibole Member have a morphology most comparable to the late Miocene hipparions from the Lower and Upper Nawata Members at Lothagam Hill, Kenya, and are broadly referable to *Eurygnathohippus*. cf. *turkanense* and *Eurygnathohippus* cf. "*sitifense*." The Tinde Member has a very meager hipparion assemblage that appears to have a larger form, perhaps more derived than *Eurygnathohippus* cf. *turkanense*. The Kiloleli Member hipparion assemblage exhibits a stage of evolution most comparable to the Hadar hipparion *Eurygnathohippus hasumense* from the Sidi Hakoma and Denen Dora members, but of distinctly different postcranial proportions. The Kiloleli Member hipparion may be a distinct species, but we believe it most prudent to refer it here to *Eurygnathohippus aff. hasumense*. The elongate slender limbs of this species suggests that it was highly cursorial. The elongate snout suggests that it was a selective feeder, while the hypertrophied and grooved incisors and increased ectostylid height suggests that it was a dedicated grazer which is characteristic of later Pliocene/Pleistocene African hipparions (Bernor and Armour-Chelu, in press).

In conclusion, the assemblage of hipparion remains from the Manonga Valley likely includes two sizes of hipparion and probably samples an earliest–medial Pliocene interval. Further cranial and postcranial remains will be needed to test this chronological hypothesis and better establish biogeographic relationships between East and South Africa.

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Appendixes

Appendix 1: Measurements of Eisenmann *et al.* 1988

SKULL

1. Muzzle length
2. Palatal length
3. Vomerine length
4. Post-vomerine length
5. Post-palatal length
6. Basilar length
7. Premolar length
8. Molar length
9. Upper cheek teeth length
10. Choanal length
11. Minimal breadth of the choanae
12. Maximal breadth of the choanae
13. Palatal breadth
14. Minimal muzzle breadth
15. Muzzle breadth: between the posterior borders of the I^3
16. Length of fossa temporalis: maximal
17. Length between basion and the foramen ethmoidalis
18. Frontal breadth: greatest breadth between orbital processes: compass
19. Bizygomatic breadth: greatest breadth between the most exterior points of the zygomatic arches
20. Occipital breadth: greatest breadth of the supraoccipital crest
21. Basioccipital breadth: greatest breadth at the base of the paroccipital processes
22. Occipital height: from the middle of the dorsal border of the foramen magnum to the middle of the supra-occipital crest
23. Anterior ocular line: from prosthion to the most exterior point of the orbital process
24. Posterior ocular line: from the most exterior point of the orbital process to the middle of the supra-occipital crest
25. Facial height: with the compass, in front of P^2
26. Cranial height: with the compass, at the level of the posterior margin of the orbital process
27. Exterior height of the meatus auditivus externus
28. Anteroposterior orbital diameter
29. Orbital diameter perpendicular to the former

30. Length of the nasoincisival notch: from prosthion to the back of the narial opening
31. Cheek length: from the back of the narial opening to the most anterior point of the orbit
32. Distance between the orbit and preorbital fossa.
33. Length of the preorbital fossa: maximal
34. Distance between the back of the preorbital fossa and the foramen infra-orbitale
35. Height of the preorbital fossa: perpendicular to its maximal length (33)
36. Distance between the preorbital fossa and the facial crest.
37. Height of back of the foramen infra-orbitale above the alveolar border
38. Height of the back of the preorbital fossa above the alveolar border

HUMERUS

1. Maximal length
2. Maximal length from caput
3. Minimal breadth
4. Diameter perpendicular to, and at the level of measurement 3
5. Proximal maximal breadth
6. Proximal depth at the level of the median tubercule
7. Maximal breadth of the trochlea
8. Distal maximal depth
9. Maximal trochlear height (medial)
10. Minimal trochlear height
11. Trochlear height at the sagittal crest

RADIUS

1. Maximal length
2. Medial length
3. Minimal depth
4. Depth of the diaphysis at level of 3
5. Proximal articular breadth
6. Proximal articular depth
7. Proximal maximal breadth
8. Distal articular breadth
9. Distal articular depth
10. Distal maximal breadth
11. Breadth of the radial condyle
12. Breadth of the ulnar condyle

ULNA

1. Maximal length
2. Length of the olecranon
3. Maximal articular breadth
4. Minimal depth of the olecranon
5. Depth across the processus anconaeus

METACARPAL III

1. Maximal length
2. Medial length
3. Minimal breadth (near the middle of the bone)
4. Depth of the diaphysis at level of 3
5. Proximal articular breadth
6. Proximal articular depth
7. Maximal diameter of the articular facet for the third carpal
8. Diameter of the anterior facet for the fourth carpal
9. Diameter of the articular facet for the second carpal
10. Distal maximal supra-articular breadth
11. Distal maximal articular breadth
12. Distal maximal depth of the keel
13. Distal minimal depth of the lateral condyle
14. Distal maximal depth of the medial condyle

ASTRAGALUS

1. Maximal length
2. Maximal diameter of the medial condyle
3. Breadth of the trochlea (at the apex of each condyle)
4. Maximal breadth
5. Distal articular breadth
6. Distal articular depth
7. Maximal medial depth

METATARSAL III

1. Maximal length
2. Medial length
3. Minimal breadth (near the middle of the bone)
4. Depth of the diaphysis at level of 3
5. Proximal articular breadth
6. Proximal articular depth
7. Maximal diameter of the articular facet for the third tarsal
8. Diameter of the anterior facet for the fourth tarsal
9. Diameter of the articular facet for the second tarsal
10. Distal maximal supra-articular breadth
11. Distal maximal articular breadth
12. Distal maximal depth of the keel
13. Distal minimal depth of the lateral condyle
14. Distal maximal depth of the medial condyle

Appendix 2. Measurements in Table 2 and Figures 5–9.

SPEC_ID = specimen number

SPECSHORT = Eu. lg. is a larger member of the *Eurygnathohippus* lineage; Eu. sm. is a smaller member of the *Eurygnathohippus* lineage; indet. is unidentifiable for size.

SITE = 1 is specimens derived from the Ibole Member; 2 from the Tinde Member; 3 from the Kiloleli Member; 4 without stratigraphic proveniance.

SIDE = 1 is for right, 2 is for left side.

Postcranials: ast = astragalus; mciii = MC III; mtiii = MT III; measurements follow Eisenmann *et al.*, 1988.

tx = teeth maxillary: M1 = occlusal length; M2 = base length; M3 = occlusal width; M4 = base width; M5 = mesostyle height; M6 = number of plis on anterior surface of prefossette; M7 = number of plis on posterior surface of prefossette; M8 = number of plis on anterior surface of postfossette; M9 = number of plis on anterior surface of prefossette; M10 = protocone length; M11 = protocone width.

tm = teeth mandible: M1 = occlusal length; M2 = base length; M3 = metaconid-metastylid length; M4 = length of preflexid; M5 = length of postflexid; M6 = occlusal width; M7 = base width; M8 = width across protoconid band/metaconid; M9 = width across hypoconid metastylid; M10 = height of anterior surface; M11 = height of parastylid; M12 = height of ectostylid; M13 = length of ectostylid; M14 = width of ectostylid.

skull = measurements follow Eisenmann *et al.*, 1988.

Appendix 3. Character State Attributions for Tables 3 and 4

Hipparionine Character States (following Bernor *et al.*, 1989 and Bernor & Lipscomb, 1991)

1) Relationship of lacrimal to the preorbital fossa: A = lacrimal large, rectangularly shaped, invades medial wall and posterior aspect of preorbital fossa; B = lacrimal reduced in size, slightly invades or touches posterior border of preorbital fossa; C = preorbital bar (POB) long with the anterior edge of the lacrimal placed more than 1/2 the distance from the anterior orbital rim to the posterior rim of the fossa; D = POB reduced slightly in length but with the anterior edge of the lacrimal placed still more than 1/2 the distance from the anterior orbital rim to the posterior rim of the fossa; E = POB vestigial, but lacrimal as in D; F = POB absent; G = POB very long with anterior edge of lacrimal placed less than 1/2 the distance from the anterior orbital rim to the posterior rim of the fossa; H = POB becomes vestigial, but lacrimal as in G; I = lacrimal as in G. POB absent.
2) Nasolacrimal fossa: A = POF large, ovoid shape and separated by a distinct medially placed, dorsoventrally oriented ridge, dividing POF into equal anterior (nasomaxillary) and posterior (nasolacrimal) fossae;

B = nasomaxillary fossa sharply reduced compared to nasolacrimal fossa; C = nasomaxillary fossa absent (lost), leaving only nasolacrimal portion (when a POF is present).

3) Orbital surface of lacrimal bone: A = with foramen; B = reduced or lacking foramen.
4) Preorbital fossa morphology: A = large, ovoid shape, anteroposteriorly oriented; B = POF truncated anteriorly; C = POF further truncated, dorsoventrally restricted at anterior limit; D = subtriangular shaped and anteroventrally oriented; E = subtriangularly shaped and anteroposteriorly oriented; F = egg-shaped and anteroposteriorly oriented; G = C-shaped and anteroposteriorly oriented; H = vestigial but with a C-shaped or egg-shaped outline; I = vestigial without C-shape outline, or absent; J = elongate, anteroposteriorly oriented; K = small, rounded structure; L = posterior rim straight, with non-oriented medial depression.
5) Fossa posterior pocketing: A = deeply pocketed, greater than 15 mm in deepest place; B = pocketing reduced, moderate to slight depth, less than 15 mm; C = not pocketed but with a posterior rim; D = absent.
6) Fossa medial depth: A = deep, greater than 15 mm. in deepest place; B = moderate depth, 10–15 mm in deepest place; C = shallow depth, less than 10 mm in deepest place; D = absent.
7) Preorbital fossa medial wall morphology: A = without internal pits; B = with internal pits.
8) Fossa peripheral border outline: A = strong, strongly delineated around entire periphery; B = moderately delineated around periphery; C = weakly defined around periphery; D = absent with a remnant depression; E = absent, no remnant depression.
9) Anterior rim morphology: A = present; B = absent.
10) Placement of infraorbital foramen: A = placed distinctly ventral to approximately 1/2 the distance between the preorbital fossa's anteriormost and posteriormost extent; B = inferior to, or encroaching upon anteroventral border or the preorbital fossa.
11) Confluence of buccinator and canine fossae: A = present; B = absent, buccinator fossa is distinctly delimited.
12) Buccinator fossa: A = unpocketed posteriorly; B = pocketed posteriorly.
13) Caninus (= intermediate) fossa: A = absent; B = present.
14) Malar fossa: A = absent; B = present.
15) Nasal notch position: A = at posterior border of canine or slightly posterior to canine border; B = approximately 1/2 the distance between canine and P2; C = at or near the anterior border of P2; D = above P2; E = above P3; F = above P4; G = above M1; H = posterior to M1.
16) Presence of dP1: A = persistent and functional; B = lost early.
17) Curvature of maxillary cheek teeth: A = very curved; B = moderately curved; C = slightly curved; D = straight.
18) Maximum cheek tooth crown height: A = < 30 mm; B = 30–40 mm; C = 40–60 mm; D = > 60 mm maximum crown height.

19) Maxillary cheek tooth fossette ornamentation: A = complex, with several deeply amplified plications; B = moderately complex with fewer, more shortly amplified, thinly banded plications; C = simple complexity with few, shortly amplified plications; D = generally no plis; B = very complex.
20) Posterior wall of postfossette: A = may not be distinct; B = always distinct.
21) Pli caballin morphology: A = double; B = single or occasionally poorly defined double; C = complex; D = plis not well formed.
22) Hypoglyph: A = hypocone frequently encircled by hypoglyph; B = deeply incised, infrequently encircled hypocone; C = moderately deeply incised; D = shallowly incised.
23) Protocone shape: A = round q-shape; B = oval q-shape; C = oval; D = elongate-oval; E = lingually flattened-labially rounded; F = compressed or ovate; G = rounded; H = triangular; I = triangular-elongate; J = lenticular; K = triangular with rounded corners.
24) Isolation of protocone: A = connected to protoloph; B = isolated from protoloph.
25) Protoconal spur: A = elongate, strongly present; B = reduced, but usually present; C = very rare to absent.
26) Premolar protocone/hypocone alignment: A = anteroposteriorly aligned; B = protocone more lingually placed.
27) Molar protocone/hypocone alignment: A = anteroposteriorly aligned; B = protocone more lingually placed.
28) P2 anterostyle (28U)/paraconid(28L): A = elongate; B = short and rounded.
29) Incisor morphology: A = not grooved; B = grooved.
30) Incisor curvature: A = curved; B = straight.
31) I3 lateral aspect: A = elongate, not transversely constricted; B = very elongate, transversely constricted; C = atrophied.
32) Premolar metaconid: A = rounded; B = elongated; C = angular on distal surface; D = irregular shaped; E = square shaped; F = pointed.
33) Molar metaconid: A = rounded; B = elongated; C = angular on distal surface; D = irregular shaped; E = square shaped; F = pointed.
34) Premolar metastylid: A = rounded; B = elongate; C = angular on proximal surface; D = irregular shaped; E = square shaped; F = pointed.
35) Premolar metastylid spur: A = present; B = absent.
36) Molar metastylid: A = rounded; B = elongate; C = angular on mesial surface; D = irregular shaped; E = square shaped; F = pointed.
37) Molar metastylid spur: A = present; B = absent.
38) Premolar ectoflexid: A = does not separate metaconid and metastylid; B = separates metaconid and metastylid.
39) Molar ectoflexid: A = does not separate metaconid and metastylid; B = separates metaconid and metastylid; C = converges with preflexid and postflexid to abutt against metaconid and metastylid.
40) Pli caballinid: A = complex; B = rudimentary or single; C = absent.

41) Protostylid: A = present on occlusal surface; B = absent on occlusal surface, but may be on side of crown buried in cement; C = strong, columnar; D, a loop; E, a small, poorly developed loop; F = a small, pointed projection continuous with the buccal cingulum.
42) Protostylid orientation: A = courses obliquely to anterior surface of tooth; B = less oblique coursing, placed on anterior surface of tooth; C = vertically placed, lies flush with protoconid enamel band; D = vertically placed, lying lateral to protoconid band; E = open loop extending posterolabially.
43) Ectostylids: A = present; B = absent.
44) Premolar linguaflexid: A = shallow; B = deeper, V-shaped; C = shallow U-shaped; D = deep, broad U-shape; E = very broad and deep U-shape.
45) Molar linguaflexid: A = shallow; B = V-shaped; C = shallow U-shaped; D = deep, broad U-shape; E = very broad and deep U-shape.
46) Preflexid morphology: A = simple margins; B = complex margins; C = very complex.
47) Postflexid morphology: A = simple margins; B = complex margins; C = very complex.
48) Postflexid invades metaconid/metastylid by anteriormost portion bending sharply lingually: A = no; B = yes.
49) Protoconid enamel band morphology: A = rounded; B = flattened.

Chapter 9

Fossil Proboscidea from the Wembere–Manonga Formation, Manonga Valley, Tanzania

WILLIAM J. SANDERS

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1. Introduction

Between 1990–1994, the Wembere–Manonga Paleontological Expedition (WMPE) recovered the remains of *Deinotherium, Anancus*, several species from the subfamily Elephantinae, and possibly *Stegotetrabelodon* from fossil localities in the Manonga Valley, north-central Tanzania. The inferred age of these localities is late Miocene–early Pliocene (see below). African proboscideans

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underwent rapid morphological transformation and taxonomic diversification during and subsequent to the late Tertiary, and their fossils are well documented from isotopically calibrated localities (Cooke and Maglio, 1972; Maglio, 1972a, 1973; Coppens *et al.*, 1978; Beden, 1980, 1983, 1987; Hill *et al.*, 1986; Kalb and Mebrate, 1993). Consequently, they have proven particularly useful for biochronological correlation (e.g., Maglio, 1970a; Cooke and Maglio, 1972; Cooke, 1974; Beden, 1983). Evolutionary alterations in the structure of teeth and skulls in African proboscideans since the late Miocene correspond with an adaptive shift from grinding-crushing to more horizontal grinding mastication (in *Anancus*), and an increased emphasis on fore and aft horizontal shearing mastication (in elephants), probably in response to changes in climate, environment, and habitat utilization (Maglio, 1972a,b, 1973, 1974; Cooke, 1984; Beden, 1987; Kalb and Mebrate, 1993). Proboscideans occur in each fossil horizon of the Manonga Valley, and show distinct morphological changes through time. Thus, they provide an important line of evidence for reconstructing the paleoecological record of the Manonga Valley, and for dating sedimentary deposits from that region.

The fossil proboscidean sample from the 1990–1994 field seasons comprises 323 specimens. Of these, 235 are either molars, partial molars, or pieces of incisor. Two specimens are cranial fragments, and two are partial mandibles. Eighty-two catalog entries refer to individual postcranial elements. Two partial skeletons, WM 325/92 from Shoshamagai 2 and WM 840/94 from Beredi South 5, were also collected and cataloged. All of these fossils derive from fine-grained lacustrine sediments of the Wembere–Manonga Formation, which is subdivided into the Ibole, Tinde, and Kiloleli Members (Table I; see Verniers, this volume, Chapter 2). In addition, an elephantine dentary fragment preserving the remnants of several teeth was recovered during paleontological survey of the Tinde area in 1929 (Hopwood, 1931; Harrison and Mbago, this volume, Chapter 1).

In this chapter, molars from the proboscidean sample are described and identified taxonomically. Preliminary review of the material indicates (1) the presence of *Primelephas gomphotheroides*, *Anancus kenyensis*, and possibly *Stegotetrabelodon* in the Ibole Member; (2) the occurrence of *Deinotherium bozasi* and an archaic elephantine species, probably either *P. gomphotheroides* or *Mammuthus subplanifrons*, in the Tinde Member; and (3) the replacement of these taxa by more derived elephantine and anancine gomphothere species in the Kiloleli Member. The former of these has affinities to *Loxodonta exoptata*, and the latter resembles *Anancus* sp. "Sagantole-type," documented from the upper Sagantole Formation, Middle Awash, Ethiopia (Kalb and Mebrate, 1993). The co-occurrence of *Anancus* with elephantines is particularly useful for relative dating of the sediments. Biochronological correlation of proboscideans from the Wembere–Manonga Formation indicates a temporal range of 4.0–6.0 Ma for deposition of the lower fossil-bearing beds, and an approximate age of 3.8 Ma for the Kiloleli Member. The occlusal morphology of taxa in the Ibole and Tinde Members correlates with mixed feeding or browsing in wooded, closed areas, suggesting the presence of such habitats near paleolake Manonga during the late Miocene–early Pliocene. In contrast, parallel development in Kiloleli

Table I. Stratigraphic Distribution of Manonga Valley Proboscideans

		Taxa			
	Member	Deinotheriidae	Gomphotheriidae	Elephantidae	Inferred age (Ma)
Wembere–Manonga Fm.	Kiloleli		*Anancus* cf. *Anancus* sp. (Sagantole-type)	*Loxodonta* cf. *Loxodonta exoptata* ?*Elephas ekorensis*	≈3.8
	Tinde	*Deinotherium bozasi*		Elephantinae, gen.et sp. indet.	4.0–6.0
	Ibole		*Anancus kenyensis*	cf. *Stegotetrabelodon* sp. indet. *Primelephas gomphotheroides*	4.5–6.0
Mwansarara Formation					
Precambrian Basement					

Member proboscideans of derived occlusal traits, such as greater hypsodonty and cementum deposition, is consistent with feeding in more open conditions and possibly increased exploitation of coarser foliage, including grasses.

2. Terminology and Measurements

Terms used in this chapter to describe proboscidean teeth follow Maglio (1973), Tobien (1973), Kalb and Mebrate (1993), and Tsoukala and Melentis (1994). The measurements and indices used in the present study, and the procedures used to obtain them, are taken from Maglio (1973). These are standard for quantitative evaluation of proboscidean molars (see Kalb and Mebrate, 1993), and are summarized in Table II.

Deinothere molars are either bi- (M2–3) or trilophodont (M1), composed of continuous, low transverse ridges. From anterior to posterior, these ridges are

Table II. Abbreviations of Measurements and Terms Used in the Text and Table III

Abbreviation	Measurement or term
P	Number of plates (in elephants)
L	Molar length—measured perpendicular to the average lamellar plane
W	Molar width—taken across the widest plate, ridge, or loph(id), including cementum
H	Maximum molar crown height—measured parallel to the vertical axis of the plate, ridge, or loph(id) from the base of the enamel covering to the apex of the tallest conelet or pillar (greatest width and height of a molar may occur on different plates, ridges, or loph(id)s)
ET	Enamel thickness—averaged from a series of measurements taken on worn enamel figures of plates along the molar
HI	Hypsodonty index—an index of relative molar crown height, represented as H × 100/W
LF	Lamellar frequency—the number of plates per 10 cm, averaged from measurements taken at the base and apex along both sides of the molar
+	Indicates a missing portion of a molar
x	Anterior or posterior platelets or crescentoids not constituting full plates (an elephant molar with seven plates and a posterior platelet, but broken anteriorly, has a plate formula of "+7x")
C	Accessory intravalley columns or conules
P1, P2, . . .	Plates, ridges, or loph(id)s counted from the anterior end of the tooth
PI, PII, . . .	Plates, ridges, or loph(id)s counted from the posterior end of the tooth
M	Molar—"M/" refers to an upper molar and "/M" to a lower molar
dP	Deciduous premolar
I	Incisor—"/I" refers to a lower incisor
pre	Pretrite half-loph(id)
post	Posttrite half-loph(id)
BMNH	Natural History Museum, London (formerly "British Museum [Natural History]")
WM	Prefix for Manonga valley specimens, housed in the National Museums of Tanzania (Dar es Salaam)
MMK	Accession designation, McGregor Memorial Museum (Kimberly, South Africa)
KNM	Accession designation, Kenya National Museum (Nairobi)
LT	Prefix for Lothagam Hill specimens
LU	Prefix for Lukeino specimens

labeled protoloph(id), metaloph(id), and tritoloph(id). Cingula may be present anteriorly and posteriorly.

Anancus molars are constructed of a series of alternating and interlocking half-loph(id)s, separated by a median longitudinal sulcus and roughly aligned as oblique transverse ridges. Each half-loph(id) consists of a variable number of conelets. "Pretrite" refers to the more worn half of each loph(id), which is buccal in lower molars and lingual in upper molars; "posttrite" refers to the corresponding half of each loph(id) (Tobien, 1973, p. 119). Loph(id)s are separated anteroposteriorly by transverse valleys. Accessory conules may be present in the transverse valleys, usually toward the midline of the tooth. *Anancus* molars may also have small conelets arranged into an anterior crescentoid at the front of molars, or forming talon(id)s posteriorly. Cementum is variably developed between the loph(id)s.

Elephant molars consist of a series of parallel transverse plates made up of fused pillars, which are superficially subdivided into apical digitations. Worn plates form continuous enamel loops. Median longitudinal clefts are absent or weakly expressed in elephantines (*sensu* Maglio, 1973). Plates are connected at their bases, but otherwise are separated anteroposteriorly by transverse valleys, which may be covered or filled with cementum. Accessory intravalley columns (= accessory conules of *Anancus*) are variably expressed.

3. Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Proboscidea Illiger, 1811
Suborder Deinotherioidea Osborn, 1921
Family Deinotheriidae Bonaparte, 1845
Genus *Deinotherium* Kaup, 1829

3.1. *Deinotherium bozasi* Arambourg, 1934

Referred Specimens, Tinde Mbr. Ngofila 5:WM 834/94, left M^1 or M^2, anterior cingulum, protoloph and metaloph (Fig. 1).

Description. WM 834/94 is an unworn, but damaged, left upper molar, probably M^1, preserving an anterior cingulum, protoloph, and part of a metaloph (Fig. 1A,B,C). The tooth is broken along its buccal and posterior margins. In addition, the metaloph is expanded anteroposteriorly by a vertical crack filled with sediment, and enamel is spalled off of the anterior face of the protoloph. In lateral view, the lophs are triangular, broad at their bases, and low (Fig. 1A). They are separated by a wide, V-shaped transverse valley. The anterior cingulum juts forward as a prominent ledge. The lophs exhibit no pillars or columns, and apically form continuous transverse ridges (Fig. 1B,C). These features are characteristic of unworn molars in deinotheres (see Harris, 1975, 1978; Tsoukala and Melentis, 1994). Widths across the cingulum, protoloph, and metaloph are 84.9+

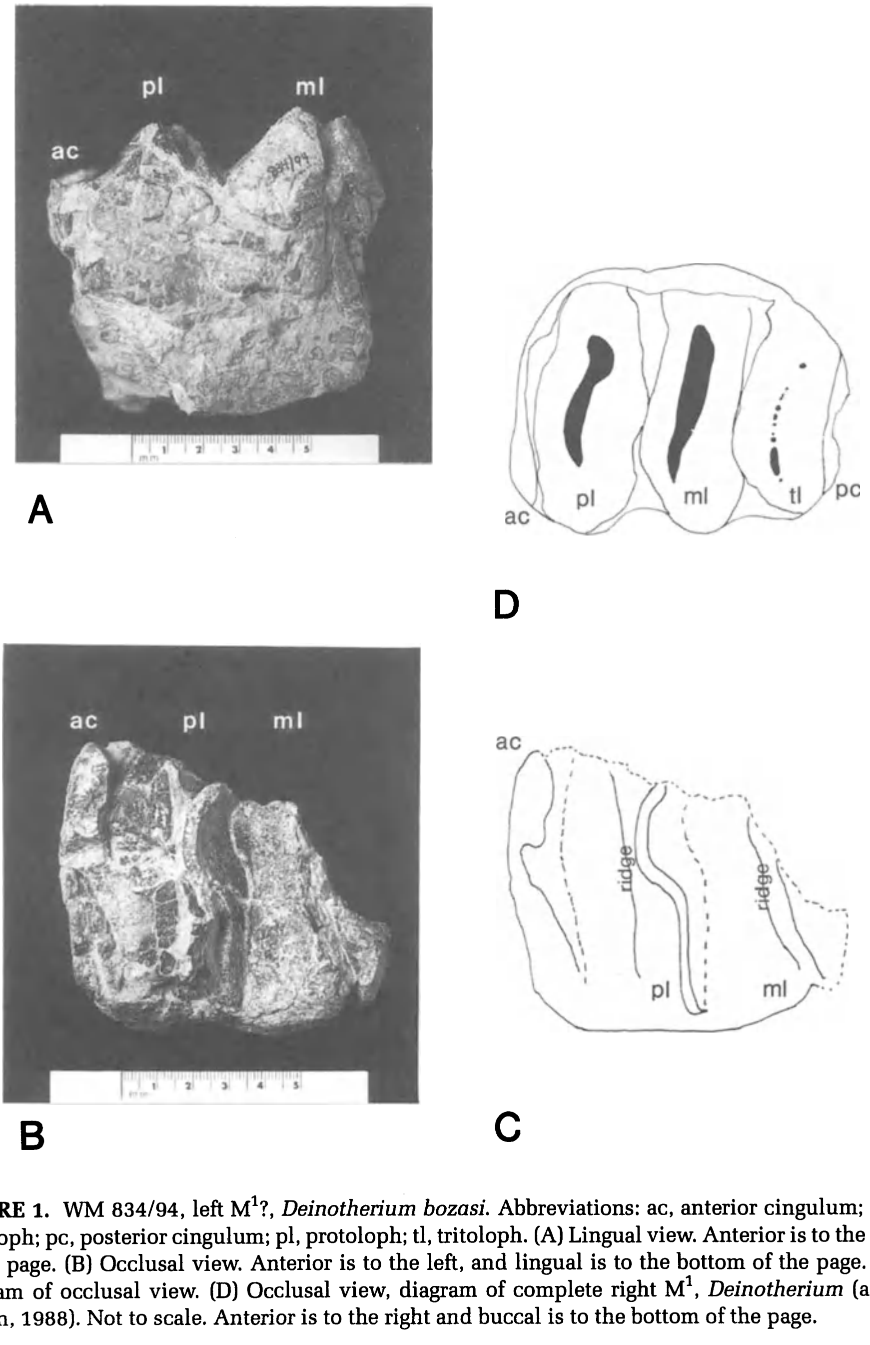


FIGURE 1. WM 834/94, left M^1?, *Deinotherium bozasi.* Abbreviations: ac, anterior cingulum; ml, metaloph; pc, posterior cingulum; pl, protoloph; tl, tritoloph. (A) Lingual view. Anterior is to the left of the page. (B) Occlusal view. Anterior is to the left, and lingual is to the bottom of the page. (C) Diagram of occlusal view. (D) Occlusal view, diagram of complete right M^1, *Deinotherium* (after Tobien, 1988). Not to scale. Anterior is to the right and buccal is to the bottom of the page.

mm, 80.0+ mm, and 73.6+ mm, respectively. Length of the crown is 95.0+ mm, and height of the metaloph is 41.0 mm. Enamel thickness averages 3.9 mm.

In occlusal view, the protoloph has a flattened S-shape; its posterior face is buccally concave and lingually convex (Fig. 1B,C). In deinotheres, this feature is most pronounced in M^1 (Fig. 1D; see also Harris, 1983, Pl. 2.5; Tobien, 1988, Pl. 4, Pl. 5 fig. 22; Tsoukala and Melentis, 1994, Pl. 1b). The transverse valley is broadest at the lingual side of the crown. Deinothere M1s have three transverse loph(id)s (Fig. 1D; Harris, 1975); if WM 834/94 is an M^1, it is missing its tritoloph.

The family Deinotheriidae is successively represented in Africa during the Miocene–early Pleistocene by *Prodeinotherium hobleyi* and *Deinotherium bozasi* (Harris, 1975, 1976, 1978, 1983). WM 834/94 is similar in morphology and size to M^1s in *Deinotherium*, and exceeds the dimensions of molars in *Prodeinotherium* (Harris, 1973, 1976, 1978, 1983). Thus, WM 834/94 is assigned to *D. bozasi.*

Suborder Elephantiformes Tassy, 1988
Family Gomphotheriidae Hay, 1922
Genus *Anancus* Aymard, 1855

3.2. *Anancus kenyensis* (MacInnes, 1942)

Referred Specimens, Ibole Mbr. Shoshamagai 2:WM 1046/92, molar fragment, five loph(id) pieces; WM 1088/92, right M_2?, posterior two lophids; WM 1089/92, right M^3?, posteriormost two lophs and talon; WM 1097/92, molar fragment, parts of three half loph(id)s; WM 1800/92, mandible with left and right dP_4s, left and right M_1s (Fig. 3), and left M_2 (incompletely formed in crypt) (Fig. 4); WM 307/94, right M_3?, parts of anterior crescentoid and first two lophids; WM 554/94, molar fragment, parts of several loph(id)s.

Inolelo 1:WM 1012/92, right M^2?, posteriormost two lophs and talon; WM 1017/92, molar fragment, parts of two loph(id)s; WM 148/94, left M^3 (Fig. 2).

Inolelo 3:WM 1199/92, molar fragment, parts of two loph(id)s; WM 673/94, molar fragment, parts of several loph(id)s.

Mwambiti 3:WM 1413/92, left dP_4, parts of four lophids (Fig. 5).

Description. WM 148/94 is a complete left M^3. Although its occlusal surface is heavily excavated by wear, it is possible to discern the outline of five lophs and a large talon (Fig. 2A). Anteriorly, the first two lophs are supported by two sharply curved roots that diverge laterally (Fig. 2B). A stouter posterior root supports the remainder of the crown. Crown length is 160.5 mm, and greatest width is 73.6 mm at P4. Enamel remains only on the posteriormost loph and talon. It is unfolded, and ranges in thickness from 4.3 to 5.5 mm. Each half-loph of P5 appears to be formed of two conelets. A sizable anterior conule is incorporated into the worn pretrite half-loph of P5 (Fig. 2A). The talon is composed of eight conelets in close formation. There is no interproximal facet on the posterior face of the tooth.

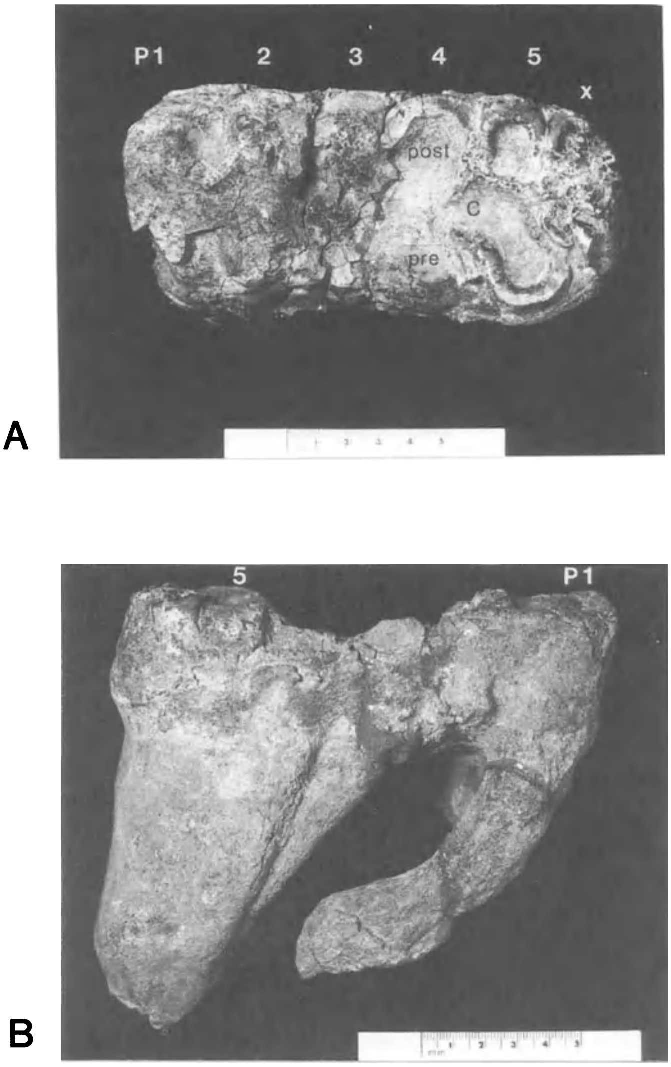


FIGURE 2. WM 148/94, left M^3, *Anancus kenyensis*. Abbreviations: C, accessory conule; P1, 2, . . . , loph 1, loph 2, . . . ; pre, pretrite half-loph; post, posttrite half-loph; x, talon. (A) Occlusal view. Anterior is to the left, and lingual is to the bottom of the page. (B) Buccal view. Anterior is to the right of the page.

The worn condition of WM 148/94 makes it difficult to assess its structural affinities with *Anancus* from other East African localities. Nonetheless, its thick, unfolded enamel and possession of five lophs suggest that it is from a relatively primitive form of *A. kenyensis* (Mebrate and Kalb, 1985; Kalb and Mebrate, 1993). In morphology and size, WM 148/94 is similar to M^{3}s of *A. kenyensis* from Lukeino (Tassy, 1986, Table 17).

WM 1800/92 is the most complete proboscidean mandible collected by the WMPE. It is composed of partial left and right dentaries, an intact symphysis, left and right dP_4s, M_1s, and an unerupted, incompletely formed left M_2. The anterior symphysis is blunt and shows no trace of lower incisors. Absence of mandibular tusks and abbreviated symphyses are characteristic of *Anancus* (Coppens *et al.*, 1978).

The dP_4s are very worn anteriorly, but nonetheless show evidence of large anterior crescentoids and four lophids. The length of these teeth on the left and

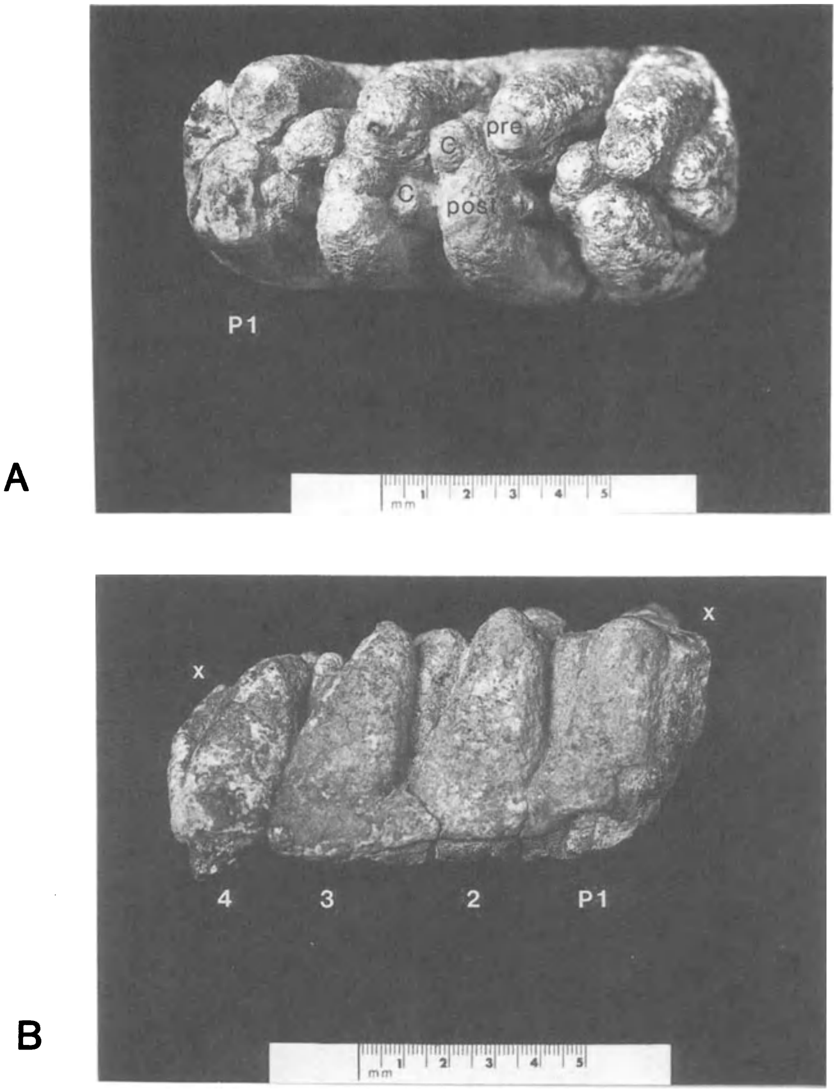


FIGURE 3. WM 1800/92, right M_1, *Anancus kenyensis*. Abbreviations: C, accessory conule; P1, 2, . . . , lophid 1, lophid 2, . . . ; pre, pretrite half-lophid; post, posttrite half-lophid; x, anterior crescentoid, talonid. (A) Occlusal view. Anterior is to the left, and lingual is to the bottom of the page. (B) Buccal view. Anterior is to the right of the page.

right sides is +87.3 mm and +91.4 mm, respectively. On each side, greatest width is 52.0 mm at P3. The posttrite half-lophids, at least of P2 and P3, are formed of two conelets, while the pretrite half-lophids have one conelet. Each lophid was apparently accompanied by single posterior pretrite and posttrite conules. The right dP$_4$ ends in a posterior conule, which is incorporated into the pretrite half-lophid of P4. Enamel is unfolded and ranges in thickness from 4.2 to 5.0 mm.

Both M$_1$s are complete and only slightly worn anteriorly. These molars have four lophids, accompanied by well-developed anterior crescentoids and small talonids (lophid formula = x4x) (Fig. 3A,B). The length of the left M$_1$ is 126.9

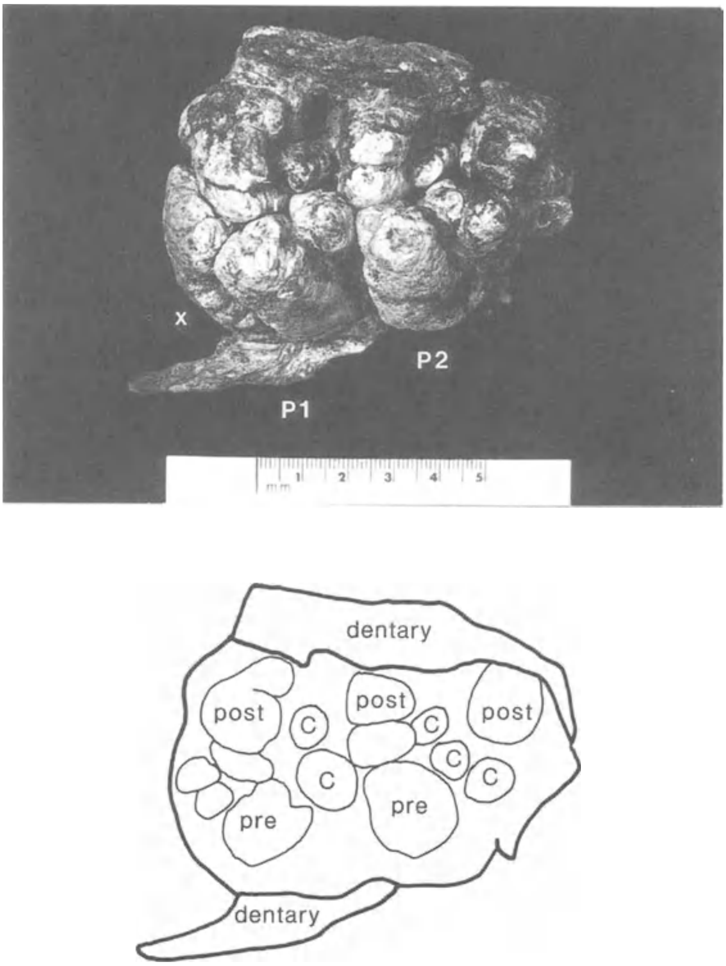


FIGURE 4. WM 1800/92, left M$_2$, *Anancus kenyensis*. Abbreviations: C, accessory conule; P1, lophid 1; P2, lophid 2; pre, pretrite half-lophid; post, posttrite half-lophid; x, anterior crescentoid. Occlusal view. Anterior is to the left, and lingual is to the top of the page.

mm, and the right M_1 is 124.6 mm. Greatest width of the right M_1 is 65.0 mm at P3, and unworn crown height measures 57.3 mm on the pretrite side of P3. Posttrite half-lophids are composed of one or two conelets, and pretrite half-lophids each have a single, stout conelet. The talonid is formed of two moderate-size conelets. P1 and P2 have single posterior posttrite and pretrite accessory conules, and P3 has a single small posterior posttrite conule and a large, doubled posterior pretrite conule (Fig. 3A). There is no cementum on these molars.

The left M_2 was developing in its mandibular crypt, and therefore is not complete (Fig. 4). It exhibits an anterior crescentoid and two and one-half lophids. At P1, greatest width measures 65.0 mm, and height on the pretrite side is 56.7 mm. The posttrite half-lophids have three conelets at P1, and two conelets at P2 and P3. On the pretrite side, the half-lophids are made up of two conelets of unequal size. Posterior conules are present behind each half-lophid of P1 and P2 (Fig. 4).

On the basis of lophid formulae of its intermediate molars (dP_4–M_1), WM 1800/92 is a tetralophodont *Anancus* (see Kalb and Mebrate, 1993). In this and

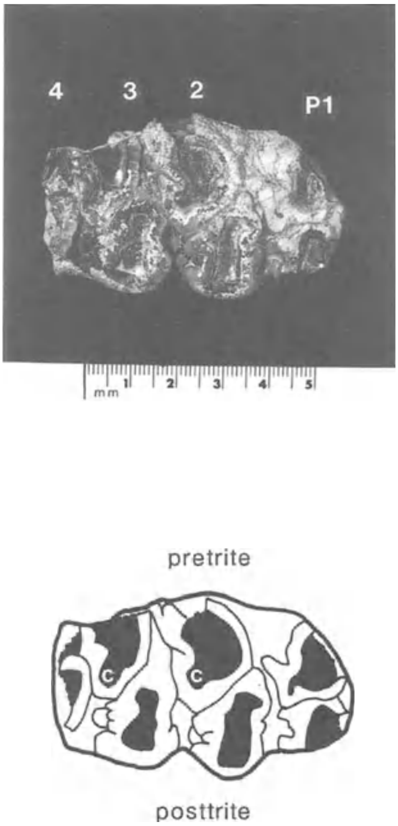


FIGURE 5. WM 1413/92, left dP_4, *Anancus kenyensis*. Abbreviations: C, accessory conule; P1, 2, . . . , lophid 1, 2 . . . Occlusal view. Anterior is to the right, and lingual is to the bottom of the page.

other traits, such as lack of cementum, simple development of talonids, conservative expression of accessory conules, and the presence of thick, unfolded enamel, WM 1800/92 is comparable to other primitive forms of *Anancus kenyensis.* These features also characterize the rest of the *Anancus* molar sample from the Ibole Mbr. Morphologically, the closest affinities of WM 1800/92 are broadly with *A. kenyensis* from Lukeino, Kanam East and West, and the upper Adu-Asa Fm. (MacInnes, 1942; Tassy, 1986; Kalb and Mebrate, 1993).

WM 1413/92 is a worn, posteriorly broken left dP_4 (Fig. 5). It preserves parts of four lophids, a trace of an anterior enamel fold, and stubs of an anterior root under P1 and a more substantial root under P3–P4. The specimen measures 68.8+ mm in length, and is 43.0 mm wide at P2. Posterior conules have been incorporated by wear into their respective pretrite half-lophids. Small enamel "buds" (= accessory conules?) are situated posterior to the posttrite half-lophids. Enamel ranges in thickness from 3.0 to 4.0 mm, and is weakly folded. Structurally, this specimen fits well with the molar series in WM 1800/94.

3.3. *Anancus* cf. *Anancus* sp. (Sagantole-type)

Referred Specimens, Kiloleli Mbr. Kiloleli 3:WM 927/92, right M^3?, parts of posteriormost two lophs and talon (Fig. 6).

Ngofila 1:WM 493/94, molar fragment, parts of three loph(id)s.

Ngofila 2:WM 791/94, molar fragment, parts of two loph(id)s.

Beredi South 3:WM 1706/92, molar fragment, five loph(id) pieces.

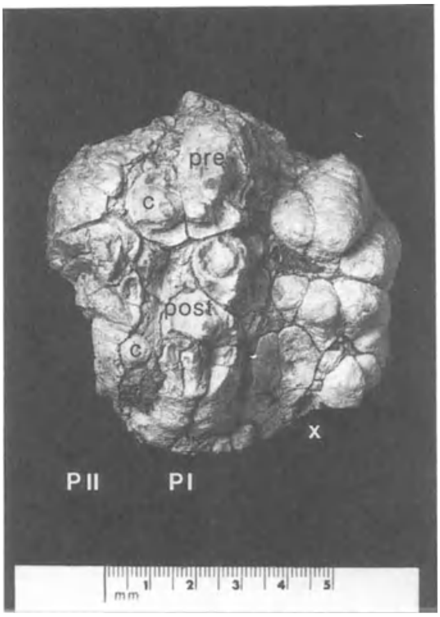


FIGURE 6. WM 927/92, right M^3?, *Anancus* cf. *Anancus* sp. (Sagantole-type). Abbreviations: C, accessory conule; PI, last loph; PII, penultimate loph; pre, petrite; post, posttrite; x, talon. Occlusal view. Anterior is to the left, and buccal is to the bottom of the page.

Description. WM 927/92 is a weathered and pitted, but unworn, posterior molar segment (Fig. 6). It preserves portions of the last two lophs, and a talon. At PI, width is 83.0 mm and height is 44.0+ mm. Each half-lophid is constructed of two conelets, and accessory conules are present on both the pretrite and posttrite side between PI and PII. Sectioning of the crown reveals that the enamel is thick (5.5–5.8 mm) and strongly folded. Cementum fills the spaces around the conelets and conules. The talon is large and complex, with numerous conelets.

Other molars in the *Anancus* sample from the Kiloleli Mbr. are morphologically similar to WM 927/92. The presence of cementum, degree of enamel folding, and talon(id) complexity in these specimens suggest that they are from a more derived form of *Anancus* than is found in the Ibole Mbr. Morphologically, the *Anancus* sample from the Kiloleli Mbr. is comparable to molars from a progressive species of *Anancus* (*Anancus* sp. [Sagantole-type]) from the upper Sagantole Fm., Middle Awash (see Kalb and Mebrate, 1993, Fig. 17).

Family Elephantidae Gray, 1821
Subfamily Stegotetrabelodontinae Aguirre, 1969

3.4. cf. *Stegotetrabelodon* Petrocchi, 1941

Referred Specimens, Ibole Mbr.: Lubeho:WM 110/94, left dentary fragment with left M_3 (Fig. 9) and associated right M_3 (Figs. 7 and 8) and isolated tusk, left molar with anterior platelet and anterior five plates, right molar with anterior platelet and anterior four plates.

Description. WM 110/94 includes a left dentary fragment with a partial M_3 in place, and an isolated partial right M_3. The right M_3 conserves a trace of an anterior fold of enamel, P1-P3, and half of P4 (Fig. 7A). Posterior view of the specimen shows the plates to be broad and low (Fig. 8A and Table III). In occlusal view, the plates are worn into enamel loops that are transversely nearly straight (Fig. 7A). Indentations on the vertical faces of P3 indicate that in a less worn condition it exhibited seven apical digitations. In lateral view, the plates are basally thick, pyramidal, and separated by deep V-shaped valleys (Fig. 7B). Because the plates are massive, lamellar frequency is low (Table III and Fig. 10). Cementum is largely abraded away, but still partially fills the valleys. Enamel is moderately thick (Table III and Fig. 10), and unfolded. Prominent posterior columns (C) occupy the valleys between each plate, and abut against the plates anterior to them. Thus, C1 is fused to P1, C2 to P2, and so on. The left M_3 preserves an additional plate, and has a posterior column (C4) between P4 and P5. A longitudinal break through the dentary reveals that this molar has a large, stout posterior root, a small root beneath P3 and P4, and a long, narrow root under P1 and P2 that curves strongly backward.

The dentary of WM 110/94 (Fig. 9A, B) is missing its ascending ramus and much of its posterior corpus. The surviving section of the corpus, including the symphyseal part, measures 400.0 mm. Anteriorly, the corpus is turned downward at an angle of 17°, for a length of +130.0 mm. Evidently, the symphyseal

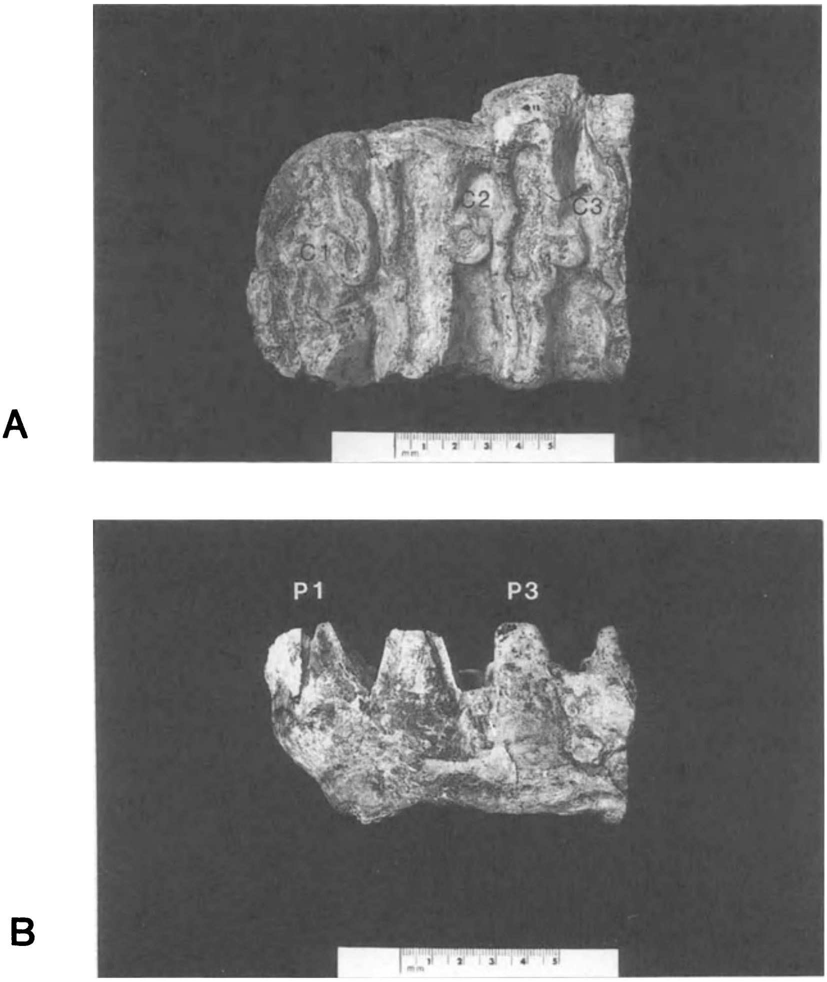


FIGURE 7. WM 110/94, right M_3, cf. *Stegotetrabelodon*. Abbreviations: C1, C2, C3, posterior accessory conules associated with plates 1, 2, and 3; P1, plate 1; P3, plate 3. (A) Occlusal view. Anterior is to the left, and lingual is to the bottom of the page. (B) Lingual view. Anterior is to the left of the page.

region was relatively long. At M_3, the dentary has a height of 140.0 mm and width of 100.0 mm. A mandibular foramen is situated at a point two-thirds the height of the dentary and below the first plate of the M_3. Numerous incisor fragments were found with the dentary, and appear to have formed a tusk of modest girth and length. However, damage to the anterior portion of the dentary makes it difficult to determine with certainty whether it had an alveolus to accommodate a lower incisor. This is unfortunate, as mandibular incisors have important implications for elephantid systematics. Within the Elephantidae, the genus *Stegotetrabelodon* is characterized by the presence of moderately to very long lower tusks (Coppens *et al.*, 1978), whereas the development of lower tusks in *Primelephas* is controversial (Maglio, 1970b, 1973; Maglio and Ricca, 1977; Tassy, 1986; Kalb and Mebrate, 1993; Kalb *et al.*, 1996) and does not normally occur in other elephantines. For this reason, WM 110/94 is referred to *Stegotetrabelodon* for comparison. However, the formation of full enamel loops with only moderate plate wear (which is a progressive feature), and retention of posterior columns behind each plate (which is probably a primitive trait), suggest that this specimen represents a (possibly new) form of *Stegotetrabelodon* different from the Mio-Pliocene East African species *Stegotetrabelodon orbus* (see Coppens *et al.*, 1978).

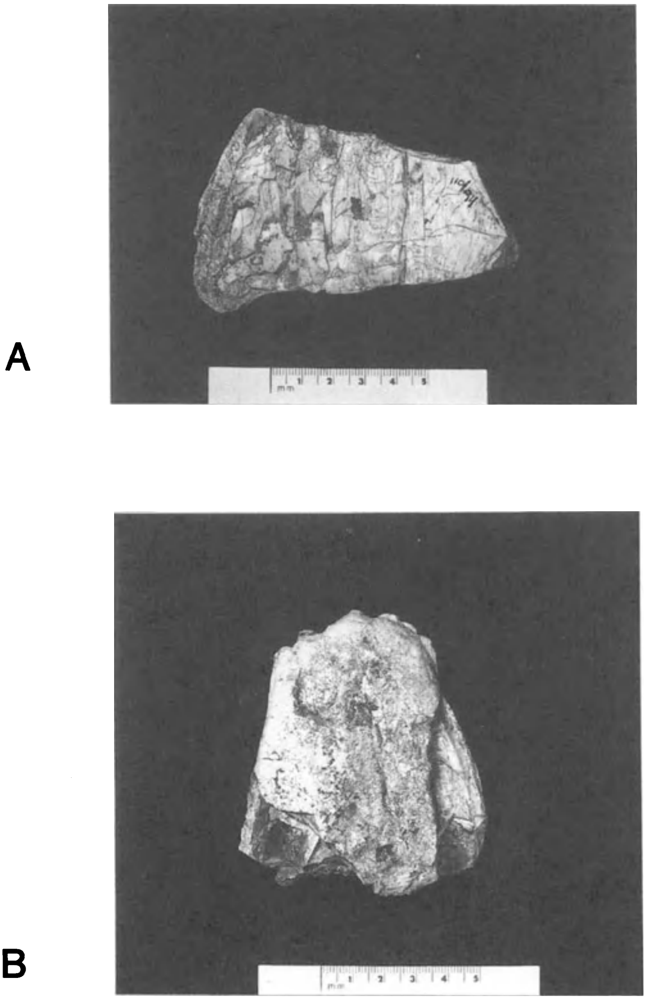


FIGURE 8. (A) WM 110/94, right M_3, cf. *Stegotetrabelodon*. Posterior view, cross-section of plate 4. Lingual is to the left of the page. (B) WM 904/92, isolated plate, *Loxodonta* cf. *Loxodonta exoptata*. Posterior view, plate cross-section.

Table III. Comparison of Dimensions (in mm) and Indices of M3s in Selected Primitive Elephantines and in Fossils from the Wembere–Manonga Formation, Manonga Valley, Tanzania

Species/specimen	Horizon/locality	Molar	P	L	W	H	HI	LF	ET
Primelephas gomphotheroides[1] (species mean and range)		M^3	7	208.0 208.0–208.1	96.1 86.9–109.5	57.6 52.1–60.1	61.3 57.0–63.8	3.3 3.0–3.7	4.9 4.3–5.5
KNM-LT 351[a] *P. gomphotheroides* (type)[1,2]	Lothagam 1, Lothagam Hill, Kenya	r. M^3	7x	208.0	94.3	60.1	63.8	3.2	4.3–5.6
KNM-LT 351[a] *P. gomphotheroides* (type)[1,2]	Lothagam 1, Lothagam Hill, Kenya	l. M^3	7x	208.1	93.8	59.5	63.4	3.2	3.4–5.2
KNM-LU 58 *P. gomphotheroides*[3]	Lukeino Fm., Baringo Basin, Kenya	l. M^3	5+	190.0+	99.0+	57.0	≤57.6	3.6	5.6–7.0
M 25160[a] *P. gomphotheroides*[1,4]	Kaiso Fm., Nyawiega, Uganda	l. M^3	+4	+112.2	104.0	52.1	50.0	3.7	4.0–4.9
Mammuthus subplanifrons[1] (species mean and range)		M^3	7.5 7–8	215.3 202.8–229.2	96.9 81.0–122.0	67.8 49.0–85.0	74.5 56.3–91.0	3.3 2.6–4.1	4.0 3.4–5.0
M15410 *M. subplanifrons*[1,5]	Kanam East, Kenya	l. M^3	+7x	213.3	114.2	59.2+	51.8+	3.0	—
L27-1b *M. subplanifrons*[6,7]	Sagantole Fm., Middle Awash, Ethiopia	l. M^3	+5+	154.0+	102.0	91.0	89.0	3.0	2.0–4.0
WM 1093-92	Ibole Mb., Shoshamagai 2, Manonga, Tanzania	l. M3	x7x	235.0	94.3	54.6	58.0	3.2	(unworn)
WM 1099-92	Ibole Mb., Shoshamagai 2, Manonga, Tanzania	r. M^3	7x	—	92.7	—	—	—	(unworn)
WM 1232-92	Ibole Mb., Inolelo 3, Manonga, Tanzania	r. M^3	+5x	+170.8	99.1	56.0+	56.5+	3.4	4.9–5.6
WM 1794-92	Ibole Mb., Shoshamagai 2, Manonga, Tanzania	l. M^3	+3x	+96.5	84.7	54.0	—	—	5.4

Primelephas gomphotheroides[1,2] (species mean and range)		M_3	7.5 7–8	247.5 —	94.5 89.2–103.0	60.4 52.8–68.0	63.8 59.2–66.0	3.1 3.1–3.3	4.9 4.3–5.4
KNM-LT 351[a] *P. gomphotheroides*[1,2] (type)	Lothagam 1, Lothagam Hill, Kenya	l. M_3	8x	247.5	93.2	61.2	65.6	3.3	3.5–5.1
KNM-LU 7597 *P. gomphotheroides*[3]	Lukeino Fm., Baringo Basin, Kenya	l. M_3	9x	279.4	107.6	—	—	3.5	—
Chemeron[a] no # *P. gomphotheroides*[1,5]	Chemeron Fm, Baringo Basin,Kenya	l. M_3	x7x	242.6	96.2	59.6	61.9	3.1	4.5–5.3
L302-1, *P.* cf. *gomphotheroides*[7]	Adu-Asa Fm., Middle Awash, Ethiopia	r. M_3	8x	219.0	97.0	65.0+	67.0+	3.6	4.0–5.0
Mammuthus subplanifrons[1] (species mean and range)		M_3	8.5 8–9	292.0 259.0–325.1	94.4 88.5–111.5	67.4 45.0–80.9	72.7 59.0–89.0	3.5 3.1–4.3	4.5 3.5–5.5
Ishasha, no # *M. subplanifrons*[8]	Kaiso Fm., Ishasha, Zaïre	l. M_3	+4+	—	109.6	60.0[c]	54.7[c]	3.2	3.7
L27-1a *M. subplanifrons*[6,7]	Sagantole Fm., Middle Awash, Ethiopia	l. M_3	x8x	254.0	101.0	77.0	76.2	3.6	4.0–5.0
L210 *M. subplanifrons*[6]	Adu-Asa Fm., Middle Awash, Ethiopia	r. M_3	+4+	+133.0+	96.0	64.0+	66.6+	4.0	3.0–4.0
MMK 3920[b] *M. subplanifrons*[1] (type)	Vaal River, South Africa	r. M_3	+5x	+151.0	102.0	80.0[c]	78.4[c]	3.7	3.0–4.0
MMK 4334 *M. subplanifrons*[1]	Vaal River, South Africa	r. M_3	+5x	+181.0	104.0	75.0[c]	72.7[c]	3.1	4.0–5.0
MMK 4333[b] *M. subplanifrons*[1]	Vaal River, South Africa	l. M_3	8x	259.0	105.0	70.0	66.7	3.2	3.7–4.0
M 15411 (K.E.1)[b] *M. subplanifrons*[5,9]	Kanam East, Kenya	l. M_3	+5x	218.5+	87.0+	41.0+	—	3.0	4.0–6.0

(continued)

Table III. (Continued)

Species/specimen	Horizon/locality	Molar	P	L	W	H	HI	LF	ET
L 12723B[b] *M. subplanifrons*[10,11,12]	Varswater Fm., Langebaanweg, South Africa	l. M_3	x9x	325.0	112.0	76.0	67.9	3.2	4.1–5.6
KNM-LU 67, cf. *Loxodonta* sp.[3]	Lukeino Fm., Baringo Basin, Kenya	r. M_3	x8x	220.0	86.5	—	—	4.2	3.7–4.1
WM 1106-92	Ibole Fm., Shoshamagai 2, Manonga, Tanzania	r. M_3	x7x	229.0	88.4	56.0	63.3	3.5	4.0–5.0
WM 110-94	Ibole Fm; Lubeho, Manonga, Tanzania	r. M_3	x4+	119.3+	107.6	66.2+	61.5+	3.0	4.4–5.4
WM 110-94	Ibole Fm., Lubeho, Manonga, Tanzania	l. M_3	x5+	160.0+	99.2+	—	—	3.0	4.8–5.1

Abbreviations: P, number of plates; L, length; W, width; H, height; HI, hypsodonty index; LF, lamellar frequency; ET, enamel thickness.

Sources: 1. Maglio (1973); 2. Maglio (1970b); 3. Tassy (1986); 4. Cooke and Coryndon (1970); 5. Collections note, Natural History Museum, London; 6. Kalb and Mebrate (1993); 7. Mebrate (1977); 8. Vanoverstraeten *et al.* (1990); 9. MacInnes (1942); 10. Maglio and Hendey (1970); 11. Hendey (1978); 12. Hendey (1982).

[a] Specimen included in Maglio's (1973) calculations of mean and range for *P. gomphotheroides.*

[b] Specimen included in Maglio's (1973) calculations of mean and range for *M. subplanifrons.*

[c] Estimated.

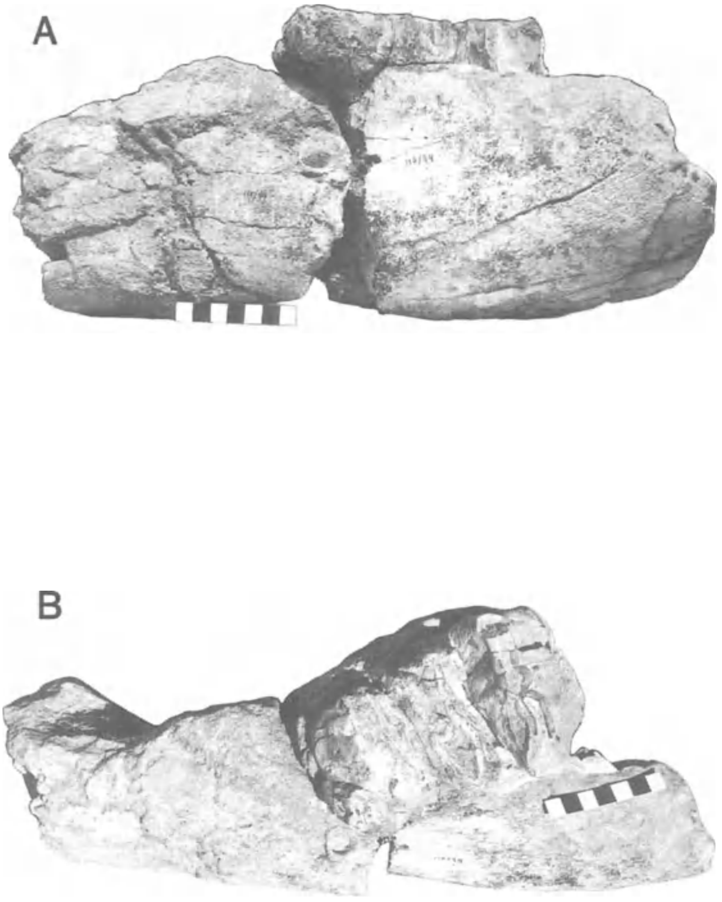
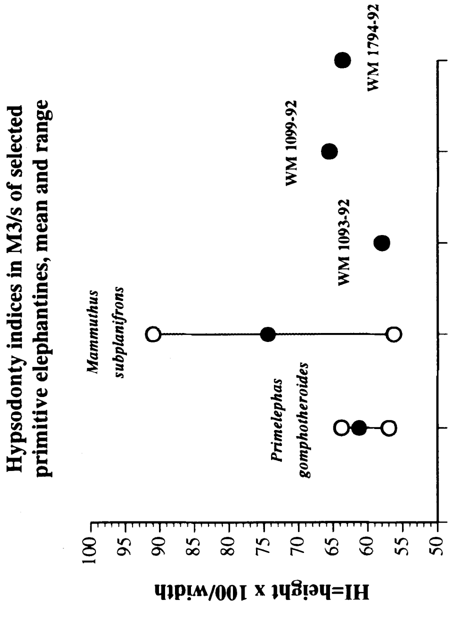


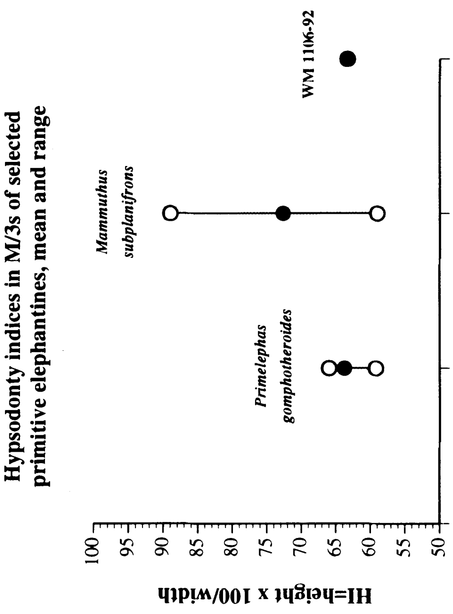
FIGURE 9. WM 110/94, left dentary and M_3, cf. *Stegotetrabelodon*. (A) Buccal view. Anterior is to the left of the page. (B) Occlusal view. Anterior is to the left, and buccal is to the bottom of the page.

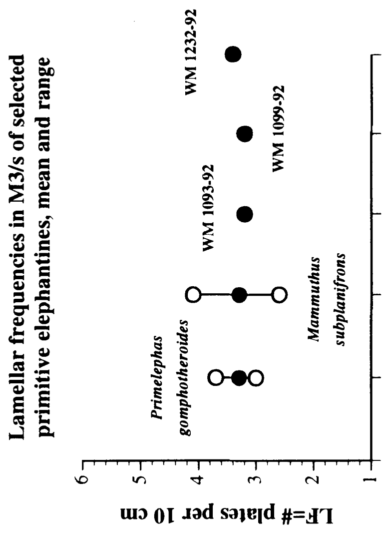
Subfamily Elephantinae Gray, 1821
Genus *Primelephas* Maglio, 1970

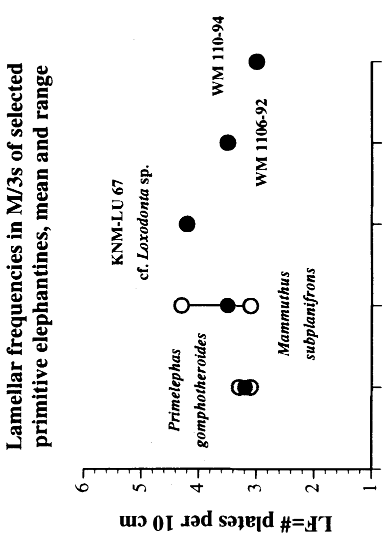
3.5. *Primelephas gomphotheroides* Maglio, 1970

Referred Specimens, Ibole Mbr. Shoshamagai 2:WM 1091/92, molar fragment, two partial plates; WM 1093/92, left M^3 (Fig. 11); WM 1099/92, right M^3, seven associated plates and a posterior platelet (Fig. 12); WM 1105/92, molar fragment, posteriormost plate and heel; WM 1106/92, right M_3, and left M_2 (Fig. 15); WM


Hypsodonty indices in M3/s of selected primitive elephantines, mean and range


Hypsodonty indices in M/3s of selected primitive elephantines, mean and range


Lamellar frequencies in M3/s of selected primitive elephantines, mean and range


Lamellar frequencies in M/3s of selected primitive elephantines, mean and range

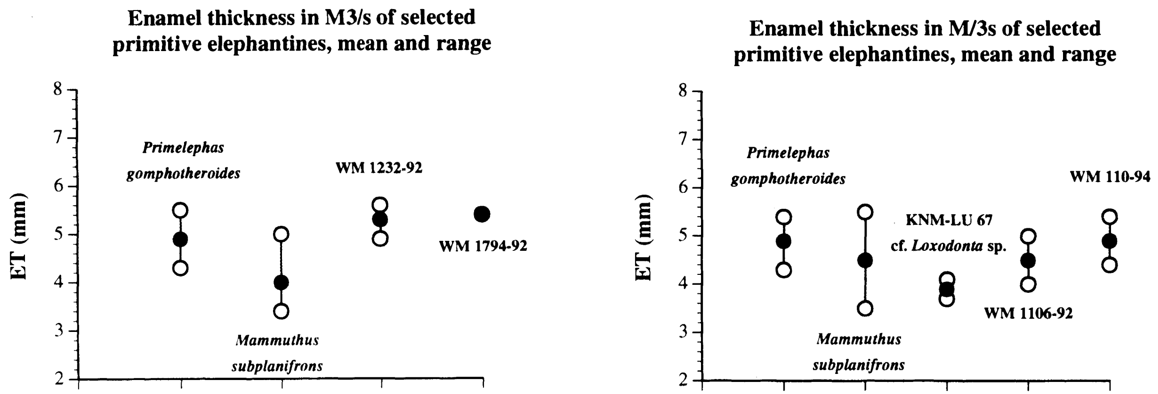


FIGURE 10. Comparative M3 indices and enamel thickness in selected primitive elephantines.

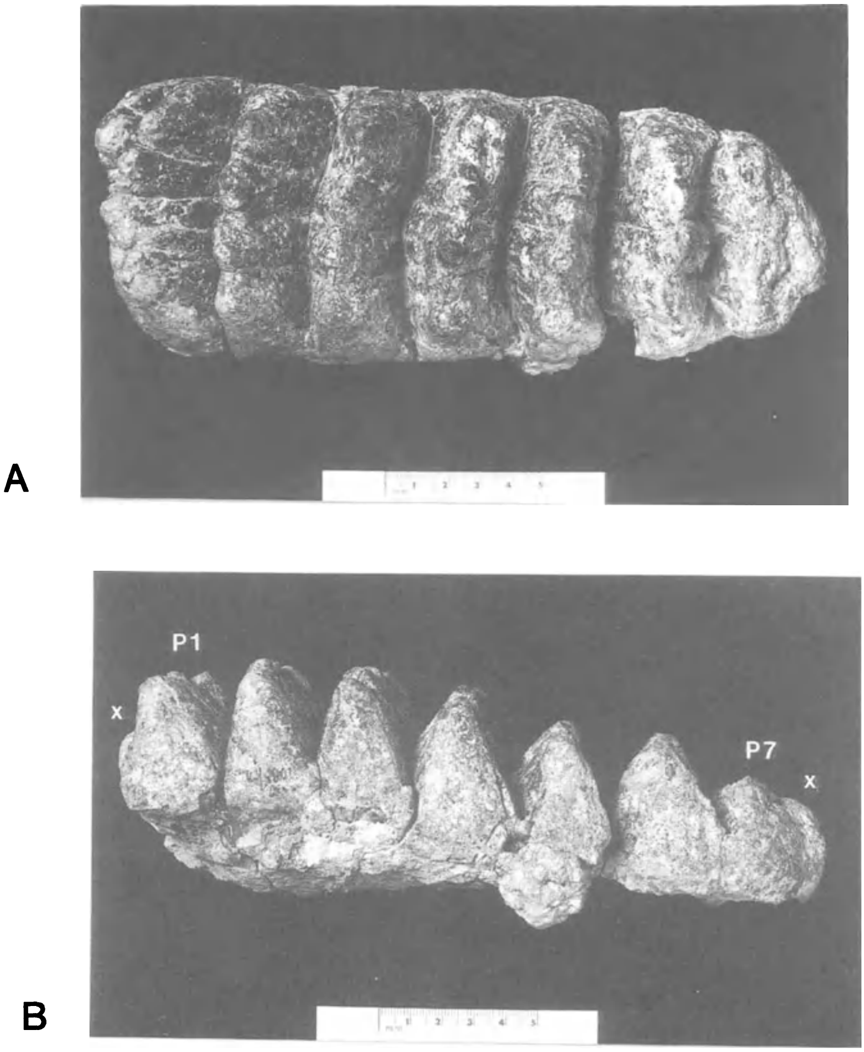


FIGURE 11. WM 1093-92, left M^3, *Primelephas gomphotheroides*. Abbreviations: P1, plate 1; P7, plate 7; x, anterior or posterior platelet. (A) Occlusal view. Anterior is to the left, and lingual is to the bottom of the page. (B) Lingual view. Anterior is to the left of the page.

1186/92, right M_2?, anterior platelet and anterior two plates; WM 1793/92, left M_3, posterior two plates and heel; WM 1794/92, M^3, posterior three plates and heel; WM 1795/92, molar fragment, two partial plates; WM 203/94, molar fragment, posteriormost plate and posterior platelet; WM 204/94, molar fragment, posteriormost plate and heel; WM 205/94, molar fragment, three partial plates; WM 308/94 to 311/94, molar fragments, pieces of several plates.

Inolelo 1:WM 1065/92, left dP^3, anterior platelet and anterior two plates (Fig. 17); WM 1955/92, M3, anterior platelet and first plate; WM 1972/92, molar

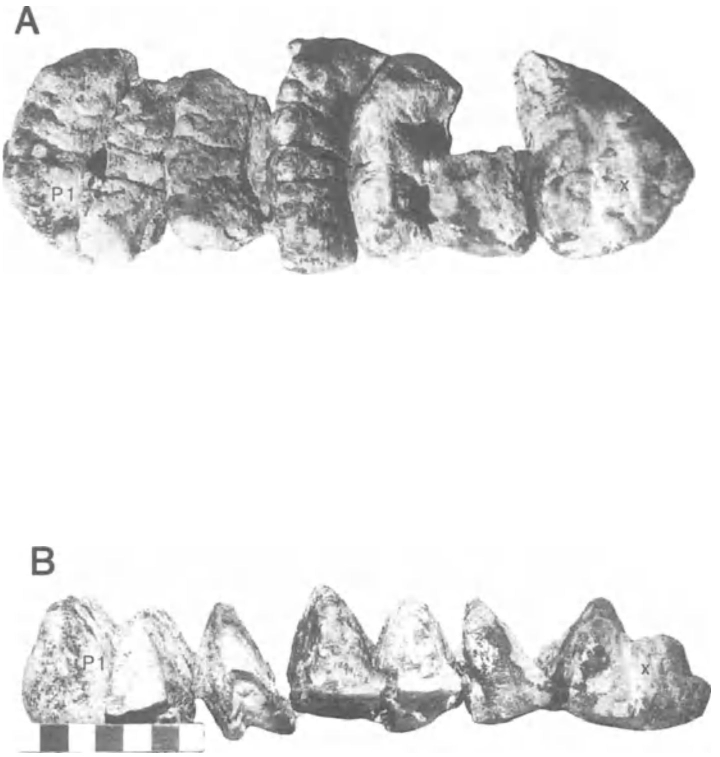


FIGURE 12. WM 1099/92, right M^3, *Primelephas gomphotheroides*. Abbreviations: P1, plate 1; x, posterior platelet. (A) Occlusal view. Anterior is to the left, and buccal is to the bottom of the page. (B) Buccal view. Anterior is to the left of the page.

fragment, two partial plates; WM 143/94, molar fragment, posteriormost plate and heel.

Inolelo 2:WM 211/94, left dP^3 (Fig. 17).

Inolelo 3:WM 1232/92, right M^3, posterior five plates and posterior platelet (Fig. 13); WM 180/94, right M_3, anterior enamel fold and anterior two and one-half plates (Fig. 14). WM 181/94, left dP^3, posterior two and one-half plates and posterior platelet (Fig. 18).

Description. WM 1093/92 is a complete left M^3 composed of seven wide, low plates (Table III), an anterior cingulum, and a small posterior platelet (Fig. 11A). It is unworn, with no development of roots or cementum, and probably had not emerged from its maxillary crypt. In occlusal view, the crown is rectangular and of uniform width except at the heel, which is tapered (Fig. 11A). The plates are formed of four stout pillars demarcated by strong grooves and superficially subdivided into as many as seven apical digitations. In lateral view, the plates are bulbous and pyramidal, broad at their bases, and separated by V-shaped valleys (Fig. 11B). Due to the basal thickness of the plates, the lamellar frequency is low (Table III). There are no intravalley columns. The enamel is thick but could not be measured accurately. While it is longer than other M^3s of *P. gomphotheroides*, in other dimensions WM 1093/92 is metrically close to this species (Table III and Fig. 10), and in most details of its morphology resembles the M^3s from the species type, KNM-LT 351 (see Maglio, 1970b, Pl. III, 1973; Maglio and Ricca, 1977).

WM 1099/92 is a virtually complete, unworn right M^3 formed of seven plates and a posterior platelet. The plates are broken at their bases and cannot be entirely reassembled. Each plate is wide and low (Table III and Fig. 10), broadest at the base, and composed of four to six conules (Fig. 12A). The posterior platelet has two pillars. In lateral view, the plates are basally thick and pyramidal, and the transverse valleys are V-shaped (Fig. 12B). There are no median clefts through the plates, and no accessory columns. Breaks in the plates reveal the enamel to be thick, but do not permit accurate measurements. WM 1099/92 is similar in size and structure to WM 1093/92.

WM 1232/92 is a right M^3 preserving PI–PIV, part of PV, and a small posterior platelet (Fig. 13A). It is longitudinally convex, and has no median clefts or accessory columns. The plates are bulbous, pyramidal, and interspersed by V-shaped transverse valleys (Fig. 13B). Cementum covers unworn PI and PII up to their apices, but does not fill the valleys. In PII–PV, vertical grooves demarcate five pillars, which are partitioned superficially into seven or eight apical digitations of unequal size. PI has four pillars subdivided into six apical digitations. The plates are low, broad, and widely spaced (Table III and Fig. 10). Enamel is unfolded and thick (Table III and Fig. 10). Structurally and metrically, WM 1232/92 closely resembles M^3s attributed to *P. gomphotheroides*, especially KNM-LU 58 from the Lukeino Fm. (see Tassy, 1986, Pl. XIV, Fig. 3), and a left M^3 from Kolinga mistakenly attributed to *Stegodon* (see Coppens, 1967, Fig. 2).

WM 1794/92, a remnant of an M^3, retains only the last two and one-half plates, and a small posterior platelet. The plates are pyramidal and thick in lateral view, and exhibit five apical digitations. In addition, the plates are low and wide, and the enamel is thick (Table III and Fig. 10). Cementum covers the plates and is invested into, but does not fill, the V-shaped transverse valleys. The morphology of this specimen closely matches that of the posterior portion of WM 1232/92.

WM 180/94 is a worn anterior fragment of a right M_3, preserving an anterior enamel ridge and parts of P1–P3 (Fig. 14). Greatest width of the tooth is 78.0+ mm at P2. It has coarsely folded enamel ranging in thickness from 4.2 to 4.7 mm. P1 retains the trace of a median cleft. P2 is worn into a complete, anteriorly concave enamel loop. A posterior column is present to the buccal side of the transverse valley between P1 and P2. The anterior ridge also has a strong median pillar, which is pressed against the buccal enamel loop of P1. The plates are pyramidal in shape and thick at their bases, suggesting a low lamellar frequency. In lateral view, the transverse valley between P1 and P2 is V-shaped. These features are compatible with the species diagnosis of *Primelephas gomphotheroides* (Maglio, 1970b).

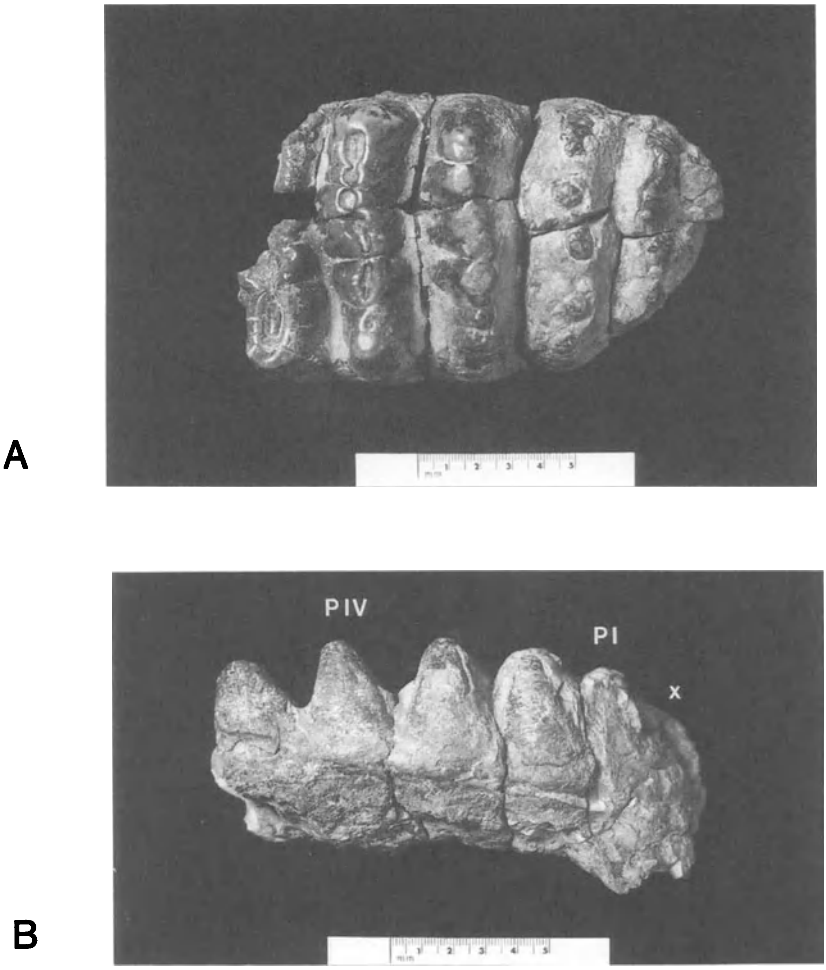


FIGURE 13. WM 1232/92, right M^3, *Primelephas gomphotheroides*. Abbreviations: PI, last plate; PIV, fourth plate, counted from the posterior end; x, posterior platelet. (A) Occlusal view. Anterior is to the left, and buccal is to the bottom of the page. (B) Buccal view. Anterior is to the left of the page.

WM 1106/92 includes a complete right M_3 composed of a small anterior fold of enamel, seven plates, and a prominent posterior platelet (Fig. 15A). Its anterior root is positioned under P1 and P2 and is strongly curved posteriorly, while a more massive root supported P3–P7. The plates are widest at their bases and low (Table III and Fig. 10). Unworn P4–P7 and their intervening transverse valleys are liberally covered with cementum. In lateral view, the transverse valleys are V-shaped, and the plates are pyramidal (Fig. 15B). Because of their cementum covering, P4–P7 appear to impinge closely on each other. Nevertheless, as a consequence of plate thickness, lamellar frequency is low (Table III and Fig. 10).

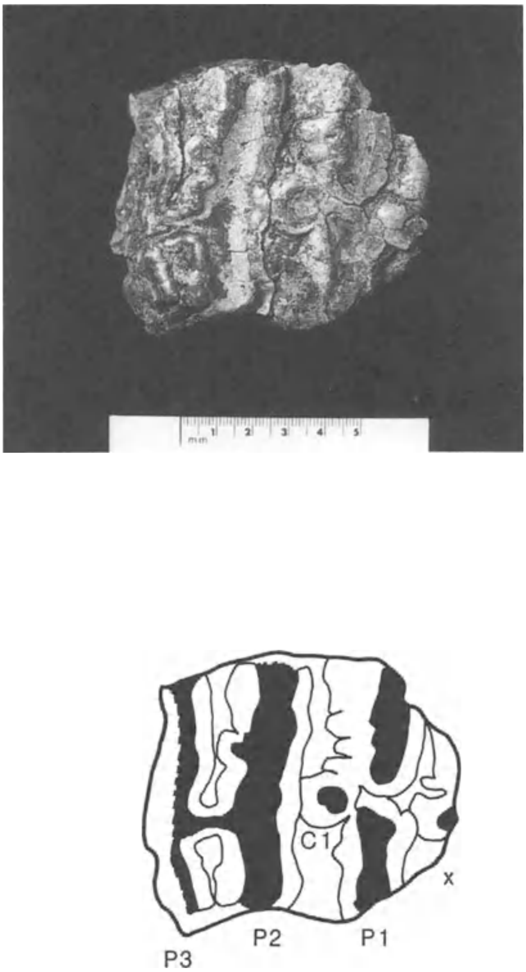


FIGURE 14. WM 180/94, right M_3, *Primelephas gomphotheroides*. Abbreviations: C1, posterior accessory column associated with plate 1; P1, plate 1; P2, plate 2; P3, plate 3; x, anterior enamel ridge. Anterior is to the right, and buccal is to the bottom of the page.

Each plate is made up of four main pillars superficially subdivided into as many as six apical digitations. P5–P7 and the posterior platelet exhibit slight median clefts, and a trace of a median sulcus is apparent on P1. A small accessory column is fused to the anterior face of P3. Enamel is moderately thick (Table III and Fig. 10) and unfolded.

The crown proportions of WM 1106/92 are similar to those of KNM-LU 67, a right M_3 from the Lukeino Fm. that has been referred to cf. *Loxodonta* sp. (Tassy, 1986). However, the Lukeino specimen differs from WM 1106/92 in having plates that are more anteroposteriorly compressed and not expanded at their bases, closer spacing of plates and a higher lamellar frequency, U-shaped transverse

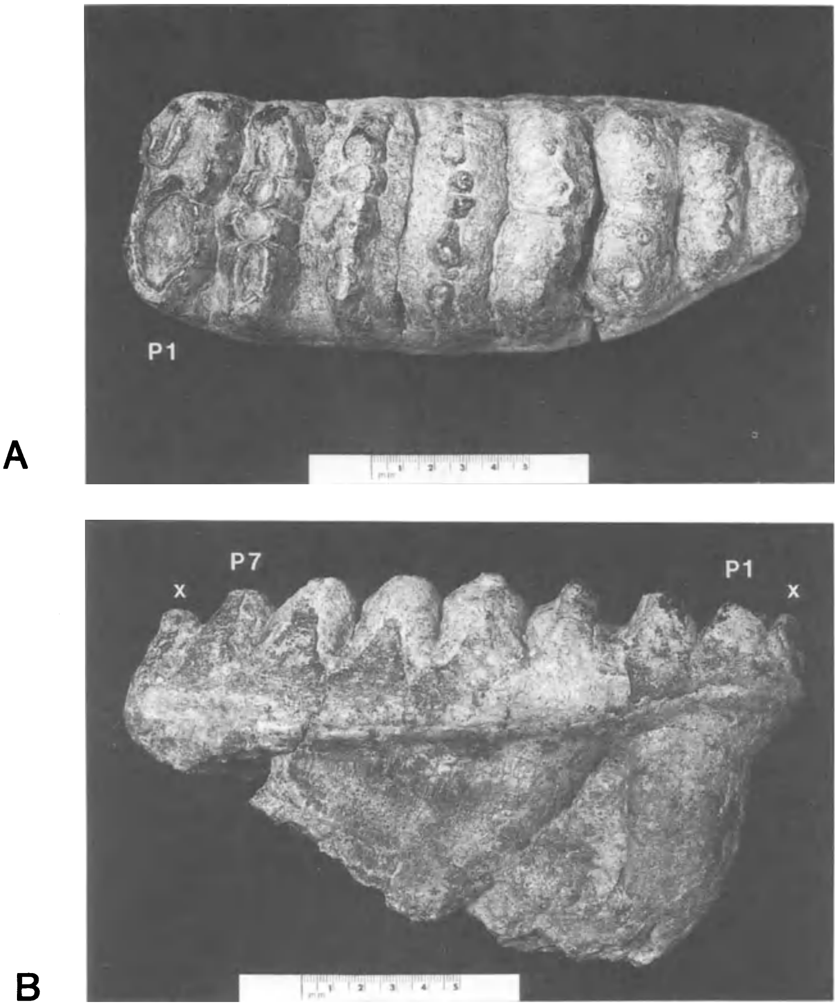


FIGURE 15. WM 1106/92, right M_3, *Primelephas gomphotheroides*. Abbreviations: P1, plate 1; P7, plate 7; x, anterior or posterior platelet. (A) Occlusal view. Anterior is to the left, and lingual is to the bottom of the page. (B) Buccal view. Anterior is to the right of the page.

valleys, and thinner enamel (Table III and Fig. 10; Tassy, 1986). In contrast, the occlusal morphology of WM 1106/92 is consistent with the species diagnosis of *Primelephas gomphotheroides* (Maglio, 1970b), and its dimensions and indices compare well with other M_3s attributed to that species (Table III and Figs. 10 and 16). Morphologically and metrically, WM 1106/92 most closely matches the left M_3 from the species type of *P. gomphotheroides*, KNM-LT 351 (see Maglio, 1970b, Pl. III).

WM 1793/92, a posterior fragment of a left M_3, was found with WM 1106/92 and may be from the same individual. It preserves the last two plates and a

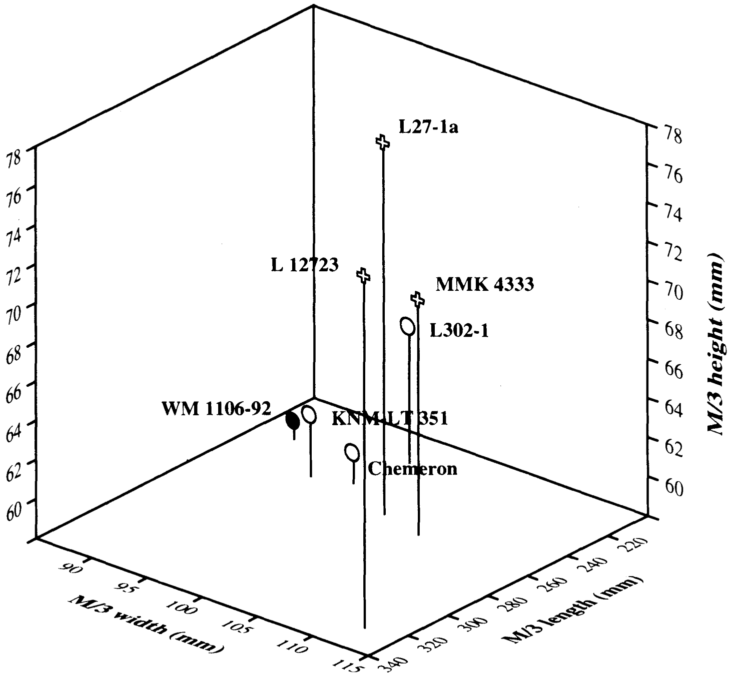


FIGURE 16. Three-dimensional plot of M/3 dimensions in selected primitive elephantines. Symbols: ○, *Primelephas gomphotheroides*; ✣, *Mammuthus subplanifrons*; ●, WM 1106-92. Data from Maglio and Hendey (1970); Maglio (1973), and Mebrate (1977).

prominent posterior platelet. At PII, width is 82.6 mm and unworn crown height is 54.3 mm. Enamel thickness averages 5.0 mm. PI and PII each exhibit four apical digitations, and the posterior platelet is composed of two conules. In lateral view, the plates are pyramidal and the transverse valleys are V-shaped. Abundant cementum covers the plates to their apices, and almost fills the transverse valleys.

WM 211/94 is a left dP^3 composed of four plates and an anterior platelet worn into enamel loops. The posteriormost enamel figure is anteroposteriorly broad and may represent incorporation of a posterior platelet into P4. In occlusal view, the crown is broad posteriorly and tapered anteriorly (Fig. 17A). This shape is typical of dP3s in other fossil elephants (e.g., *Loxodonta exoptata*, see Beden, 1987, Plate 8.1), and also in modern elephants. The crown is also more worn posteriorly than anteriorly, a condition found in extant elephant dP3s. Crown length is 52.4 mm, height is 16.2+ mm at P3, and greatest width is 36.7 mm at P4. The enamel is weakly folded and has a mean thickness of 2.2 mm. In lateral view, the crown is anteroposteriorly convex (Fig. 17B). Remnants of an anterior root are under the anterior platelet and P1, and a larger posterior root or roots supported the remainder of the plates. A small contact facet for dP^2 is present on the anterior face of the crown, and a broader facet for dP^4 is present posteriorly.

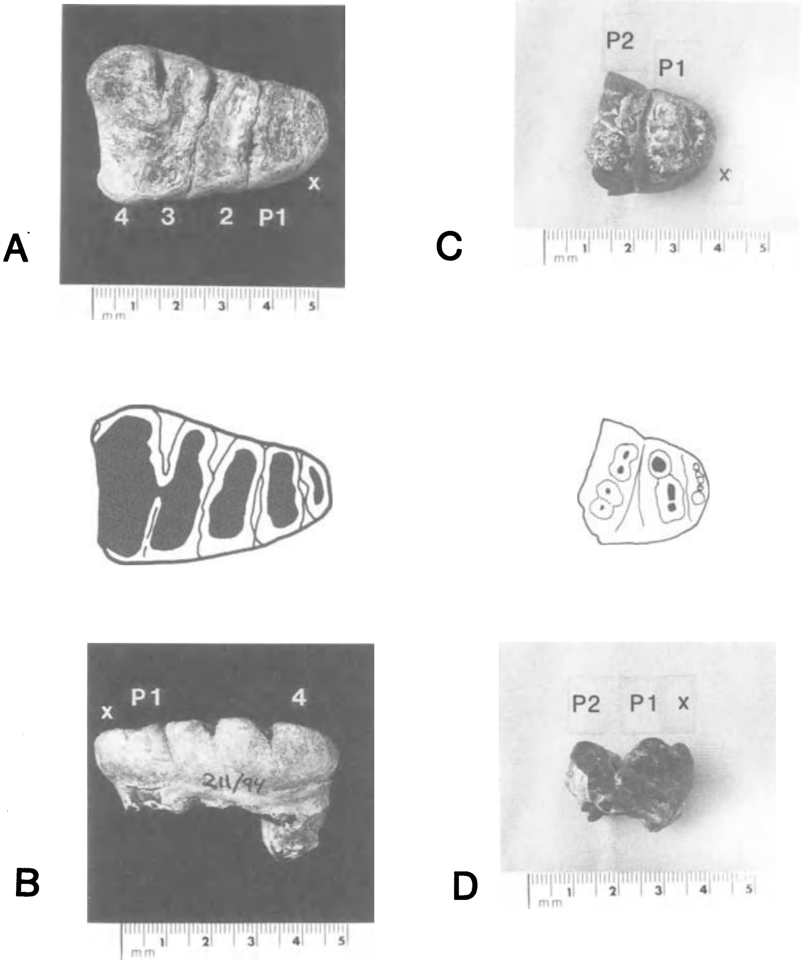


FIGURE 17. WM 211/94, left dP^3, *Primelephas gomphotheroides*. Abbreviations: P1, 2, . . . , plate 1, 2, . . . ; x, anterior platelet. (A) Occlusal view. Anterior is to the right, and buccal is to the bottom of the page. (B) Lingual view. Anterior is to the left of the page. (C) WM 1065/92, left dP^3, *Primelephas gomphotheroides*. Occlusal view. Anterior is to the right, and buccal is to the bottom of the page. (D) Buccal view. Anterior is to the right of the page.

In number of plates and occlusal morphology, WM 211/94 closely resembles a dP_3 from the Lukeino Fm. (KNM-LU 663) that is attributed to *Primelephas gomphotheroides* (Tassy, 1986, Pl. XIV, Fig. 4). The dP3s of *P. gomphotheroides* differ from those of *Stegotetrabelodon orbus* in having a greater number of full plates and in lacking prominent accessory columns (see Maglio and Ricca, 1977). The presence of fewer plates also distinguishes dP3s of *P. gomphotheroides* from those of *Loxodonta*, *Elephas*, and *Mammuthus* (Maglio, 1973; Maglio and Ricca, 1977; Tassy, 1986; Beden, 1987). In modern African and Asian elephants, dP3s

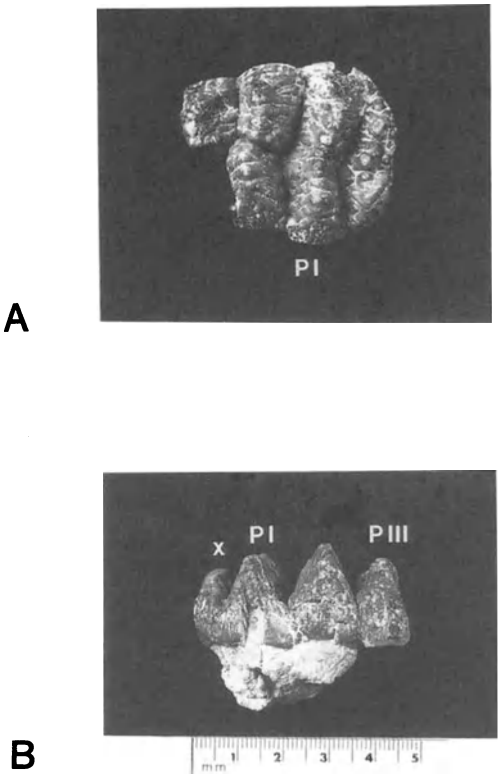


FIGURE 18. WM 181/94, left dP^3, *Primelephas gomphotheroides*. Abbreviations: PI, last plate; PIII, antepenultimate plate; x, posterior platelet. (A) Occlusal view. Anterior is to the left and lingual is to the bottom of the page. (B) Buccal view. Anterior is to the right of the page.

worn to the same extent as WM 211/94 are found in calves four to six years old (Johnson and Buss, 1965; Sikes, 1966; Laws, 1966; Roth and Shoshani, 1988).

WM 1065/92 is an incomplete left dP^3, preserving an anterior platelet and the first two plates. It is morphologically similar to the anterior portion of WM 211/94, but considerably less worn, and therefore probably from a younger calf. P1 and P2 are obliquely oriented relative to the long axis of the crown and are set at an angle to one another, leaving the V-shaped transverse valley between them open buccally (Fig. 17C). Median clefts divide the anterior platelet and plates into lingual and buccal moieties. P1 is composed of a buccal pillar exhibiting two apical digitations, and a smaller lingual pillar. P2 has two pillars, each apically partitioned into two digitations. Crown length is 28.3+ mm, and crown height reaches 20.0+ mm at P1. P1 and P2 are 24.0 mm and 27.8 mm wide, respectively. Corresponding plates in WM 211/94 have widths of 23.7 mm and 27.9 mm. In lateral view, the plates are broadest at the base and pyramidal in shape (Fig. 17D). Fine vertical striations adorn the enamel. Contact with dP^2 is marked by a small interproximal facet on the anterior face of the tooth.

WM 181/94 is an unworn, unerupted left dP^3 without root formation. It preserves a prominent posterior platelet, PI, PII, and the buccal half of PIII (Fig. 18A,B). Length is +49.6 mm, greatest width is 40.9 mm at the base of PI, and height is 25.5 mm at PII. In occlusal view, the plates are anteriorly convex (Fig. 18A). Median clefts divide each plate into buccal and lingual moieties, each comprised of three or four tiny mammillae. In lateral view, the plates are pyramidal and interspersed by V-shaped valleys (Fig. 18B). Enamel "buds" (= accessory columns?) adorn the anterior and posterior faces of PI-PIII and the posterior platelet. The outer rim of enamel is marked by fine vertical crenulations.

Finely crenulated enamel and diminutive mammillae are found in deciduous premolars of fossil elephantines (see Osborn, 1942: Fig. 987, 1064; Beden, 1983: Fig. 3.4A–D, 1987: Plate 8.1, Fig. 6). In size, shape of worn enamel figures (as seen from the underside of the crown of WM 181/94), and presence of median clefts WM 181/94 resembles dP3s in *Primelephas gomphotheroides* (Tassy, 1986), which is relatively abundant in the Ibole Mbr.

3.6. Elephantinae, Genus and Species Indeterminate

Referred Specimens, Tinde Mbr. Tinde: BMNH M14125, left dentary fragment with dP_4? (Fig. 19) and unerupted partial P_3?

Tinde West: WM 289/90, molar fragment, partial plate.

Tinde East: WM 83/94, left P_4? (Fig. 20).

Description. BMNH M14125 is a left dentary fragment collected at Tinde by Grace in 1929. It was first described by Hopwood (1931), who attributed it to *Elephas* sp. Subsequently, it was diagnosed as *Mammuthus subplanifrons* by Harrison and Verniers (1993), who added to Hopwood's initial description. It is an unusual specimen in that it has a permanent premolar. Among elephantids (*sensu* Maglio, 1973), permanent premolars have been documented only in *Stegotetrabelodon* from Mpesida and Lothagam 1, *Primelephas* from Lukeino, and *Elephas planifrons* from the Siwaliks (Hopwood, 1931; Morrison-Scott, 1938; Maglio, 1973; Maglio and Ricca, 1977; Tassy, 1986), and are lost in extant species (Morrison-Scott, 1938; Coppens *et al.*, 1978).

The premolar is still in its crypt, and preserves the last two plates and a distal conule (plate formula = +2x). A median cleft divides the plates into buccal and lingual halves, each of which is composed of two small conelets. Length is +18.0 mm, greatest width is 21.0 mm, and unworn height is 17.0 mm (Hopwood, 1931). This tooth is considerably smaller than recognized elephantid P_4s (see Tassy, 1986), and is more likely a P_3 (*contra* Hopwood, 1931). Root fragments of a deciduous precursor (dP_3?) are present above the unerupted permanent premolar.

The Tinde dentary also primitively retains an incisor alveolus, though there is no sign that a lower tusk projected externally from it. In addition, a moderately worn cheek tooth is present. Examination of the corpus below this tooth failed to reveal another permanent premolar, and on this basis it was concluded that it is an M_1 (Hopwood, 1931). The molar retains parts of the first four plates (Fig.

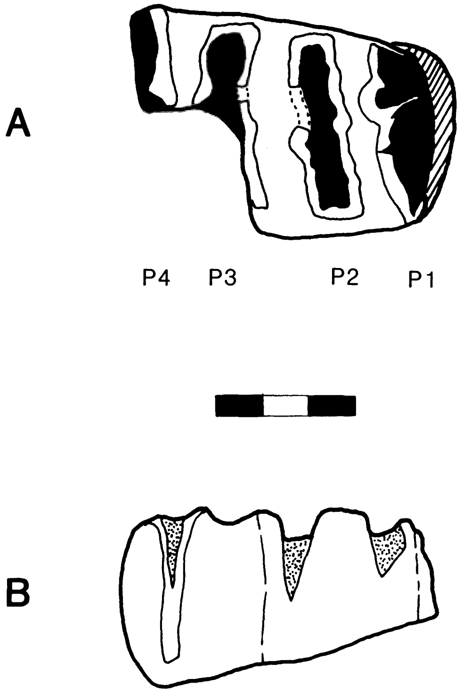


FIGURE 19. BMNH M14125, left dP_4 or M_1 (incomplete), Elephantidae gen. et sp. indet. Abbreviations: P1, 2 . . . , plate 1, 2, . . . (A) Occlusal view. Anterior is to the right, and lingual is to the bottom of the page. (B) Lingual view. Anterior is to the right of the page. Scale bar = 3 cm.

19A, B), and evidence of at least another plate. The first two plates are supported by a long, posteriorly curved root; a thicker posterior root buttresses the rest of the crown. Length of the complete tooth would have been at least 86.5 mm; width is 42.0 mm at P2, and crown height at P3 is 28.0+ mm. The worn plates form simple, rectangular enamel loops (Fig. 19A). Evidence of a median cleft is seen on P1. Enamel figures range from 2.2 to 2.7 mm in thickness and are unfolded. In lateral view, the plates are broad at the base, pyramidal, and separated by deep, V-shaped transverse valleys (Fig. 19B). Cementum is abundant in the valleys. There are no accessory columns. WM 289/90, a molar fragment from Tinde West, also exhibits thick enamel and pyramidal plate shape.

Compared with teeth of other elephantines, the molar of M14125 is small for M_1 (Maglio, 1973; Beden, 1983, 1987), and is closer in size to dP_4, which was recognized by Hopwood (1931). If this tooth is dP_4, the absence of P_4 beneath it could be accounted for by delayed development. Although the Tinde molar resembles specimens assigned to *Mammuthus subplanifrons*, its morphology is primitive for the Elephantinae and is also found in cheek teeth of *Primelephas gomphotheroides* (Maglio, 1970b, 1973; Maglio and Ricca, 1977). Contrary to the suggestion of Harrison and Verniers (1993), there is insufficient evidence to unequivocally place M14125 in *M. subplanifrons* or any other species.

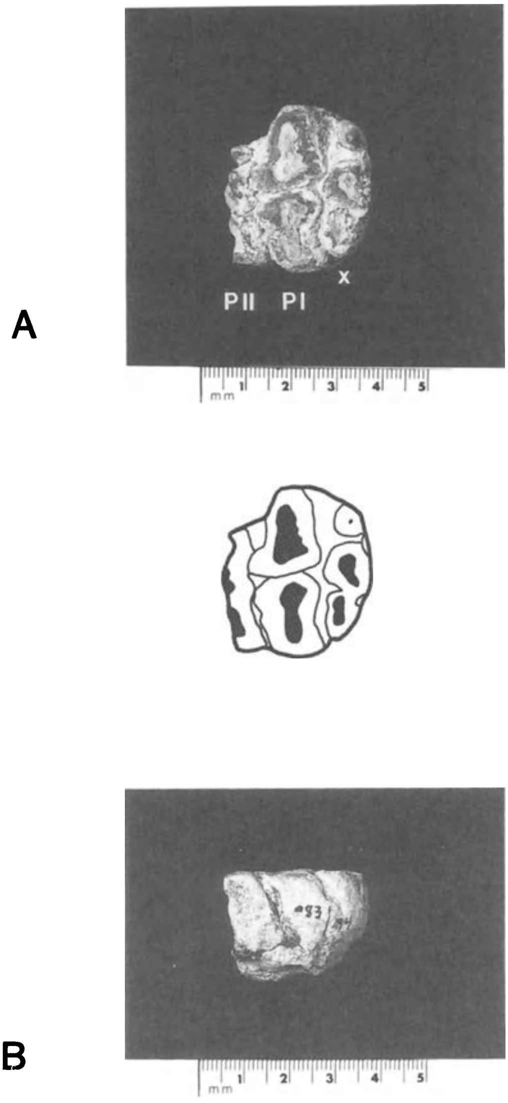


FIGURE 20. WM 83/94, left P4?, Elephantidae gen. et sp. indet. Abbreviations: PI, last plate; PII, penultimate plate; x, posterior platelet. (A) Occlusal view. Anterior is to the left, and buccal is to the bottom of the page. (B) Buccal view. Anterior is to the left of the page.

WM 83/94 is a moderately worn left P_4?, with parts of the last two plates and a relatively large posterior platelet (Fig. 20A,B). The posterior platelet has three pillars composed of five conelets. PI is divided into buccal and lingual halves by a median cleft. Each half has two pillars worn into "keyhole"-shaped enamel figures (Fig. 20A). PII was evidently worn into a single enamel loop. Length is

+32.7 mm, greatest width is 38.6 mm at PI, and height is 19.7+ mm at PII. Enamel is moderately thick (2.5–3.0 mm) and coarsely folded.

In size and occlusal composition, WM 83/94 compares well with a less worn P_4, of *Primelephas gomphotheroides*, from Lukeino (KNM-LU 925) (see Tassy 1986, Pl. IX, Fig. 7). The anteroposterior expansions of median pillars, lingual broadening of transverse valleys, and median clefts observed in WM 83/94 are characteristic of permanent premolars in archaic elephants (see Tassy, 1986, Fig. 42, Pl. IX, Figs. 7–9). This specimen further substantiates the occurrence of a primitive elephantine species in the Tinde Mbr.

Genus *Loxodonta* Cuvier and Geoffroy Saint-Hilaire, 1825

3.7. *Loxodonta* cf. *Loxodonta exoptata* (Dietrich, 1941)

Referred Specimens, Kiloleli Mbr. Kiloleli 2: WM 904/92, molar fragment, isolated plate (Fig. 16); WM 905/92, molar fragment, parts of two plates; WM 907/92, molar fragment, partial plate; WM 908/92, molar fragment, part of one plate.

Kiloleli 3: WM 639/90, molar fragment, parts of two plates.

Kiloleli 4: WM 652/90, molar fragment, parts of two plates; WM 809/90, molar fragment, parts of two plates; WM 810/90, molar fragment, pieces of several plates; WM 1314/92, upper molar fragment, parts of last two plates and posterior platelet (Fig. 21); WM 1315/92, molar fragment, parts of two plates; WM 1318/92, molar fragment, parts of last two plates and posterior platelet (Fig. 22).

Mwambiti 1: WM 663/90, molar fragment, last plate and posterior platelet.

Description. WM 1314/92 is a moderately worn, posterior fragment of an upper molar, with parts of the last two plates and a posterior platelet. The posterior platelet and PI are formed of three stout pillars, and PII exhibits traces of at least four pillars. Length is +55.0 mm, and width and height at PII are 62.0+ mm and 47.8+ mm, respectively. In lateral view, the plates are subparallel in shape, slightly broader at their bases than apically. The transverse valleys are U-shaped and completely filled with cementum. These features are derived, relative to the construction of elephantine molars from the Ibole and Tinde Mbrs. Enamel is mostly unfolded and ranges in thickness from 3.0 to 4.2 mm.

Horizontal sectioning of the specimen shows that at midheight of the crown, the plates and platelet are strongly convex anteriorly (Fig. 21A). PI and the posterior platelet also exhibit salient median sinuses along their anterior margins, which is a feature characteristic of *Loxodonta* (Maglio, 1973; Beden, 1987). Small enamel tubercles are situated lateral to the posterior platelet and PI. The occlusal morphology of WM 1314/92, including the odd development of lateral tubercles, has a particular resemblance to molars of *Loxodonta exoptata* from the Matabaietu Fm. in the Middle Awash (see Fig. 21B; Kalb and Mebrate, 1993, Figs. 30 and 31). Thus, WM 1314/92 is provisionally referred to *L. exoptata*. However, differences in the degree of enamel folding and spacing of plates suggest that WM 1314/92 is from a more primitive form of *Loxodonta* (compare Fig. 21A and B; see Beden, 1983). More complete molars are needed to better assess the species-level affinities of the Kiloleli Mbr. elephantine sample.

WM 1318/92 is a molar fragment comprising parts of the last two plates and a posterior platelet. PI is formed of four equal-size pillars. In lateral view, the plate faces are almost parallel and are separated by a tall, U-shaped transverse valley filled abundantly with cementum (Fig. 22A). This morphology is characteristic of the entire elephantine molar sample from the Kiloleli Mbr. At PI, unworn height (71.0 mm) is greater than width (57.0 mm). In anterior view, greatest plate width is at the base, but the lateral sides of the plates almost parallel one another (Fig. 22B). Horizontal sectioning of this specimen reveals that at midcrown, the enamel loops are strongly convex anteriorly and have distinct anterior median sinuses, as in WM 1314/92. Enamel is coarsely folded and averages 3.5 mm in thickness.

WM 904/92 is a single, virtually complete molar plate (Fig. 8B). Cementum covers both plate faces nearly to the apices of its pillars. There are six apical

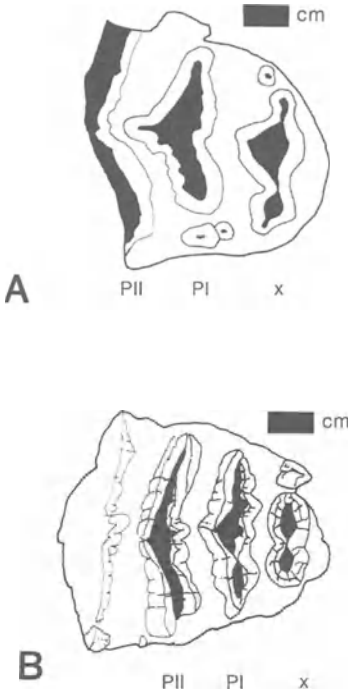


FIGURE 21. (A) WM 1314/92, molar fragment, *Loxodonta* cf. *Loxodonta exoptata*. Occlusal view. Anterior is to the left of the page. Abbreviations: PI, last plate; PII, penultimate plate; x, posterior platelet. (B) L4-12, upper molar fragment, *Loxodonta exoptata*, from the Matabaietu Fm., Middle Awash, Ethiopia (redrawn after Kalb and Mebrate, 1993). Occlusal view. Anterior is to the left of the page.

FIGURE 22. WM 1318/92, molar fragment, *Loxodonta* cf. *Loxodonta exoptata*. Abbreviations: PI, last plate; PII, penultimate plate; V, transverse valley; x, posterior platelet. (A) Lateral view. Anterior is to the right of the page. (B) Anterior view, cross section of PII.

digitations. In lateral view, the plate faces are almost parallel. Enamel thickness averages 3.7 mm along broken plate margins. Greatest width occurs at the base and measures 82.0 mm; unworn crown height is 92.5 mm. It is, therefore, relatively high (HI = 112.8)—as are other unworn molars from the Kiloleli Mbr., and differs markedly in shape from the plates of more primitive elephant molars from the Ibole and Tinde Mbrs. (see Fig. 8A). The morphological and metric qualities of this specimen link it with other elephantine molars from the Kiloleli Mbr., which appear to belong to a single loxodont species with similarities to *L. exoptata*.

4. Discussion

4.1. Biochronological Correlation

Analysis of proboscidean fossils from the Manonga Valley demonstrates the presence of archaic elephantines in the Ibole and Tinde Members, the lowermost fossiliferous units of the Wembere–Manonga Fm. They are accompanied in the Ibole Mbr. by anancine gomphotheres, and possible *Stegotetrabelodon*, and by *Deinotherium* in the Tinde Mbr. More derived forms of elephantines and *Anancus* appear higher in the sequence, in the Kiloleli Mbr. The co-occurrence of elephantines and *Anancus* is especially fortuitous for relative dating of the Wembere–Manonga Formation.

Elephantine molars from the Ibole Mbr. are characterized by a moderate number of broad, low plates, composed of bulbous, pyramidal pillars; thick, unfolded enamel; V-shaped transverse valleys; wide spacing of plates; and cementum covering (but not filling) transverse valleys. These features indicate close affinities between Ibole Mbr. specimens and molars of the most primitive elephantines, particularly *Primelephas gomphotheroides*. In contrast, the Ibole Mbr. elephantine specimens are distinguished from molars of *Stegotetrabelodon* by a greater number of plates (M^3s); thinner enamel; lower relative crown height (as expressed by hypsodonty indices); anterior concavity of lower molar plates; and lack of pronounced median clefts along the crown (Maglio, 1970b, 1973; Maglio and Ricca, 1977).

Maglio (1970b, 1973, p. 20) originally proposed *Primelephas* to accommodate "very early, unspecialized Elephantinae whose characters are not sufficiently modified to permit reference to any of the . . . later genera of elephants." A second species of *Primelephas, P. korotorensis* (Coppens), 1965, was recognized from two molar fragments from Kolinga, Chad (Maglio, 1973; Coppens *et al.*, 1978). However, these are morphologically indistinguishable from molars of *P. gomphotheroides*. In addition, although *P. korotorensis* was diagnosed on the basis of its relatively higher molar crowns (Maglio, 1970b, 1973), hypsodonty indices for the Kolinga teeth were calculated from plates at the distal ends of molars, and are proportionally similar to posterior molar plates in *P. gomphotheroides*. Thus, *P. korotorensis* and *P. gomphotheroides* may be conspecific.

Molars of *Mammuthus subplanifrons* purportedly differ from those of *P. gomphotheroides* in having a greater number of plates, higher lamellar frequencies, thinner enamel, greater hypsodonty, U-shaped transverse valleys, and more parallel-sided plates (Maglio 1970b, 1973; Tassy and Darlu, 1986). In practice, however, it is difficult to distinguish isolated molars of these species, especially if they are fragmentary, because their dimensions and indices overlap extensively (Table II and Fig. 10). Furthermore, some molars currently placed in *M. subplanifrons*, such as those from Kanam East (Maglio, 1973), are identical in occlusal morphology to *P. gomphotheroides*. Almost certainly, the hypodigm of *M. subplanifrons* is a "heterogeneous assemblage" requiring revision (Maglio and Hendey, 1970, p. 87). The suggestion that M_3s of *P. gomphotheroides* may be differentiated from those of *M. subplanifrons* by the presence of posterior accessory columns extending to the posterior end of the crown (Kalb and Mebrate, 1993; Kalb *et al.*, 1996), however, has little diagnostic value for these species *as constituted*, as the distribution of accessory columns in their molars appears to be highly variable intraspecifically. Nevertheless, the Ibole Mbr. specimens are unquestionably more primitive than molars exhibiting diagnostic traits for *M. subplanifrons* (as defined by Maglio, 1973) (e.g., L27-1b, left M^3 from the Sagantole Fm. [Kalb and Mebrate, 1993]; L 12723, left M_3 from the Varswater Fm., Langebaanweg [Maglio and Hendey, 1970]). They are also more primitive than the earliest known molars of *Loxodonta* and *Elephas* (Maglio, 1970b, 1973; Tassy, 1986), and should, therefore, be referred to *P. gomphotheroides*.

Primelephas gomphotheroides is known from Lothagam 1, the Lukeino Fm., the lower Chemeron Fm., the "earlier" Kaiso Fm., Kanam East and Central, and the Asa and Kuseralee Mbrs. of the Adu-Asa Fm., and dates to between approximately 4.5 and 6.0 Ma (Cooke and Coryndon, 1970; Maglio, 1970b, 1973; Mebrate, 1977; Hill *et al.*, 1986; Tassy, 1986; Sanders, 1990; Kalb and Mebrate, 1993; Hill, 1994). Therefore, on the basis of biochronological correlation of elephantines, the Ibole Mbr. fits within a time range of about 4.5–6.0 Ma. This is consistent with the possible occurrence of *Stegotetrabelodon* in the Ibole Mbr.; *Stegotetrabelodon* is known in East Africa from the late Miocene-early Pliocene localities of Lothagam and Mpesida, and the Kaperyon Beds (Coppens *et al.*, 1978).

These dates are supported by the presence of *Anancus kenyensis* in the Ibole Mbr. Fossil remains of *A. kenyensis* have been recovered from late Miocene–early Pliocene localities throughout East Africa (Coppens *et al.*, 1978). This species first appears in the Mpesida Beds, dated around 6.5 Ma or slightly older (Maglio, 1974; Tassy, 1979, 1986; Hill, 1985, 1994; Hill *et al.*, 1986). *Anancus kenyensis* has also been recorded from the Lukeino and lower Chemeron Fms., Lothagam 1, Aterir, Kanam East and West, the Kubi Algi beds, the "earlier" Kaiso Fm., the Mursi Fm., the Adu-Asa Fm. and the Haradaso Mbr. of the Sagantole Fm., and Unit 2 of the Chiwondo Beds (MacInnes, 1942; Cooke and Coryndon, 1970; Maglio, 1972a; Beden, 1976 Tassy, 1979, 1986; Mebrate and Kalb, 1985; Hill *et al.*, 1986; Tassy, 1986; Haileab and Brown, 1992; Kalb and Mebrate, 1993; Bromage *et al.*, 1995). This stratigraphic distribution indicates a last occurrence of no younger than 4.0 Ma (Tassy, 1986; Ward and Hill, 1987).

The evolutionary history of *A. kenyensis* is characterized by the progressive addition of loph(id)s to its molars, multiplication of conelets in half-loph(id)s, elaboration of accessory conules in the transverse valleys, greater complexity of talon(id)s, and development of cementum on molar crowns (Coppens *et al.*, 1978; Kalb and Mebrate, 1993). Mebrate and Kalb (1985) used these changes to divide *A. kenyensis* from the Middle Awash into a series of time-successive stages. In addition, a more derived species of pentalophodont *Anancus* ("Sagantole-type") is recognized from the Aramis Mbr. and Beearyada beds of the Sagantole Fm., and may also be present at Kanapoi and in the lower Laetolil Beds (Kalb and Mebrate, 1993). The stratigraphic occurrence of this unnamed species suggests an approximate temporal range of 3.8 Ma to 4.3 Ma (Harris, 1987a; Ward and Hill, 1987; Haileab and Brown, 1992; Kalb and Mebrate, 1993).

Anancus kenyensis intermediate molars (dP4–M2) from the Ibole Mbr. are tetralophodont; lack cementum; and have thick, unfolded or coarsely folded enamel; modest development of accessory conules; and relatively simple talon(id)s. Third molars are apparently pentalophodont, and share this morphology. Although more derived in conule complexity than *A. kenyensis* from the lower-middle Adu-Asa Fm. ("Stage A"), the Ibole Mbr. sample is similar in occlusal composition to molars from Lukeino, Kanam East and West, and the upper Adu-Asa Fm, ("Stage B"), temporally bracketed between about 4.5–6.0 Ma (MacInnes, 1942; Mebrate and Kalb, 1985; Tassy, 1986; Kalb and Mebrate, 1993). These dates coincide with the time range for deposition of Ibole Mbr. sediments estimated from biochronological correlation of elephantines.

The sparse elephantine sample from the Tinde Mbr., including the specimen collected by Grace in 1929 (M14125), exhibits features consistent with the primitive morphology of the Ibole Mbr. material. It is possible that this sample represents *Primelephas*. Alternatively, the Tinde Mbr. elephantines could belong to another archaic species, such as *Mammuthus subplanifrons*, as was suggested by Harrison and Verniers (1993). *Mammuthus subplanifrons* is primarily an early Pliocene species, and is best known from southern Africa (Clark, 1966; Maglio and Hendey, 1970, Maglio, 1973; Cooke and Maglio, 1972; Cooke, 1974; Bromage *et al.*, 1995). In East Africa, *M. subplanifrons* has been reported from Kanam East and West, the lower Chemeron Fm., and the upper Adu-Asa and lower Sagantole Fms., dated about 4.0–5.6 Ma or possibly slightly older, depending on differing age estimates for Kanam (Maglio, 1973; Hill, 1994; Kalb and Mebrate, 1993). Despite their unresolved taxonomic status, the elephantine fossils suggest that the sediments of the Tinde Mbr. were also deposited sometime during the latest Miocene–early Pliocene, within the span of 4.0–6.0 Ma.

The Tinde Mbr. has also produced a single specimen of *Deinotherium bozasi*. Unfortunately, the presence of this species is of little help in calibrating the age of the Wembere–Manonga Fm., as it has a long geological record without significant morphological evolution (Harris, 1975, 1978). The earliest record of *Deinotherium* in East Africa is from the Muruyur Beds, slightly older than 12.0 Ma (Hill *et al.*, 1986). It is also reported from the Ngorora Fm., Lukeino Fm., lower Chemeron Fm., Chemoigut Fm., Lothagam 1, Kanapoi, Kanam East, the upper Laetolil Beds, Olduvai Beds I and II, the Mursi, Usno, and Shungura Fms., and the Hadar Fm., apparently going extinct around 1.2 Ma (MacInnes, 1942; Beden, 1976; Smart, 1976; Harris, 1976, 1978, 1983, 1987a,b; Bishop *et al.*, 1978; White *et al.*, 1984; Cooke, 1984; Hill *et al.*, 1986).

Elephantine molars from the Kiloleli Mbr. are distinguished from archaic specimens of the Ibole and Tinde Mbrs. by thinner enamel; greater hypsodonty; more parallel-sided, narrowly spaced plates; more compressed and U-shaped transverse valleys; and thicker cementum filling the valleys completely. The occlusal morphology of these teeth generally resembles a grade of organization seen in Pliocene elephantines such as *Loxodonta adaurora, L. exoptata, Elephas ekorensis*, and *Elephas recki brumpti* (Maglio, 1970b, 1973; Beden, 1980, 1983, 1987). Although poor preservation hinders precise taxonomic identification, an affinity between Kiloleli Mbr. elephantines and *L. exoptata* is suggested by the "propeller-shaped" configuration of (sectioned) plates, which is especially characteristic of that species (Kalb and Mebrate, 1993, p. 59).

Loxodonta exoptata is known from the lower Koobi Fora Fm. (below the Tulu Bor Tuff), the upper Laetolil Beds, the Shungura Fm., and the Denen Dora Mbr. of the Hadar Fm., dated between approximately 3.2 and 3.8 Ma (Beden, 1983, 1987; White *et al.*, 1984; Harris, 1987a). The recovery of this species from the lower Matabaietu Fm. has greatly extended its temporal range to ≈2.3 Ma (Kalb and Mebrate, 1993). Weak folding of enamel and broad spacing of plates in the Kiloleli Mbr. specimens suggest that they are from an early part of the lineage. This interpretation is consistent with the coincidence of an apparently derived form of *Anancus*, possibly *Anancus* sp. "Sagantole-type" (Kalb and Mebrate, 1993), in the Kiloleli Mbr. Overlap of temporal ranges for *L. exoptata* and *Anancus* sp. "Sagantole-type" (see above) indicates that the Kiloleli Mbr. dates to ≈3.8 Ma. A worn, partial elephantid molar from the Kiloleli Mbr. collected in 1996 may belong to *Elephas ekorensis* (N. Todd, personal communication), which would support this interpretation (see Coppens *et al.*, 1978).

Biochronological correlation of proboscideans suggests that the fossiliferous sediments of paleolake Manonga were deposited sometime between ≈3.8 and 6.0 Ma. Thus, fossil localities of the Manonga Valley apparently antedate hominid-bearing levels at Hadar and Laetoli, and are comparable in age to the early hominid sites of Lothagam, Lukeino, Kanapoi, Tabarin, Fejej, Aramis, Maka, and Belohdelie (Drake and Curtis, 1979, 1987; Hay, 1987; Haileab and Brown, 1992; Kalb and Mebrate, 1993; Hill, 1994; White *et al.*, 1994). If this initial assessment is correct, the fauna from the Manonga Valley will add substantially to current understandings of evolutionary and ecological changes that occurred in East Africa during a period of time (latest Miocene–early Pliocene) marked by a dramatic shift from faunas of "archaic" nature to those of more modern aspect, including the first appearance of hominids (Hill *et al.*, 1986), yet represented at only a few localities.

4.2. Paleoecological Considerations

The late Miocene–Pleistocene fossil record of Africa documents phyletic trends among elephant lineages to increase the number of plates on each molar, decrease the thickness of enamel and increase enamel folding, increase plate height, increase the amount of cementum covering the crown, and to narrow spacing between plates (Maglio, 1973). Progressive changes in these features over time are thought to be functionally correlated with cranial adaptations to enhance the effectiveness of fore–aft horizontal shearing mastication, and to increase individual longevity (Aguirre, 1969; Maglio, 1972b, 1973; Cooke, 1984; Beden, 1987). This type of chewing is effective for the initial processing of low-grade food high in cellulose (which large herbivorous mammals inevitably ingest in abundant quantities) (Eltringham, 1982), especially grasses, and permits elephants to exploit a wide variety of foods. In addition to grazing, modern elephants (*Loxodonta africanus* and *Elephas maximus*) are mixed feeders of trees and shrubs (fruit, bark, pith, stems, leaves), "forbs" (leafy herbaceous plants), and sedges (Eltringham, 1982, p. 95).

Studies of feeding behavior in modern elephants show that they prefer grasses where available, and that grasses predominate in their diet during wet seasons (Buss, 1961; Field, 1971; Field and Ross, 1976; Olivier, 1978; Kabigumila, 1993; Tchamba and Seme, 1993). The correspondence between the importance of grasses and fore–aft shearing mastication in modern species suggests that morphological evolution of elephant molars was associated with increasing emphasis on grazing. In modern ungulates, however, hypsodonty is highly correlated with feeding at ground level in open habitats but does not differentiate grazers from mixed feeders living in those conditions (Janis, 1986). This suggests that elephant evolution could have been adaptively driven by the increasing prevalence of open conditions, with varying degrees of selection for grazing in different lineages. In East Africa, the origin of the Elephantidae at ≈7.0 Ma (Maglio, 1973) apparently coincided with the advent of more seasonal environments and the spread of savanna grasslands (Morgan *et al.*, 1994).

Adaptive trends in the development of elephant molars were paralleled during the late Miocene–Pliocene by *Anancus*. Progressive changes in molar size, loph(id) number, cementum distribution, enamel folding, and complexity of accessory conules are well documented over time for *Anancus* (Kalb and Mebrate, 1993). These changes appear to have been correlated with a transformation in masticatory function from grinding-crushing to horizontal grinding, attributable to gradual changes in dietary habits (Mebrate and Kalb, 1985). However, it appears that elephants were more successful than *Anancus* at coping with environmental shifts during the Pliocene; while *Anancus* disappeared in East Africa before the end of the Pliocene, *Elephas recki* flourished and continued to evolve through the Pleistocene (Coppens *et al.*, 1978; Beden, 1980).

Co-occurrence of archaic elephants with *Anancus kenyensis* in the Ibole Mbr., and with *Deinotherium bozasi* in the Tinde Mbr., indicates the presence of relatively closed, wooded habitats near paleolake Manonga during the late Miocene–early Pliocene. Although species such as *Primelephas gomphotheroides* may have been forced by increasing seasonality to explore new food sources in a variety of habitats, the brachydont configuration of their molars suggests that they were primarily adapted to mixed feeding or browsing in closed conditions (Janis, 1986). *Anancus kenyensis* is considered to have been a forest form (Smart, 1976). In addition, the low-crowned cheek teeth and inferred maneuverability of the head in deinotheres have been interpreted as adaptations for browsing soft foliage above the level of the ground, and they are also thought to have inhabited densely vegetated areas (Harris, 1975,1978).

Elephantines of the Kiloleli Mbr. are more derived with regard to hypsodonty, enamel thickness, plate spacing, and cementum thickness, and therefore probably habitually occupied more open areas than earlier elephantines from the Wembere–Manonga Fm. Differences between the simple molars of *Anancus kenyensis* from the Ibole Mbr. and the complex occlusal morphology in specimens referred to *Anancus* sp. "Sagantole-type" from Kiloleli Mbr. sediments complement the contrasts between the elephantines from these units. These differences include greater folding of enamel, development of cementum, and elaboration of talon(id)s, and support the idea that at ≈3.8 Ma, climatic and environmental changes placed new constraints on the feeding behavior of Manonga Valley proboscideans. The inferred exploitation of open habitats by proboscideans coincides with a dramatic increase in rhinos and equids, as a percentage of large mammals collected from the Kiloleli Mbr. (Bernor and Armour-Chelu, this volume, Chapter 8; Harrison, this volume, Chapter 4).

5. Summary

During fieldwork in 1990–1994, the WMPE recovered a large sample of proboscidean fossils from the Manonga Valley, north-central Tanzania. Comparative morphological and metrical analysis of molars from this collection reveals the presence of the archaic elephantine *Primelephas gomphotheroides*, *Anancus kenyensis*, and possibly *Stegotetrabelodon* in the Ibole Mbr. The *Primelephas* sample is especially important in that it substantially expands the modest hypodigm of the species. *Deinotherium bozasi* and archaic elephantines, probably either *Primelephas* or *Mammuthus subplanifrons*, are documented from the overlying Tinde Mbr. Specimens from the Kiloleli Mbr. are identified as belonging to more derived elephant species, cf. *Loxodonta exoptata* and perhaps *Elephas ekorensis*, and a progressive stage of *Anancus*, referred to *Anancus* sp. "Sagantole-type." Comparisons between taxa of the Kiloleli Mbr. and those of the Ibole and Tinde Mbrs. indicate that climatic and environmental changes occurred between the time of earliest and latest deposition of sediments. It is inferred from the occlusal morphology of Ibole and Tinde Mbr. taxa that they were mixed feeders or browsers, and that closed, wooded areas were present around paleolake Manonga during the late Miocene–early Pliocene. Morphological changes evident in Kiloleli Mbr. proboscideans imply shifts in resource acquisition at ≈3.8 Ma, involving greater intake of coarse forage, possibly including grasses, and suggest that open-country habitats were exploited with greater frequency by these taxa. This is supported by a dramatic increase in the relative occurrence of rhinos and equids in the Kiloleli Mbr.

Biochronological correlation of these fossils with proboscideans from other, isotopically well-calibrated, East African localities indicates that the Wembere–Manonga Fm. was deposited sometime between ≈3.8 and 6.0 Ma. The individual stratigraphic units appear to best fit the following time ranges:

1. Ibole Mbr. = 4.5–6.0 Ma
2. Tinde Mbr. = 4.0–6.0 Ma
3. Kiloleli Mbr. = ≈3.8 Ma

These results place the Manonga Valley localities in a time period poorly represented elsewhere in East Africa, during which faunas of archaic composition were replaced by those of more modern aspect. Thus, geological and paleontological data from the Manonga Valley are especially valuable for reconstructing the paleoecological contexts within which these modern faunas, including hominids, first appeared.

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Chapter 10

Systematics, Paleobiogeography, and Paleoenvironmental Significance of Rodents from the Ibole Member, Manonga Valley, Tanzania

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1. Introduction

The late Miocene and Pliocene fossil record documents important changes in rodent faunal composition heralding the advent of the modern East African fauna. Most significant among these changes is the beginning of the radiation of the Murinae, the true rats and mice, whose earliest African record is 12–10 Ma, and which currently dominate rodent assemblages in sub-Saharan Africa. The rodent record for the late Miocene and Pliocene is better than that for the middle Miocene, but still woefully inadequate. Hence the significance of late Neogene rodent remains from the Manonga Valley, in north-central Tanzania.

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The Manonga rodent sample currently includes a small undetermined species of the thryonomyid genus *Thryonomys* (cane rat), the cricetomyine (pouched mouse) *Saccostomus major*, a new genus and species of murine, *Tectonomys africanus*, and a new species of the extinct murine genus *Saidomys*. Although numerically small, this collection includes new taxa and is biogeographically significant. In addition, the Manonga rodents help refine the age of the Ibole Member, Wembere–Manonga Formation, and contribute to an understanding of local paleoenvironments.

Screen-washing operations for micromammals in the Manonga Valley were initiated in 1992 and resumed in 1994. The combined collection includes 41 isolated cheek teeth, 10 isolated small incisor fragments, and a few postcrania possibly assignable to Rodentia. Rodent remains are known from lacustrine sediments at two localities, Inolelo 1 and Shoshamagai 2 (two specimens), both in the Ibole Member. These two localities sample the same stratigraphic horizon, and have no discernable macrofaunal differences, so the incorporated fossils are considered a single fauna. The two rodent specimens from Shoshamagai 2 (*Saccostomus major* and cf. *Saidomys parvus*) represent taxa also recovered at Inolelo 1, and there are no morphological differences between specimens from the two localities.

The Ibole Member fauna, which also includes mollusks, fish, reptiles, and larger mammals, represents the geologically oldest fossil material from the study area (Harrison, 1993; Verniers, this volume, Chapter 3). Harrison (1993) estimated its age to be 6–5 Ma based on faunal similarities with other East African sites. The rodents discussed herein suggest the age may be slightly younger, perhaps earliest Pliocene (5–4 Ma).

Abbreviations. KNM-TH, National Museums of Kenya, Tugen Hills; KNM-LT, National Museums of Kenya, Lothagam; M or P with a superscript number indicates upper molars or premolars; M with a subscript number indicates lower molars; N, number of specimens; WM, Wembere–Manonga (Tanzania); YGSP, Yale-Geological Survey of Pakistan. The Wembere–Manonga rodents are housed at the National Museums of Tanzania in Dar es Salaam.

2. Description of Specimens

2.1. Family Thryonomyidae, *Thryonomys* sp.

Order Rodentia Bowdich, 1821
Family Thryonomyidae Pocock, 1922
Thryonomys sp.

Referred Material. Cheek tooth fragment, WM 1346/92; left M^1, WM 1351/92; right M^2, WM 1101/94; all from Inolelo 1.

Description. These teeth are assigned to the Thryonomyidae based on bunodonty and the presence of simple transverse lophs instead of individual cusps. The cheek tooth fragment, WM 1346/92, is moderately worn and includes two

Table I. Measurements (in mm) of *Paraulacodus indicus*, *P. johanesi*, and *Thryonomys* spp.

			M^1		M^2	
Taxon	Geologic age	Source	Length	Width	Length	Width
P. indicus	Late Miocene	Pakistan	2.53	3.09	2.91	3.64
P. johanesi[a]	Late Miocene	Ethiopia	3.02 3.03	3.78 3.93	3.16	4.06
Thryonomys sp.	Early Pliocene	Manonga, Tanzania	3.07	3.79	3.22	3.44
Thryonomys sp.[b]	Late Pliocene	Laetoli, Tanzania	4.10	4.80	—	—
T. gregorianus	Recent	Various	$N = 4$ $\bar{X} = 3.35$ 2.50–4.70	$N = 4$ $\bar{X} = 4.22$ 3.00–5.60	3.92	5.17
T. swinderianus	Recent	Various	$N = 4$ $\bar{X} = 4.52$ 4.33–4.78	$N = 4$ $\bar{X} = 6.03$ 5.75–6.25	$N = 3$ $\bar{X} = 4.95$ 4.83–5.11	$N = 3$ $\bar{X} = 6.71$ 6.67–6.91

[a] Measurements from Jaeger *et al.* (1980).

[b] Measurements from Denys (1987).

incomplete transverse lophs. This specimen is tentatively assigned to the same taxon as the two upper molars based on similar size.

The crown of WM 1351/92 (Fig. 1), the left M^1, is complete, but only the upper portions of the roots are present. Tooth occlusal wear and hypsodonty are moderate. The specimen is rectangular in outline, with three transverse lophs that run slightly oblique to the long axis of the tooth. Tooth terminology follows

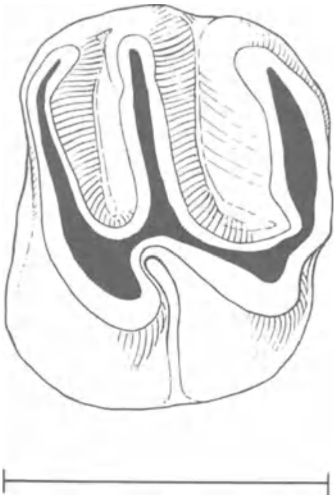

FIGURE 1. Occlusal view of *Thryonomys* sp., left M^1, WM 1351/92, from Inolelo 1. Anterior is to the left, labial is toward the top of the page. Bar scale = 3 mm.

Winkler (1992). The anteroloph turns posteriorly at its labial edge to contact the protoloph. Both the anteroloph and protoloph are narrow, but the posteroloph is inflated anteroposteriorly. The anterior and posterior labial sulci are narrow, giving the tooth an anteroposteriorly compressed appearance. A metaloph and mesoloph are lacking. The tooth has anterior and posterior labial roots, and fused anterior and posterior lingual roots.

The right M^2, WM 1101/94, is essentially unworn and from a young individual. The crown is complete, but no roots are preserved. Overall morphology is similar to that of the M^1, except that the M^2 has a small metaloph.

Discussion. The simple three-lophed morphology (derived in lacking a mesoloph) of the upper molars is of taxonomic significance and indicates that these specimens most closely match the extinct Miocene genus *Paraulacodus* and the Pliocene–Recent genus *Thryonomys* (see cladogram of Winkler, 1992). The lack of a metaloph on the Tanzanian M^1 is a derived character. In the derived condition, a metaloph is absent on P^4–M^1, and present on M^2–M^3. This is the condition seen in more recent thryonomyids, such as *Thryonomys* and *Paraulacodus.* Presence of a metaloph on P^4–M^1 is a primitive character (Winkler, 1992), seen in early middle Miocene thryonomyids, such as *Paraphiomys pigotti* and *Kochalia.*

The fossil record of *Paraulacodus* includes *P. indicus* from the middle Miocene (12.9–12.5 Ma) of Pakistan (Flynn and Winkler, 1994), and *P. johanesi* from the early late Miocene of Ethiopia (10.7–10.5 Ma; Jaeger *et al.*, 1980), and a report (without description) from the early late Miocene of Namibia (Mein in Conroy *et al.*, 1992). *Thryonomys* is an exclusively African genus, whose present distribution includes much of sub-Saharan Africa. Its oldest published record is a small form from the upper Ndolanya Beds at Laetoli, Tanzania (ca. 2.5 Ma; Denys, 1987).

The Ibole molars are close in size to those of *Paraulacodus* (Table I), and smaller species of *Thryonomys* [*T. gregorianus* and an undescribed species from the Upper Nawata Member, Lothagam, Kenya (unfortunately lacking M^1–M^3; Winkler, in preparation)]. Assignment of the Ibole specimens to *Thryonomys* and not *Paraulacodus* is based on anteroposterior compression and relative obliqueness of the lophs. These traits are apomorphic for *Thryonomys* (Winkler, 1992).

2.2. Family Muridae, *Saccostomus major* Denys, 1987

Family Muridae Gray, 1821
Subfamily Cricetomyinae Roberts, 1951
Genus *Saccostomus* Peters, 1846
Saccostomus major Denys, 1987

Referred Material. Three left M^1s, WM 1342/92, WM 1357/92, WM 1107/94; three left M^2s, WM 1104/94, WM 1108/94, WM 1110/94; two left M_1s, WM 1106/94, WM 1121/94; right M_1, WM 1343/92; two left M_2s, WM 1350/92, WM

Table II. Occlusal Measurements (in mm) of *Saccostomus major* from the Manonga Valley and Laetoli, and *S.* cf. *S. mearnsi* from Olduvai

	Length			Width		
Tooth and locality	*N*	Mean	Observed range	*N*	Mean	Observed range
M^1						
Manonga	—	—	—	3	2.19	2.16–2.25
Laetoli[a]	21	3.0	2.83–3.38	21	2.08	1.80–2.40
Olduvai[b]	43	2.66	2.52–2.81	46	1.77	1.63–1.91
M^2						
Manonga	3	1.96	1.88–2.04	3	2.05	2.00–2.12
Laetoli[a]	13	2.01	1.80–2.37	13	1.90	1.78–2.07
Olduvai[b]	61	1.63	1.53–1.87	61	1.67	1.57–1.84
M_1						
Manonga	3	2.71	2.60–2.83	5	1.83	1.75–1.92
Laetoli[a]	38	2.78	2.48–3.03	38	1.83	1.63–2.00
Olduvai[b]	139	2.35	2.19–2.57	140	1.57	1.42–1.77
M2						
Manonga	2	—	1.84–1.88	2	—	1.84–1.96
Laetoli[a]	34	2.06	1.85–2.33	34	1.93	1.75–2.15
Olduvai[b]	135	1.69	1.54–1.89	134	1.65	1.49–1.78

[a] Measurements from Denys (1987).

[b] Measurements from Denys (1992): Stratigraphic level M2 for M^1, level M3 for M^2, and level M4 for M_1, and M_2.

1123/94; all from Inolelo 1. Right M_1, WM 1951/92, from Shoshamagai 2. Incomplete left M_1, WM 1114/94, from Inolelo 1, is tentatively referred.

Description. Measurements are given in Table II. Tooth terminology follows that for murines (Fig. 3), except that the M^1 lacks an anterostyle and the anterior portion of M_1 has a single medial anteroconid, and lacks lingual and labial anteroconids. Note that in Fig. 3B, labial cingular cusps on lower molars are numbered to show their approximate location. Their numbering does not imply homology between cricetomyines and murines, nor even within those subfamilies.

M^1 WM 1107/94 (Fig. 2A) has moderately heavy occlusal wear, and is complete except for the anterolingual corner of the tooth. WM 1342/92 (Fig. 2B) has light occlusal wear and includes the middle and posterior chevrons. WM 1357/92 has moderate occlusal wear and includes the middle and posterior chevrons and the posterior aspect of the lingual cingular shelf between the anterior and middle chevrons. The anterior end of M^1 (preserved only on WM 1107/94) includes two transversely aligned cusps: larger lingual and smaller labial anterocones. There is a low precingulum. A wide lingual cingular shelf is present between the enterostyle and lingual anterocone. There is a low labial cingulum between the labial anterocone and paracone. On all M^1s, very faint labial and lingual cingula are present between the middle and posterior chevrons.

The middle chevron includes a smaller enterostyle (tA, anterior tubercle of Denys, 1987), and larger protocone and paracone. On WM 1342/92 and WM

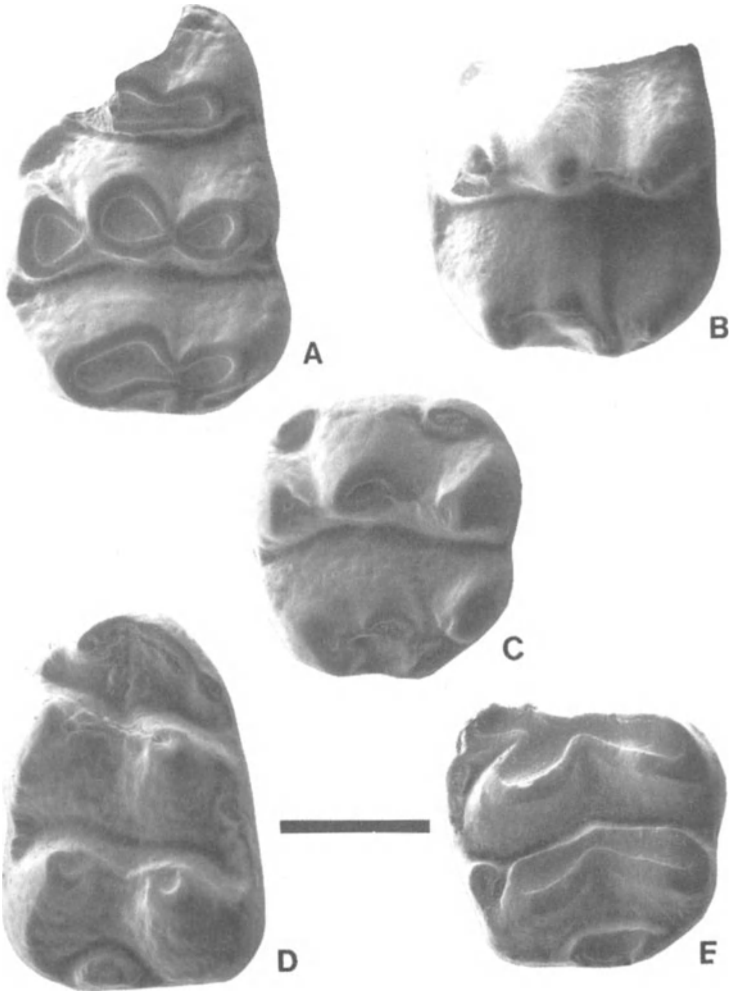

FIGURE 2. Occlusal views of *Saccostomus major* from Inolelo 1. (A) Left M^1, WM 1107/94; (B) left M^1, WM 1342/92; (C) left M^2, WM 1108/94; (D) right M_1, WM 1343/92; (E) left M_2, WM 1350/92. Bar scale = 1 mm. Anterior is to the top of the page.

1107/94 the protocone is larger than the paracone. WM 1357/92 has a protocone that is somewhat smaller than the paracone. On all three teeth the protocone and paracone are oriented transverse to one another with the enterostyle slightly posterior. The enterostyle is linked well to the protocone. The base of the enterostyle is slightly compressed labiolingually; its occlusal wear outline is roughly circular.

The posterior chevron has a large hypocone and metacone (hypocone only slightly larger) separated by a distinct sulcus. There is a faint sulcus separating the hypocone and smaller posterostyle (posterior tubercle of Denys, 1987). The metacone is a little posterior to the hypocone; the posterostyle more posterior.

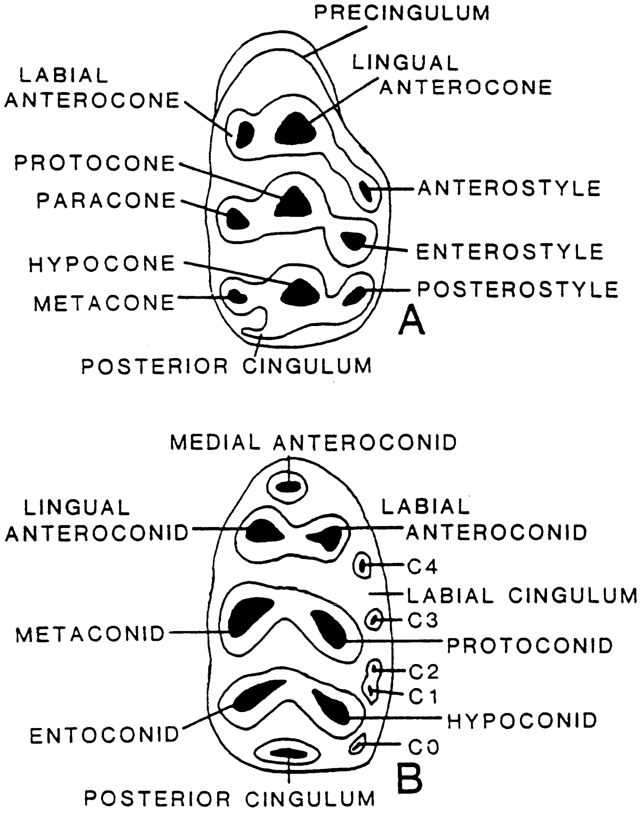

FIGURE 3. Murine tooth terminology (after Jacobs, 1978) for (A) upper and (B) lower molars.

These teeth have a low posterior cingulum with a small cusp connected to the hypocone on WM 1357/92, to the metacone on WM 1107/94, and to the hypocone and metacone on 1342/92. M^1 has large lingual and posterior roots and a small labial root under the paracone. There may also be a large anterolabial root.

Three essentially complete M^2s are known. Occlusal wear on these specimens ranges from very light (WM 1104/94) to light (WM 1108/94; Fig. 2C) to heavy (WM 1110/94). Two of these teeth have a small lingual anterocone; on WM 1110/94 there is no cusp, but a low anterior cingular shelf is present. The anterior chevron includes a large protocone and smaller paracone and enterostyle, which are located a little posterior to the protocone. The enterostyle is slightly labiolingually compressed and is a little smaller and more posterior than the paracone.

On the posterior chevron the hypocone is the largest cusp and the posterostyle the smallest. The metacone may be somewhat anterior to, or transversely aligned with, the hypocone. A deep sulcus separates the hypocone and metacone. The posterostyle, which is compressed labiolingually, is located posterior to the hypocone. A weak sulcus separates the posterostyle and hypocone. The posterior cingulum is low on WM 1108/94, but higher on WM 1104/94, similar to its development on the Laetoli specimens (Denys, 1987). WM 1110/94 is too worn to ascertain original height of the posterior cingulum. There is a small posterior cingular cusp connected to the metacone on WM 1110/94, to the hypocone on WM 1108/94, and to the crest connecting the hypocone and metacone on WM 1104/94. The M^2 has three roots: anterolabial, posterolabial, and longer anterolingual.

M_1s WM 1343/92 (Fig. 2D) and WM 1106/94 have light occlusal wear; WM 1951/92 and WM 1121/94 (only the anterior two thirds of the tooth preserved) have heavy occlusal wear. These teeth have a large medial anteroconid, which on three of the four specimens is connected by an anterior mure to the midpoint of the anterior chevron. There is no trace of an anterior mure on WM 1106/94. The anterior chevron includes a large metaconid and slightly larger protoconid. The metaconid is located a little anterior to the protoconid, and the entire chevron is slightly oblique relative to the long axis of the tooth. With wear, the chevron has a concave posterior border.

The posterior chevron includes a larger hypoconid and somewhat smaller entoconid. These cusps and the chevron they form are oriented as on the anterior chevron, with the entoconid anterior. There is an elongate posterior cingular cusp. This cusp is attached to a thin ridge extending to the hypoconid and entoconid on WM 1106/94. The ridge is present only on the lingual side on WM 1343/92. On lightly worn teeth a labial cingulum is nearly continuous from the medial anteroconid to the labial side of the hypoconid. A cuspule (not corresponding to any shown on Fig. 3) may be present directly lateral to the protoconid. WM 1343/92 has a small C4 and WM 1106/94 a small C1. There is a short lingual cingulum extending posteriorly from the medial anteroconid. This cingulum is weak on WM 1343/92 and WM 1106/94, but strong on the other two M_1s. Large anterior and posterior roots are present and there is a rootlet under the protocone.

The two known M_2 specimens have moderately heavy wear (Fig. 2E). Anterior and posterior chevrons are slightly oblique, with the lingual cusp positioned a little more anteriorly. The posterior borders of the chevrons are concave. Labial and lingual major cusps are close in size. There is a large anterolabial cusp (about one-half the size of the major cusps) attached to the anterior border of the protoconid. An anterolabial cingulum continues posteriorly from the anterolabial cusp to the posterolabial border of the protoconid. WM 1350/92 has a small C1. There is a large elongate posterior cingular cusp. On WM 1350/92 it is attached to a thin ridge that extends to the hypoconid and entoconid.

The M_2 has anterolingual and anterolabial roots (with a thin connection between them on WM 1123/94) and a large elongate posterior root. The posterior roots on WM 1123/94 divide inferiorly into labial and lingual rootlets.

Discussion. The Ibole *Saccostomus* are assigned to *S. major* based on their large size and overall morphology. *Saccostomus major* was described by Denys (1987) from craniodental remains in the Laetolil Beds, Laetoli, Tanzania, dated at 3.7–3.5 Ma. The Manonga Valley specimens compare well in size with those from the Laetolil Beds, and are larger than teeth of the extant species *S. mearnsi* and *S. campestris*, and other fossil specimens (Table II and compare to scatter diagrams Figs. 6.8 and 6.9 in Denys, 1987, and Fig. 5 in Denys, 1992).

In addition to large size, the M^1 of *S. major* is diagnosed as having the lingual anterior tubercle [enterostyle] of M^1 much larger than in other species of *Saccostomus* (Denys, 1987, p. 131). This cusp is described as being on average much larger than the protocone, and displaced posteriorly from the transverse protocone and paracone. In the extant species, the protocone is the largest cusp in the anterior chevron. Although the enterostyles of the Manonga specimens are smaller than the protocones, their size and orientation fall within the range of variation observed in the Laetolil Beds material. The one Manonga M^1 preserving much of the anterior end of the tooth differs from the Laetoli specimens in the former having the labial and lingual anterocones transverse. On the Laetoli M^1s, the labial anterocone is located anterior to the lingual, forming a slightly oblique lamina. The Manonga *Saccostomus* M^1s and M^2s differ from those of Laetoli in the former possessing a weaker sulcus between the posterostyle and hypocone. Manonga M^1s and one of two M^2s have a low posterior cingulum, not developed as the high ridge seen on the teeth from Laetoli.

An interesting difference between the M_1s from the two localities is that one of the four specimens from Manonga lacks any evidence of an anterior mure. An anterior mure, which with relatively little wear connects the medial anteroconid to the first chevron, is present on *S. major* from Laetoli and *S. mearnsi.* This connection was observed on only one of five specimens of extant *S. campestris* in collections at the American Museum of Natural History, New York. Denys (1987, p. 133) did not observe this connection in the comparative material of *S. campestris* she examined, although she noted some specimens did have a "small distal crest" extending from the medial anteroconid. Additional collection of *Saccostomus* from the Manonga Valley is important to determine if the differences observed between Manonga and Laetoli samples are statistically significant. The Manonga *Saccostomus* may prove to be a distinct species.

Saccostomus, the African pouched rat, includes one or two extant species from eastern (*S. mearnsi*) and southern (*S. campestris*) Africa. *Saccostomus* is nocturnal, and is found in savannas, grassy places in open forests, cultivated fields, and sandy plains (Nowak and Paradiso, 1983). Denys (1992) summarizes the fossil record of *Saccostomus* in East Africa, which includes (1) *S. major* from the Laetolil Beds (3.7–3.5 Ma); (2) *S.* sp. from the upper Ndolanya Beds, Laetoli (3–2.5 Ma); (3) *S.* cf. *S. mearnsi* from Olduvai Bed I, Tanzania (1.7 Ma); (4) *S.* cf. *S. mearnsi* from Lake Natron, Peninj, Tanzania (early Pleistocene); (5) *S.* sp. from Isenya, Kenya (middle Pleistocene); and (6) *S.* cf. *S. mearnsi* from East Turkana, Kenya (Plio-Pleistocene).

2.3. Family Muridae, *Tectonomys africanus*, gen. & sp. nov.

Family Muridae Gray, 1821
Subfamily Murinae Gray, 1821
Tectonomys, gen. nov.

Type and only known species. *Tectonomys africanus.*

Table III. Occlusal Measurements (in mm) of *Tectonomys africanus* from Tabarin and Inolelo 1

	Length			Width		
Tooth position	*N*	Mean	Observed range	*N*	Mean	Observed range
M^1	3	2.74	2.56–2.92	3	1.72	1.67–1.75
M^2	6	1.85	1.76–1.96	7	1.67	1.64–1.75

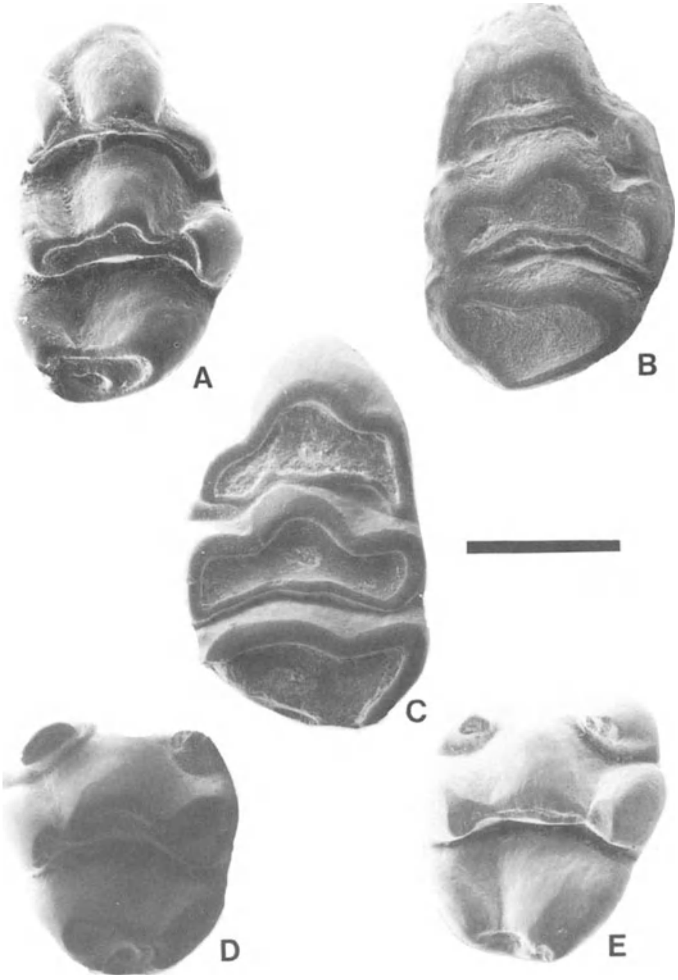

FIGURE 4. Occlusal views of *Tectonomys africanus* from (A) Tabarin, Kenya, and (B–E) Inolelo 1. (A) Right M^1, KNM-TH 18477, holotype; (B) right M^1, WM 1338/92; (C) left M^1, WM 1339/92; (D) left M^2, WM 2011/92; (E) right M^2, WM 2010/92. Bar scale = 1 mm. Anterior is to the top of the page.

Type Locality. Baringo Paleontological Research Project (BPRP) locality #77a, Tabarin locality, Chemeron Formation, Baringo District, Kenya.

Age. Early Pliocene (5.25–4.15 Ma) based on K-Ar dating and faunal correlation (Ward and Hill, 1987).

Diagnosis. Large size. Brachydont and relatively elongate. M^1 with posteriorly displaced anterostyle. Small labial anterocone on M^2. Cusps in the middle chevron of M^1 and M^2 oriented transverse to each other. Hypocone transversely elongate and at the same transverse level as the metacone. Hypocone extends lingually relative to the lingual anterocone and protocone. Strong posterior cingulum contacts the metacone to enclose an ellipsoidal basin. Three large roots.

Etymology. "*Tectono-*" refers to plate tectonics, and is in reference to the East African Rift Valley, from which this genus has been recovered. *Mys* is Greek for mouse.

Tectonomys africanus, sp. nov.

Holotype. Right M^1, KNM-TH 18477

Referred Specimens. Left M^1, WM 1339/92; right M^1, WM 1338/92; left M^2s, WM 2011/92, WM 1105/94, WM 1112/94; right M^2s, WM 2010/92, WM 1113/94, WM 1117/94, WM 1120/94.

Horizons and Localities. The holotype is from BPRP locality #77a, Tabarin, Chemeron Formation, Baringo District, Kenya. All WM specimens are from Inolelo 1, Ibole Member, Manonga Valley, Tanzania.

Age. The holotype is early Pliocene in age (5.25–4.15 Ma; Ward and Hill, 1987). The Manonga Valley specimens date to the late Miocene/early Pliocene based on overall faunal correlation (Harrison, 1993; Harrison and Baker, this volume, Chapter 13), or to the early Pliocene based only on the rodents.

Diagnosis. Same as for genus.

Etymology. *africanus* refers to the continent where this species is found.

Description. The holotype M^1 (KNM-TH 18477) (Fig. 4A) has light occlusal wear, and the Tanzanian teeth (Figs. 4B,C) both have heavy occlusal wear (Table III). The teeth are essentially complete except for the posterolingual edge of the crown of WM 1339/92. The M^1 is relatively elongate and has cusps arranged in three transverse chevrons. Cusps in the median row (lingual anterocone, protocone, and hypocone) are the largest. An anterostyle is displaced posteriorly relative to other cusps in the anterior chevron. It is strongly compressed labiolingually on KNM-TH 18477, somewhat compressed on WM 1338/92, and little compressed on WM 1339/92. The large lingual anterocone is situated transverse to the smaller labial anterocone. Projecting posterolabially from the labial anterocone is an elongate spur, which contacts the paracone with wear. A precingulum and stylar cusps are lacking. The middle chevron is relatively transverse with the paracone and enterostyle only slightly posterior to the protocone. The paracone and enterostyle are similar in size. The posterior chevron is wide, with a transversely elongate hypocone (about twice the size of the metacone). The hypocone is at the same transverse level as the metacone.

The hypocone extends lingually relative to the lingual anterocone and protocone. A posterostyle is lacking. The posterior cingulum is well developed, semilunar in shape, and posteriorly connects the hypocone to the metacone, enclosing an ellipsoidal basin. Chevrons of M^1 are separated by deep transverse valleys and the cusps of each chevron are separated by shallow wide valleys. There are three large roots, anterior, posterior, and lingual.

Known M^2s of *T. africanus* range in occlusal wear from light (Fig. 4E) to moderate (Fig. 4D). Like the M^1s, the M^2s are anteroposteriorly elongate. Anteriorly, there is a small labial anterocone and larger anterostyle. Cusps in the first chevron are relatively transverse with the enterostyle and paracone a little posterior. Labiolingual compression of the enterostyle varies from none to slight. The enterostyle and paracone are generally similar in size (four of seven specimens), but the paracone is slightly larger on two specimens. On WM 2011/92 the paracone is about three times the size of the enterostyle. The posterior portion of M^2 is morphologically similar to that of M^1. There are deep valleys separating the major rows of cusps and shallow wide valleys separating cusps within a chevron. These teeth have large anterolingual, anterolabial, and posterior roots.

Discussion. *Tectonomys africanus* has a combination of primitive and derived traits that make it unique among known fossil and extant rodents. The most striking primitive character is a very strong posterior cingulum, as strong as that observed in the most primitive murid genus *Antemus* (Jacobs *et al.*, 1989, Figs. 3, 4). Presence of such a strong posterior cingulum on *Tectonomys* suggests it represents a lineage that originated very early in murine evolutionary history. Other primitive traits of *Tectonomys* include three roots (versus four or more) on M^1 and M^2, and a labial anterocone present on M^2. Derived characters include large size and the transverse position of the enterostyle on M^1 and M^2. On the primitive murid *Antemus* the anterostyle (on M^1) and enterostyle (on M^1 and M^2) are positioned posteriorly relative to the other cusps in their respective chevrons.

Tectonomys appears to be most closely related to extant and fossil representatives of the genera *Acomys* and *Praomys*, in particular to *Acomys*. Extant representatives of the spiny mouse, *Acomys*, form a systematically complex group that ranges geographically from Pakistan to South Africa (Denys, 1990). It is generally, but not exclusively, associated with arid environments. *Tectonomys* was compared with the earliest and best represented fossil *Acomys*, *A. mabele* from Langebaanweg, South Africa (ca. 4.5 Ma; Denys, 1990), and with illustrations and descriptions of extant species. Many aspects of the morphology of *Tectonomys* are within the range of variation of *Acomys*, including teeth relatively elongate; labial and lingual anterocones on M^1 at about the same level, with the anterostyle displaced posteriorly; labial anterocone present on M^2; cusps in the middle chevron of M^1 and M^2 fairly transverse to each other; metacone large and at a similar level as the transversely elongate hypocone; and three roots on M^1 and M^2. Compared to *Tectonomys*, *Acomys* is derived in lacking (usually) or having a small posterior cingulum. Intriguingly, an M^2 of *A. transvaalensis* illustrated by Petter [1983, Fig. 5 (1)] has a posterior cingulum as strongly developed as that of *Tectonomys*. However, such strong development in *Acomys* is extremely rare. *Tectonomys* is large in size (derived); *Acomys* tends to be small.

Tectonomys was also compared with the extant African monotypic genus *Uranomys*, which is considered to be closely related to *Acomys* (Misonne, 1969; Denys *et al.*, 1992). *Tectonomys* is less closely related to *Uranomys* than to *Acomys*. *Uranomys* lacks a posterior cingulum (derived) on M^1 and M^2, and has a posteriorly displaced enterostyle (primitive) on M^1.

The Tanzanian teeth were compared to published illustrations and descriptions and some comparative skeletons of extant members of the *Praomys* group, including representatives of the subgenera (or genera) *Hylomyscus*, *Mylomyscus*, *Mastomys*, and *Praomys*. This is a large group whose members may be difficult to separate and whose systematics are in need of revision (Misonne, 1974). In addition, *Tectonomys* was compared with extinct members of the *Praomys* group, including *P.* (*Mastomys*) *minor*, *Mastomys cinereus*, and species of the subgenus *Berberomys*. *Praomys* (*M.*) *minor* is reported from Olduvai Beds I and II, Tanzania (type locality; 1.75–1.1 Ma; Jaeger, 1976, 1979), upper Member B–lower Member G, Shungura Formation, lower Omo Valley, Ethiopia (3.03–1.98 Ma; Wesselman, 1984), and tentatively referred from Locality 130-A, East Turkana, Kenya (ca. 1.6 Ma; Black and Krishtalka, 1986). *Mastomys cinereus* is known from the Laetolil Beds, and is tentatively referred from the upper Ndolanya Beds, Laetoli, Tanzania (Denys, 1987). Jaeger (1975) describes four species of a new subgenus of *Praomys*, *Berberomys*, from the upper Pliocene and lower and middle Pleistocene of north Africa. *Tectonomys* was also compared with *Praomys* sp. from Hadar, Ethiopia (>3 Ma; Sabatier, 1982).

As for *Acomys*, many aspects of the morphology of *Tectonomys* are within the range of variation of *Praomys*. These include teeth relatively elongate; size (although most extinct fossil *Praomys* are smaller); labial and lingual anterocones on M^1 at about the same level, with the anterostyle displaced posteriorly; labial anterocone present on M^2; depth of valleys between the labial and lingual anterocones on M^1 and between the protocone and paracone on M^1 and M^2; and three roots on M^1 and M^2. Compared to *Tectonomys*, the hypocone of *Praomys* is not elongate and does not extend as far lingually compared to the lingual anterocone and protocone. *Praomys* is derived in almost always lacking a posterior cingulum; a small posterior cingulum is rarely present. However, *Tectonomys* is derived relative to *Praomys* in the transverseness of cusps in the middle chevron of M^1 and M^2.

2.4. Family Muridae, *Saidomys parvus*, sp. nov.

Genus *Saidomys* James and Slaughter, 1974

Emended Diagnosis. Relatively large size. M^1 broad with nearly symmetrical transversely aligned cusps on the first two chevrons and often with a precingulum along the lingual anterocone. Posterior cingulum weak on M^1, weaker to absent on M^2. M^2 with small labial anterocone; M^3 elongate with small to vestigial labial anterocone. M_1 with large medial anteroconid and large C1. C1 reduced on M_2 relative to M_1. An anterior mure on M_1 is lacking. Strong posterior cingulum on M_1 and M_2.

Saidomys parvus, sp. nov.

Holotype. Left M^1, WM 2012/92.

Referred Specimens. Right M^1, WM 2013/92; left M^2s, WM 1111/94, WM 1122/94; right M^2s, WM 1358/92, WM 1362/92, WM 1103/94; left M^3, WM 1354/92; left M_1s, WM 1348/92, WM 1355/92; right M_1s, WM 1340/92, WM 1349/92, WM 1100/94. Left M_1, WM 2014/92, is tentatively referred.

Horizons and Localities. The holotype and all definitively referred specimens are from Inolelo 1. The tentatively referred specimen, WM 2014/92, is from Shoshamagai 2. All specimens are from the Ibole Member, Manonga Valley, Tanzania.

Age. Late Miocene/early Pliocene based on overall faunal correlation (Harrison, 1993; Harrison and Baker, this volume, Chapter 13). Early Pliocene based on faunal correlation using only the rodents.

Table IV. Occlusal Measurements (in mm) of *Saidomys parvus*, *S. natrunensis*, *S. afarensis*, and *S. afghanensis*

	Length			Width		
Tooth and taxon	*N*	Mean	Observed range	*N*	Mean	Observed range
M^1						
S. parvus	2	—	2.42–2.50	2	—	1.83–1.92
S. natrunensis	2	—	3.04–3.16	2	—	2.24–2.32
S. afarensis[a]	59	3.06	2.89–3.29	59	2.35	2.22–2.49
S. afghanensis[b]	11	3.25	3.09–3.38	14	2.28	2.18–2.41
M^2						
S. parvus	5	1.94	1.72–2.16	5	1.97	1.80–2.20
S. natrunensis	4	2.05	2.00–2.16	4	2.44	2.40–2.52
S. afarensis[a]	62	2.48	2.25–2.69	62	2.32	2.10–2.47
S. afghanensis[b]	16	2.50	2.23–2.75	21	2.47	2.25–2.67
M^3						
S. parvus	1	—	2.08	1	—	1.88
S. natrunensis	1	—	2.30	1	—	1.90
S. afarensis[a]	41	2.22	2.06–2.44	41	1.83	1.67–2.10
S. afghanensis[b]	13	2.12	2.10–2.36	13	1.88	1.76–2.02
M_1						
S. parvus[c]	3	2.52	2.33–2.67	3	1.73	1.67–1.79
S. natrunensis	3	2.81	2.76–3.00	3	1.96	1.88–2.08
S. afarensis[a]	60	2.97	2.78–3.15	60	2.06	1.85–2.27
S. afghanensis[b]	6	2.91	2.71–3.07	13	2.03	1.90–2.19

[a] Measurements from Sabatier (1982).
[b] Measurements from Sen (1983).
[c] Does not include measurements of WM 2014/92, tentatively referred.

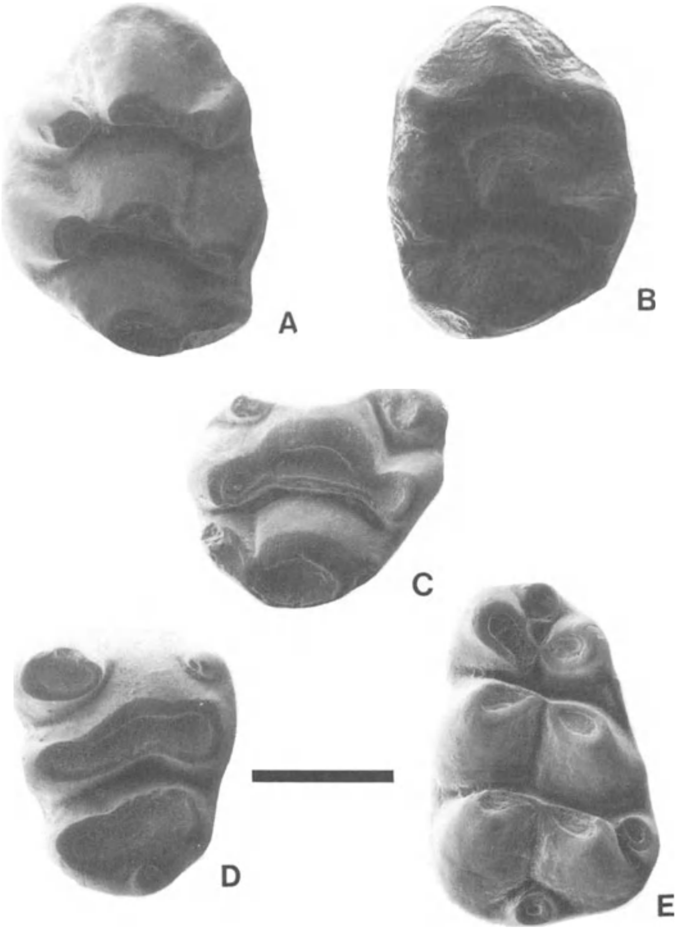

FIGURE 5. Occlusal views of *Saidomys parvus* from Inolelo 1. (A) Left M^1, WM 2012/92, holotype; (B) right M^1, WM 2013/92; (C) right M^2, WM 1362/92; (D) left M^3, WM 1354/92; (E) right M_1, WM 1349/92. Bar scale = 1 mm. Anterior is to the top of the page.

Diagnosis. Smaller than *S. natrunensis*, *S. afarensis*, and *S. afghanensis* by 10–26%. M^1 may have a precingulum along the lingual anterocone. Posterior cingulum vestigial to absent on M^2. M^3 with a small conical posterior cingular cusp. M_1 with a small conical posterior cingulum in two of three specimens.

Etymology. parvus is Latin for "little," referring to the relatively smaller size of this species compared to other species of *Saidomys*.

Description. Measurements for all tooth positions are given in Table IV. Both first upper molars (Fig. 5A,B) show moderately light occlusal wear. The surface of WM 2013/92 is corroded and the tooth may have been digested. The two teeth are broad in occlusal outline and consist of three transverse chevrons, with the first two symmetrical with respect to the longitudinal axis of the tooth. Cusps in the first two chevrons are weakly connected. The first chevron consists of a large lingual anterocone and smaller labial anterocone and anterostyle. The latter two cusps are approximately equal in size and located slightly posterior to the lingual anterocone. There is a weak precingulum on WM 2012/92 extending from the anterior aspect of the lingual anterocone to the labial anterocone. The middle chevron includes a large protocone (slightly larger than the lingual anterocone) and somewhat smaller paracone and enterostyle, which are similar in size and located somewhat posterior to the protocone. A large hypocone is elongate transversely and connected to a smaller anteriorly placed metacone. A weak posterior cingulum is present. The posterostyle is lacking, but may be represented by a thickening of the enamel. This thickening continues as an indistinct crest connecting the enterostyle and hypocone on WM 2013/92, but not on the holotype. Large anterolabial, posterolabial, and lingual roots and a small labial root are present.

Second upper molars are broad anteriorly and taper posteriorly (Fig. 5C). The present sample includes teeth with occlusal wear ranging from light to heavy. The teeth have a small conical labial anterocone and a conical anterostyle, which is about 2 1/2 times the size of the labial anterocone. There are two transverse chevrons. The anterior chevron includes a large protocone and smaller posteriorly placed paracone and enterostyle. On the posterior chevron, the large hypocone is connected to a much smaller anteriorly placed metacone. A distinct posterostyle is absent, but enamel on the lingual side of the hypocone is thickened and extends as a low crest to the enterostyle. The posterior cingulum is vestigial ($N = 2$) to absent ($N = 2$; cannot tell on one additional specimen). Large anterolabial and posterolabial roots are present. Large anterolingual and lingual roots may be fused or separate.

The M^3 shows moderately heavy occlusal wear (Fig. 5D). It is wider anteriorly and tapers posteriorly. There is a large oval anterostyle and a small conical labial anterocone. There are two transverse chevrons, both with the lingual cusps posterior to the rest of the chevron. In both chevrons, cusps within the chevron are fused. The posterior cingulum is a small conical cusp. There is a very large anterolabial root, large anterolingual and posterior roots, and a small lingual root.

Five M_1s of *S. parvus* are currently known. They range in occlusal wear from moderately light to heavy. The M_1 has six major cusps (labial and lingual anteroconid, protoconid, metaconid, hypoconid, entoconid) in three transverse rows, which are separated by moderately deep furrows (Fig. 5E). The labial cusps are located slightly posterior to, but are comparable in size with, the lingual cusps. A large medial anteroconid is variable in its location relative to the lingual and labial anteroconids. There is a high labial cingulum between the labial anteroconid and protoconid, with a small C4. A short weak labial cingulum connects the protoconid with a moderately large C1. Of four specimens, three have a small conical, and one has a small elongate, posterior cingulum. A low ridge extending labially and lingually from the posterior cingulum is variably developed. There are large anterior and posterior roots (the latter formed by two fused roots), and small labial and lingual roots.

WM 2014/92, a left M_1, is tentatively referred to this species. The specimen has heavy occlusal wear and is extremely abraded (perhaps digested). It is similar to *S. parvus* in size (length × width = 2.25 × 1.42 mm) and overall cusp morphology, including a probable large medial anteroconid and a C1. In contrast to the small usually conical posterior cingulum of *S. parvus*, that of WM 2014/92 is a slender elongate loph connecting the hypoconid and entoconid.

Discussion. The genus *Saidomys* was erected by James and Slaughter (1974) based on three isolated teeth from Wadi Natrun, Egypt. The genus was subsequently revised, although not formally rediagnosed (Slaughter and James, 1979), after the recovery of 22 additional isolated teeth from Wadi Natrun. Since description of the type species, *S. natrunensis*, four other species have been assigned to this genus, including *S. afarensis* from Hadar, Ethiopia (Sabatier, 1982), and *S. afghanensis* (Sen, 1983), *S. ?transversus* (Sen, 1983), and "*S.*" *magnus* (Brandy *et al.*, 1980), from Afghanistan. "*Saidomys*" *magnus* is now considered the monotypic species of the genus *Dilatomys* (Sen, 1983). Wesselman (1984) assigned a single M_1 from Member G, Shungura Formation, Ethiopia, to *Saidomys* sp. indet. *Saidomys* is also known from unpublished material from Tabarin, Chemeron Formation, and Kapcheberek, Lukeino Formation, central Kenya (Winkler, 1990), and Lothagam, Upper Nawata Beds, northern Kenya (Winkler, in preparation). The chronological range of the genus is ca. 6.5 (Wadi Natrun)–2 Ma (upper Member G, Shungura Formation).

A single M_1 of *Saidomys* sp. indet. is described from locality P.939, upper Member G, Shungura Formation, lower Omo Valley, Ethiopia (late Pliocene, >1.87 Ma; Wesselman, 1984). This tooth is close in size to *S. parvus* and to specimens from Tabarin.

There are a number of differences between *S. parvus* and *S. natrunensis* from Wadi Natrun. The most obvious discrepancy is in size: teeth of *S. parvus* are 10–21% smaller than *S. natrunensis*, although the observed ranges for the two species overlap for length of M^2 and width of M^3 (Table IV). In addition, the M^2s of *S. parvus* are proportionally less wide than those of *S. natrunensis* (length:width ratio of *S. parvus* = 0.91–0.94; *S. natrunensis*, mean = 0.84). There is slightly stronger development of the precingulum on *S. natrunensis*. Comparisons of M^3 are difficult because those of *S. natrunensis* have extremely heavy occlusal wear and the morphology is also obscured by postmortem abrasion. However, *S. natrunensis* appears to lack a labial anterocone and posterior cingular cusp on M^3. On *S. natrunensis* M_1s, the C1 is larger, the posterior cingulum is larger and usually oval in outline, and the labial and lingual cingula are more strongly developed. *Saidomys parvus* is derived relative to *S. natrunensis* in its conical posterior cingulum on M_1 and presence of a posterior cingular cusp on M^3.

The largest sample of *Saidomys*, nearly 300 specimens of *S. afarensis*, is from two localities in the Sidi Hakoma Member, Hadar Formation, Ethiopia (Sabatier, 1982). Sabatier diagnosed this species as being similar in size to *S. natrunensis*, but differing from it in possessing a conical posterior cingulum on M_1 and M_2, a larger hypocone and metacone on M^3, and a posterior cingulum on M_3. Some M_1 posterior cingula of *S. natrunensis* are as conical as those of *S. afarensis*, but overall the posterior cingula of M_1s and M_2s of *S. natrunensis* are oval in outline (elongate transversely). Evaluating differences in relative size of the hypocone and metacone on M^3 is difficult because M^3s of *S. natrunensis* are heavily worn and corroded. The posterior cingula on M^3s of *S. afarensis* are absent to vestigial, but present on 44 of 47 specimens (Sabatier, 1982). This cingulum appears to be lacking on the two specimens of *S. natrunensis*, but both teeth are damaged. Thus, while the latter two distinctions between the two species are difficult to substantiate, differences in morphology of the posterior cingulum on M_1 and M_2 indicate that *S. afarensis* is a distinct species. *Saidomys afarensis* is derived compared to other species of *Saidomys* in having a conical posterior cingulum on M_1 and M_2, and an M_3 with the labial anteroconid reduced to absent.

Compared to *S. afarensis*, *S. parvus* differs primarily in its smaller size: *S. parvus* is 10–22% smaller (but size ranges overlap for width of M^2). Excepting size, $M^1/_1$s are quite similar. M^2s of *S. parvus* are proportionally shorter (length:width ratio of *S. parvus* = 0.91–0.94; *S. afarensis* = 1.07) and have a less complex system of roots than those of *S. afarensis*. Although the posterior cingulum is vestigial to absent on M^2s of *S. parvus*, it is absent on *S. afarensis*. The M^3s of the two species are generally similar, but differ in *S. parvus* having a less reduced paracone. Sabatier (1982) describes the posterior end of M^3 as a small depressed rim on *S. afarensis*. However, the two illustrated M^3s of this taxon (Sabatier, 1982, Plate 1, figs. 9, 11) show small posterior cingular cusps, one conical and one slightly elongate. *Saidomys afarensis* is derived relative to *S. parvus* in the former being larger in size, possessing a more complex root pattern on M^2, and lacking a posterior cingulum on M^2.

Saidomys afghanensis from Pul-e Charkhi and Dawrankhel 14 and 15, Afghanistan (all early Pliocene), was originally diagnosed as *Karnimata afghanensis* by Brandy (1979, 1981). Subsequently, Sen (1983) reallocated the species to *Saidomys*. *Saidomys afghanensis* is a large form, comparable in size to *S. natrunensis* and *S. afarensis*. *Saidomys parvus* is 12–26% smaller than *S. afghanensis* (Table IV). Based on published descriptions and illustrations, other autapomorphies of *S. parvus* compared to *S. afghanensis* include (1) reduced posterior cingulum on M^2; (2) M^3 elongated (see below) and with a posterior cingular cusp (a cingulum on *S. afghanensis*); and (3) M_1 usually with a conical posterior cingulum, while that of *S. afghanensis* is transverse.

Sen (1983) described six teeth from Pul-e Charkhi as *Saidomys ?transversus* n. sp. (generic identification in question). From the illustrations and descriptions these specimens may represent a primitive *Arvicanthis*. These fossils are larger than any described *Saidomys* (approaching, but still smaller than, *Dilatomys magnus*) and have more transverse lophs. The posterior cingulum on M^1 is reduced. Labial cingula are greatly reduced on both M_1 and M_2. There does not appear to be a medial anteroconid on the one M_1 illustrated, but presence or absence of this cusp is not discussed. If it pertains to *Arvicanthis*, this is a primitive form because it has strong posterior cingula as cusps on M_1 and M_2, and the cusps on M^1 are fairly distinct.

In summary, compared to *S. afghanensis*, *S. natrunensis*, and *S. afarensis*, *S. parvus* is primitive in its smaller size. *Saidomys parvus* is close to *S. afarensis*, and derived with respect to *S. afghanensis* and *S. natrunensis*, in having (usually) an M_1 with a conical posterior cingulum, and an M^3 that may have a posterior cingular cusp. An undescribed sample of *Saidomys* from the Tabarin and Kapcheberek localities, Kenya (Winkler, 1990), includes 17 teeth and likely represents an additional species close in size to *S. parvus*, but differing with it in other aspects of its morphology. A small undescribed *Saidomys* is also present at Lothagam (Winkler, in preparation). A detailed discussion of the relationships within the genus *Saidomys* (including the new Kenyan material) and between *Saidomys* and other extinct (e.g., *Karnimata*, *Parapelomys*, *Euryotomys*) and extant (e.g., *Pelomys*, *Arvicanthis*) taxa is outside the scope of the present chapter and is in preparation.

3. Discussion and Conclusions

Rodent remains from the Ibole Member include the cane rat, *Thryonomys* sp., the cricetomyine *Saccostomus major*, a new genus and species of murine, *Tectonomys africanus*, and a new species of an extinct murine, *Saidomys parvus*. This small sample provides a tantalizing insight into Manonga paleoenvironments, the age of the Ibole Member, and paleobiogeography during the late Neogene.

A paleoenvironmental reconstruction for the Inolelo 1 and Shoshamagai 2 localities using four (Inolelo 1) or two (Shoshamagai 2) species, most of which are extinct, is speculative. Nevertheless, the presence of *Thryonomys* and *Saccostomus* is suggestive of open-country environments, based on habitat preferences of extant species. At present, *Thryonomys* includes two species: (1) *T. gregorianus*, ranging from northern Cameroon to the East African coast, is found in moist savannas; and (2) the generally larger *T. swinderianus*, more widely distributed in sub-Saharan Africa, and essentially semiaquatic, is associated with reed beds and grassy areas (Kingdon, 1974). *Saccostomus* is associated with a wide variety of savanna habitats (Nowak and Paradiso, 1983).

Harrison (1993) estimated the age of the Ibole Member to be late Miocene or early Pliocene (6–5 Ma) based on faunal correlation with other East African localities. This is close to the age suggested by the fossil rodents. The Manonga *Thryonomys* is a small form most comparable with specimens from the Upper Nawata Beds at Lothagam (ca. 5 Ma) and the lower part of the Chemeron Formation at Tabarin (5.25–4.15 Ma). *Saccostomus major* is otherwise known only from the Laetolil Beds (3.7–3.5 Ma). The holotype of *Tectonomys africanus* is from Tabarin. The genus *Saidomys* is known from faunas dating from about 6 Ma (Wadi Natrun, Kapcheberek) to 2 Ma (lower Omo Valley). The new species from Manonga is small, like specimens from Tabarin and Lothagam, but derived compared to them (and similar to material from Hadar, early Pliocene) in usually possessing a conical posterior cingulum on M_1. Overall the rodents suggest an early Pliocene age for the Ibole Member, ca. 5–4 Ma.

Rodents from the Manonga Valley are especially interesting and significant in terms of paleobiogeography during the Neogene. There are taxa in common between the Manonga Valley and Laetoli (*Saccostomus major, Thryonomys*), Tabarin and Kapcheberek (*Saidomys, Tectonomys africanus, Thryonomys*), and Lothagam (*Saidomys, Thryonomys*). The Manonga Valley records the southernmost occurrence for *S. major, Tectonomys*, and *Saidomys*. These localities are all found within the eastern branch of the developing East African Rift, which had been active since the late Oligocene, and was certainly tectonically active during the early Pliocene (Baker *et al.*, 1972, and others). Allowing for differences in age, depositional environment, and sample size, taxa in common among these sites indicate that tectonic activity in the developing Eastern Rift during the early Pliocene did not prevent dispersal within the rift. This is in contrast to Denys's (1985; Denys *et al.*, 1986) findings for younger localities within the East African Rift (Laetoli, Hadar, Omo Members B and F, and Olduvai Bed I), which show strong endemism and independent evolutionary development of their rodent faunas.

Saidomys had an extensive distribution during the late Miocene and Pliocene. It ranged from Afghanistan into Egypt, Ethiopia, Kenya, and northern Tanzania. The absence of this genus from the well-documented Laetoli fauna may possibly reflect a preference for a moister environment. Denys (1987) suggests rodents from the Laetolil Beds lived in a dry savanna (but Andrews, 1989, suggests a more wooded habitat for Laetoli).

Saidomys probably had its origins in Asia and subsequently dispersed to Africa. The immigration of *Saidomys* may have coincided with lowered sea levels associated with the Messinian stage (6.3–4.8 Ma; Steininger *et al.*, 1990). Dispersal of rodents and other taxa between Africa and Eurasia during this time period has been discussed by many authors (e.g., Brandy and Jaeger, 1980; Denys *et al.*, 1986; Azzaroli, 1990).

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Chapter 11

Fossil Fish from the Manonga Valley, Tanzania

Description, Paleoecology, and Biogeographic Relationships

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1. Introduction

This chapter reports on fossil fish elements collected from the Manonga Valley by the author and members of the Wembere–Manonga Paleontological Expedition (WMPE), during the 1990, 1992, and 1994 field seasons. Previous expeditions to the region had collected and reported on fossil mammal elements at the Tinde site (e.g., Stockley, 1930; Grace and Stockley, 1931; Hopwood, 1931), but little attention was paid to the abundant fish fossils, other than to report their presence (e.g., Grace and Stockley, 1931).

The Manonga basin was formed as a result of rifting and warping of the basement complex, probably during the late Miocene (Harrison and Verniers, 1993). The resulting lake was shallow and extensive; most fish fossils were recovered from these deposits. Further rifting, during the Pliocene, created the Eyasi basin to the northeast, into which Lake Manonga subsequently drained. The present-day Manonga and Wembere Rivers are seasonal, draining into Lake Kitangiri and Lake Eyasi during the rainy season.

WMPE collected fish elements from 14 sites in the Manonga Valley, representing all three members of the Wembere–Manonga Formation. Sites and formations are described by Harrison and Mbago in Chapter 1, this volume. Collection involved both surface recovery of larger fossil elements, and microscreening, using a 1-mm mesh screen, with some material further sieved through a 0.5-mm mesh screen. A total of 1591 fish elements were collected by the expedition and reported on here. Of these elements, 76 were teeth and the remainder were bone elements. Because of the large numbers of fish elements at many of the sites, only representative samples were collected.

2. History of Research

Analysis of fossil fish remains has suggested that a reasonably uniform fish fauna inhabited most of the African continent during the Miocene, and possibly earlier[*] (e.g., Greenwood, 1974; Van Couvering, 1977; Beadle, 1981). This fauna has been termed "Nilotic" or "Soudanien," and presumably formed the stock for later diversification into regional faunas, such as the Zaire, Nile, and Zambezi faunas (e.g., Beadle, 1981; also see Lowe-McConnell, 1987, for description of faunal provinces).

While little has been reported on fossil fish in the Wembere–Manonga basin, research on fish from nearby western and central rift localities indicates that the original Nilotic fauna underwent considerable evolutionary and biogeographic change in the late Cenozoic. Data, however, are still incomplete. Early Miocene deposits from Chianda Uyoma[†] (located in the northeastern section of modern

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[*] A pre-Nilotic fauna may have existed, with the recovery of fossils of ?mid-Tertiary age from the Singida Region south of Manonga. These were assigned to *Palaeodenticeps* and *Singida*, both belonging to families not previously known from modern or fossil eastern Africa fish faunas (Greenwood, 1960; Greenwood and Patterson, 1967).

Lake Victoria) contained the remains of *Lates* and other taxa, indicating the existence of a Nilotic fauna (Greenwood, 1951), which has since disappeared. The fish fauna of modern Lake Victoria is chiefly endemic, and other than brief reports of fossil fish remains (e.g., Trewavas, 1937), the post-Miocene history of fish fauna in the basin is unknown.

Miocene-aged deposits from Sinda, near Lake Albert, contained endemic, extinct species of *Sindacharax* and *Lates*, indicating the presence of a fauna with both Nilotic and Zaire affinities, and suggesting that proto–Lake Albert was isolated for a long period of time (Greenwood and Howes, 1975; Van Neer, 1992). Collections of fish specimens from Plio-Pleistocene deposits in the Lake Albert basin and in the nearby Lake Edward basin have documented a diverse ichthyofauna consisting of 18 genera, which show changes through time from a Nile–Zaire fauna to a purely Nilotic fauna (Stewart, 1989; Van Neer, 1992).

Late Miocene and Pliocene deposits at the Lothagam site, west of Lake Turkana, contained remains of a Nilotic fauna, including the extinct *Sindacharax* (Stewart, 1994). Some suggestion has been made of Plio-Pleistocene hydrological connections between the Lake Albert and Lake Edward basins and the proto–Lake Turkana basin (Pickford *et al.*, 1993), which could explain the existence of the Nilotic fauna in the later levels of the Lake Edward basin.

Fossil faunas are poorly known from the eastern rivers of Tanzania and Kenya (referred to by Roberts, 1975, and Lowe-McConnell, 1987, as the East Coast Ichthyofaunal Province); however, the modern fauna is distinct from the Nilotic fauna. The Manonga Valley lies between this eastern region and the western rift. Of considerable interest, therefore, in analysis of the Manonga fish fauna are possible relationships with the later Neogene faunas just mentioned.

3. Description of Fossils

Class Osteichthyes
Subclass Dipneusti
Order Dipnoi
Family Protopteridae

3.1. *Protopterus* sp. (Lungfish)

Provenance. Beredi South 4: 1 toothplate; Kiloleli 2: 2 toothplates; Mwambiti 3: 2 toothplates; Shoshamagai 2: 1 toothplate; Tinde West: 4 toothplates.

[†] Miocene sediments from Chianda Uyoma, Rusinga Island, and other localities provided evidence of a lake or series of lakes in what is today the northeastern section of Lake Victoria. Earlier researchers had suggested the presence of an extensive lake, which was named Lake Karunga (e.g., Kent, 1944; Wayland, 1931). Later researchers suggested the deposits represent small lake basins, possibly connected by rivers or streams, rather than one extensive body of water (e.g., Bishop and Trendall, 1967; see discussion in Van Couvering, 1982). The presence at Chianda Uyoma of relatively large *Lates* (Greenwood, 1951) suggests well-oxygenated waters.

Description. A total of 10 toothplates are identified as *Protopterus*; unfortunately, toothplates alone cannot be used for species identification. The elements represent a diversity of lengths, from an estimated total length (TL) of fish from 30 cm to over 1 m. While lungfish elements were not common, they were found consistently at Tinde and Kiloleli Member sites.

Discussion. Lungfish are an archaic group, dating from the Paleozoic. Lungfish toothplates are robust, and preserve well as fossils. They are known from ?Eocene and Oligocene deposits in northern Africa, Miocene deposits in eastern Africa, and Pliocene deposits in northern and eastern Africa (Van Couvering, 1977). *Protopterus* is present in modern Lakes Kitangiri and Eyasi, into which the Manonga and Wembere Rivers now drain, and also throughout Africa.

Subclass Actinopterygii
Superorder Ostariophysi
Order Characiformes
Family Characidae

3.2. *Hydrocynus* sp. (Tigerfish)

Provenance. Inolelo 1: 16 teeth; Shoshamagai 2: 2 teeth.

Description. Eighteen teeth have been assigned to this genus. The teeth are unicuspid and range in length from 2.6 to 6.5 mm from base of enameloid to the point. The estimated total length of the fish would be from ca. 29 to 70 cm. The fossil teeth are identical to modern *Hydrocynus* teeth. However, no species designation can be made, as *Hydrocynus* teeth vary little among species. Unfortunately, other *Hydrocynus* elements are not robust, and rarely preserve as fossils.

Discussion. Hydrocynus does not inhabit the modern Lake Kitangiri–Eyasi basin, but it is common in the modern Nile and Zaire River systems. Its fossil remains have been recovered from late Miocene and Pliocene deposits at Lothagam, Kenya (Stewart, 1994), and at Sinda, Zaire (Van Neer, 1992), from Plio-Pleistocene deposits in the Lake Edward basin (Greenwood, 1959; Stewart, 1990) and eastern Lake Turkana (Schwartz, 1983), and from Pliocene deposits at Wadi Natrun, Egypt (Stromer, 1916; Weiler, 1926; Greenwood, 1972).

3.3. *Alestes*

Provenance. Inolelo 1: 7 first inner premaxillary teeth, 13 second inner premaxillary teeth, 1 third inner premaxillary tooth, 1 fourth inner premaxillary tooth, 6 outer premaxillary teeth, 2 inner dentary teeth, 4 first outer dentary teeth, 16 second or third outer dentary teeth, 1 tooth fragment; Kininginila: 1 second inner premaxillary tooth; Shoshamagai 2: 2 outer dentary teeth.

Description. A total of 54 teeth attributable to *Alestes* were recovered, with all but one derived from the lowest fossiliferous stratigraphic unit (Ibole Member). *Alestes* remains are rarely recovered as fossils, due to the small, fragile structure of the bones, and the very small teeth. Only screening with a 1-mm screen will allow recovery of these elements. The teeth from the Manonga sites represent fish with an estimated total length of about 15 to 30 cm.

The Manonga *Alestes* teeth were compared with those of extant species, including *A. affinis, A. baremose, A. dentex, A. imberi, A. jacksonii, A. liebrechtsii, A. macrolepidotus, A. macrophthalmus, A. nurse*, and *A. stuhlmanni*. The teeth are morphologically similar to those of four of these species—*A. affinis, A. dentex, A. nurse*, and *A. stuhlmanni*. Teeth resembling *A. stuhlmanni* were most numerous, and are discussed first.

3.4. *Alestes* aff. *A. stuhlmanni*

Provenance. Inolelo 1: 5 first inner premaxillary teeth, 9 second inner premaxillary teeth, 1 third inner premaxillary tooth, 1 fourth inner premaxillary tooth, 2 first outer dentary teeth, 6 second/third outer dentary teeth.

Description. Three of the first inner premaxillary teeth (PI1) (Figure 1a) are almost identical to the PI1 teeth of *A. stuhlmanni*, both in shape and cusp morphology. While there is considerable individual variation in *A. stuhlmanni* teeth, the PI1 teeth of *A. stuhlmanni* are distinctive from all other modern *Alestes* PI1 teeth examined in that the dominant lingual-distal cusp and its surrounding cusps form a long oval-shaped ridge, the center of which is deeply excavated. In all other *Alestes* PI1 teeth examined, the dominant lingual cusp is separated from surrounding cusps, which are discrete and do not show ridging. In the Manonga PI1 teeth, the lingual-distal cusps form an oval-shaped ridge almost identical to that of *A. stuhlmanni*, although the cusps that make up the ridge are slightly better defined in the fossil teeth. In some *A. stuhlmanni* specimens there is also a second shorter ridge anterior to the oval ridge. In the fossil teeth this ridge is well defined in one specimen, but vestigial or nonexistent in the other two teeth. Two of the fossil teeth are within the size range of modern *A. stuhlmanni*; however, one is about a third again larger than the longest reported modern individual (ca. 26.8 cm TL). Two other PI1 teeth are too worn for positive identification, but also appear similar to the *A. stuhlmanni* teeth.

A total of 13 second inner premaxillary teeth (PI2) are identified from the fossil sample, and these fall into three distinct morphological types. Three of the teeth (Figure 1b) are very similar to the PI2 teeth of *A. stuhlmanni*. The chief difference is that in the modern specimens, anterior to the dominant lingual cusp, there is a largely unbroken ridge crossing from the mesial to distal surface of the tooth. In the fossil specimens, this ridge also exists, but the small cusps composing the ridge are more distinct. Six other teeth are also very similar to modern *A. stuhlmanni* PI2 teeth, but with two differences. First, in place of the ridge just described are two distinct cusps. Second, the fossil teeth are more triangular than rounded, as in the modern specimens. All fossil teeth fall within the size range of the modern species.

The fossil tooth assigned as PI3 is identical to that of *A. stuhlmanni* in shape, size, cusp morphology and arrangement (Figure 1c).

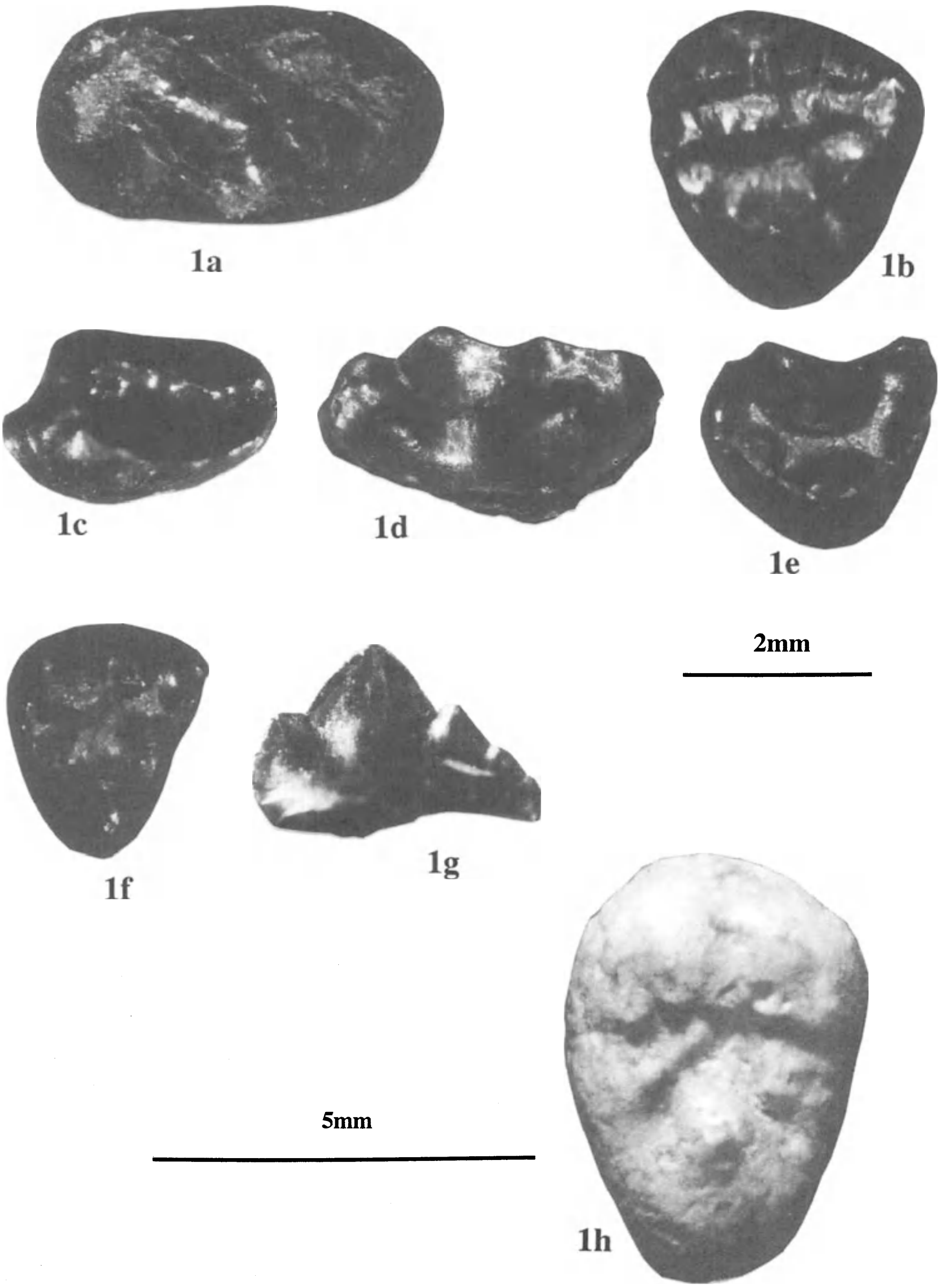

FIGURE 1a. Occlusal view of first inner premaxillary tooth - *Alestes* aff. *A. stuhlmanni;* **1b.** Occlusal view of second inner premaxillary tooth - *Alestes* aff. *A. stuhlmanni*; **1c.** Occlusal view of third inner premaxillary tooth - *Alestes* aff. *A. stuhlmanni*; **1d**. Occlusal view of fourth inner premaxillary tooth - *Alestes* aff. *A. stuhlmanni;* **1e.** Occlusal view of first outer dentary tooth - *Alestes* aff. *A. stuhlmanni*; **1f.** Occlusal view of second outer dentary tooth - *Alestes* aff. *A. dentex*; **1g.** Lingual view of third outer dentary tooth - *Alestes* cf. *Alestes affinis/A. nurse;* **1h.** Occlusal view of second inner premaxillary tooth - *Sindacharax* sp.

The fossil PI4 tooth (Figure 1d) is also identical to that of PI4 of *A. stuhlmanni*. It represents an individual that is slightly larger than the largest reported modern *A. stuhlmanni*.

A total of 20 fossil teeth are identified as outer dentary teeth. These are robust teeth, which have a similar morphology in many *Alestes* species. These teeth tend to show more wear than premaxillary teeth, and distinctive characters may not be apparent, so position is not always clear. Four teeth were assigned as first outer dentary teeth (DO1). Two of these (Figure 1e) were identical to the DO1 of modern *A. stuhlmanni*, which is distinctive from those of other *Alestes* in having a small ridge on its lingual edge. In other *Alestes* the lingual edge has no ridge, but is smooth.

Fourteen teeth are assigned as either DO2 or DO3, as exact position could not be determined. Six of these are identical to DO2/3 teeth of *A. stuhlmanni*; the others are described below.

Given the similarity between the fossil teeth and those of modern *A. stuhlmanni*, and the contrast with any other modern *Alestes* examined, they are designated *Alestes* aff. *A. stuhlmanni*.

3.5. *Alestes* aff. *A. dentex*

Provenance. Inolelo 1: 2 second inner premaxillary teeth, 1 first outer dentary tooth, 2 second/third outer dentary teeth.

Description. Two fossil PI2 teeth (Figure 1f) are very similar to PI2 teeth of *A. dentex*. The cusp patterns of the fossil and modern teeth are similar, with *A. dentex* having a dominant lingual cusp, and several discrete cusps anterior to it. While the fossil teeth have a similar arrangement, the pattern of the discrete cusps is slightly different. Similar to modern *A. dentex* PI2 teeth, the lingual side of the fossil teeth is pinched in rather than rounded as in other species of *Alestes*.

One fossil DO1 tooth and two fossil DO2/3 teeth were very similar to those of modern *A. dentex*.

3.6. *Alestes* cf. *A. nurse* and *A. affinis*

Provenance. Inolelo 1: 2 first inner premaxillary teeth, 2 second inner premaxillary teeth, 1 first outer dentary tooth, 6 second/third outer dentary teeth.

Description. Two of the Manonga PI1 teeth are identical to the modern PI1 teeth of *A. nurse* and *A. affinis*, which are virtually indistinguishable from each other. The size of the fossil teeth puts them in the size range of modern *A. nurse*, however, rather than *A. affinis*, which is somewhat smaller.

Two fossil teeth are identical to the PI2 teeth of *A. affinis* and *A. nurse*, which are again indistinguishable from each other. The modern and fossil teeth all have a dominant lingual cusp and two smaller nonridged cusps paired anterior to the dominant cusp. Modern *A. affinis* and *A. nurse* have reported total lengths of approximately 14 cm and 23 cm, respectively, and the fossil teeth fall within this size range.

One fossil DO1 was identical to the DO1 of *A. nurse* and *A. affinis*, which were again indistinguishable from each other. Six fossil DO2/3 teeth were assigned as *A. affinis/A. nurse* (Figure 1g).

Teeth assigned as *A. nurse/A. affinis* are fossilized differently from all other Manonga *Alestes* teeth, with a fresher appearance. Because they resemble their modern counterparts exactly, they, unlike the other fossil *Alestes* teeth, were assigned as "cf." While it is unusual to designate "cf." for two species, I found it impossible to distinguish between the teeth of the two species.

3.7. *Alestes* sp.

Provenance. Inolelo 1: 6 outer premaxillary teeth, 2 first inner dentary teeth, 2 outer dentary teeth, 1 indet. tooth; Kininginila: 1 second inner premaxillary tooth; Shoshamagai: 2 second/third outer dentary teeth.

Description. The PI2 tooth from Kininginila differs from the other fossil teeth in its size and cusp morphology. It is twice the length and width of the other fossil *Alestes* teeth, and while the overall cusp morphology is similar to that of other *Alestes*, the lingual cusp is positioned more anteriorly. The large size of the tooth means that the estimated length of the individual is greater than that of any known modern *Alestes*. For these reasons it is referred here only as *Alestes* sp.

Six fossil teeth are assigned as outer premaxillary teeth. Outer premaxillary teeth are very similar in morphology among all modern *Alestes* specimens, and no species designation can be given to the fossil specimens.

Two fossil teeth are assigned as inner dentary teeth (DI1), and again, as these are similar among modern *Alestes* specimens, no further identification can be made.

Two outer dentary teeth from Shoshamagai (DO2/3) can only be identified as *Alestes* sp.

Two remaining teeth were worn and could only be identified as outer dentary teeth of *Alestes*. A final tooth fragment was also left as *Alestes* sp.

Discussion. Very little morphological analysis of modern *Alestes* teeth has been undertaken, other than absolute counts of teeth, with most taxonomic work based on external meristic and morphometric characters. In an examination of the teeth of modern *Alestes* species, primarily the inner premaxillary teeth, it became clear that the teeth fell into three distinct groups. Most species in each group had the same geographic distribution; therefore the groups were called the "Zaire" group (*A. liebrechtsii, A. macrophthalmus*), with a Zaire River basin distribution; the "Eastern" group (*A. stuhlmanni*), with a distribution in the eastern rivers of Tanzania; and the "Nile" group (*A. baremose, A. dentex, A. jacksonii, A. macrolepidotus, A. nurse*), with a Nilotic (Nile River system *sensu lato*) distribution. *A. macrolepidotus*, known primarily from the Nile system, is also present in the Zaire basin. In addition, two species had teeth that fell into the Nilotic group, but which did not have a Nilotic distribution. These were *A. affinis* and *A. imberi*, which are found only in the eastern rivers and the Zaire/Zambesi basin systems respectively.

The Zaire group had the most simple cusp patterns on their inner premaxillary teeth, with a dominant row of lingually positioned cusps, but no, or minor, cusps anterior to these. The Nile group had at least two, and occasionally three, rows of well-developed cusps on their PI1 and PI2 teeth, and one row of cusps on their PI3 and occasionally on their PI4 teeth. The Eastern group was distinctive in having their PI1, PI2, and PI3 teeth with one or sometimes two ridges. The teeth of these three groups are easily distinguished from each other.

The Manonga teeth patterns fell consistently into both Nile and Eastern groups, with no teeth resembling the Zaire group teeth. I suggest therefore that the Manonga teeth have direct and/or indirect relationships with the Nile River and Eastern *Alestes* groups, and no relationship with the Zaire River fauna. I will discuss this further below.

Alestes is not present in modern Lake Kitangiri–Lake Eyasi. It has a poor fossil record, but teeth are known from late Miocene–Pliocene deposits at Lothagam (Stewart, 1994) and Plio-Pleistocene deposits in the Lake Edward basin (Stewart, 1990).

3.8. *Sindacharax* sp.

Provenance. Kininginila: 1 first inner premaxillary tooth, 1 second inner premaxillary tooth, 1 second inner premaxillary fragment, 1 outer dentary tooth.

Description. Fossil teeth of this genus were only recovered at Kininginila. The teeth are very worn, but can be identified to position. Only the PI2 (Figure 1h) retains enough morphology to compare it with other *Sindacharax* teeth. In comparison to the two known species of *Sindacharax*, there is little similarity either with *S. lepersonnei*, known only from Miocene deposits in the Lake Albert basin and Sinda area, Zaire (Greenwood and Howes, 1975; Van Neer, 1992), or with the *S. deserti* specimens from Pliocene-aged Wadi Natrun (Greenwood, 1972). There is however considerable similarity with several *Sindacharax* sp. PI2 specimens from late Miocene–Pliocene deposits at Lothagam, and from Plio-Pleistocene specimens from the upper Semliki River (Stewart, 1990).

Discussion. *Sindacharax* is an extinct genus, with the latest recorded specimen, from East Turkana, dating to about 0.7 Ma according to Feibel (1988).

Order Siluriformes
Family Clariidae

3.9. *Clarias* sp. (Mudfish)

Provenance. Beredi South 1: 1 dermethmoid fragment, 1 prefrontal, 1 supraorbital fragment, 1 pterotic, 1 supraoccipital, 1 articular, 2 trunk vertebra centra; Beredi South 3: 1 dermethmoid fragment, 1 articular, 1 caudal vertebral centrum, 3 nonidentifiable fragments; Beredi South 4: 1 frontal, 1 sphenotic, 1 dermosphenotic, 1 pterotic fragment, 1 dentary, 1 articular, 2 ceratohyals, 1 epihyal; Inolelo 1: 3 parasphenoid fragments, 2 supraoccipital fragments, 1 jugal, 4 dentary fragments, 8 articular fragments, 1 quadrate fragment, 1 operculum fragment, 5 urohyal fragments, 1 dorsal hypohyal fragment, 1 ceratohyal fragment, 3 trunk vertebra centra, 3 caudal vertebra centra; 49 vertebral fragments, 9 pectoral spine fragments; Kiloleli 2: 2 dermethmoids, 1 frontal, 3 frontal fragments, 2 supraorbital fragments, 2 sphenotic fragments, 2 pterotics, 3 supraoccipitals, 3 supraoccipital fragments, 1 parasphenoid fragment, 1 dentary, 1 operculum, 4 ceratohyals, 1 ceratohyal fragment, 1 epihyal, 4 cleithrum fragments, 1 trunk vertebra, 5 pectoral spine fragments, 73 nonidentifiable fragments; Kininginila: 2 frontal fragments, 1 supraorbital fragment, 1 ceratohyal, 2 pectoral spine fragments; Mwambiti 4: 2 neurocranial fragments, 1 articular, 5 vertebral fragments; Ngofila 4: 2 articulars, 4 vertebral fragments; Nyawa: 1 dermethmoid, 1 pterotic, 1 supraoccipital, 2 ceratohyals, 2 epihyals, 1 trunk vertebra, 1 pectoral spine; Shoshamagai 1: 1 supraoccipital fragment, 3 cranial fragments, 1 articular fragment; Shoshamagai 2: 2 frontals, 1 parasphenoid fragment, 1 dentary fragment, 5 articulars, 1 articular fragment, 1 quadrate, 1 weberian apparatus fragment, 8 trunk centra, 5 caudal centra, 13 vertebral fragments, 3 pectoral spine fragments; Tinde East: 1 articular fragment; Tinde West: 8 dermethmoids, 72 dermethmoid fragments, 38 prefrontals, 9 prefrontal fragments, 1 frontal, 12 frontal fragments, 190 supraorbital fragments, 19 sphenotics, 2 dermosphenotics, 2 pterotic fragments, 3 posttemporals, 4 supraoccipitals, 57 supraoccipital fragments, 1 vomer fragment, 1 parasphenoid, 42 parasphenoid fragments, 35 neurocranial fragments, 3 jugals, 1 jugal fragment, 1 palatine, 2 pterygoids, 5 pterygoid fragments, 1 dentary, 19 dentary fragments, 64 articulars, 38 articular fragments, 7 quadrate fragments, 13 operculum fragments, 9 urohyals, 2 urohyal fragments, 3 dorsal hypohyals, 1 ventral hypohyal, 22 ceratohyals, 7 ceratohyal fragments, 5 epihyal fragments, 14 cleithrum fragments, 1 coracoid fragment, 3 weberian apparatus fragments, 70 trunk vertebra centra, 80 caudal vertebra centra, 2 vertebral fragments, 117 pectoral spine fragments, 78 nonidentifiable fragments.

Description. A total of 1364 *Clarias* remains were collected. *Clarias* remains were ubiquitous at all sites surveyed, and those collected represent only a sample. *Clarias* cranial elements are robust, and preserve distinctively as fossils. A diverse range of estimated lengths of individuals is represented, from about 10 to 120 cm total length. Unfortunately, disarticulated elements are not diagnostic to species, particularly given the considerable individual variation in *Clarias* morphology.

Discussion. Clarias is known from late Miocene deposits in Sinda, Zaire (Van Neer, 1992), Chalouf, Egypt (Priem, 1914), and Lothagam, Kenya (Stewart, 1994), Pliocene deposits from Wadi Natrun (Egypt) (Greenwood, 1972), and Plio- Pleistocene sites from eastern Turkana, Kenya (Schwartz, 1983; Stewart, 1994). At present *Clarias* has a wide distribution in Africa, with at least 34 species. *C. mossambicus* inhabits the modern Lake Kitangiri/Eyasi basin.

3.10. Siluriformes Indet.

Provenance. Inolelo 1: 1 cranial spine fragment, 60 vertebral fragments, 18 pectoral spine shaft fragments; Shoshamagai 2: 2 frontal fragments, 1 quadrate fragment; 5 vertebral fragments; Tinde West: 10 cranial fragments, 13 vertebral fragments, 19 pectoral spine fragments.

Description. Most of these remains were too fragmentary for identification, except as siluriform. However, four of the pectoral spine fragments, as well as a cranial spine fragment, from Inolelo were clearly not of *Clarias*. The pectoral spines have strongly bilateral barbing on the shaft, similar to either *Synodontis* or *Clarotes*, and the cranial spine also bears a resemblance to those of these two genera.

Discussion. These shaft fragments indicate the rare presence of a nonclariid siluriform in the Manonga Valley sites.

Superorder Acanthopterygii
Order Perciformes
Family Centropomidae

3.11. *Lates* sp.

Provenance. Beredi South 4: 2 lepidotrichia; Kininginila: 1 cleithrum fragment, 1 trunk vertebra centrum; Ngofila 4: 1 basioccipital fragment.

Description. Few *Lates* remains were found, and these were restricted to sites in the Tinde and Kiloleli Members. The fish represented were small to medium-size for *Lates*, with estimated total lengths ranging from 60 to 150 cm.

While the remains were few and fragmentary, the vertebra and cleithrum closely resemble those of *L. niloticus*, and not those of *L. rhachirhinchus*, a species known from the Mio-Pliocene of the Lake Albert basin (Greenwood and Howes, 1975).

Discussion. Lates is widely distributed in Africa, with seven modern species. The closest modern occurrence of *Lates* is Lake Tanganyika. Fossil *Lates* are known from Eocene deposits in Egypt (Weiler, 1929), early Miocene deposits in Kenya (Greenwood, 1951), Sinda, and the Lake Albert basin (*L. rhachirhinchus*) (Greenwood and Howes, 1975), late Miocene deposits at Lothagam (Stewart, 1994), Lake Albert basin (Greenwood and Howes, 1975) and Egypt (Priem, 1914), and early to mid Pliocene in Lothagam and East Turkana (Schwartz, 1983; Stewart, 1994), Lakes Edward–Albert basins (Greenwood and Howes, 1975; Stewart, 1990; Van Neer, 1992) and Wadi Natrun, Egypt (Stromer, 1916; Weiler, 1926; Greenwood, 1972).

3.12. Cichlidae

Provenance. Inolelo 1: 1 trunk vertebral centrum; Kininginila: 1 operculum fragment, 1 caudal vertebra centrum, 1 lepidotrichia; Nyawa: 3 lepidotrichia, 2 lepidotrichia fragments.

Description. Cichlid remains from the Manonga Valley were few and, with one exception, were restricted to the Tinde Member. The fish are estimated to have total lengths ranging from about 20 to 25 cm. Unfortunately, the taxonomy of the well-documented radiation of modern cichlids in African rift lakes is based largely on differences in cranial and tooth features, which means that most disarticulated remains are not identifiable beyond the level of family.

Discussion. Modern cichlids are widespread in Africa, with upwards of 600 described species. *Oreochromis amphimelas* is present in modern Lakes Kitangiri and Eyasi, and two introduced cichlid species are also present in Lake Kitangiri (Trewavas, 1983). Fossil cichlid elements are common in African deposits from the Oligocene to the present (e.g., Van Couvering, 1977; see in particular Van Couvering, 1982). They are reported from early Miocene (and possibly earlier) deposits in Mahenge (Greenwood and Patterson, 1967) and Rusinga (Greenwood, 1951; Van Couvering, 1982), late Miocene and Pliocene deposits in the Lakes Albert–Edward basins (Greenwood and Howes, 1975; Stewart, 1990; Van Neer, 1992), and Lothagam and East Turkana (Schwartz, 1983; Stewart, 1994).

3.13. Perciformes Indet.

Provenance. Inolelo 1: 2 lepidotrichia fragments.

Description, Discussion. These specimens are too fragmentary to assign to family, but belong to either the centropomids or the cichlids.

4. Composition of the Manonga Fish Fauna and Relationships with Other Fish Faunas

The Manonga fish fauna demonstrates considerable change from the earlier to the later deposits (Table I). The earlier, Ibole Member fauna (sites: Inolelo 1, Mwambiti 3 & 4, Shoshamagai 2) is more diverse than later faunas, including *Protopterus*, several species of *Alestes*, as well as *Hydrocynus*, *Clarias*, a non-clariid catfish, and at least one species of cichlid. In the lower Tinde Member (sites: Beredi South 4, Kininginila, Nyawa), several species of *Alestes* and *Hydrocynus* have disappeared, while *Sindacharax* and *Lates* have appeared. By the time of deposition of the later Tinde Member (sites: Tinde West and Tinde East) and the Kiloleli Member (sites: Beredi South 1 & 3, Kiloleli 2, Ngofila 4, Shoshamagai 1) only *Protopterus*, *Clarias*, and a second catfish are still in evidence. One *Lates* element from Ngofila 4 is suggested to have derived from the earlier levels, rather than the Kiloleli Member levels. It must be emphasized, however, that although collection of fossils was exhaustive at all sites, presence/absence may still be an artifact of sampling.

Of interest are the biogeographic relationships of the Manonga fish fauna. The Lake Manonga (Lake "Wembere" in Pickford *et al.*, 1993) basin was formed as a result of warping of the basement complex at the end of the Miocene (Williams and Eades, 1938; Harrison and Verniers, 1993). Pickford *et al.* (1993) suggest that this action led to interruption of the east–west drainage and the subsequent formation of Lake "Wembere." While it is not certain whether the ponded-back

Table 1. Listing of Fish Taxa Found at Manonga Valley Sites, by Stratigraphic Member

Taxa	Ibole Member	Lower Tinde Member	Upper Tinde Member	Kiloleli Member
Protopterus sp.	x	x	x	x
Hydrocynus sp.	x			
Alestes aff. *A. dentex*	x			
Alestes aff. *A. stuhlmanni*	x			
Alestes cf *A. nurse/affinis*	x			
Alestes sp.	x	x		
Sindacharax sp.		x		
Clarias sp.	x	x	x	x
Siluriformes indet.	x		x	
Lates sp.		x		x?
Cichlidae	x	x		
Perciformes indet.	x			

rivers were east or west flowing, the map by Pickford *et al.* (1993) suggests that the rivers were eastern flowing. Further support for this suggestion comes from maps by both Cooke (1958) and Beadle (1981), which show the pre-Pleistocene Manonga–Wembere drainage as part of the Pangani River system, an easterly flowing river system that is part of the East Coast Ichthyofaunal Province (Boulenger, 1905; Lowe-McConnell, 1987). The probable presence in the early levels of the Lake Manonga deposits of *A. stuhlmanni*, known today only from eastern flowing rivers in Tanzania, suggests the early lake was indeed drained by eastern-flowing rivers. There were no *Alestes* specimens recovered that showed Zaire River affiliations, which would be expected if western-flowing rivers had contributed to Lake Manonga.

The presence in the Ibole Member of one, and possibly two other, *Alestes* species not known in eastern-flowing rivers suggests contribution from other hydrological systems. The presence of *A. dentex*, and possibly *A. nurse*, indicates a contribution from a Nilotic system, as both these species are known only from the Nile River and affiliated systems.

Later in the history of Lake Manonga, the appearance in the Tinde Member of *Sindacharax* and *Lates* indicates inflows from another hydrological system, as these genera were not present in the Ibole Member sites. Neither genus is known from the east coast rivers. Three other systems can be considered as having possible inflows to the Pliocene Manonga basin—the Zaire system via Lake Tanganyika, the proto–Lake Victoria[*] and Lakes Edward–Albert[†] systems, and the Lake Turkana system. Because the Kininginila *Alestes* specimen is

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[*] The term "proto–Lake Victoria" refers to the pre-Pleistocene lacustrine/fluvial deposits in the location now occupied by present day Lake Victoria. It is not meant to imply an evolutionary relationship between the present Lake Victoria basin and earlier formations.

[†] Pickford *et al.* (1993) have hypothesized that in the late Miocene and Pliocene the Lakes Albert and Edward basins were one, creating a large lake called Lake Obweruka. They suggest the lake was divided into two basins at the end of the Pliocene.

morphologically most similar to Nile system *Alestes*, and because *Sindacharax* is known from proto-Nile Miocene–Pliocene sites, but not from Zaire River sites, it seems clear that the connection into Lake Manonga must come from a Nilotic system, being either the proto–Lake Victoria and Lakes Albert–Edward systems or the proto–Lake Turkana system, or both.

The possibility of a connection between Lake Manonga and the proto–Lake Victoria and Lakes Edward–Albert systems, most likely via a southern tributary of the Kagera River, is not new in the literature (e.g., Grace and Stockley, 1931; de Heinzelin, 1959; Barth in Pickford *et al.*, 1993). Early Miocene deposits at Chianda Uyoma (in the proto–Lake Victoria basin) indicated that *Lates* and other Nilotic species inhabited the lakes or rivers (Greenwood, 1951). However, little is known of late Miocene and Pliocene fish fossils, and whether the fish disappeared or moved to other systems. Both *Lates* and *Sindacharax* are known from Pliocene deposits in the Lake Edward basin (Stewart, 1990), which may have had an inflow from the Kagera River (e.g. Cooke, 1958), which in turn may have indirectly been periodically connected to the Manonga basin. Pickford *et al.* (1993) have suggested that the Lakes Albert–Edward basins may have been connected on occasion with the Lake Turkana basin during the Plio-Pleistocene, based on similarity of molluscan faunas in the two basins (see also Williamson, 1985). While few elements of *Sindacharax* and *Lates* were recovered from the Manonga sites, further examination of the Lake Edward and Lake Turkana taxa is needed, to determine any such affiliations.

By the time of deposition of the Kiloleli Member sites, the lake had apparently undergone some shrinkage. Fish which required well-oxygenated water, such as *Alestes* and *Lates*, had disappeared, leaving only taxa more tolerant of deoxygenated waters, including *Clarias* and *Protopterus*.

The fresher-appearing *A. nurse*/*A. affinis* fossils may indicate more recent fossilization and, therefore, a more recent connection between the Manonga River system and a Nilotic system. *A. nurse*/*A. affinis* are not now present in the Manonga River or Lakes Kitangiri–Eyasi systems, but *A. nurse* is present in Lake Victoria and *A. affinis* is present in eastern Tanzanian rivers. Evidence reported by Verniers (this volume, Chapter 2) supports a Holocene overflow of Lake Victoria into the Manonga Valley.

5. Evolutionary Relationships

Unfortunately, because only disarticulated elements were recovered, little can be said about evolutionary relationships for most taxa. One exception is *Alestes*, whose oral teeth are molariform (unusual in fish), and may show changing cusp morphology through time. The clear separation of modern *Alestes* teeth into groups that have geographic (and presumably phylogenetic) significance requires further investigation. However, *Alestes* teeth are rarely reported from fossil deposits, and more are needed for study.

While large numbers of elements were recovered of *Clarias*, this genus has considerable individual variation, and complete, articulated skeletons are needed for more specific identification.

6. Paleoecological Implications

During deposition of the Ibole Member sites, the fish, with the exception of *Clarias*, were of small body size. While this may be an artifact of collection or taphonomy, it is unlikely that the remains of small fish would have survived to the exclusion of large elements, especially when a variety of sites were surveyed. The presence of *Alestes* and *Hydrocynus* in the Ibole Member, both pelagic fish, suggests a shallow, well-oxygenated lake or slow-moving river with open water (i.e., not marshy or swampy). *Clarias* is also present, and is highly tolerant of most hydrological conditions; therefore its habits are not incompatible with an open, shallow lake or river.

In the lower Tinde Member there is a clear change in the composition of the fish fauna. The presence of a much larger-size fauna than in the Ibole Member, in particular *Lates* up to 1.5 m in length, as well as large *Alestes* and *Sindacharax* individuals, indicates a large, moderately deep, well-oxygenated lake. The appearance of *Sindacharax* and *Lates* indicates a new inflow/outflow into Lake Manonga, possibly associated with the increased size of the lake.

The disappearance in the upper Tinde Member and Kiloleli Member of the large fish fauna, and the presence of only *Clarias* and *Protopterus*, seems to indicate a shrinking lake or river. Both *Clarias* and *Protopterus* are air-breathers, and, therefore, are tolerant of deoxygenated, swampy waters, unlike *Alestes, Hydrocynus*, and *Lates*. The disappearance of these latter taxa seems to indicate some period of regression of lake waters and cessation of the early Tinde member inflow/outflow to the point where the three taxa disappeared and could not recolonize.

7. Summary

Fossil fish elements collected from sites in the Manonga Valley indicate a changing fish fauna throughout the late Miocene–Pliocene. Fish from the earlier Ibole Member include several species of *Alestes*, as well as *Protopterus, Hydrocynus, Clarias*, a second catfish, and at least one species of cichlid. The *Alestes* specimens show affinities with modern species from the eastern rivers and from Nilotic systems. The lake at this time was probably shallow, but with open waters.

In the lower Tinde member, new taxa appear, including *Sindacharax* and *Lates*, while several Ibole Member taxa disappear. The new taxa have Nilotic affinities, and indicate a new inflow/outflow from a Nilotic system, possibly the proto–Lake Victoria and Lakes Edward–Albert systems, or Lake Turkana. The much increased size and changed composition of the fauna suggests Lake Manonga was a large, reasonably deep, well-oxygenated lake.

By the time of the upper Tinde and Kiloleli members, the lake appears to have shrunk. The only taxa recovered are *Protopterus* and *Clarias*, air breathers that are tolerant of deoxygenated, swampy conditions.

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Chapter 12

Late Cenozoic Freshwater Mollusks of the Wembere–Manonga Formation, Manonga Valley, Tanzania

DIRK VAN DAMME and ACHILLES GAUTIER

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1. Introduction

The fossil freshwater mollusks described and analyzed in this chapter were collected by members of the Wembere–Manonga Paleontological Expedition (WMPE) in the Manonga Valley during the 1992 and 1994 field seasons. The following list summarizes basic information about the seven localities from which fossil mollusks were obtained. The abbreviations in parentheses are those used in Table I.

Fossil mollusks have been recovered from each of the main stratigraphic units within the Wembere–Manonga Formation: the Kiloleli, Tinde, and Ibole Members.

- Kiloleli Member: Beredi South 1 (BE), Ngofila 1 (N1), Ngofila 2 (N2); three sites located within 5 km of each other, but yielding finds from the same fossiliferous beds; estimated age ca. 4 Ma.
- Tinde Member: Kininginila (KI); estimated age between 4 and 5 Ma.

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Table I. Late Cenozoic Freshwater Mollusks from the Wembere–Manonga Formation[a]

	Ibole Mb			Tinde Mb	Kiloleli Mb		
	I1	I3	SH	KI	BE	N1	N2
Bellamya aff. *capillata*	(2)	—	—	(R)	(3)	—	(F)
Pila ovata	—	—	—	—	(R)	—	(3)
Lanistes ovum	(1)	(1)	(2)	(3)	(8)	(1)	(8)
Gabbiella aff. *humerosa*	—	—	—	(F)	—	—	(F)
Melanoides aff. *anomala*	—	—	—	(2)	—	—	—
Cleopatra aff. *ferruginea*	(20)	—	—	(F)	—	(10)	(R)
Spathopsis wahlbergi	(12)	—	(12)	—	(5)	—	—
Mutela dubia	(2)	—	(1)	—	—	—	—
Number of species	5	1	3	5	4	2	5

[a] For abbreviations of the fossil localities see the list in the text introduction. The numbers of specimens are given in parentheses because they are of limited information content (see text for discussion). F and R mean frequent and rare, respectively, and are used for occurrences that could not be counted properly.

- Ibole Member: Inolelo 1 (I1), Inolelo 3 (I3), Shoshamagai 2 (SH); three localities within 3 km of each other, but yielding specimens from the same fossiliferous beds; estimated age between 5 and 6 Ma.

The precise location of the fossiliferous sites discussed here, as well as details of their stratigraphic contexts, are described elsewhere in this volume (Harrison and Mbago, Chapter 1; Verniers, Chapter 2). No absolute dates are currently available for the Wembere–Manonga Formation, but fossil mammals from all of the sites mentioned above, and from additional sites without mollusks, allow the beds to be dated by comparison with other localities in East Africa for which radiometric ages are well established (Harrison and Baker, this volume, Chapter 13).

The sediments composing the Wembere–Manonga Formation were deposited in a shallow lake, and consist predominantly of fine clastics. Swelling clays occur frequently in the Ibole and Tinde Members, and their formation may have had a negative effect on the preservation of shells. However, the restricted sampling does not provide evidence of such differential destruction, especially with respect to the Kiloleli Member (see Table I). Fluctuations in the level of the Wembere–Manonga paleolake resulted in repeated emersion phases, with subsequent leaching, red soil development, and calcium carbonate precipitation in various forms. These conditions undoubtedly also had a generally destructive effect on the molluscan taphocoenoses. The foregoing, as well as the restricted sampling, make it difficult to gauge the original extent of the shell-bearing deposits in the paleolake.

The finds consist of internal molds, shells or shell fragments, and external molds, occurring separately or in combination. The matrix is made of fine, sometimes yellowish or reddish, gray limestone. A few internal molds are partially filled with saccharoid calcite, probably resulting from recrystallization. The shells of bivalves are often better preserved than those of gastropods. In the latter, the outer shell has frequently been destroyed by dissolution, obliterating growth lines and other surface details. The bivalves occur as doublets, generally completely closed. No opercula are associated with the gastropod shell remains, except in two samples (N1, KI).

Well-preserved mollusks, quite often still retaining part of their original coloration, were collected by J. Verniers at localities situated several kilometers distant from the extant Manonga River. These finds include landsnails of the genus *Limicolaria* and another, as yet unidentified, smaller landsnail, as well as various freshwater mollusks: *Bellamya capillata*, *Pila ovata*, *Lymnaea natalensis*, *Bulinus* sp., and *Spathopsis wahlbergi*. *Pila ovata* and the pulmonates may have originated from recent local marshy waterbodies (which are common in the area today following heavy seasonal rains), but *B. capillata* and *S. wahlbergi* are undoubtedly related to a former lacustrine phase or phases, subsequent to the deposition of the Wembere–Manonga Formation. On the basis of their fresh appearance, we attribute a late Quaternary (Holocene?) age to these finds, and relate them tentatively to the overflow of Lake Victoria into the Manonga basin, as discussed by Verniers (this volume, Chapter 2). These latter specimens have not been included in the following analysis.

Table I summarizes the species and number of molluscan specimens represented at each of the fossil localities in the Manonga Valley. The collection is housed at the National Museums of Tanzania, Dar es Salaam.

In the systematic descriptions and general interpretations presented here, information concerning the biology and distribution of present-day species is based mainly on the works of Brown (1994), for gastropods, and Mandahl-Barth (1988), for bivalves. Data on fossil freshwater mollusks from other sites in eastern Africa can be found in Gautier and Van Damme (1973), Van Damme (1984), Pickford *et al.* (1993), and Van Damme and Pickford (1995). As a rule, these references will not be repeated. Original authors of taxonomic names referred to in the systematic description do not appear in the list of references.

2. Taxonomy

Several finds have been assigned using the Latin abbreviation aff. (*affinis*: near to) to imply that the specimens concerned seem phylogenetically closely related to or identical with the taxon named after the abbreviation. Measurements of gastropods include height and width (H × W), while those of bivalves include length, height, and total width (L × H × W). All measurements are given in millimeters, and these represent the largest measurable specimen(s), unless indicated otherwise. Field numbers are provided following each entry in the inventories.

Class Gastropoda
Family Viviparidae
Genus *Bellamya* Jousseaume, 1886
Bellamya aff. *capillata* (Frauenfeld, 1865)

Material. Inolelo 1, two small specimens (WM 1365/92). Kininginila, a few specimens in limestone (WM 779/94). Beredi South 1, three fragments (WM 1960/92). Ngofila 2, several small specimens in a block of limestone (WM 957/94).

Description. Small, thin shell (11.2 × 9.0), consisting of five whorls with flattened periphery, and a subsutural and basal blunt angulation (Fig. 1a). Umbilicus closed.

Remarks. Today *B. capillata* is the most common viviparid in southern Africa, with its northern limit in southern Tanzania, while *B. unicolor* (Olivier, 1804) is found in the northern part of Tanzania. The distinction between *B. capillata* and *B. unicolor* is not based on conchological features, for these strongly overlap, but on the number of rows of embryos. It is difficult, therefore, to identify fossil material to species level. The Manonga Valley material is referred to *B. capillata* because, in general morphology, it resembles that species more closely than it does *B. unicolor.*

B. capillata is found in slow-flowing rivers, lakes, and permanent marshes. Representatives of the genus *Bellamya* are sensitive to high salinity, and do not occur in waters with salinity levels in excess of 730 µmhos. In our material, *B.* aff. *capillata* is represented by a few fragmentary shells only, whose small size and thin shells suggest suboptimal living conditions.

Fossils of viviparids are extremely rare in pre-Pliocene African deposits, and were until now known only from late middle to late Miocene sediments (Kakara and Oluka Formations) in the Albertine Rift, and Miocene/Pliocene boundary deposits at Lothagam in northern Kenya.

Family Ampullariidae
Genus *Pila* Röding, 1798
Pila ovata (Olivier, 1804)

Material. Ngofila 1, 12 fragments of several opercula (WM 1121/94). Ngofila 2, two small specimens (51 × 49) and one larger one (WM 734/94, WM 1423/92). Shoshamagai 2, one fragmentary small specimen (WM 1058/92).

Description. Low spired, small forms, with typical *P. ovata* characteristics (Fig. 1b).

Remarks. Nowadays *P. ovata* is a widespread species, usually found in temporary waterbodies linked to floodplains, and in swampy fringes of rivers and lakes. It survives drought by aestivating in the mud. Due to this burrowing habit, it is the most commonly preserved freshwater mollusk in Miocene deposits of East and Central Africa. The specimens under study, however, did not die during aestivation. They were accumulated along with other dead mollusks, as indicated by the occurrence of smaller shells preserved within the matrix that fills them.

Genus *Lanistes* Montfort, 1810
Lanistes ovum Peters, 1845

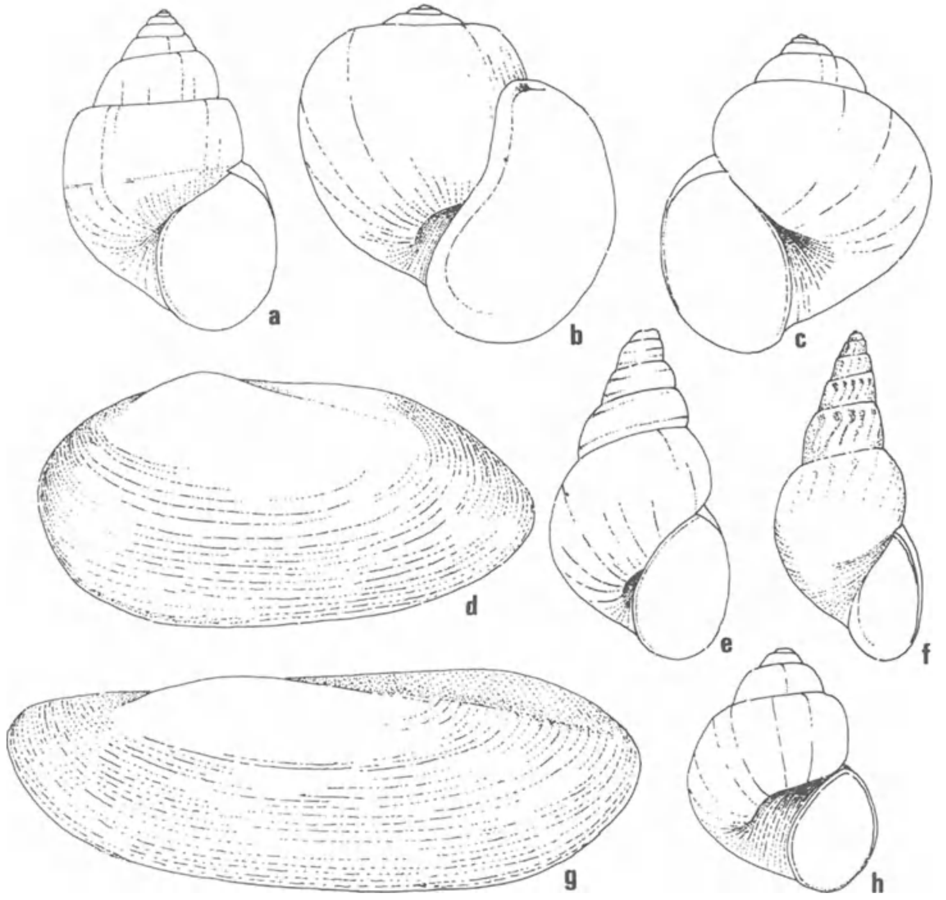

FIGURE 1. Reconstruction of freshwater mollusks from the Wembere–Manonga Formation, based on single shells. (a) *Bellamya* aff. *capillata* (11.2 × 9.0; WM 1365/92); (b) *Pila ovata* (51 × 49; WM 734/94); (c) *Lanistes ovum* (40 × 39; WM 733/94); (d) *Spathopsis wahlbergi* (85 × 42; WM 1101/92); (e) *Cleopatra* aff. *ferruginea* (11.3 × 6.2; WM 1365/92); (f) *Melanoides* aff. *anomala* (16.6 × 7.0; WM 779/94); (g) *Mutela dubia* (93.2 × 37.5; WM 1038/92); (h) *Gabbiella* aff. *humerosa* (3.7 × 2.8; WM 956/94). Various scales. Some reconstructions are incomplete because the material is fragmentary. Drawings by Van Damme.

Material. Inolelo 1, one fragment of a juvenile (WM 950/94). Inolelo 3, one fragment (WM 699/94). Shoshamagai 2, one high-spired fragmentary specimen (WM 590/94) and one low-spired specimen (34.5 × 40.5) (WM 1058/92). Kininginila, three specimens, partly decalcified, one very large (72 × 53) (WM 779/94, WM 956/94). Beredi South 1, one adult specimen (52 × 44) (WM 1527/92), six fragmentary smaller ones (WM 1960/92, WM 367/94). Ngofila 1, one juvenile (WM 1122/94). Ngofila 2, eight medium-size specimens (41 × 37) (WM 1423/92, WM 733/94, WM 957/94).

Description. The material is highly variable is size, most specimens being medium-size to small. Most closely resemble the nominal form, with a relatively high spire, strongly convex whorls, and open umbilicus (Fig. 1c).

Remarks. The present-day *L. ovum* has a wide distribution, and occurs in different types of waterbodies, including lakes, rivers, and temporary pools. *Lanistes* is quite common in Miocene deposits of eastern Africa, but most identifications pertain to *L. carinatus* (Olivier, 1804). As to *L. ovum*, up until now, this ampullariid was known only from lower middle Miocene deposits at Maboko Island on Lake Victoria in western Kenya.

Family Bithyniidae
Genus *Gabbiella* Mandahl-Barth, 1968
Gabbiella aff. *humerosa* (Martens, 1879)

Material. Kininginila, numerous specimens and opercula in blocks of limestone (WM 779/94, WM 956/94). Ngofila 2, numerous poorly preserved specimens in limestone (WM 1123/94).

Description. Globose or somewhat higher shell (3.7 × 2.8), consisting of four and a half whorls that are somewhat flattened at the periphery and shouldered (Fig. 1h). Umbilicus open. Rim of the inner margin slightly expanded. Operculum with a large spiral part.

Remarks. The specimens undoubtedly belong to the *G. humerosa* group, and may well represent *G. humerosa* s.s. *G. humerosa* is the only recent representative of the genus that is widespread in East Africa, where it lives on bottom sediments in the major lakes, their tributaries, and surrounding marshes.

The oldest fossil occurrence, *G. humerosa mohariensis*, dates from the late middle Miocene (Mohari Formation) of the Albertine Rift.

Family Thiaridae
Genus *Melanoides* Olivier, 1804
Melanoides aff. *anomala* (Dautzenberg and Germain, 1914)

Material. Kininginila, two partly decalcified specimens in a block of limestone (WM 779/94).

Description. Internal molds and remnants of the shell of a small *Melanoides* (16.6 × 7.0) with a relatively short spire, and a large, somewhat globose, body whorl (Fig. 1f).

Remarks. In general form, the specimens resemble *M. anomala* (Dautzenberg and Germain, 1914), occurring today in the Zaire River basin, and not *M. tuberculata* (Müller, 1774), which is the only species now found in East Africa. The material is too poorly preserved to make a definitive identification.

Genus *Cleopatra* Troschel, 1856
Cleopatra aff. *ferruginea* (Lea and Lea, 1850)

Material. Inolelo 1, 20 small specimens (WM 1366/92, WM 950/94). Kininginila, several partially decalcified, generally small specimens in a block of limestone (WM 956/94). Ngofila 1, 10 internal molds and fragments (WM

1124/94). Ngofila 2, some poorly preserved specimens in limestone (WM 1125/94).

Description. Small *Cleopatra* (11.3 × 6.2) consisting of 5 and a half whorls (Fig. 1e). The apex is shorter than the aperture. Last whorl fairly convex. Carination present on the apex only. Aperture acuminate ovate. Umbilicus closed.

Remarks. The recent species, *C. bulimoides* (Olivier, 1804), *C. ferruginea* (Lea and Lea, 1850), and *C. africana* (Martens, 1878) are difficult to distinguish, since the diagnostic characters relate to differences in size and coloration. Specific identification of the material, based on dwarfed specimens, is inadvisable. The material under consideration seems to resemble most closely *C. ferruginea*, which is presently the common *Cleopatra* in Tanzania. All East African Miocene material has also to be referred to this species. The small size of the specimens suggests suboptimal environmental conditions.

Class Bivalvia
Family Mutelidae
Genus *Spathopsis* Simpson, 1900
Spathopsis wahlbergi (Krauss, 1848)

Material. Inolelo 1, 12 juveniles and fragments of small specimens (61.5 × 33) (WM 1038/92, WM 1366/92, WM 603/94). Shoshamagai 2, 12 doublets (89 × 48 × 27.5) (WM 1101/92, WM 326/94). Beredi South, five small specimens (52 × 33) (WM 1642/92, WM 1976/92, WM 364/94).

Description. Relatively small specimens with a straight to slightly downward sloping posterior dorsal margin and an evenly curved ventral margin (Fig. 1d). Beak anteriorly situated and prominent in young individuals, sometimes showing the sculpture of concentric ridges typical of the genus.

Remarks. Mandahl-Barth (1988) recognizes several subspecies, but the fossil material resembles the nominate subspecies in the position of the beak, which lies relatively near to the anterior end, and in the straight, slightly sloping dorsal margin. Today *S. wahlbergi wahlbergi* occurs from Natal to southern Tanzania. According to the same author, *Spathopsis* species are chiefly lacustrine, as opposed to the mainly fluviatile related genus *Aspatharia.*

Part of the material from lower Miocene deposits in East Africa, described as *Aspatharia*, was assigned to this genus before Mandahl-Barth (1988) elevated *Spathopsis* to full generic level. *S. wahlbergi* from the Wembere–Manonga Formation is the oldest record of the genus. It seems to be the dominant bivalve in our samples. The material consists exclusively of closed doublets, suggesting fossilization in or close to the living position.

Genus *Mutela* Scopoli, 1777
Mutela dubia (Gmelin, 1791)

Material. Inolelo 1, one doublet (94.2 × 38.5 × 18.3) and one fragment of a doublet (WM 1038/92). Shoshamagai 2, one doublet (93.2 × 22.0) (WM 1101/92).

Description. Relatively small form with an anteriorly situated, small, and low beak (Fig. 1g). Dorsal anterior margin slightly curved and posterior margin straight. Anterior end broadly rounded, posterior end pointed. Ventral margin straight and parallel to the dorsal margin.

Remarks. The specimens show strongest resemblance to small representatives of the subspecies *M. dubia nilotica* (Caillaud, 1823), as figured by Mandahl-Barth (1988, Figs. 69–70).

Today the genus *Mutela* is absent from Tanzania, except for *M. bourguignati* Bourguignat, 1885, an endemic of Lake Victoria. According to Mandahl-Barth (1988), this form is closely related to the *M. dubia* complex. There is no doubt that the Manonga Valley specimens belong to this complex, which today occurs in large rivers and lakes of the Nile, Senegal, Niger, Congo, and Chad basins.

In all pre-Pliocene associations, representatives occur of the genus *Pleiodon* Conrad, 1834, characterized by a taxodont hinge, while anodont mutelids (i.e., *Mutela*) are conspicuously absent. In our opinion, *Mutela* is a taxon that evolved somewhat later. The material under study constitutes the oldest record of the genus. As in the case of *S. wahlbergi*, only doublets were collected, suggesting fossilization in autochthonous positions.

3. Paleoecology and Zoogeography

Since sampling of fossil mollusks was nonsystematic, and differential destruction may have affected the qualitative and quantitative composition of the collections from individual localities or stratigraphic unit, the few local differences observed are probably of no biostratigraphic significance. Most likely, the molluscan fauna had basically the same general composition throughout the time span represented by the Wembere–Manonga Formation. Moreover, the faunas in Table I are not derived from single horizons or taphocoenoses, and they combine, no doubt, remains from different biotopes separated in time and space. Taking the foregoing limitations into consideration, the following inferences can be made concerning the ecology of the Wembere–Manonga paleolake. The presence of large bivalves, such as *Spathopsis* and *Mutela*, is indicative of the existence of large open stretches of well-oxygenated, relatively shallow water (depth not more than about 20 m, but probably closer to 5 m?). The relative abundance of ampullariids (i.e., *Lanistes* and *Pila*) suggests the existence of a swampy fringe, while the concentrations of *Gabbiella* may point to shallow water, with dense plant growth. Thus, the main molluscan biotopes of "normal" freshwater lakes are represented by our specimens.

As to the chemical composition of the water, the fact that the calcium of the shells was preserved and that the matrix is limestone suggest hard water (>40 mg/l Ca, > 200 mg/l $CaCO_3$), while the small size of gastropods, such as *Bellamya* and *Cleopatra*, as well as of the bivalve *Spathopsis*, indicates that there was a limiting growth factor other than calcium, usually high temperature or high salinity. Neither *Mutela* nor *Bellamya* are found in waters with a salinity in excess of 730 μmhos. Such a concentration has been measured in Lake Albert, and can be considered as the maximal salinity at the time of the formation of the deposits containing the fossil mollusks.

As to the zoogeographic implications of the Wembere–Manonga fauna, the latter includes wide-ranging species, which still occur in the region and in other parts of Tanzania. The sole exception may be the specimens tentatively identified as *Melanoides* aff. *anomala*, which imply a hydrographic link with the Congo drainage system. The material is too poorly preserved, however, to go beyond this suggestion.

The banality of this fauna constitutes its main interest. Late Miocene molluscan assemblages are extremely rare in Africa, and are restricted to the nascent rift lakes of Lake Albert and Lake Turkana, in which endemic populations rapidly developed, and exhibit dramatic evolutionary change. Conversely, the Wembere–Manonga fauna indicates that in the non rift aquatic environments of East Africa the molluscan fauna of the late Cenozoic had essentially the same composition as today. This demonstrates a surprising degree of morphological inertia, and implies that the general conditions of the common aquatic environments (in contrast to rift lakes) have changed little during the last six million years. Consistent with previous observations (Van Damme, 1984), however, is the absence of pulmonates, a group that seems to have become highly successful only since the end of the Pliocene.

4. Conclusions

The species composition of the molluscan assemblages of the Wembere–Manonga Formation is indicative of the existence of an extensive shallow waterbody. This lake was well oxygenated and calcium-rich and it probably had a maximum salinity concentration comparable to the highest levels measured in present-day Lake Albert.

The total absence of conchological adaptations to lacustrine environments indicates that the lake was not permanent in terms of geological age, and should be considered as a temporary expansion (again geologically speaking) of a river and its fauna.

The Wembere–Manonga fauna is of interest zoogeographically, because it indicates that by the late Miocene the composition of the molluscan fauna of the common aquatic environments in East Africa was, in general, already the same as today.

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Chapter 13

Paleontology and Biochronology of Fossil Localities in the Manonga Valley, Tanzania

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1. Introduction

Comparisons of the Manonga Valley faunas with those from other East African localities for which radiometric dates have been obtained allow the Manonga Valley sequence to be placed within a broader chronological framework. The results of a biochronological analysis produce consistent estimates of the age range of the sequence, and indicate that the fossiliferous sediments were laid down during the late Miocene and early Pliocene. Nevertheless, it should be noted that there are several constraining factors that limit the degree of precision of such correlations, as follows: (1) There are few late Miocene and early Pliocene sites that have been dated radiometrically, and these are restricted geographically to the East African Rift valley (i.e., the Turkana basin, the Baringo basin, the Samburu Hills, and the Middle Awash Valley); (2) with the exception of Lothagam in northern Kenya and Langebaanweg in South Africa, the mammalian faunas from this time period are either poorly known or have not been the subject of detailed study; and (3) few researchers have made detailed firsthand comparisons between late Miocene and early Pliocene faunas from fossil localities in North, East, and South Africa. What makes the Manonga Valley fauna so important from a paleontological perspective is that it adds significantly to our limited appreciation of the diversity and provinciality of African faunas from this period, but this also means that there is a lack of an extensive comparative base that limits the degree of reliability of any assessments of age and zoogeographic relationships. Obviously, as new information becomes available on the dating and taxonomy of faunas from other African localities, biochronological estimates of the Manonga Valley faunas may have to be refined, but for the time being we consider the correlations and age estimates presented here to be well founded.

2. Fossil Mammals from the Wembere–Manonga Formation

Most of the mammalian taxa from the Manonga Valley have been studied in some detail in Chapters 5–10, this volume, and these chapters provide the basis for the biochronological correlation of the main stratigraphic units presented below. A list of the mammalian fauna from the Manonga Valley is presented in Table I.

Age estimates for key paleontological sites in other parts of Africa that are mentioned in the text, and are used to correlate the Manonga Valley faunas (estimates based on radiometric dates are indicated by a †), can be summarized as follows:

Ngorora Formation, Baringo basin, Kenya (~9.0–12.3 Ma †) (Hill *et al.*, 1985, 1986; Deino *et al.*, 1990).

Namurungule Formation, Samburu Hills, Kenya (~8–10 Ma †) (Nakaya *et al.*, 1984; Nakaya, 1994).

Mpesida Beds, Baringo basin, Kenya (6.4–7.0 Ma †) (Hill *et al.*, 1985).

Table I. List of Mammals from the Wembere–Manonga Formation

	Ibole Mb	Tinde Mb	Kiloleli Mb
Bovidae			
?*Tragelaphus* sp.	X	X	
Kobus aff. *porrecticornis*	X		
Kobus aff. *subdolus*		X	X
Praedamalis sp.	X		X
Damalacra sp.	X	X	X
Aepyceros sp.			X
Alcelaphini, larger sp.			X
Alcelaphini, smaller sp.	X		X
Giraffidae			
Giraffa sp.		X	
?*Sivatherium* sp.		X	X
Hippopotamidae			
Hexaprotodon harvardi	X	X	X
Hexaprotodon sp.		X	
Suidae			
Nyanzachoerus kanamensis	X	X	X
Equidae			
Eurygnathohippus cf. "*sitifense*"	X		
Eurgnathohippus cf. *turkanense*	X		
Eurygnathohippus sp.		X	
Eurygnathohippus aff. *hasumense*			X
Rhinocerotidae			
Ceratotherium praecox			X
Deinotheriidae			
Deinotherium bozasi		X	
Gomphotheriidae			
Anancus kenyensis	X		
Anancus sp.			X
Elephantidae			
cf. *Stegotetrabelodon*	X		
Primelephas gomphotheroides	X		
Elephantinae, gen. et sp. indet.		X	
Loxodonta cf. *exoptata*			X
Elephas ekorensis			X
Felidae			
Machairodus sp.	X		
Viverridae			
gen. et sp. indet.		X	
Mustelidae			
gen. et sp. indet.	X		
Cercopithecidae			
gen. et sp. indet.			X
Thryonomyidae			
Thryonomys sp.	X		
Muridae			
Saccostomus major	X		
Tectonomys africanus	X		
Saidomys parvus	X		
gen. et sp. indet.		X	

Lothagam, Nawata Formation (Lower Nawata, 6.57–7.91 Ma †; Upper Nawata, 5.5–6.24 Ma †) and Apak Member, Kenya (~4.72–5.5 Ma †), Kenya (Patterson *et al.*, 1970; Hill *et al.*, 1992; Stewart, 1994; Leakey *et al.*, 1996).
Lukeino Formation, Baringo basin, Kenya (5.6–6.2 Ma †) (Hill *et al.*, 1985, 1986; Hill, 1994).
Nkondo Formation, Nkondo Member (~6.0–6.5 Ma) and Nyaweiga Member (~4.5–5.0 Ma), Western Rift, Uganda (Pickford *et al.*, 1993).
Adu-Asa Formation, Middle Awash Valley, Ethiopia (~4.5–6.0) (Kalb *et al.*, 1982a,b; Kalb, 1993).
Sahabi, Libya (~5 Ma) (Bernor and Pavlakis, 1987).
Wadi Natrun, Egypt (~4–5 Ma) (James and Slaughter, 1974; Cooke, 1978a).
Langebaanweg, 'E' Quarry, Varswater Formation, South Africa (~4–5 Ma) (Hendy, 1970a,b, 1976, 1981, 1982).
Aramis, Sagantole Formation, Middle Awash Valley, Ethiopia (4.3–4.5 Ma †) (WoldeGabriel *et al.*, 1994).
Tabarin, lower Chemeron Formation, Baringo basin, Kenya (4.15–5.0 Ma †) (Ward and Hill, 1987).
Mursi Formation, Omo Valley, Ethiopia (≥4.15 Ma †) (Brown and Lajoie, 1971; Brown, 1994).
Kanapoi, Kenya (3.9–4.2 Ma †) (Leakey *et al.*, 1995).
Laetoli, Upper Unit (3.5–3.8 Ma †), Lower Unit (3.8–4.3 Ma †), Laetolil Beds, Tanzania (3.5–4.3 Ma †) (Drake and Curtis, 1987; Hay, 1987).
Warwire Formation (~3.5–4.0 Ma), Western Rift, Uganda (Pickford *et al.*, 1993).
Hadar, Kada Hadar Member (2.5–3.0 Ma †), Denen Dora Member (3.0–3.1 Ma †), Sidi Hakoma Member (3.1–3.4 Ma †), Hadar Formation, Ethiopia (Haileab and Brown, 1992; Walter and Aronson, 1993).
Shungura Formation, Members A–C, Omo Valley, Ethiopia (2.5–3.7 Ma †) (Harris *et al.*, 1988; Brown and Feibel, 1991; Brown, 1994).

In the following sections the taxonomy, temporal range, and biogeographic relationships of each of the mammalian and nonmammalian groups represented in the Manonga Valley are briefly reviewed. The primary objective is to place the Manonga Valley faunas into a regional biochronological framework that will allow an estimation of the age ranges of the main stratigraphic units of the Wembere–Manonga Formation. This is followed by a brief discussion of the late Quaternary faunal remains recovered from the mbuga clay and yellow clay horizons, the youngest of the fossil-bearing sediments in the Manonga Valley.

2.1. Bovidae

Bovids are well represented in each of the major stratigraphic units of the Wembere–Manonga Formation, although their diversity remains relatively low throughout. Nevertheless, they represent a significant component of the fauna, and they provide a potentially valuable source of information for estimating the age of sites in the Manonga Valley. The following observations concerning the biochronological implications of the bovid fauna are based on Gentry's contribution to this volume (Chapter 5).

?*Tragelaphus* sp. is known from several isolated teeth from the Ibole and Tinde Members. These are similar in size and morphology to teeth of early Tragelaphini from the late Miocene and early Pliocene (~4–7 Ma) of Mpesida, Lothagam, Lukeino Formation, Adu-Asa Formation, and Langebaanweg (Gentry, 1978a, 1980; Thomas, 1980; Kalb *et al.*, 1982a,b; Hendey, 1984). Tragelaphini do not occur in the earlier Ngorora Formation, and evidence indicates that the tribe differentiated from the Boselaphini sometime during the ~7–9 Ma interval.

The absence of Boselaphini at sites in the Manonga Valley could be of some biochronological significance. Boselaphini occur at several late Miocene and Pliocene localities in Africa (i.e., Ngorora Formation, Namurungule Formation, Sahabi, Adu-Asa Formation, Lothagam, Langebaanweg), but become extinct, at least in sub-Saharan Africa, during the early Pliocene (Gentry, 1978a,b; 1980; Thomas, 1981; Kalb *et al.*, 1982a,b; Hendey, 1984; Lehmann and Thomas, 1987; Nakaya, 1994; Leakey *et al.*, 1996). Three general biochronological associations can, therefore, be identified: (1) occurrence of Boselaphini, but no Tragelaphini (late Miocene, ≥7 Ma); (2) co-occurrence of Boselaphini and Tragelaphini (late Miocene and early Pliocene, ~7.0–4.5 Ma); and (3) occurrence of Tragelaphini, but no Boselaphini (from early Pliocene, ≤4.5 Ma). The absence of Boselaphini in the Manonga sequence might be construed as evidence that the fossil horizons are younger than 4.5 Ma. However, negative evidence is an inadequate basis for biochronological correlation, especially given that boselaphines are also not recorded from the late Miocene Mpesida Beds or the Lukeino Formation. A further complicating matter is that the dentitions of boselaphines and early tragelaphines are not easily distinguished, and the two tribes may possibly co-occur prior to 7 Ma (see Gentry, 1978b, this volume, Chapter 5).

At least two species of *Kobus* are represented at sites in the Manonga Valley. *Kobus* aff. *porrecticornis* is known from the Ibole Member, while the slightly more advanced *Kobus* aff. *subdolus* is known from the Tinde and Kiloleli Members. *Kobus porrecticornis* is from the late Miocene upper Dhok Pathan and early Pliocene Tatrot of the Siwalik Hills (Gentry, 1978a). Material identified as *K.* aff. *porrecticornis* has been recognized from Mpesida and Lukeino (Thomas, 1980), and also from the Baard's Quarry 'lower level' assemblage at Langebaanweg, which is of uncertain age (Hendey, 1978). The horn cores of *Kobus* aff. *subdolus* are similar to reduncines from the early Pliocene of Langebaanweg (i.e., *Kobus* sp. B, *K. subdolus*), Sahabi (i.e., *Redunca* aff. *darti*) and Wadi Natrun (i.e., *Kobus* sp.) (Gentry, 1980; Hendey, 1984; Lehmann and Thomas, 1987), although the dentition appears to be somewhat more derived than that from Langebaanweg (Gentry, this volume, Chapter 5). The reduncines indicate that the Ibole Member is comparable in age to the Mpesida Beds and Lukeino Formation (late Miocene, ~5–7 Ma), while the Tinde and Kiloleli Members are younger (early Pliocene, ~4–5 Ma). The specimens are clearly more primitive than comparable material from the Shungura Formation, and this indicates an age prior to 3.4 Ma.

Hippotragini is represented by horn cores from the Ibole and Kiloleli Members referred to *Praedamalis* sp. The specimen from the Kiloleli Member is similar in morphology to *Praedamalis deturi* from Laetoli and the Denen Dora Member of the Hadar Formation (Gentry, 1981, 1987), but is considerably smaller. Hippotragini are not common at earlier sites, but they have been provisionally identified at Sahabi (Lehmann and Thomas, 1987), Djebel Krechem, Tunisia (Geraads, 1989), Mpesida (Thomas, 1980) and Lothagam (Hill *et al.*, 1992). Earlier reports of hippotragines from Wadi Natrun and Langebaanweg appear to be unfounded (Gentry, 1978a). Given the paucity of the comparative material from late Miocene and Pliocene sites in Africa, it is not possible to assess the taxonomic or biochronological relationships of the Manonga Hippotragini.

At least three species of Alcelaphini are represented in the collections from the Manonga Valley. Most of the specimens (from the Ibole, Tinde, and Kiloleli Members) are referable to *Damalacra* sp. This genus is known from Langebaanweg (Gentry, 1980), and is provisionally identified as occurring at Sahabi (Lehmann and Thomas, 1987), Wadi Natrun (Gentry, 1980) and Kanapoi (Leakey *et al.*, 1995). *Damalacra* represents the earliest alcelaphine in Africa, and it is apparently restricted to the early Pliocene. The only earlier occurrence of Alcelaphini is from the late Miocene site of Lothagam (Hill *et al.*, 1992; Leakey *et al.*, 1996).

The occurrence of *Aepyceros* sp. in the Manonga Valley is based on two horn cores from the Kiloleli Member. Several different species of impalas are common at sites in East Africa throughout the Plio-Pleistocene (Gentry, 1976, 1978a, 1981, 1985; Harris *et al.*, 1988; Harris, 1991a; Geraads and Thomas, 1994). The earliest definitive occurrence of the genus is in the Lukeino Formation (Thomas, 1980), and it has been identified, at least provisionally, from Lothagam (Smart, 1976; Harris, 1991a; Hill *et al.*, 1992; Leakey *et al.*, 1996).

Overall, the bovid fauna from the Manonga Valley shows its strongest affinities to those from Lukeino, Lothagam, Langebaanweg, and Kanapoi, and this indicates a broad age estimate of ~4–7 Ma. The evidence best supports an age of ~5–7 Ma for the Ibole Member and ~4–5 Ma for the Tinde and Kiloleli Members. The Manonga Valley bovids are certainly more conservative than those from the Shungura Formation and from Laetoli, confirming that the sediments are older than 4 Ma.

2.2. Giraffidae

Giraffids are not common at sites in the Manonga Valley. Gentry (this volume, Chapter 5) describes only two isolated teeth, although additional craniodental and postcranial specimens have been recovered.

A partial M_3 from Tinde West (Tinde Member) is tentatively assigned to *Giraffa* sp. The tooth is comparable in size to extant *Giraffa camelopardalis*, but it is more brachyodont. Several isolated postcranials from Tinde and Kiloleli that are metrically and morphologically consistent with modern *Giraffa* probably belong to the same species. However, postcranial bones of a giraffine recovered from Tinde are somewhat smaller than the living species (about 30% smaller), indicating that a second species was present. Without more complete material it is difficult to assign these fossils to particular species. At least three species of *Giraffa* are represented at Plio-Pleistocene sites in East Africa: *G. pygmaea*, *G. stillei*, and *G. jumae*. The Tinde dental specimen is most comparable in size to *G. jumae*, which is common at Pliocene and early to middle Pleistocene sites. The earliest occurrence of this species is at the mid-Pliocene sites of Laetoli and Kanapoi, although a similar form has been reported from the early Pliocene at Langebaanweg (Harris, 1976, 1987, 1991b; Churcher, 1978; Hendey, 1984). The fossil record for *Giraffa* apparently extends back to the late Miocene, where it occurs in the Lukeino Formation and at Lothagam (Geraads, 1986; Hill *et al.*, 1985; Gentry, this volume, Chapter 5). It is also known in South Asia from the Dhok Pathan (~5–7 Ma) of the Siwalik Hills (Barry and Flynn, 1990). As noted by Gentry (this volume, Chapter 5), the Tinde lower molar is more brachyodont than those of living and fossil species of *Giraffa*, and this implies an age antedating the mid-Pliocene (~4 Ma).

A third species of giraffid is represented by an isolated lower molar of a large sivatheriine from Kiloleli 2 (Kiloleli Member). Distal metapodials from Kiloleli 2 and Tinde can probably be attributed to the same species on the basis of size. *Sivatherium hendeyi* (from Langebaanweg) and *S. maurusium* (from all other sites) are the only sivatheriines currently recognized from Plio-Pleistocene sites in sub-Saharan Africa (Churcher, 1978; Harris, 1987, 1991b). These species range in age from early Pliocene (at Langebaanweg) to late middle Pleistocene (Churcher, 1978; Harris, 1987, 1991b). Gentry (this volume, Chapter 5) tentatively retains the Kiloleli specimen in *Sivatherium*, although he identifies some morphological features that serve to distinguish it, and possibly to link it more closely with other late Miocene Eurasian taxa, such as *Decennatherium*, *Helladotherium*, and *Bramatherium*. Giraffids with possible affinities to *Helladotherium* have been reported from late Miocene and Pliocene sites in North Africa (Joleaud, 1937; Churcher, 1978; Geraads, 1985). More primitive sivatheriines, including *Palaeotragus*, *Giraffokeryx*, and *Samotherium*, are known from late Miocene sites in East Africa, and from late Miocene to early Pliocene sites in North Africa (Aguirre and Leakey, 1974; Hamilton, 1978; Churcher, 1978; Harris, 1987, 1991b; Nakaya, 1994; Leakey *et al.*, 1996). The giraffid from Kiloleli appears to correlate best with material from early Pliocene sites, although this inference is limited by the lack of adequate material, and by the currently confused state of the taxonomy of early African and Eurasian giraffids.

In addition to these few specimens from the Tinde and Kiloleli Members, undescribed teeth belonging to a small giraffid of uncertain taxonomic affinities have been recovered from Inolelo 3 (Ibole Member).

The giraffids from the Manonga Valley are too incomplete to determine their precise taxonomic affinities, but they do permit a crude estimation of the possible age range of the Tinde and Kiloleli Members. The teeth are most closely similar in their morphology to better-preserved material from late Miocene and early Pliocene sites in East and South Africa, and so we can be reasonably confident that the Manonga Valley sediments are older than those at Laetoli.

2.3. Hippopotamidae

Hippopotamids are generally well represented at all of the major fossil sites in the Manonga Valley. The taxonomy and paleobiology of the Manonga hippopotamids have been reviewed by Harrison (this volume, Chapter 6). Almost all specimens from sites in the Manonga Valley can be referred to *Hexaprotodon harvardi.* They are indistinguishable from material from Lothagam, the type site for the species. However, an isolated phalanx from the Tinde Member indicates the occurrence of a second smaller species of a hexaprotodont hippopotamid. A diminutive form, much rarer than *Hex. harvardi,* is also present at Lothagam (Leakey *et al.*, 1996). The specimens from the Kiloleli Member are attributed to *Hex. harvardi,* but they possibly represent a slightly more derived form than the material from the Ibole and Tinde Members.

Hex. harvardi is found at sites in Ethiopia and northern Kenya ranging in age from ~7–4 Ma. The youngest material attributed to this species is from Kanapoi, and has a number of derived features of the cranium and dentition that distinguishes it from material from earlier sites, such as Mpesida, Lothagam, and Lukeino. Comparisons demonstrate that the material from the Ibole and Tinde Members is morphologically and metrically identical to that from Lothagam and Lukeino, and more conservative than that from Kanapoi. The fossil hippopotamids support a biochronological age of 5–7 Ma for the lower fossiliferous beds in the Manonga Valley sequence, while the material from Kiloleli is possibly somewhat younger, although not less than 4 Ma.

2.4. Suidae

Only a single species of suid is represented throughout the Neogene sequence in the Manonga Valley: *Nyanzachoerus kanamensis.* It is best represented by a number of relatively complete jaws from the Ibole Member (see Bishop, this volume, Chapter 7). *Nyanzachoerus kanamensis* has a broad temporal range in East Africa, being commonly found at late Miocene and Pliocene sites. Nevertheless, the presence of this species, without any other suids in association, may have important implications for estimating the ages of the sites in the Manonga Valley. Sites at which *Ny. kanamensis* is the only suid represented are apparently confined to the early Pliocene. Late Miocene faunas in East Africa (as well as the early Pliocene site of Sahabi in North Africa) are typically dominated by the more conservative species *Ny. devauxi* and *Ny. syrticus.* (=*Ny tulotos*), while late Pliocene faunas tend to have *Ny. kanamensis* in association with *Ny. jaegeri* (see Table II). Based on this evidence, age estimates for sites in the Manonga Valley might be constrained to a relatively narrow temporal range of 4.5–5.5 Ma. However, it cannot be entirely ruled out that the lack of association of *Ny. kanamensis* with other species of suids in the Manonga Valley is not a consequence of ecological, zoogeographic, or preservational factors, rather than chronology. The rarity of suids in general in the Tinde and Kiloleli Members might be an important consideration in this regard. Conservatively, however, the suids from the Manonga Valley indicate an age of ~4.5–5.5 Ma, at least for the Ibole

Table II. Temporal Distribution and Faunal Associations of Fossil Suids from the Late Miocene and Pliocene of Africa[a]

Locality[c]	*Nyanzachoerus devauxi*	*Nyanzachoerus syrticus*	*Nyanzachoerus kanamensis*	*Nyanzachoerus jaegeri*	*Notochoerus euilus*	*Kolpochoerus afarensis*	Faunal association[b]
Lothagam, Nawata Fm	X	X					I (4.5–7.0 Ma)
Lukeino Fm		X					
Adu and Asa Mbs		X					
Sahabi	cf.	X	X				
Wadi Natrun			X				
Kuseralee Mb			X				
Langebaanweg (QSM)			X				
Lothagam, Apak Mb			X	X			II (3.9–5.0 Ma)
Langebaanweg (PPM)			X	X			
Tabarin				X			
Aramis Mb			X	X			
Kanapoi			X	X			
Mursi Fm			X	X		?	
Laetoli (upper Laetolil)					X		III (2.8–3.9 Ma)
Hadar, SH, DD Mb			X		X	X	
Shungura Mb A-C			X	X	X	X	
Hadar, KH Mb					X	X	

[a] Sources. Cooke, 1978b, 1983, 1985, 1987; Cooke and Wilkinson, 1978; Kalb *et al.*, 1982a; White *et al.*, 1984; Hill *et al.*, 1985; Ward and Hill, 1987; Hill *et al.*, 1992; Cooke and Hendey, 1992; WoldeGabriel *et al.*, 1994; Leakey *et al.*, 1995; Leakey *et al.*, 1996.

[b] After Cooke, 1983, 1985.

[c] Abbreviations: DD, Denen Dora; KH, Kada Hadar; PPM, Pelletal Phosphate Member; QSM, Quartzose Sand Member; SH, Sidi Hakoma.

Member. The Tinde and Kiloleli Members may be somewhat younger, although the absence of *Notochoerus euilus* and *Kolpochoerus afarensis* clearly indicates an age older than 4 Ma.

In relation to zoogeographic affinities, it is interesting to note that the sample of *Nyanzachoerus kanamensis* from the Manonga Valley (the southernmost occurrence of the species in East Africa) appears to have its closest morphological affinities with *Ny. kanamensis australis* from Langebaanweg (Quartzose Sand Member) in South Africa. According to Cooke and Hendey (1992), the subspecies from Langebaanweg is distinguished from East African material in the following features: retention of P^1 in a slightly longer diastema and possession of relatively larger and more robust cheek teeth and of a distinct hump on the nasals in front of the canine flanges in male individuals. Unfortunately, the Manonga Valley material does not preserve the P^1 or pertinent cranial regions for comparison. Nevertheless, the mandibular diastema is relatively long in the Manonga Valley sample, being comparable in length to specimens from Langebaanweg. The large size of the cheek teeth is, perhaps, the most striking similarity between the Manonga Valley and Langebaanweg samples, although Bishop (this volume, Chapter 7) suggests that the material from other East African sites is not significantly different in this respect.

2.5. Equidae

The Manonga Valley hipparionines provide potentially very useful information for biochronological correlation of the Manonga Valley faunas. However, comparisons are limited by the relative paucity of sites from the relevant time period, and by the lack of detailed study of equid fossils from a number of key East African sites. Bernor and Armour-Chelu (this volume, Chapter 8) present a preliminary assessment of the taxonomic and biochronological relationships of the Manonga Valley equid material. The hipparionines from the Ibole Member are referred to *Eurygnathohippus* cf. "sitifense" and *E.* cf. *turkanense*. Both species have long temporal ranges. *Eurygnathohippus sitifense* is known from localities in North Africa and East Africa ranging in age from late Miocene until at least the late Pliocene (~8–2 Ma), while the larger *E. turkanense* is recorded from late Miocene to early Pliocene sites in East Africa (~7–4 Ma), but is best known from the type locality of Lothagam (Hooijer and Maglio, 1973, 1974; Churcher and Richardson, 1978; Cooke, 1983; Eisenmann, 1983, 1985, 1994). These two species (or closely similar forms) are known to co-occur at Lothagam, Lukeino, Kanapoi, and Ekora in northern Kenya (~4–7 Ma), the Nkondo and Warwire Formations in Uganda (~4–7 Ma), and possibly also Sahabi in Libya (~5 Ma). The Ibole hipparionines are most closely similar to those from the Nawata Formation at Lothagam (Bernor and Amour-Chelu, this volume, Chapter 8), and this supports a late Miocene age.

The hipparion material from the Tinde Member is not adequate to determine its biochronological affinities. Bernor and Amour-Chelu (this volume, Chapter 8) note, however, that the presence of a well-developed ectostylid on one of the lower molars from Tinde may indicate a somewhat younger age than that inferred for the Ibole Member. Better-preserved equid material has been recovered from the overlying Kiloleli Member, and the dental remains are clearly more derived than those from the Ibole Member. Bernor and Amour-Chelu note that the Kiloleli hipparionine is most similar to *Eurygnathohippus hasumense* from the Hadar Formation, although its lower cheek teeth are more primitive and its limbs are shorter and more gracile. They conclude that the Kiloleli Member best correlates with the Sidi Hakoma and Denen Dora Members at Hadar, or possibly slightly older, indicating an age of 3.1–3.4 Ma.

2.6. Rhinocerotidae

Rhinocerotids are generally rare at sites in the Manonga Valley, but they do occur quite commonly at Kiloleli (Kiloleli Member). The material consists mainly of isolated postcranial elements, especially phalanges, metacarpals, and podials, but a partial mandible and several isolated teeth are also included in the collections. These have not yet been studied in any detail, but a mandibular fragment (WM 500/94) and a right dP^2 (WM 1238/92) from Kiloleli 2 are clearly identifiable as *Ceratotherium praecox*. The dP^2 is identical in size and morphology to the corresponding tooth from Langebaanweg figured by Hooijer (1972, Pl. 29). *Ceratotherium praecox* is known from sites in East Africa (i.e., Mpesida Beds, Lothagam, Lukeino Formation, Kanapoi, Mursi Formation, Ekora, Aterir Beds, Laetoli, lower Koobi Fora Formation, Chemeron Formation, Nkondo and Warwire Formations, and Sidi Hakoma Member) and South Africa (Langebaanweg and Swartlinjes Farm), ranging in age from ~7–3 Ma (Hooijer, 1978; Guérin, 1987, 1994; Feibel *et al.*, 1991). At about 3 Ma this species is replaced in the fossil record by *Ceratotherium simum germanoafricanum*, an extinct subspecies of the modern white rhino (Hooijer, 1978; Harris, 1983; Guérin, 1985, 1987, 1994; Feibel *et al.*, 1991). The occurrence of *C. praecox* in the Kiloleli Member indicates that the main Manonga Valley sequence predates 3 Ma. Guérin (1987), however, notes that the material from Laetoli and Hadar can be distinguished from earlier samples (older than ~4 Ma) in being slightly larger in size, and in having more complex upper molars and lower premolars with closed valleys. With further study, and the recovery of additional rhinocerotid material, it might be possible to provide a more refined age estimation for the Kiloleli Member.

2.7. Primates

A single isolated tooth from the Manonga Valley has tentatively been identified as belonging to a primate. The specimen, from Kiloleli 2 (Kiloleli Member), consists of a lower canine of a large cercopithecid monkey. Unfortunately, the crown, which is weathered and abraded, cannot be identified further.

2.8. Carnivora

Carnivores are not common at localities in the Manonga Valley, and the material consists mainly of isolated teeth and fragmentary postcranial elements. Specimens have been recovered from nine different localities, from horizons within the Ibole, Tinde, and Kiloleli Members. The best material comes from the Ibole Member. A right lower canine, two incisors, left and right lower M_1s, and several mandibular fragments from Shoshamagai 2 can be attributed to a species of machairodotine felid. Comparisons suggest that the dental remains are closely similar in size and morphology to material from the Lower Nawata Member at Lothagam referred to *Machairodus* sp. (Leakey *et al.*, 1996). Isolated canines from Inolelo 3, as well as some postcranial elements from Shoshamagai 2 and Inolelo 1, might also belong to this taxon. Interestingly, concentrations of coprolites of large carnivores (of suitable size for *Machairodus*) have been recovered from the Ibole Member at Shoshamagai 2 and Beredi South 5 in close association with partial skeletons of proboscideans. Dental and postcranial remains of small carnivores have also been recovered from the Ibole Member at Inolelo 1, including an upper canine, probably belonging to a mustelid.

Carnivores are less common in the Tinde and Kiloleli Members. Material from the Tinde Member includes a humerus shaft from Tinde East and a distal radius from Kininginila. Both belong to small carnivores, probably viverrids. Distal humeri and a scapula fragment of a very large felid (possibly *Homotherium*) have also been recovered from the Tinde Member at Ngofila Hill and Tinde West. A small collection of isolated teeth and postcranial specimens of small to medium-size carnivores has been recovered from the Kiloleli Member at Kiloleli 2, Kiloleli 3, and Beredi South 4.

An assessment of the taxonomic and biochronological relationships of the carnivore fauna from the Manonga Valley will have to await a more detailed study of the material. Nevertheless, the provisional identification of *Machairodus* at Shoshamagai 2 may be of some help in correlating the Ibole Member. *Machairodus* makes its first appearance in Europe at sites correlated with MN9 (early Vallesian, ~11–12 Ma) (Mein, 1989), although it has been recorded from slightly earlier middle Miocene localities in China (Qiu, 1989). Machairodontines appear to have immigrated into Africa at the end of the Miocene, and members of this group are not recorded at sites younger than early Pliocene (Savage, 1978; Howell, 1987; Nakaya, 1994; Petter, 1994). *Machairodus* has been identified at Gafsa, Lothagam, Sahabi, Wadi Natrun, and Langebaanweg (QSM) (Hendey, 1976; Savage, 1978; Howell, 1987). This indicates a late Miocene to early Pliocene age (~4–7 Ma) for the Ibole Member.

2.9. Proboscidea

Fossil proboscideans from the Manonga Valley have been described in detail by Sanders (this volume, Chapter 9). The material, especially that from the Ibole Member, is adequate to allow a reasonably good age estimation. The proboscideans from the Ibole Member include *Anancus kenyensis*, *Primelephas gom-*

photheroides, and possibly *Stegotetrabelodon*. The latter two species are known from Lothagam, the Lukeino Formation, Kanam East, the lower Kaiso beds, the lower Chemeron Formation, and the Adu-Asa Formation, and indicate a best age estimate for the Ibole Member of 4.5–6.2 Ma.

Proboscideans from the Tinde Member include an elephantine, with possible affinities to *Mammuthus subplanifrons*, as well as a single specimen referable to *Deinotherium bozasi*. The primitive morphology of the elephantine from Tinde is consistent with an age estimation of 4.0–6.0 Ma. The deinothere does not help refine this correlation, as *D. bozasi* is identified at sites ranging in age from late Miocene (Nakali and Namurungule Formation) to early Pleistocene (Chemoigut Beds, Baringo basin) (Harris, 1978; Nakaya, 1994).

The proboscideans from the Kiloleli Member are more derived than those from the Ibole and Tinde Members. Sanders (this volume, Chapter 9) has tentatively suggested that the material might be referable to *Anancus* sp. (Sagantole-type), *Elephas ekorensis*, and *Loxodonta exoptata*. The limited temporal overlap between these three species would indicate a best-fit age estimate of ~3.8 Ma. However, the material is also generally consistent in morphology and evolutionary stage with proboscideans from the upper Sagantole Formation of the Middle Awash and from Kanapoi. This may provide a broader temporal range for the Kiloleli Member of ~3.8–4.4 Ma.

In conclusion, the proboscidean material recovered from the Manonga Valley indicates an age range of between 3.8 and 6.2 Ma for the Wembere–Manonga Formation.

2.10. Rodentia

Winkler (this volume, Chapter 10) has described a small, but important, collection of fossil rodents from the Ibole Member. The occurrence of *Thryonomys* sp. and *Tectonomys africanus* in the Ibole Member suggests a late Miocene to early Pliocene age, comparable to that of Tabarin and the Upper Nawata Member at Lothagam. However, *Saidomys parvus* from the Manonga Valley is more derived than comparable material from Tabarin and Lothagam, and appears to have closer affinities with *S. afarensis* from the Sidi Hakoma Member at Hadar (Sabatier, 1982), while *Saccostomus major* is otherwise known only from the upper Laetolil Beds (Denys, 1987). According to Winkler (this volume, Chapter 10), the rodent fauna from the Ibole Member correlates best with an early Pliocene age (~4–5 Ma).

3. Nonmammalian Fossils from the Wembere–Manonga Formation

Of the nonmammalian remains from the Manonga Valley, only the fish and mollusks have been studied in detail (Stewart, this volume, Chapter 11; Van Damme and Gautier, this volume, Chapter 12). A list of the nonmammalian fauna is presented in Table III.

Table III. List of Nonmammalian Taxa from the Wembere–Manonga Formation

	Ibole Mb	Tinde Mb	Kiloleli Mb
Osteichthyes			
Dipnoi			
Protopteridae			
Protopterus sp.	X	X	X
Characiformes			
Characidae			
Hydrocynus sp.	X		
Alestes aff. *A. stuhlmanni*	X		
Alestes aff. *A. dentex*	X		
Alestes cf. *A. nurse/A. affinis*	X		
Alestes sp.	X	X	
Sindacharax sp.		X	
Siluriformes			
Clariidae			
Clarias sp.	X	X	X
nonclariid	X	X	
Perciformes			
Centropomidae			
Lates sp.		X	X?
Cichlidae			
indet.	X	X	
Reptilia			
Chelonia			
Trionychidae			
indet.	X	X	X
Pelomedusidae			
indet.	X	X	X
Crocodylia			
Crocodylidae			
Crocodylus sp.	X	X	X
Aves			
indet.	X	X	
Gastropoda			
Viviparidae			
Bellamya aff. *capillata*	X	X	X
Ampullariidae			
Pila ovata			X
Lanistes ovum	X	X	X
Bithyniidae			
Gabbiella aff. *humerosa*		X	X
Thiaridae			
Melanoides aff. *anomala*		X	
Cleopatra aff. *ferruginea*	X	X	X
Bivalvia			
Mutelidae			
Spathopsis wahlbergi	X		X
Mutela dubia	X		
Insecta			
Isoptera			
Termitidae			
indet.	X		
Hymenoptera			
indet.			X

3.1. Birds and Reptiles

Remains of fossil birds are scarce at sites in the Manonga Valley, but several postcranial elements have been recovered at Mwambiti 3 (Ibole Member) and Tinde West (Tinde Member).

Freshwater aquatic reptiles are ubiquitous throughout the sequence. The turtles are attributable to both Trionychidae and Pelomedusidae, although specimens of the former are much more common than the latter. Detailed comparisons are needed before the material can be identified further. Species of trionychids and pelomedusids occur together commonly at North and East African sites from the early Miocene onwards (Broin and Gmira, 1994).

Crocodiles are also quite common. Unfortunately, no relatively complete cranial specimens are known, so it is not possible to identify the species represented. The collection consists of a number of jaw fragments, dermal plates, and isolated teeth that are basically similar in morphology to *Crocodylus niloticus* and *C. lloidi.* An analysis of the breadth–height proportions of the isolated teeth from the Manonga Valley shows that the sample is comparable to *C. niloticus*, in that the majority of teeth are moderately short and stout (Table IV). Since there is a reasonable correlation between the breadth of the largest tooth and maximum skull length in *C. niloticus*, we are able to provide an approximation of the size range of the fossil crocodiles from the Manonga Valley. We estimate that skull length exceeded 30 cm in at least 66.5% of individuals, 40 cm in at least 15.9% of individuals, and 50 cm in at least 2.0% of individuals. The largest individuals may have had a skull length close to 60 cm (which translates into a crocodile almost 4 m in total length).

The evidence presently available suggests that the dominant crocodile in the Manonga Valley was a large brevirostrine representative of *Crocodylus*, somewhat similar to *C. niloticus* or *C. lloidi.* There is no evidence as yet for the occurrence of any longirostrine forms, such as *Tomistoma* or *Euthecodon*, which are represented at other late Neogene and Plio-Pleistocene sites in East Africa (Tchernov, 1986; Pickford, 1994). Since pelagic fish, the major prey of such forms, are generally lacking at sites in the Manonga Valley, we may conclude that the

Table IV. Breadth–Height Proportions of Crocodile Teeth from the Manonga Valley Compared with Those of Modern Crocodylids

	Breadth–height index[a]		
	N	≤ 40	≥ 80
Manonga Valley sample	301	2.0	7.3
Crocodylus niloticus	231	9.5	12.1
Crocodylus palustris	70	7.1	28.6
Mecistops cataphractus	146	32.2	4.1
Tomistoma schlegeli	50	30.0	0.0

[a] Numbers are percentages of the samples that fall within each category.

niche for piscivorous crocodylids in the paleolake basin may have been quite restricted. The fossil crocodiles presumably preyed on catfish and mammals, similar to modern-day Nile crocodiles. The estimated size of some of the individual specimens suggests that crocodiles would have been formidable predators and very effective scavengers.

3.2. Fishes

Stewart (this volume, Chapter 11) has recognized at least six genera of fish from the Wembere–Manonga Formation (i.e., *Protopterus*, *Hydrocynus*, *Alestes*, *Sindacharax*, *Clarias*, and *Lates*), as well as unidentified representatives of the Cichlidae.

Protopterus has a widespread distribution in Africa today, and the genus occurs commonly at fossil sites throughout the Tertiary (Greenwood, 1974; Van Couvering, 1977). Its earliest reported occurrence is at Eocene and Oligocene localities in Egypt, Mali, and Angola (Greenwood, 1974). In East Africa, *Protopterus* is known from the early and middle Miocene sites of Rusinga Island, Loperot, Chianda Uyoma, and Karungu in Kenya (Greenwood, 1951), late Miocene and early Pliocene sites in the Albertine Rift valley of Uganda and Zaire, and Lothagam in Kenya (Greenwood, 1959; Greenwood and Howes, 1975; Van Neer, 1992, 1994; Stewart, 1994), and Plio-Pleistocene localities in the Turkana Basin in Kenya (Schwartz, 1983).

Hydrocynus is common in the modern-day Nile and Zaire River systems, and is represented in East African fossil fish faunas from the Miocene onward. It is known from late Miocene and Pliocene deposits at Lothagam in Kenya, Wadi Natrun in Egypt, the Omo Valley in Ethiopia, and various localities in the Western Rift of Uganda and Zaire (Greenwood, 1959, 1972, 1974; Stewart, 1990, 1994; Van Neer, 1992, 1994).

Alestes has a wide distribution in East Africa today, but is generally poorly represented in the fossil record. It has been identified from the late Miocene and Pliocene deposits from Lothagam and the Albertine Rift valley in Zaire and Uganda (Stewart, 1990, 1994; Van Neer, 1994). *Alestes*-like characids have also been reported from the Ngorora Formation and the early Miocene of Loperot in Kenya (Van Couvering, 1977). *Sindacharax*, an extinct genus of characid, is known from sites in East and North Africa ranging in age from late Miocene to middle Pleistocene (Greenwood and Howes, 1975; Stewart, 1990, 1994; Van Neer, 1992, 1994).

Clarias is widely distributed today throughout Africa and Asia. Fossil representatives of the genus are first recorded in Africa at late Miocene and early Pliocene localities in Tunisia, Egypt, Libya, Kenya, Uganda, and Zaire (Greenwood, 1972, 1973, 1974; Gaudant, 1987; Stewart, 1994; Van Neer, 1992, 1994). *Clarias* is also extremely common at Plio-Pleistocene sites in East Africa, and has been reported from similar-aged sites in tropical Asia (White, 1926; Thomson, 1966; Greenwood, 1957, 1959, 1974; Greenwood and Todd, 1970; Greenwood and Howes, 1975; Schwartz, 1983; Van Neer, 1992).

Lates is very common at fossil sites in North and East Africa ranging in age from Oligocene to Holocene (Greenwood, 1951, 1972, 1974; Greenwood and Howes, 1975; Gaudant, 1987; Stewart, 1990, 1994; Van Neer, 1992, 1994). Similarly, cichlids are recorded in Africa from the late Oligocene in Somalia (Van Couvering, 1977, 1982), and are common at sites in East and North Africa throughout the later Tertiary (Greenwood, 1951, 1974; Greenwood and Howes, 1975; Van Couvering, 1977, 1982; Schwartz, 1983; Stewart, 1990; Van Neer, 1992, 1994). The fossil cichlids from the site of Mahenge in Tanzania, which have previously been estimated to be of Oligocene or possibly even Miocene in age (Greenwood, 1960; Greenwood and Patterson, 1967), are more likely to be derived from early Eocene deposits (Harrison, 1996). Such an early occurrence for cichlids in Africa is not entirely unexpected. The modern geographic distribution of cichlids (i.e., Africa, Madagascar, South and Central America, southern India, and Sri Lanka) and their occurrence in early Tertiary sediments in Brazil and East Africa suggest that the family was broadly distributed across Gondwanaland at the time of the breakup of the African–South American plates during the Cretaceous (Rabinowitz and LaBrecque, 1979; Pitman *et al.*, 1993; Lundberg, 1993).

The fish fauna from the Manonga Valley provides no information that might help to constrain the biochronological correlation of the Wembere–Manonga deposits. The genera represented in the fauna belong to taxa that are common components of a freshwater community in East Africa that originated at least by the late Miocene, and probably considerably earlier, and continued more or less intact until recent times. Stewart's (this volume, Chapter 11) analysis of the fossil fish, however, does provide useful zoogeographic information. Although the hydrological relationships of the region during the later Neogene are difficult to reconstruct because of subsequent tectonic activities (Cooke, 1958; Pickford *et al.*, 1993; Harrison and Mbago, this volume, Chapter 1), the fish fauna suggests that the Manonga lake basin had contact with the Nile drainage system, and possible also intermittent connections with the Zaire basin and the East Coast Ichthyofaunal Province during the late Miocene and early Pliocene (Stewart, this volume, Chapter 11).

3.3. Invertebrates

A diverse freshwater molluscan fauna has been recovered from horizons within each of the main stratigraphic units of the Manonga Valley (Van Damme and Gautier, this volume, Chapter 12). Although not so informative from a biostratigraphic perspective, the fossil mollusks do contribute useful data for reconstructing the paleoecology and zoogeographic relationships (Harrison, this volume, Chapter 4; Van Damme and Gautier, this volume, Chapter 12). They indicate the presence of well-oxygenated water in shallow, open lakes during deposition of the Ibole Member, with more swampy conditions prevailing during deposition of the Tinde and Kiloleli Members. Most of the molluscan taxa have a wide geographic distribution in modern-day eastern Africa, but the occurrence of *Melanoides* aff. *anomala* implies a past zoogeographic connection with the Zaire basin.

Few other fossil invertebrates are known from the Manonga Valley, but a number of interesting examples of their traces have been identified. At Ngofila 1, for example, the red beds in the Ibole Member contain numerous termitaries. These are preserved as small ovoid, bun-shaped structures, about 10–20 cm in diameter, with well-preserved nest architecture. In terms of their size and shape, they appear to be most similar to those of *Odontotermes* (see Sands, 1987). The only other traces of Termitidae in the fossil record of sub-Saharan Africa are recorded from the mid-Pliocene site of Laetoli, Tanzania (Sands, 1987) and the late Pliocene of Senegal (Tessier, 1959). In addition, at the site of Nyawa, a thin band of hard calcareous clay in the Kiloleli Member contains numerous vertical tunnels made by burrowing invertebrates. These could also represent the traces of termites, but further study at the site is required to confirm this. Finally, the Kiloleli Member at Ngofila 2 has a clay layer that preserves numerous brood cells of solitary bees. These are flask-shaped cells (8–10 mm in length), mostly with distinct caps. The only other described occurrence of hymenopterous brood cells in the fossil record of Africa is that from Laetoli (Ritchie, 1987).

4. Biochronological Implications of the Fauna from the Wembere–Manonga Formation

Based on the information presented above, the mammalian faunas from the main stratigraphic units of the Wembere–Manonga Formation can be reliably correlated with other sites in East Africa, especially those for which radiometric dates are available. The chronological distributions of the mammalian taxa in the Ibole, Tinde, and Kiloleli Members are summarized in Figs. 1–3, and from these data best-fit estimates of the age ranges of the deposits can be inferred.

The Ibole Member correlates best with an age estimate of ~5.0–5.5 Ma (Fig. 1). All of the mammalian taxa for which there are reliable dates are consistent with this estimated age. The only exception is *Saccostomus major*, which is known only from the upper Laetolil Beds (3.5–3.8 Ma). The fauna from the Ibole Member has its closest affinities to that from the upper Nawata Formation and Apak Member at Lothagam (4.72–6.24 Ma). The main difference between the two faunas is that the Lothagam fauna still retains a number of archaic taxa not definitively represented in the Manonga Valley sequence (i.e., *Stegotetrabelodon orbus*, *Miotragocerus* sp., *Brachypotherium lewisi*, and *Palaeotragus germaini*). This further supports the inference that the Ibole Member correlates best with the younger age limit for Lothagam.

The Tinde Member is more difficult to correlate because of the limited taxonomic diversity of the mammalian fauna, and because of the generally poorer preservation of the material. Nevertheless, the fauna is obviously slightly younger than that from the Ibole Member, and seems to be most consistent with an age estimation of ~4.0–5.0 Ma (Fig. 2). Furthermore, the absence of *Nyanzachoerus jaegeri* and the occurrence of a form of *Hexaprotodon harvardi* that

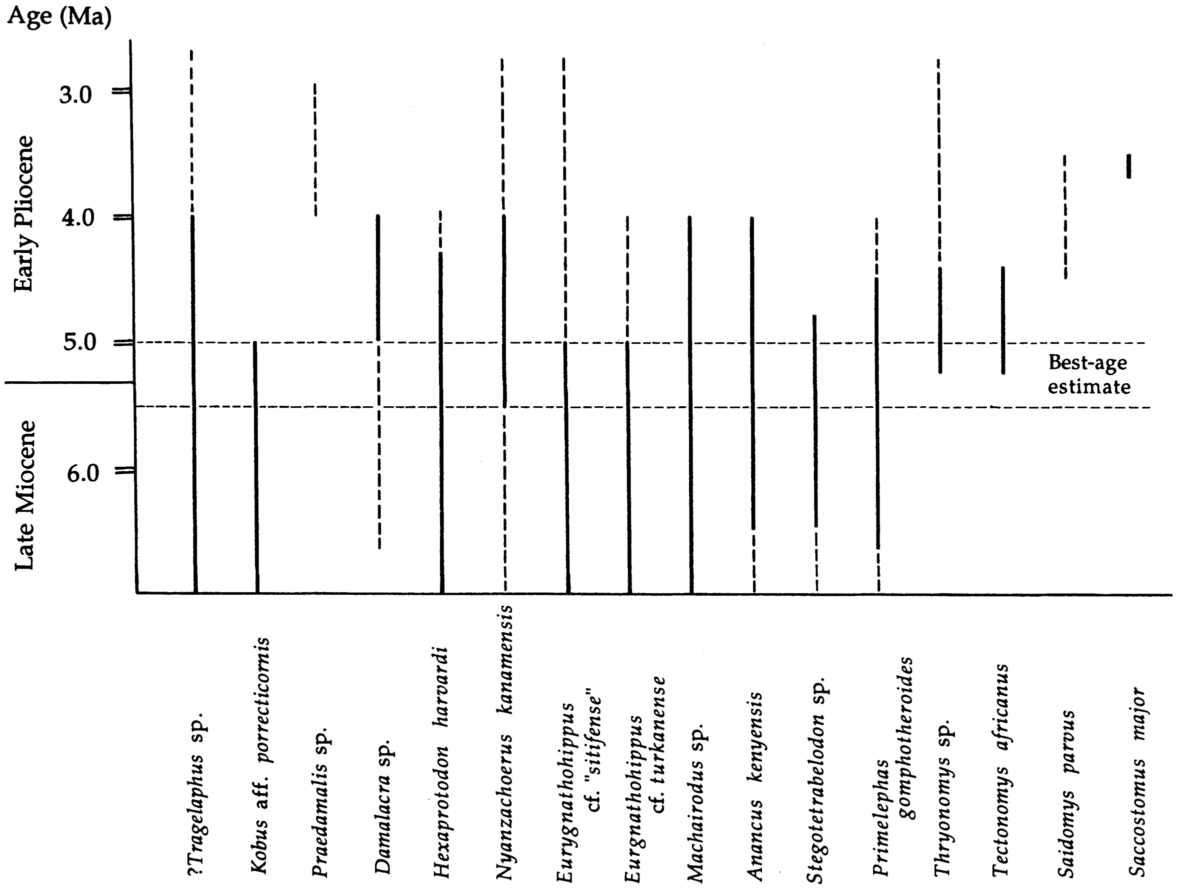

FIGURE 1. Chart showing the temporal ranges of mammalian taxa from the Ibole Member. Solid vertical lines represent that part of the temporal range of the taxon that is most consistent with the material from the Ibole Member. The broken vertical lines represent the full temporal range of the taxon. The best-age estimate is obtained by determining the time period in which maximal overlap occurs between the constituent taxa.

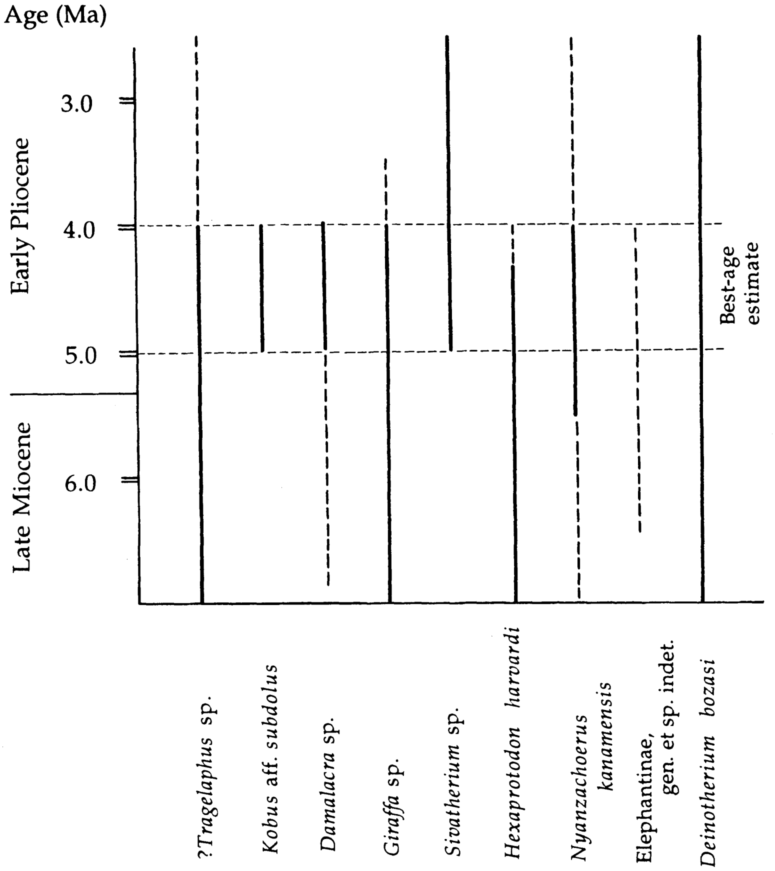

FIGURE 2. Chart showing the temporal ranges of mammalian taxa from the Tinde Member. Solid vertical lines represent that part of the temporal range of the taxon that is most consistent with the material from the Tinde Member. The broken vertical lines represent the full temporal range of the taxon. The best-age estimate is obtained by determining the time period in which maximal overlap occurs between the constituent taxa.

is morphologically more primitive than that from Kanapoi both indicate that the Tinde Member may be at the older end of this range, perhaps ~4.5–5.0 Ma.

The mammalian fauna from the Kiloleli Member appears to be most consistent with a biochronological age of ~4.0–4.5 Ma (Fig. 3). The degree of primitiveness of the bovids, the occurrence of *Hexaprotodon harvardi*, and the absence of *Notochoerus euilus* and *Kolpochoerus* spp. provide good evidence to support an estimated age older than 4 Ma. However, a somewhat younger age might be indicated by the occurrence of *Eurygnathohippus hasumense* and *Loxodonta exoptata*. However, these latter taxonomic assignments are tentative only, and it is possible that the Kiloleli species might later prove to be earlier and somewhat more primitive representatives of their respective lineages. One of the key problems in trying to assess the biochronological age of the Kiloleli Member is

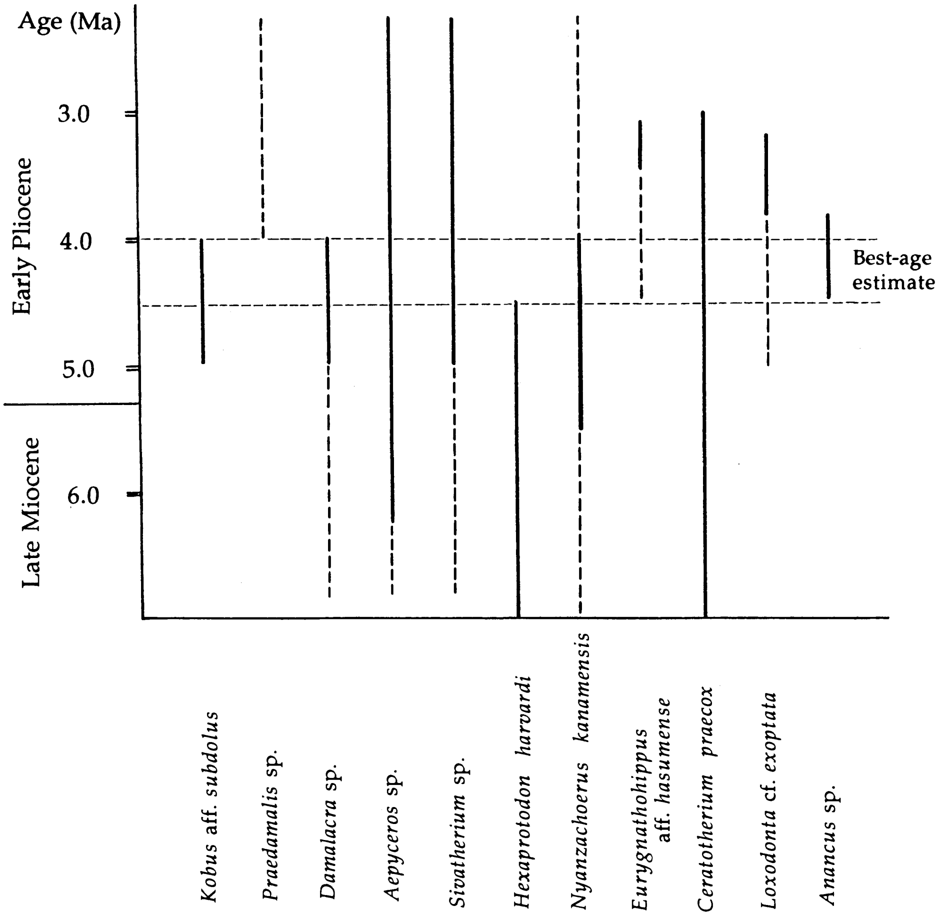

FIGURE 3. Chart showing the temporal ranges of mammalian taxa from the Kiloleli Member. Solid vertical lines represent that part of the temporal range of the taxon that is most consistent with the material from the Kiloleli Member. The broken vertical lines represent the full temporal range of the taxon. The best-age estimate is obtained by determining the time period in which maximal overlap occurs between the constituent taxa.

that there are few faunas of comparable age (~4.0–4.5 Ma) known from East Africa (i.e., Tabarin, Sagantole Formation, Kanapoi, and the Mursi Formation), and these are relatively small faunas that have not yet been studied in detail.

Simpson's index of faunal resemblance (i.e., the number of taxa in common between two faunas divided by the total number of taxa in the smaller fauna × 100) provides an objective measure of the degree of similarity between two faunas (Simpson, 1960; Shuey *et al.*, 1978). Using this index, we have compared the Manonga Valley fauna with those from all late Miocene and early Pliocene sites in Africa for which detailed and comprehensive faunal lists are currently available. At the species level, the fauna from the Ibole Member is most similar to Lothagam (75.0%) and the Adu-Asa Formation (73.5%), that from the Tinde Member is also most similar to Lothagam (75.0%), while that from the Kiloleli Member is most similar to the Sagantole Formation (66.7%). At the genus level, the Ibole Member fauna is again most similar to Lothagam (72.7%), as well as to Langebaanweg (54.5%) and Kanapoi (54.5%), the Tinde Member fauna is most similar to Kanapoi (87.5%), Lothagam (75.0%), Langebaanweg (62.5%), and the Sagantole Formation (62.5%), and the Kiloleli Member fauna is most similar to Kanapoi (72.7%) and the Sagantole Formation (63.6%). Overall, the strongest similarities are as follows: the Ibole Member with Lothagam, the Tinde Member with sites ranging in age from Lothagam to Kanapoi, and the Kiloleli Member with the Sagantole Formation. These associations are generally consistent with the inferred biochronological age estimates presented above based on the overlapping temporal ranges of the constituent taxa. The Manonga Valley faunas show least similarity, at both the species and genus levels, with the late Miocene faunas from the Ngorora Formation and the Namurungule Formation, as well as with the mid-Pliocene fauna from Laetoli. These data provide wider limits that serve to bracket the age of the Wembere–Manonga Formation between 8.0 Ma and 3.8 Ma.

In conclusion, a synthesis of the available evidence from the mammalian faunas indicates that the Wembere–Manonga Formation was deposited during the latest Miocene and early Pliocene, with an approximate age of 4.0–5.5 Ma. This is close to previously published age estimates for the fossiliferous sediments in the Manonga Valley (Harrison, 1991, 1993; Harrison and Verniers, 1993; Harrison *et al.*, 1993). The faunal evidence supports observations based on the stratigraphic succession that there were no major interruptions in sedimentation during this time period. The main stratigraphic units of the Wembere–Manonga Formation are, therefore, inferred to have the following biochronological ages: Ibole Member, ~5.0–5.5 Ma; Tinde Member, ~4.5–5.0 Ma; Kiloleli Member, ~4.0–4.5 Ma.

5. Fossil Mammals from the Mbuga Clay and Yellow Clay Horizons

A representative sample of fossil mammals has been recovered from late Quaternary sediments at various sites throughout the Manonga Valley (Table V). Most of the fossils are derived from the mbuga clay horizon, which represents a superficial layer of black to dark gray sediments covering much of the floor of the Manonga Valley. The fossils consist mainly of isolated teeth and fragmentary cranial and postcranial bones. Identifiable material can almost all be attributed to extant species, indicating a late Pleistocene or Holocene age. The Late Stone Age lithic assemblages found in association (characterized by geometric microliths, backed blades, and scrapers made of quartz and chert flakes) suggest that the horizon is probably younger than 22,000 BP (Marean, 1990). The deposition of the mbuga clays might possibly coincide with a warm and wet climatic phase (12,700–11,100 BP), during which East African lake levels reached their

Table V. Late Quaternary Fossil Sites in the Manonga Valley

Locality	Taxa identified
Beredi South 1	*Connochaetes taurinus, Equus burchelli*
Beredi South 2	*Equus burchelli, Phacochoerus africanus,* Bovidae
Inolelo 1	*Phacochoerus africanus, Damaliscus dorcus, Equus burchelli, Connochaetes taurinus,* ?*Taurotragus oryx*
Inolelo 2	*Loxodonta africana, Phacochoerus africanus, Equus burchelli,* Alcelaphini
Inolelo 3	*Phacochoerus africanus, Equus burchelli,* Bovini
Ipembe	*Homo sapiens, Phacochoerus africanus*
Kalitu	*Alcelaphus buselaphus, Connochaetes* sp., *Phacochoerus africanus, Equus burchelli, Taurotragus oryx,* Alcelaphini
Kiloleli 2	*Phacochoerus africanus, Damaliscus dorcus, Equus burchelli*
Kiloleli 3	*Equus burchelli, Alcelaphus buselaphus*
Kiloleli 4	*Connochaetes taurinus*
Kininginila	*Hippopotamus amphibius, Equus burchelli,* Alcelaphini
Mwambiti 3	*Connochaetes taurinus, Equus burchelli*
Ngofila 2	*Equus burchelli, Phacochoerus africanus,* Bovidae
Nyawa	*Connochaetes taurinus, Equus burchelli, Phacochoerus africanus,* cf. *Megalotragus* sp., Alcelaphini
Shoshamagai 2	*Equus burchelli,* Bovidae
Shoshamagai Hill	*Syncerus caffer*
Tinde West	*Phacochoerus africanus*

late Quaternary maxima (Kendall, 1969; Livingstone, 1975; Hamilton, 1982; Roberts, 1990; Roberts *et al.*, 1993; Harrison and Mbago, this volume, Chapter 1).

The most common mammals in the mbuga clays are *Equus burchelli, Phacochoerus africanus, Connochaetes taurinus,* and several smaller species of alcelaphines, tentatively identified as *Alcelaphus buselaphus* and *Damaliscus dorcas.* Rarer taxa include *Hippopotamus amphibius, Syncerus caffer, Taurotragus oryx,* and *Loxodonta africana.* In addition, a left M^2 indicates the occurrence of a large species of alcelaphine that falls outside the upper size range of extant *Connochaetes taurinus.* The specimen is possibly attributable to *Megalotragus,* a very large alcelaphine known to have survived to at least the late Pleistocene in both South and East Africa (Gentry and Gentry, 1978; Vrba, 1979; Gentry, 1985; Pickford and Thomas, 1984; Harris, 1991a). A further specimen of some interest is a fragmentary occipital bone of a human recovered from Ipembe. The bone is quite thick, but it is definitely identifiable as anatomically modern human (*Homo sapiens sapiens*). In addition to mammals, the mbuga clays commonly contain shells of large bivalve mollusks, and a piece of ostrich egg shell has also been recovered at Tinde West.

A similar fauna to that from the mbuga clays has been recovered from a yellow clay horizon resting unconformably on top of the Kiloleli Member at Kiloleli 2, Ngofila 2, and Beredi South 1. The stratigraphic relationship between the yellow clays and the mbuga clays is unclear, but it is likely that deposition of the former predates the latter. The fossil material from the yellow clays is often more completely preserved than that found in the mbuga clays. In addition, at Ngofila 2 there are clear signs, in the form of butchering marks, that the assemblage was accumulated by humans. Also, several bones have been gnawed by rodents, which indicates that they were exposed on the surface for a period of time prior to burial. Mammals recovered from the yellow clay horizon include *Equus burchelli*, *Hippopotamus amphibius*, *Phacochoerus africanus*, and several species of bovids. The occurrence of modern species in association with indications of human activity suggests a late Pleistocene or Holocene age for this faunal assemblage.

The fossil mammals from the mbuga clay and yellow clay horizons are generally similar to those found today in the Serengeti Plains just to the northeast of the Manonga Valley. The abundance of zebras, warthogs, and alcelaphine bovids indicates relatively extensive areas of grasslands. However, the widespread mbuga clays were evidently deposited in shallow lakes, pools, and swamps, which suggests that conditions were relatively more mesic during this period, and probably associated with a mosaic of grasslands and open woodlands. This paleoecological setting is quite different from the current situation in the Manonga Valley, in which patchy grasslands and dry acacia scrub predominate. The available evidence suggests that this ecological transition is very recent, and is due primarily to intensification by the local human population. Overexploitation of trees for fuel and for construction has caused a dramatic decline in the extent of woodlands, and overgrazing by livestock has led to widescale soil erosion and badlands formation. Williams and Eades (1939) noted that poor land management and sheet soil erosion were already becoming a serious problem in some areas as early as the 1930s. Along some stretches of major watercourses, and in areas less accessible to humans, small relict patches of the original acacia woodlands remain, and these indicate that the Manonga Valley was more densely vegetated, even in the recent past.

These recent ecological changes in the Manonga Valley have also impacted negatively on the wildlife. During the course of our expeditions, team members have sighted few large mammals in the area, and these are mainly cryptic or nocturnal forms. The list includes duiker, dik-dik, impala, gazelle, leopard, striped hyena, spotted hyena, aardwolf, genet, black-backed jackal, slender mongoose, vervet, hedgehog, rabbit, and porcupine. The apparent scarcity of mammals in the Manonga Valley may be a consequence, in part, of the fact that our expeditions take place only during the dry season, since local informants tell us that game animals are more plentiful in the area during the rainy season. Nevertheless, older informants acknowledge that wildlife has become more scarce in recent years.

The explorer Henry M. Stanley passed through the Manonga Valley in February 1875 (at the end of the rainy season) and his account of the expedition gives some insight into the ecology of the region at that time. He states that

> giraffe were numerous, feeding on the dwarf acacia, but the country was too open to permit my approaching them. However, I succeeded in dropping a stray springbok in a hunting excursion which I made in the evening. On leaving the Monangah, we struck

Table VI. Present-Day Large Mammal Fauna from the Manonga Valley[a]

English name	Scientific name	Sukuma name	Swahili name
Tropical African hedgehog	*Atelerix albiventris*	Kirungu-mifa	Kalunguyeye
Crested porcupine	*Hystrix sp.*	Nuungu	Nungu
Crawshay's hare	*Lepus crawshayi*	Lungwando kaumbu	Katiti sungura
African rabbit	*Poelagus marjorita*	Lungwando lusuga	Katita sungura
Cane rat	*Thryonomys* sp.	Ngosso	Ndezi
Anubis baboon	*Papio anubis*	Nguku	Nyani
Green monkey	*Cercopithecus aethiops*	Numbirhi	Ngedere, Tumbili
Common jackal	*Canis aureus*	Jidevwe	Mbweha
Black-backed jackal	*Canis mesomelas*	Jidevwe	Mbweha
Civet	*Viverra civetta*	Nungo	Fungo mkubwa
Common genet	*Genetta genetta*	Nirhilhi	Ngawa
Dwarf mongoose	*Helogale parvula*	Njololho	Nguchiro
Slender mongoose	*Herpestes sanguineus*	Njololho	Nguchiro
Striped hyena	*Hyaena hyaena*	Mbithi	Fisi
Spotted hyena	*Crocuta crocuta*	Mbithi	Fisi
Wild dog	*Lycaon pictus*	Mhuge	Mbwa mwitu
Aardwolf	*Proteles cristatus*	Mbithi	Fisi ndogo
Lion	*Panthera leo*	Shimba	Simba
Leopard	*Panthera pardus*	Shubi, Subi	Chui
Cheetah	*Acinonyx jubatus*	Shubi mondo	Duma
Zebra	*Equus burchelli*	N'nduulu	Punda milia
Aardvark	*Orycteropus afer*	Naga	Kiliberatili
Elephant	*Loxodonta africana*	Mhulhi	Tembo
White rhinoceros	*Ceratotherium simum*	Mhela	Kifaru
Hippopotamus	*Hippopotamus amphibius*	Nguwbo	Kiboko
Warthog	*Phacochoerus aethiopicus*	Nngiri	Ngiri
Giraffe	*Giraffa camelopardalis*	Nhiga	Twiga
Giant eland	*Taurotragus derbianus*	Mboku	Pofu
Greater kudu	*Tragelaphus strepsiceros*	Nandala	Tandala mkubwa
Brindled gnu	*Connochaetes taurinus*	Mbushi	Nyumbu ya montu
Thomson's gazelle	*Gazella thomsoni*	Lhala	Swala tomi
Grant's gazelle	*Gazella granti*	Lhala	Swala granti
Impala	*Aepyceros melampus*	Mhala	Swala pala
Kirk's dik-dik	*Rhynchotragus kirki*	Subhuya	Dikidiki
Abbot's duiker	*Cephalophus spadix*	—	Minde
African buffalo	*Syncerus caffer*	Nmbogo	Mbogo, Nyati

[a] This list is based on personal observations and on data supplied by local Sukuma informants.

> northerly across a pathless country seamed with elephant tracks, rhinoceros wallows, and gullies which contained pools of grey muddy water (Stanley, 1878 p. 106).

From such sources, and from local informants, we have been able to compile a list of large mammals that are native (in the living memories of our informants) to the Manonga Valley (Table VI). The Wembere depression, the southernmost extension of the Serengeti, just to the east of the Manonga Valley, still supports large herds of game animals, mainly because the soils and vegetation there are unsuitable for intensive cultivation and ranching.

Apparently, during the late Pleistocene or early Holocene the Manonga Valley was dominated by grasslands and open woodlands that supported a mammalian community broadly comparable in its taxonomic composition to that found in the Serengeti today. It would seem that similar (but probably less mesic) habitats occurred in the Manonga Valley until recent historic times. The relatively impoverished fauna and the sparser vegetation that is typically present in the area today appears to be the result of recent ecological disturbances by local farming populations. The increased density of humans and their dependent livestock in the area since the start of the colonial period has led to a dramatic decline in woodland habitats, and severe overgrazing of the grasslands.

6. Conclusions

The mammalian fauna indicates that the Wembere–Manonga Formation was deposited during the latest Miocene and early Pliocene, with a best-fit age of 4.0–5.5 Ma for the entire sequence. The main stratigraphic units of the Wembere–Manonga Formation are inferred to have the following biochronological ages: Ibole Member, ~5.0–5.5 Ma; Tinde Member, ~4.5–5.0 Ma; and Kiloleli Member, ~4.0–4.5 Ma. Although the paucity of well-dated and well-studied faunas from this time period for comparison limits the degree of precision of the correlations, we are confident that the biochronological age estimates of the Manonga Valley faunas presented here can be considered reasonably secure.

The lower part of the sequence appears to be comparable in age to the Nawata Formation and Apak Member at Lothagam and to the Lukeino Formation in Kenya. We have placed the lower limit of the sequence at 5.5 Ma, but this is a conservative estimate, and it is possibly slightly older. The Kiloleli Member appears to be closest in age to Tabarin (lower Chemeron Formation), Baringo basin, Kenya, and to Aramis, Middle Awash Valley, Ethiopia. Comparisons indicate that the Kiloleli fauna is more archaic than those from Hadar, Laetoli, and Kanapoi, and there seems little doubt that the upper part of the Wembere–Manonga Formation is as old or older than 4 Ma.

Future research in the Manonga Valley will obviously need to concentrate on developing a detailed geochronology. This might prove feasible given the apparently tuffaceous origin of the lake sediments (Mutakyahwa, this volume, Chapter 3). In addition, a preliminary analysis of the paleomagnetic stratigraphy is currently underway by John Kappelman (University of Texas at Austin), and this might help to further refine the biochronological age estimates presented here.

Fossil mammals have also been recovered from late Quaternary sediments in the Manonga Valley. These are almost exclusively attributable to extant species, which indicates a late Pleistocene or Holocene age. Late Stone Age lithic assemblages found in association with the fauna suggest that the deposits are younger than 22,000 BP.

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Chapter 14

Hominid Origins

A View from the Manonga Valley

TERRY HARRISON

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1. Introduction

The sequence of fossil-bearing sediments in the Manonga Valley, with an estimated age range of ~4.0–5.5 Ma, samples a critical period of time (from 4 Ma to 7 Ma) that is generally poorly represented in sub-Saharan Africa. Few other paleontological sites have sediments that fall into this time range, and many of these are difficult to date, or have relatively small faunas that have not yet been the subject of detailed study. The best paleontological information for this period comes from sites in the Baringo basin and Turkana basin in Kenya, and from sites in the Middle Awash region of Ethiopia, where sizable faunas have been recovered from sediments that have been dated using radiometric techniques. The most important fossil collections are from the Mpesida Beds (6.4–7.0 Ma) and Lukeino Formation (5.6–6.2 Ma) in the Baringo basin, the upper Nawata Formation and Apak Member at Lothagam (~4.72–6.24 Ma) in the Turkana basin, and the Sagantole Formation (~3.5–4.5 Ma) and Adu-Asa Formation (~4.5–6.0 Ma) in the Middle Awash. It is important to note that these sites are limited geographi-

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cally to two relatively restricted areas within the East African Rift valley (i.e., in north-central Kenya and northeastern Ethiopia). Other significant faunas from this time period, but without absolute dates, are known from Kenya (Kanam, ~4–6 Ma; Nakali, ~7–8 Ma), the Western Rift in Uganda (Nkondo Formation ~4.5–6.5; Oluka Formation ~6.0–7.5 Ma), North Africa (Wadi Natrun, Egypt, ~4–5 Ma; Sahabi, Libya, ~5 Ma), and South Africa ('E' Quarry, Varswater Formation, Langebaanweg, ~4–5 Ma) (see Harrison and Baker, this volume, Chapter 13 for references on the dating and paleontology of these sites).

The paleontological collections from the Manonga Valley, therefore, help to contribute significant new information to improve on our currently limited appreciation of the taxonomic diversity, evolutionary history, paleobiology, and paleoecology of fossil mammals in East Africa during the late Miocene and early Pliocene. Furthermore, the location of the Manonga Valley at the southern end of the Eastern Rift valley also extends the geographic range of faunas known from this time period. The Manonga basin is located almost 600 km from the Baringo basin and about the same distance from the Western Rift. Comparisons of African faunas from this period might ultimately allow us to recognize provincial or ecological differences that existed as a result of the formation of the rift valley.

Better documentation of mammalian faunas from the late Miocene and early Pliocene of Africa is especially significant for understanding hominid origins. This time period witnesses a significant change in the composition of the mammalian fauna. Compared with earlier East African faunas from the Namurungule Formation (~8–10 Ma) and the Ngorora Formation (~9.0–12.3), which have many archaic taxa surviving from the earlier part of the Miocene, those between 5 Ma and 7 Ma are characterized by the first appearance of a number of groups of mammals of "modern aspect" (Hill *et al.*, 1985; Leakey *et al.*, 1996). Hippopotamines, giraffines, *Nyanzachoerus*, several bovid tribes (i.e., tragelaphines, alcelaphines), *Ceratotherium*, elephantids, machairodontine felids, and ursids all make their first appearance in sub-Saharan Africa at this time. Although the fossil evidence is still rather limited, it seems likely that hominids also made their initial appearance at this time. Their earliest recorded occurrence is at Lothagam and Lukeino, estimated to be 4.7–6.2 Ma in age. This is close in time to the estimated divergence dates for hominids based on molecular evidence (Weiss, 1987; Caccone and Powell, 1989; Hasegawa *et al.*, 1989; Hasegawa, 1992; Bailey *et al.*, 1992). If hominids did indeed originate at this time, then a detailed analysis of the dynamics of this major faunal change might provide important clues to understanding the factors underlying the differentiation and subsequent divergence of hominids from their last common ancestor with the African apes.

The Manonga Valley has the potential to provide important evidence that is directly or indirectly pertinent to the study of hominid origins. With so few paleontological sites sampling the critical time period between 4 Ma and 7 Ma, the Manonga Valley, with its productive fossil localities of the appropriate age, is an ideal place to look for early hominids. Moreover, given the scarcity of fossil hominids currently known from this time period, the eventual discovery of hominids in the Manonga Valley would undoubtedly contribute significantly to our limited understanding of their anatomy and paleobiology. Even if hominids are not found, study of the Manonga Valley faunas might allow us to gain valuable insight into the ecological and biogeographical factors that led to the initial differentiation of hominids during the late Miocene of Africa.

The objective of this chapter is to present a brief critical review of some of the main issues my research in the Manonga Valley has raised that relate directly to the question of human origins. It is not intended to be a review of early hominid fossils and sites, since this has already been done in some detail elsewhere (Hill and Ward, 1988; Hill, 1994). Rather, the aim is to focus on a few key problems that emphasize just how little we actually know about the earliest hominids, and why continued research in the Manonga Valley (and at other late Neogene sites in Africa) is so important. The fact that hominid fossils have not yet been found in the Manonga Valley, with its numerous paleontologically productive sites located in close proximity to the famous hominid-bearing sites of Olduvai Gorge and Laetoli, is an interesting finding in itself. Working in the Manonga Valley has, therefore, given me a unique perspective, because it has forced me to ask different kinds of questions about early human origins. Unfortunately, I am not in a position to provide conclusive answers to any of these questions, but it is hoped that by introducing them here they will serve as a basis for stimulating further discussion and research. It is also my hope that additional researchers will take up the challenge to explore new areas in Africa that might offer valuable clues to help document and explain hominid origins.

2. What Evidence Is Available for Hominids Older Than 4 Ma?

Even though there has been a marked increase in the number of discoveries of hominid specimens from sites older than 4 Ma in recent years, there are still relatively few specimens available. The total collection comprises the following: (1) Lothagam, Kenya (~5–7 Ma)—a right mandibular fragment discovered in 1967, and two isolated teeth recovered by Meave Leakey in 1990–92 (Patterson *et al.*, 1970; Hill, 1994; Leakey *et al.*, 1996); (2) Cheboit, Lukeino Formation, Kenya (5.6–6.2 Ma)—left lower molar discovered in 1973 (Pickford, 1975; Corruccini and McHenry, 1980; McHenry and Corruccini, 1980; Kramer, 1986; Hill and Ward, 1988; Hill, 1994; Ungar *et al.*, 1994); (3) Aramis, Sagantole Formation, Middle Awash, Ethiopia (~4.3–4.5 Ma)—collection of 17 craniodental and postcranial specimens described as *Ardipithecus ramidus* (White *et al.*, 1994, 1995); (4) Tabarin, Chemeron Formation, Kenya (~4.15–5.0 Ma)—right mandibular fragment discovered in 1984 (Hill, 1985, 1994; Ward and Hill, 1987; Hill and Ward, 1988; Ferguson, 1989); (5) Chemeron Formation, Kenya (~4.2–5.0 Ma)—proximal humerus discovered in 1973 (Pickford *et al.*, 1983; Hill and Ward, 1988; Hill, 1994); (6) Kanapoi, Kenya (~3.9–4.2 Ma)—distal humerus found in 1965, and portions of a right tibia and seven craniodental specimens found in 1994 all referred to *Australopithecus anamensis* (Patterson and Howells, 1967; Leakey *et al.*, 1995).

All of the known specimens are derived from the Turkana basin, the Baringo basin, and the Middle Awash. In addition, most of the specimens are from sediments that are estimated to be 4.0–4.5 Ma, and only the isolated tooth from Lukeino and the specimens from Lothagam are likely to be appreciably older (~4.7–6.2 Ma). Possible hominoid remains (including a clavicle, a distal fibula, and a parietal fragment) have been reported from the North African early Pliocene (~5 Ma) site of Sahabi (Boaz, 1980, 1987; Boaz and Meikle, 1982). However, the purported clavicle has been identified as a rib of a dolphin (White *et al.*, 1983; White, 1987), and the other pieces are of questionable taxonomic status (Hill, 1994). Reference should also be made to the isolated upper molar from the late Miocene Ngorora Formation, discovered in 1968, which has in the past been identified as a hominid (Bishop and Chapman, 1970). However, it is quite distinctive, and, like several other isolated teeth recovered more recently from the Ngorora Formation (~12.4–12.5 Ma), it may have closer affinities with earlier Miocene catarrhines, such as *Afropithecus* (Hill and Ward, 1988; Hill, 1994).

Clearly, the hominid fossil record is exceedingly sparse before 4 Ma, and we know almost nothing about the anatomy and paleobiology of hominids prior to 4.5 Ma. The only way in which the fossil record can be improved is by finding additional specimens from existing localities that sample this time period or, perhaps more importantly, by stepping up the search for productive new localities in unexplored regions of Africa, such as the Manonga Valley, where fossiliferous deposits of the right age are likely to be found or are known to occur.

3. Why Are There No Hominids in the Manonga Valley?

Several possible explanations can be given for why no fossil hominids have been recovered from the Manonga Valley: (1) The geographical distribution of hominids did not extend as far south as Tanzania during the late Miocene–early Pliocene; (2) the ecology of the Manonga basin was not suitable to support early hominid populations at this time because (a) hominids were restricted in their habitat preferences or (b) the ecology of the Manonga Valley was in some way different from that of hominid sites in Kenya and Ethiopia; (3) hominids were an extremely rare component of the fauna, and their remains have not yet been recovered; and (4) hominids were locally common, but (a) they did not inhabit ecosystems favoring their preservation, (b) there was a selective taphonomic bias against their remains being preserved as fossils compared with other mammals, or (c) their remains are preserved as fossils, but we have been searching in the wrong parts of the basin.

I suspect that it is a combination of several of these factors. A brief consideration of the evidence from the Manonga Valley, and from other sites of similar age in Africa, allows us to rule out some options, but there are still several remaining possibilities. A review of these is instructive for possible interpretations of the ecological and geographic distribution of early hominids.

It is a distinct possibility that hominids had a restricted geographic range during the late Miocene and early Pliocene. Their known geographic distribution prior to 4.0 Ma is limited to sites in Ethiopia and Kenya associated with the East African Rift valley (if the purported hominoids from Sahabi are excluded from consideration). Could it be that hominids originated in this region, and were then limited to a relatively restricted range until just before 3 Ma, when they appear for the first time in Chad and southern Africa? There is some evidence (at least of a negative kind) from sites in other parts of Africa dated at 4–6 Ma to support this hypothesis. In addition to the Manonga Valley, no hominids have been recovered from this time period from the Western Rift of Uganda and Zaire, North Africa (Wadi Natrun, and possibly also Sahabi), or South Africa (Langebaanweg). It could be argued that the intensity of the research effort and the quality of the preservation is much higher at sites in the Eastern Rift valley, and that this has contributed to the successful recovery of fossil hominids. There is certainly some justification for this argument. However, given the size of the faunal collections from the Manonga Valley and the Western Rift, as well as the remarkably well-preserved and meticulously collected fossils from Langebaanweg, it is difficult to accept that the absence of hominids in these particular samples is simply a matter of preservation or collecting technique.

I am more inclined to accept, at present, that early hominids may have been geographically restricted to the rift valley region in Kenya and Ethiopia during the late Miocene and early Pliocene. This seems a reasonable hypothesis given the evidence currently available. Perhaps there is something unique about the ecology of the developing rift valley that lies at the root of hominid origins. Only detailed comparisons of the geology and paleoecology between sites in the Eastern Rift valley and those from other parts of Africa will allow us to test this idea. Unfortunately, if this scenario is the correct one, the asymmetric nature of the negative evidence logically means that there is no possibility of ever effectively demonstrating it to be so, no matter how much effort we put into paleontological research at sites outside the rift valley. By contrast, a single discovery of a fossil hominid in the Manonga Valley will necessitate a major rethinking of the proposed hypothesis. However, there are several other possible ways to explain the absence of hominids in the Manonga Valley.

For instance, there might be an important ecological distinction between sites that could imply that early hominids had a particular habitat preference. At first glance this does not seem to be a likely alternative. Preliminary data on the paleoecology of sites older than 4 Ma suggest that hominids were able to occupy a diversity of habitats. At Lothagam (~4.7–6.2 Ma) the paleoecology appears to have been closely similar to that inferred for the Ibole Member in the Manonga Valley (Harrison, this volume, Chapter 4). The vegetation consisted predominantly of dense woodland with broad tracts of gallery forests located along the banks of rivers and other permanent sources of water (Leakey *et al.*, 1996). Similarly, the ecology of Aramis in the Sagantole Formation of the Middle Awash (4.3–4.5 Ma) has also been reconstructed as closed woodland, although the rarity of aquatic elements in the fauna may indicate somewhat drier conditions than those at Lothagam (WoldeGabriel *et al.*, 1994). At the site of Kanapoi (3.9–4.2

Ma) dry, possibly open woodland or bushland conditions are indicated by the fauna, although the presence of a large river system may have supported a gallery forest along its flanks (Leakey *et al.*, 1995). Evidence from Laetoli, at a slightly younger date (3.5–3.8 Ma), suggests a predominantly dry grassland and open woodland setting, possibly with more densely wooded areas nearby (Harris, 1987; Andrews, 1989). We can draw two main conclusions from these data. First, early hominids appear to have been rather eclectic in their habitat preference; they are found at sites with ecologies that are inferred to range from moist woodland or forest settings to rather dry grasslands and open woodlands. Second, the paleoecology at sites such as Lothagam or Aramis is basically similar to that inferred from the Manonga Valley, with no indication of a profound ecological distinction that would serve to exclude hominids.

Although we can probably rule out the possibility that major ecological differences existed between the Manonga Valley and contemporary hominid-bearing sites in Kenya and Ethiopia, it is not possible to establish whether or not more subtle environmental or vegetational differences may have been influential in determining hominid distribution patterns. For example, hominids may have been constrained by the geographic distribution of particular plant species that were an important component of their diets. If this is the case, it will be exceedingly difficult to tease this out using paleontological evidence. However, some clues might be gained from the comparative study of other taxa from these sites. Some importance might be attributed to the observation that cercopithecids are found commonly at sites in association with early hominids, while they tend to be much rarer elements of the fauna at other sites. At Aramis, for example, monkeys are remarkably abundant, and they compose over 30% of the vertebrate fauna from the site (WoldeGabriel *et al.*, 1994). Cercopithecids are also quite common at Lothagam, Lukeino, Kanapoi, and Laetoli (Leakey and Delson, 1987; Hill *et al.*, 1985, 1992; Leakey *et al.*, 1995). They also occur at the early Pliocene sites of Wadi Natrun and Sahabi in North Africa, but are relatively uncommon components of these faunas (Szalay and Delson, 1979; Boaz and Meikle, 1982). The late Miocene site of Menacer (= Marceau) in Algeria is exceptional, however, in that the fauna (without hominids) is dominated by cercopithecids (Szalay and Delson, 1979; Thomas and Petter, 1986). By contrast, six isolated teeth represent the total complement of cercopithecids from Langebaanweg, the Manonga Valley, and from late Miocene–early Pliocene sites in the Western Rift of Uganda and Zaire (Hooijer, 1963; Senut, 1994; Grine and Hendey, 1981; Harrison and Baker, this volume, Chapter 13). The correlation between the relative abundance of cercopithecids and the occurrence of hominids certainly suggests that ecological or environmental factors are responsible for the association. It may be significant, in this regard, that cercopithecids become much more abundant and taxonomically diverse in both South and East Africa from the mid-Pliocene onwards, just at the time when the hominid fossil record is also beginning to pick up pace (Leakey *et al.*, 1996).

Another important factor that could account for the apparent absence of fossil hominids in the Manonga Valley is that they may have been very rare elements in the East African faunal community throughout the late Miocene and early

Pliocene. This is confirmed by the paleontological evidence, and is especially noticeable for sites older than 4.5 Ma. Even at Lothagam, where an intensive program of fossil collecting has been implemented in recent years, few hominid specimens have been recovered compared to the abundance and diversity of other large mammals (Leakey *et al.*, 1996). If hominids were very rare elements of the fauna during the later Neogene (they represent less than 0.3% of all large mammals at Lothagam, but combining data from all sites of this age in Africa, hominids constitute less than 0.01%), then on the grounds of probability alone, we might expect them to be missing from the fossil record, even at sites within their geographic and temporal range. Although the rarity of hominids from this time period makes the task of searching for them an extremely frustrating business, it also implies that early hominids probably occupied a very specialized niche. Research on the relative abundance and community structure of late Miocene mammals in Africa, using comparative data from modern faunas, could well prove fruitful for reconstructing the ecology of early hominids.

We may yet discover the remains of fossil hominids in the Manonga Valley, and if we do, these are most likely to come from previously established sites. Since 1990, WMPE (Wembere–Manonga Paleontological Expedition) has systematically prospected most areas in the center of the basin, and we are confident that we have now identified most of the productive localities. Perhaps the most promising sites for future research are those at Shoshamagai and Inolelo. These sites have produced well-preserved fossils, including partial skeletons, from the oldest fossiliferous beds in the Manonga Valley (~5.0–5.5 Ma), and we continue to add new species to the faunal list each season.

In conclusion, the absence of hominids from the fossil record in the Manonga Valley can be explained as a consequence of the fact that either hominids are very rare components of the East African fauna during the late Miocene and early Pliocene, or hominids were geographically restricted to a region of the rift valley in Kenya and Ethiopia at this time, and their range did not extend far enough south to encompass the Manonga Valley. Either way, this has important implications for interpretations of the ecology and zoogeography of the earliest hominids, and further research is needed on the detailed community structure and distribution of African faunas from the later Neogene.

4. How Will We Recognize a Hominid if We Find One?

A more mundane, but no less important, consideration of our research in the Manonga Valley is the problem of how to recognize a hominid if we find one. This is not as easy as it might seem. Many of the craniodental features previously employed as characteristics of hominids, such as a well-developed metaconid on P_3, a simple occlusal pattern on the cheek teeth, thickened enamel on the molars, and a relatively shallow and robust mandible, are also typical of many late Miocene hominoids from Eurasia, including *Griphopithecus*, *Graecopithecus*, and *Sivapithecus*, and these may be inferred to represent primitive features of great apes and humans (see Andrews, 1995). There appear to be few derived craniodental characters that serve to distinguish early hominids. The development of an incisiform canine of reduced size appears to be the most significant specialization shared by all hominids. If only isolated teeth and jaw fragments of early hominids are found it may be difficult to establish their affinities. For this reason, attribution of the specimens from Lukeino and Lothagam has proved problematic (Kramer, 1986; Hill and Ward, 1988; Ungar *et al.*, 1994; Hill *et al.*, 1992; Hill, 1994; Leakey *et al.*, 1996), and their hominid status might best be considered provisional. All that can be stated with certainty is that they are hominoids with relatively thick-enameled molars. It should be noted, in this regard, that thick-enameled hominoids from Africa have been traditionally recognized as hominids, while those from Eurasia are just apes. However, unless relatively complete cranial or postcranial remains are recovered it may be difficult to tell whether we are truly dealing with a hominid or a more conservative member of the clade comprising all of the African hominoids.

5. Conclusions

Research in the Manonga Valley has contributed significantly to an improved understanding of the taxonomic diversity, evolutionary history, paleoecology, and zoogeography of faunas from the late Neogene of East Africa. The region also has the potential to yield important new finds that could document the earliest stages of human evolution, and help to explain the ecological and biogeographic factors associated with the initial differentiation of hominids. The main findings and conclusions of the Manonga Valley project that relate to issues of hominid origins can be summarized as follows:

1. The sequence of fossil-bearing sediments in the Manonga Valley, with an estimated age range of 4.0–5.5 Ma, samples a critical period of time between 4 Ma and 7 Ma that is poorly represented in sub-Saharan Africa. Paleontological collections from the Manonga Valley, therefore, contribute significant new information toward improving our limited understanding of the taxonomic diversity, evolutionary history, paleobiology, and paleoecology of fossil mammals in East Africa during the late Miocene and early Pliocene.
2. The location of the Manonga Valley at the southern end of the Eastern Rift valley extends the geographic range of faunas from this time period. Contemporary faunas are known from North Africa, the Eastern Rift in Kenya and Ethiopia, the Western Rift in Uganda and Zaire, and South Africa. Detailed comparisons of these faunas might allow us to recognize possible provincial or ecological differences in Africa at this time.
3. Faunas from the late Miocene and early Pliocene of Africa are especially significant because this is a period of time that witnesses a significant change in the composition of the mammalian community. Faunas dated between 5 Ma and 7 Ma are characterized by the first appearance of a number of groups of mammals of "modern aspect." Hominids also apparently make their initial appearance at this time. As a consequence, detailed

study of the dynamics of this major faunal change could provide important clues to understanding the factors underlying the differentiation and subsequent divergence of the hominid lineage from the last common ancestor of African apes and humans.

4. Given the paucity of hominid finds from the late Miocene and early Pliocene of Africa, the Manonga Valley has the potential to yield new finds that could contribute significantly to an improved understanding of their anatomy and paleobiology. Even if hominids are not found in the Manonga Valley, study of the faunas might eventually allow us to gain valuable insight into the ecological and biogeographic factors that led to the initial differentiation of hominids in Africa.
5. A number of possible explanations have been given for why hominids do not occur in the fossil record of the Manonga Valley: (a) The geographic distribution of hominids did not extend south as far as Tanzania at this time; (b) the geographical range of hominids extended into northern Tanzania, but ecological factors excluded hominids from occupying the Manonga basin; and (c) hominids were an extremely rare component of the fauna throughout this time period, and the chances of finding their remains in the fossil record are very remote.
6. Even if fossil hominoids are recovered from the Manonga Valley at a later date, it may be difficult to identify them as members of the hominid clade. Isolated teeth and jaw fragments offer relatively few characteristics that can be used to distinguish early hominids from later Miocene Eurasian hominoids, or from the inferred primitive morphotype for African hominoids. Relatively complete cranial and postcranial remains will undoubtedly be required to establish the affinities of purported hominids from the late Miocene of Africa, but given the paucity of finds currently known from this time period, this may be an overly optimistic expectation.

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