

## Chapter 4

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

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## 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 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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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<sup>2</sup>, 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

Site	Mammals		Reptiles	Fish	Other <sup>a</sup>	Total
	Identifiable	Indeterminate				
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

<sup>a</sup> 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 <sup>a</sup>	Frequency <sup>b</sup>	MNI <sup>c</sup>	Recovery rate <sup>d</sup>
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

<sup>a</sup> Number of individual specimens.

<sup>b</sup> The number of elements expected in a single individual.

<sup>c</sup> Minimum number of individuals.

<sup>d</sup> 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 <sup>a</sup>	Frequency <sup>b</sup>	MNI <sup>c</sup>	Recovery rate <sup>d</sup>
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

<sup>a</sup> Number of individual specimens.

<sup>b</sup> The number of elements expected in a single individual.

<sup>c</sup> Minimum number of individuals.

<sup>d</sup> 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 <sup>a</sup>	Element	Recovery rate <sup>a</sup>
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

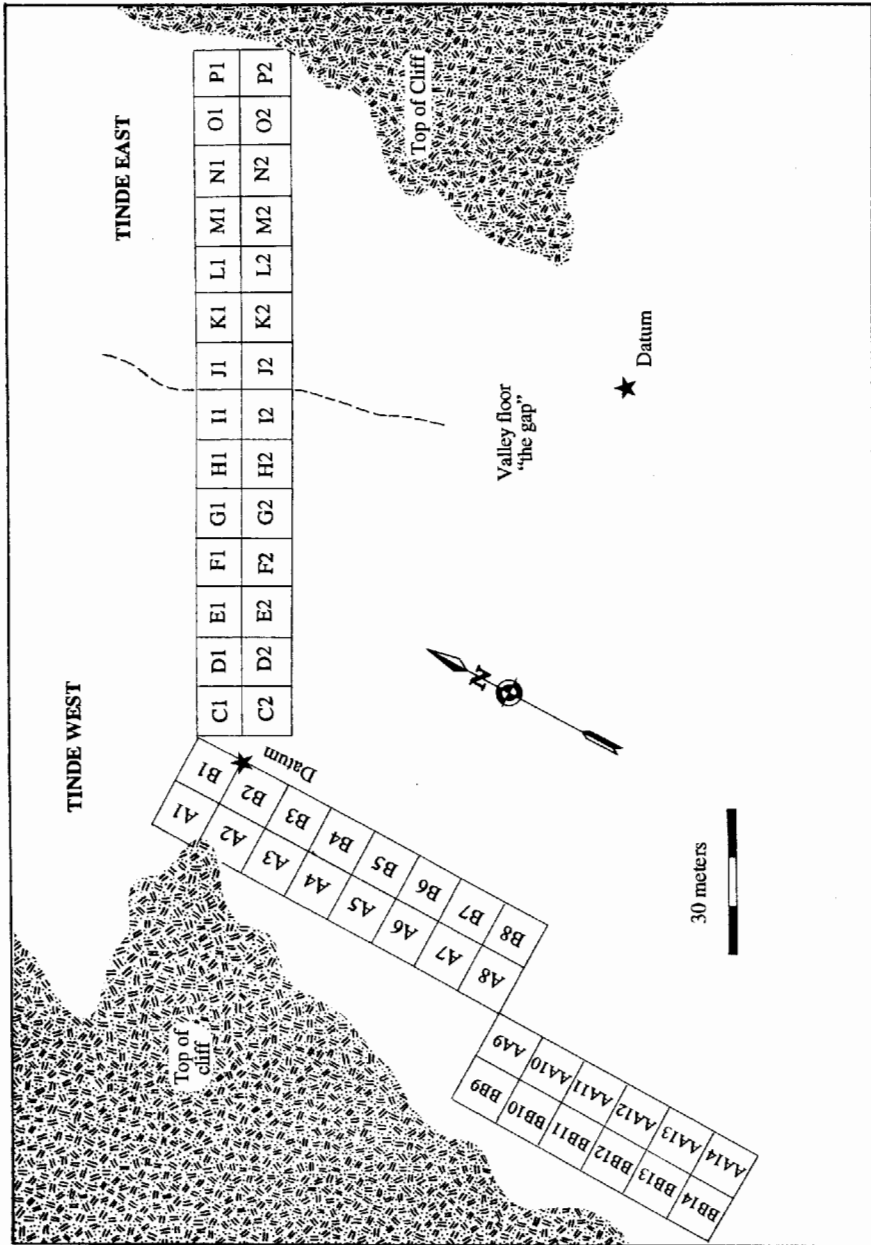
<sup>a</sup> The recovery rate represents the actual number of recovered elements expressed as a percentage of the expected number of elements for the highest minimum number of individuals (MNI). Only those elements with a recovery rate greater than 15% are included here. For a full listing see Tables 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  $10 \times 10$  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  $3.26/\text{m}^2$ , with densities ranging from  $0.36/\text{m}^2$  to  $11.33/\text{m}^2$ . 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

Square	Fish		Reptiles		Mammals		
	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)

Square	Fish	Reptiles			Mammals		
	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

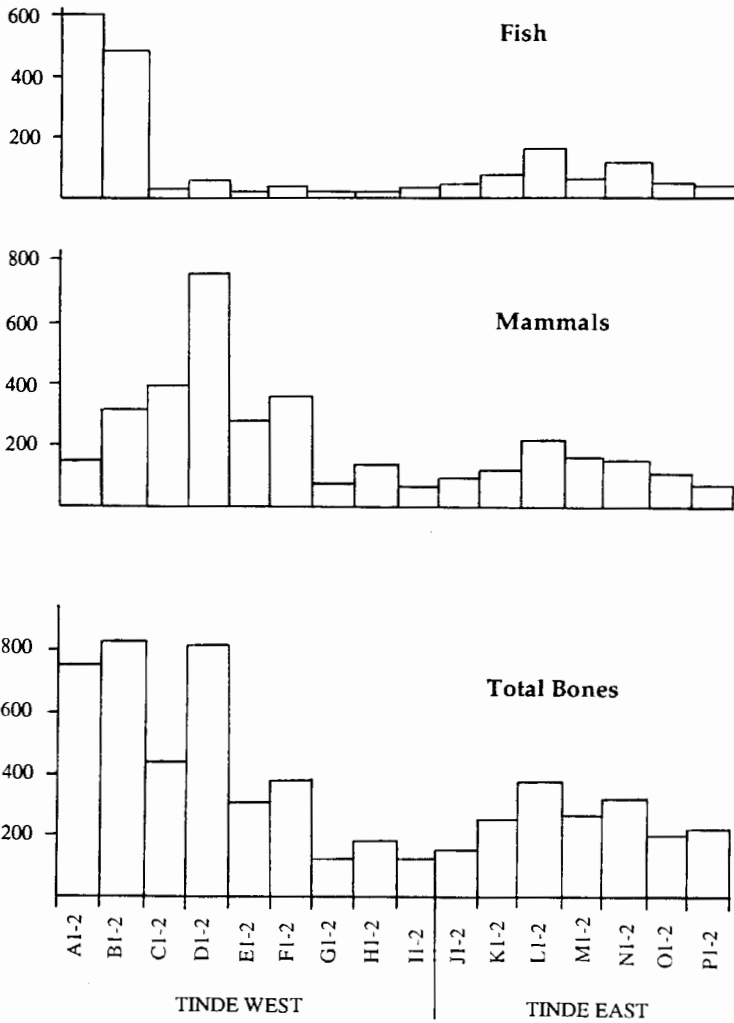


FIGURE 3. Histogram showing the frequency and distribution of bones across the gap at Tinde, based on the results of the controlled surface collection. The vertical axis represents the number of individual bones collected. The horizontal axis represents the transect squares depicted in Fig. 2.

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

Squares	Fish			Mammals		
	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. *subdolos* 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	<i>Kobus aff. subdolus</i> <i>?Tragelaphus sp.</i> <i>Damalacra sp.</i>
Giraffidae	<i>Giraffa sp.</i> <i>?Sivatherium sp.</i>
Suidae	<i>Nyanzachoerus kanamensis</i>
Hippopotamidae	<i>Hexaprotodon harvardi</i> <i>Hexaprotodon, small species</i>
Perissodactyla	
Equidae	<i>Eurygnathohippus sp.</i>
Proboscidea	
Elephantidae	indet.
Carnivora	
Viverridae	indet.
Aves	indet.
Reptilia	
Chelonia	
Trionychidae	indet.
Pelomedusidae	indet.
Crocodylia	
Crocodylidae	<i>Crocodylus sp.</i>
Osteichthyes	
Siluriformes	
Clariidae	<i>Clarias sp.</i>
Dipnoi	
Protopteridae	<i>Protopterus sp.</i>

**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	Kilolele 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<sup>2</sup>, 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	<i>Kobus aff. subdolus</i> <i>Praedamalis</i> sp. <i>Damalacra</i> sp. Alcelaphini, larger species Alcelaphini, smaller species <i>Aepyceros</i> sp.
Giraffidae	<i>?Sivatherium</i> sp.
Suidae	<i>Nyanzachoerus kanamensis</i>
Hippopotamidae	<i>Hexaprotodon harvardi</i>
Perissodactyla	
Equidae	<i>Eurygnathohippus</i> aff. <i>hasumense</i>
Rhinocerotidae	<i>Ceratotherium praecox</i> .
Proboscidea	
Gomphotheriidae	<i>Anancus</i> sp.
Elephantidae	<i>Loxodonta</i> cf. <i>exoptata</i> <i>Elephas ekorensis</i>
Primates	
Cercopithecidae	indet.
Reptilia	
Chelonia	
Trionychidae	indet.
Pelomedusidae	indet.
Crocodylia	
Crocodylidae	<i>Crocodylus</i> sp.
Osteichthyes	
Siluriformes	
Clariidae	<i>Clarias</i> sp.
Dipnoi	
Protopteridae	<i>Protopterus</i> sp.
Mollusca	
Bivalvia	
Mutelidae	<i>Spathopsis wahlbergi</i>

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

**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	<i>Crocodylus</i> sp.
Osteichthyes	
Siluriformes	
non-clariid	indet.
Clariidae	<i>Clarias</i> spp.
Perciformes	
Cichlidae	indet.
Characiformes	
Characidae	<i>Hydrocynus</i> sp. <i>Alestes</i> spp.
Dipnoi	
Protopteridae	<i>Protopterus</i>
Mollusca	
Gastropoda	
Viviparidae	<i>Bellamyia</i> aff. <i>capillata</i>
Ampullariidae	<i>Pila ovata</i> <i>Lanistes ovum</i>
Thiaridae	<i>Cleopatra</i> aff. <i>ferruginea</i>
Bivalvia	
Mutelidae	<i>Spathopsis wahlbergi</i> <i>Mutela dubia</i>

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 an 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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