

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			
? <i>Tragelaphus</i> sp.	X	X	
<i>Kobus</i> aff. <i>porrecticornis</i>	X		
<i>Kobus</i> aff. <i>subdolos</i>		X	X
<i>Praedamalis</i> sp.	X		X
<i>Damalacra</i> sp.	X	X	X
<i>Aepyceros</i> sp.			X
Alcelaphini, larger sp.			X
Alcelaphini, smaller sp.	X		X
Giraffidae			
<i>Giraffa</i> sp.		X	
? <i>Sivatherium</i> sp.		X	X
Hippopotamidae			
<i>Hexaprotodon harvardi</i>	X	X	X
<i>Hexaprotodon</i> sp.		X	
Suidae			
<i>Nyanzachoerus kanamensis</i>	X	X	X
Equidae			
<i>Eurygnathohippus</i> cf. "sitifense"	X		
<i>Eurygnathohippus</i> cf. <i>turkanense</i>	X		
<i>Eurygnathohippus</i> sp.		X	
<i>Eurygnathohippus</i> aff. <i>hasumense</i>			X
Rhinocerotidae			
<i>Ceratotherium praecox</i>			X
Deinotheriidae			
<i>Deinotherium bozasi</i>		X	
Gomphotheriidae			
<i>Anancus kenyensis</i>	X		
<i>Anancus</i> sp.			X
Elephantidae			
cf. <i>Stegotetrabelodon</i>	X		
<i>Primelephas gomphotheroides</i>	X		
Elephantinae, gen. et sp. indet.		X	
<i>Loxodonta</i> cf. <i>exoptata</i>			X
<i>Elephas ekorensis</i>			X
Felidae			
<i>Machairodus</i> sp.	X		
Viverridae			
gen. et sp. indet.		X	
Mustelidae			
gen. et sp. indet.	X		
Cercopithecidae			
gen. et sp. indet.			X
Thryonomyidae			
<i>Thryonomys</i> sp.	X		
Muridae			
<i>Saccostomus major</i>	X		
<i>Tectonoms africanus</i>	X		
<i>Saidomys parvus</i>	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 (\geq 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 M₃ 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	<i>Nyanzachoerus devauxi</i>	<i>Nyanzachoerus syrticus</i>	<i>Nyanzachoerus kanamensis</i>	<i>Nyanzachoerus jaegeri</i>	<i>Notochoerus euillus</i>	<i>Kolpochoerus afarensis</i>	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				II (3.9–5.0 Ma)
Kuseralee Mb			X				
Langebaanweg (QSM)			X				
Lothagam, Apak Mb			X	X			
Langebaanweg (PPM)			X	X			III (2.8–3.9 Ma)
Tabarin			X	X			
Aramis Mb			X	X			
Kanapoi			X	X			
Mursi Fm			X	X		?	
Laetoli (upper Laetoli)					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 P¹ 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 P¹ 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 dP² (WM 1238/92) from Kiloleli 2 are clearly identifiable as *Ceratotherium praecox*. The dP² 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 germanoaffricanum*, 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 cercopithecoid 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_1 s, and several mandibular fragments from Shoshamagai 2 can be attributed to a species of machairodontine 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 deinotherere 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			
<i>Protopterus</i> sp.	X	X	X
Characiformes			
Characidae			
<i>Hydrocynus</i> sp.	X		
<i>Alestes</i> aff. <i>A. stuhlmanni</i>	X		
<i>Alestes</i> aff. <i>A. dentex</i>	X		
<i>Alestes</i> cf. <i>A. nurse/A. affinis</i>	X		
<i>Alestes</i> sp.	X	X	
<i>Sindacharax</i> sp.		X	
Siluriformes			
Clariidae			
<i>Clarias</i> sp.	X	X	X
nonclariid	X	X	
Perciformes			
Centropomidae			
<i>Lates</i> sp.		X	X?
Cichlidae			
indet.	X	X	
Reptilia			
Chelonia			
Trionychidae			
indet.	X	X	X
Pelomedusidae			
indet.	X	X	X
Crocodylia			
Crocodylidae			
<i>Crocodylus</i> sp.	X	X	X
Aves			
indet.	X	X	
Gastropoda			
Viviparidae			
<i>Bellamyia</i> aff. <i>capillata</i>	X	X	X
Ampullariidae			
<i>Pila ovata</i>			X
<i>Lanistes ovum</i>	X	X	X
Bithyniidae			
<i>Gabbiella</i> aff. <i>humerosa</i>		X	X
Thiaridae			
<i>Melanooides</i> aff. <i>anomala</i>		X	
<i>Cleopatra</i> aff. <i>ferruginea</i>	X	X	X
Bivalvia			
Mutelidae			
<i>Spathopsis wahlbergi</i>	X		X
<i>Mutela dubia</i>	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
<i>Crocodylus niloticus</i>	231	9.5	12.1
<i>Crocodylus palustris</i>	70	7.1	28.6
<i>Mecistops cataphractus</i>	146	32.2	4.1
<i>Tomistoma schlegeli</i>	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 orbis*, *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

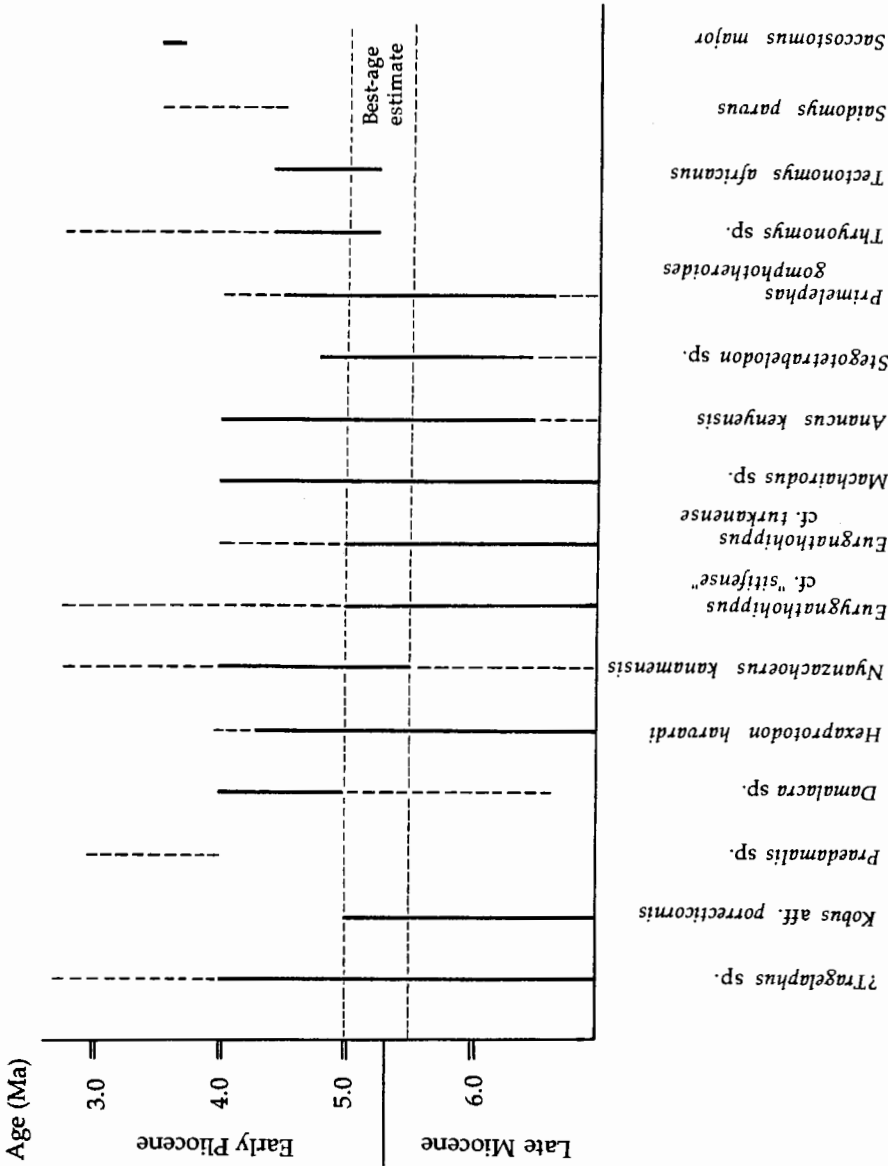


FIGURE 1. Chart showing the temporal ranges of mammalian taxa from the Ibole Member. Solid vertical lines represent that part of the temporal range of the taxon that is most consistent with the material from the Ibole Member. The broken vertical lines represent the full temporal range of the taxon. The best-age estimate is obtained by determining the time period in which maximal overlap occurs between the constituent taxa.

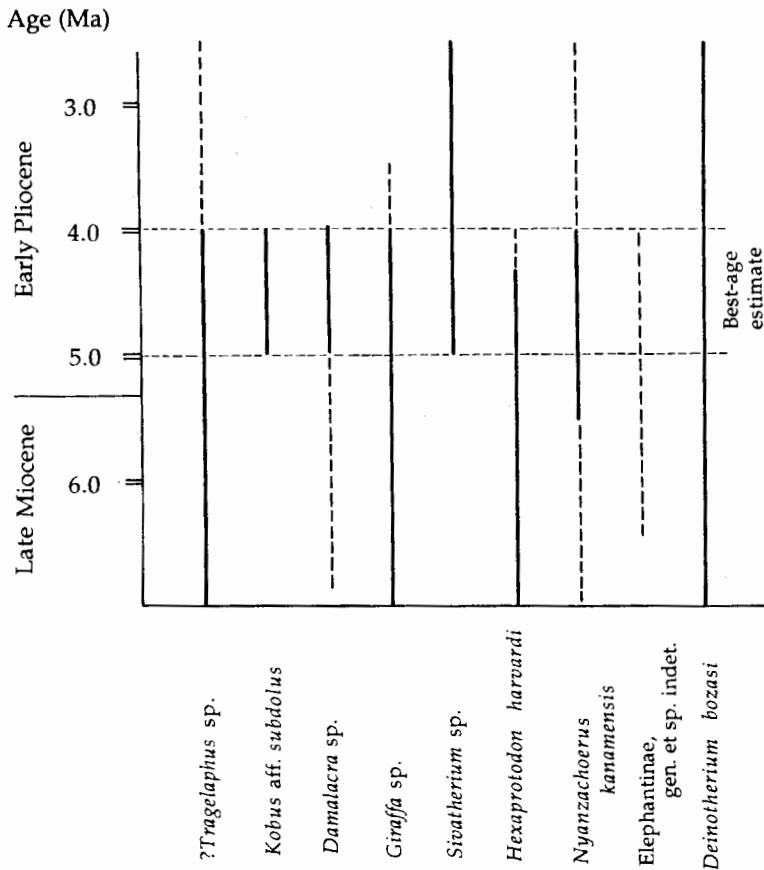


FIGURE 2. Chart showing the temporal ranges of mammalian taxa from the Tinde Member. Solid vertical lines represent that part of the temporal range of the taxon that is most consistent with the material from the Tinde Member. The broken vertical lines represent the full temporal range of the taxon. The 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

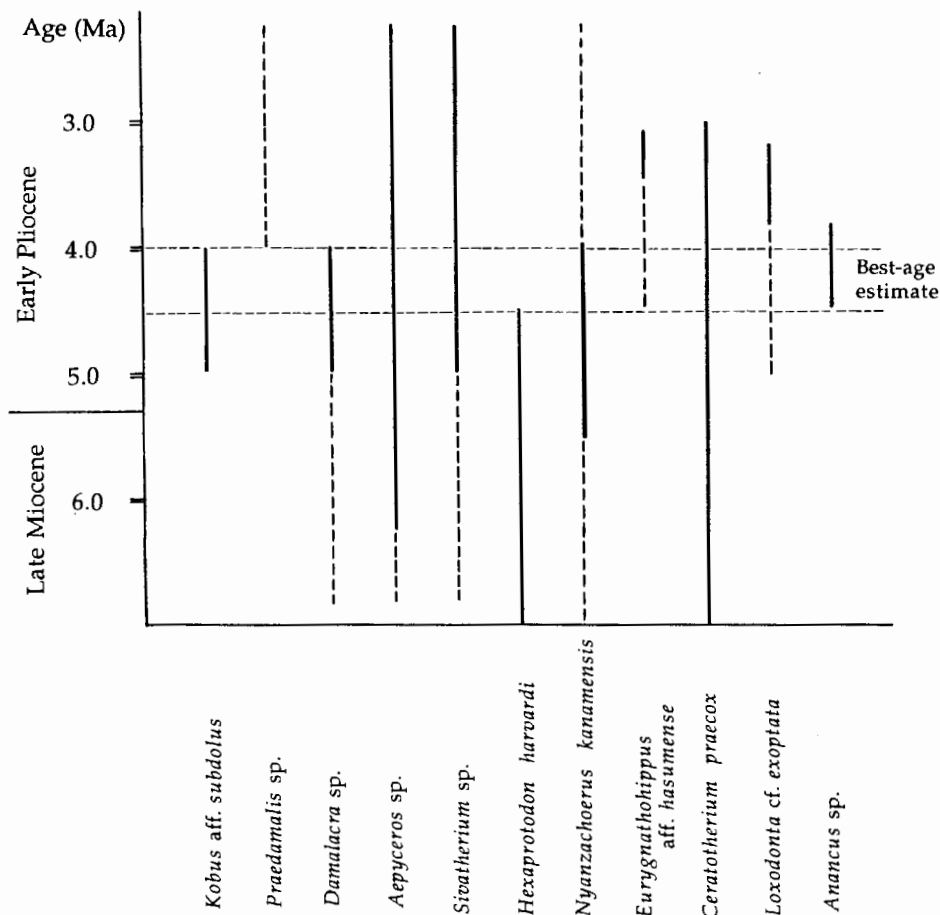


FIGURE 3. Chart showing the temporal ranges of mammalian taxa from the Kiloleli Member. Solid vertical lines represent that part of the temporal range of the taxon that is most consistent with the material from the Kiloleli Member. The broken vertical lines represent the full temporal range of the taxon. 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	<i>Connochaetes taurinus</i> , <i>Equus burchelli</i>
Beredi South 2	<i>Equus burchelli</i> , <i>Phacochoerus africanus</i> , Bovidae
Inolelo 1	<i>Phacochoerus africanus</i> , <i>Damaliscus dorcas</i> , <i>Equus burchelli</i> , <i>Connochaetes taurinus</i> , ? <i>Taurotragus oryx</i>
Inolelo 2	<i>Loxodonta africana</i> , <i>Phacochoerus africanus</i> , <i>Equus burchelli</i> , Alcelaphini
Inolelo 3	<i>Phacochoerus africanus</i> , <i>Equus burchelli</i> , Bovini
Ipembe	<i>Homo sapiens</i> , <i>Phacochoerus africanus</i>
Kalitu	<i>Alcelaphus buselaphus</i> , <i>Connochaetes</i> sp., <i>Phacochoerus africanus</i> , <i>Equus burchelli</i> , <i>Taurotragus oryx</i> , Alcelaphini
Kiloleli 2	<i>Phacochoerus africanus</i> , <i>Damaliscus dorcas</i> , <i>Equus burchelli</i>
Kiloleli 3	<i>Equus burchelli</i> , <i>Alcelaphus buselaphus</i>
Kiloleli 4	<i>Connochaetes taurinus</i>
Kininginila	<i>Hippopotamus amphibius</i> , <i>Equus burchelli</i> , Alcelaphini
Mwambiti 3	<i>Connochaetes taurinus</i> , <i>Equus burchelli</i>
Ngofila 2	<i>Equus burchelli</i> , <i>Phacochoerus africanus</i> , Bovidae
Nyawa	<i>Connochaetes taurinus</i> , <i>Equus burchelli</i> , <i>Phacochoerus africanus</i> , cf. <i>Megalotragus</i> sp., Alcelaphini
Shoshamagai 2	<i>Equus burchelli</i> , Bovidae
Shoshamagai Hill	<i>Syncerus caffer</i>
Tinde West	<i>Phacochoerus africanus</i>

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 M² 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	<i>Atelerix albiventris</i>	Kirungu-mifa	Kalunguyeye
Crested porcupine	<i>Hystrix sp.</i>	Nuungu	Nungu
Crawshay's hare	<i>Lepus crawshayi</i>	Lungwando kaumbu	Katiti sungura
African rabbit	<i>Poelagus marjorita</i>	Lungwando lusuga	Katita sungura
Cane rat	<i>Thryonomys sp.</i>	Ngosso	Ndezi
Anubis baboon	<i>Papio anubis</i>	Nguku	Nyani
Green monkey	<i>Cercopithecus aethiops</i>	Numbirhi	Ngedere, Tumbili
Common jackal	<i>Canis aureus</i>	Jidevwe	Mbweha
Black-backed jackal	<i>Canis mesomelas</i>	Jidevwe	Mbweha
Civet	<i>Viverra civetta</i>	Nungo	Fungo mkubwa
Common genet	<i>Genetta genetta</i>	Nirhilhi	Ngawa
Dwarf mongoose	<i>Helogale parvula</i>	Njololho	Nguchiro
Slender mongoose	<i>Herpestes sanguineus</i>	Njololho	Nguchiro
Striped hyena	<i>Hyaena hyaena</i>	Mbithi	Fisi
Spotted hyena	<i>Crocuta crocuta</i>	Mbithi	Fisi
Wild dog	<i>Lycan pictus</i>	Mhuge	Mbwa mwitu
Aardwolf	<i>Proteles cristatus</i>	Mbithi	Fisi ndogo
Lion	<i>Panthera leo</i>	Shimba	Simba
Leopard	<i>Panthera pardus</i>	Shubi, Subi	Chui
Cheetah	<i>Acinonyx jubatus</i>	Shubi mondo	Duma
Zebra	<i>Equus burchelli</i>	N'nduulu	Punda milia
Aardvark	<i>Orycteropus afer</i>	Naga	Kiliberatili
Elephant	<i>Loxodonta africana</i>	Mhulhi	Tembo
White rhinoceros	<i>Ceratotherium simum</i>	Mhela	Kifaru
Hippopotamus	<i>Hippopotamus amphibius</i>	Nguwbo	Kiboko
Warthog	<i>Phacochoerus aethiopicus</i>	Nngiri	Nngiri
Giraffe	<i>Giraffa camelopardalis</i>	Nhiga	Twiga
Giant eland	<i>Taurotragus derbianus</i>	Mboku	Pofu
Greater kudu	<i>Tragelaphus strepsiceros</i>	Nandala	Tandala mkubwa
Brindled gnu	<i>Connochaetes taurinus</i>	Mbushi	Nyumbu ya montu
Thomson's gazelle	<i>Gazella thomsoni</i>	Lhala	Swala tomi
Grant's gazelle	<i>Gazella granti</i>	Lhala	Swala granti
Impala	<i>Aepyceros melampus</i>	Mhala	Swala pala
Kirk's dik-dik	<i>Rhynchotragus kirki</i>	Subhuya	Dikidiki
Abbot's duiker	<i>Cephalophus spadix</i>	—	Minde
African buffalo	<i>Syncerus caffer</i>	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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