

Neogene Paleontology of the Manonga Valley, Tanzania

A Window into the Evolutionary
History of East Africa

Edited by

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Chapter 14

Hominid Origins

A View from the Manonga Valley

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1. Introduction

The sequence of fossil-bearing sediments in the Manonga Valley, with an estimated age range of ~4.0–5.5 Ma, samples a critical period of time (from 4 Ma to 7 Ma) that is generally poorly represented in sub-Saharan Africa. Few other paleontological sites have sediments that fall into this time range, and many of these are difficult to date, or have relatively small faunas that have not yet been the subject of detailed study. The best paleontological information for this period comes from sites in the Baringo basin and Turkana basin in Kenya, and from sites in the Middle Awash region of Ethiopia, where sizable faunas have been recovered from sediments that have been dated using radiometric techniques. The most important fossil collections are from the Mpesida Beds (6.4–7.0 Ma) and Lukeino Formation (5.6–6.2 Ma) in the Baringo basin, the upper Nawata Formation and Apak Member at Lothagam (~4.72–6.24 Ma) in the Turkana basin, and the Sagantole Formation (~3.5–4.5 Ma) and Adu-Asa Formation (~4.5–6.0 Ma) in the Middle Awash. It is important to note that these sites are limited geographi-

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cally to two relatively restricted areas within the East African Rift valley (i.e., in north-central Kenya and northeastern Ethiopia). Other significant faunas from this time period, but without absolute dates, are known from Kenya (Kanam, ~4–6 Ma; Nakali, ~7–8 Ma), the Western Rift in Uganda (Nkondo Formation ~4.5–6.5; Oluka Formation ~6.0–7.5 Ma), North Africa (Wadi Natrun, Egypt, ~4–5 Ma; Sahabi, Libya, ~5 Ma), and South Africa ('E' Quarry, Varswater Formation, Langebaanweg, ~4–5 Ma) (see Harrison and Baker, this volume, Chapter 13 for references on the dating and paleontology of these sites).

The paleontological collections from the Manonga Valley, therefore, help to contribute significant new information to improve on our currently limited appreciation of the taxonomic diversity, evolutionary history, paleobiology, and paleoecology of fossil mammals in East Africa during the late Miocene and early Pliocene. Furthermore, the location of the Manonga Valley at the southern end of the Eastern Rift valley also extends the geographic range of faunas known from this time period. The Manonga basin is located almost 600 km from the Baringo basin and about the same distance from the Western Rift. Comparisons of African faunas from this period might ultimately allow us to recognize provincial or ecological differences that existed as a result of the formation of the rift valley.

Better documentation of mammalian faunas from the late Miocene and early Pliocene of Africa is especially significant for understanding hominid origins. This time period witnesses a significant change in the composition of the mammalian fauna. Compared with earlier East African faunas from the Namurungule Formation (~8–10 Ma) and the Ngorora Formation (~9.0–12.3), which have many archaic taxa surviving from the earlier part of the Miocene, those between 5 Ma and 7 Ma are characterized by the first appearance of a number of groups of mammals of "modern aspect" (Hill *et al.*, 1985; Leakey *et al.*, 1996). Hippopotamines, giraffines, *Nyanzachoerus*, several bovid tribes (i.e., tragelaphines, alcelaphines), *Ceratotherium*, elephantids, machairodontine felids, and ursids all make their first appearance in sub-Saharan Africa at this time. Although the fossil evidence is still rather limited, it seems likely that hominids also made their initial appearance at this time. Their earliest recorded occurrence is at Lothagam and Lukeino, estimated to be 4.7–6.2 Ma in age. This is close in time to the estimated divergence dates for hominids based on molecular evidence (Weiss, 1987; Caccone and Powell, 1989; Hasegawa *et al.*, 1989; Hasegawa, 1992; Bailey *et al.*, 1992). If hominids did indeed originate at this time, then a detailed analysis of the dynamics of this major faunal change might provide important clues to understanding the factors underlying the differentiation and subsequent divergence of hominids from their last common ancestor with the African apes.

The Manonga Valley has the potential to provide important evidence that is directly or indirectly pertinent to the study of hominid origins. With so few paleontological sites sampling the critical time period between 4 Ma and 7 Ma, the Manonga Valley, with its productive fossil localities of the appropriate age, is an ideal place to look for early hominids. Moreover, given the scarcity of fossil hominids currently known from this time period, the eventual discovery of hominids in the Manonga Valley would undoubtedly contribute significantly to

our limited understanding of their anatomy and paleobiology. Even if hominids are not found, study of the Manonga Valley faunas might allow us to gain valuable insight into the ecological and biogeographical factors that led to the initial differentiation of hominids during the late Miocene of Africa.

The objective of this chapter is to present a brief critical review of some of the main issues my research in the Manonga Valley has raised that relate directly to the question of human origins. It is not intended to be a review of early hominid fossils and sites, since this has already been done in some detail elsewhere (Hill and Ward, 1988; Hill, 1994). Rather, the aim is to focus on a few key problems that emphasize just how little we actually know about the earliest hominids, and why continued research in the Manonga Valley (and at other late Neogene sites in Africa) is so important. The fact that hominid fossils have not yet been found in the Manonga Valley, with its numerous paleontologically productive sites located in close proximity to the famous hominid-bearing sites of Olduvai Gorge and Laetoli, is an interesting finding in itself. Working in the Manonga Valley has, therefore, given me a unique perspective, because it has forced me to ask different kinds of questions about early human origins. Unfortunately, I am not in a position to provide conclusive answers to any of these questions, but it is hoped that by introducing them here they will serve as a basis for stimulating further discussion and research. It is also my hope that additional researchers will take up the challenge to explore new areas in Africa that might offer valuable clues to help document and explain hominid origins.

2. What Evidence Is Available for Hominids Older Than 4 Ma?

Even though there has been a marked increase in the number of discoveries of hominid specimens from sites older than 4 Ma in recent years, there are still relatively few specimens available. The total collection comprises the following: (1) Lothagam, Kenya (~5–7 Ma)—a right mandibular fragment discovered in 1967, and two isolated teeth recovered by Meave Leakey in 1990–92 (Patterson *et al.*, 1970; Hill, 1994; Leakey *et al.*, 1996); (2) Cheboit, Lukeino Formation, Kenya (5.6–6.2 Ma)—left lower molar discovered in 1973 (Pickford, 1975; Corruccini and McHenry, 1980; McHenry and Corruccini, 1980; Kramer, 1986; Hill and Ward, 1988; Hill, 1994; Ungar *et al.*, 1994); (3) Aramis, Sagantole Formation, Middle Awash, Ethiopia (~4.3–4.5 Ma)—collection of 17 craniodental and postcranial specimens described as *Ardipithecus ramidus* (White *et al.*, 1994, 1995); (4) Tabarin, Chemeron Formation, Kenya (~4.15–5.0 Ma)—right mandibular fragment discovered in 1984 (Hill, 1985, 1994; Ward and Hill, 1987; Hill and Ward, 1988; Ferguson, 1989); (5) Chemeron Formation, Kenya (~4.2–5.0 Ma)—proximal humerus discovered in 1973 (Pickford *et al.*, 1983; Hill and Ward, 1988; Hill, 1994); (6) Kanapoi, Kenya (~3.9–4.2 Ma)—distal humerus found in 1965, and portions of a right tibia and seven craniodental specimens found in 1994 all referred to *Australopithecus anamensis* (Patterson and Howells, 1967; Leakey *et al.*, 1995).

All of the known specimens are derived from the Turkana basin, the Baringo basin, and the Middle Awash. In addition, most of the specimens are from sediments that are estimated to be 4.0–4.5 Ma, and only the isolated tooth from Lukeino and the specimens from Lothagam are likely to be appreciably older (~4.7–6.2 Ma). Possible hominoid remains (including a clavicle, a distal fibula, and a parietal fragment) have been reported from the North African early Pliocene (~5 Ma) site of Sahabi (Boaz, 1980, 1987; Boaz and Meikle, 1982). However, the purported clavicle has been identified as a rib of a dolphin (White *et al.*, 1983; White, 1987), and the other pieces are of questionable taxonomic status (Hill, 1994). Reference should also be made to the isolated upper molar from the late Miocene Ngorora Formation, discovered in 1968, which has in the past been identified as a hominid (Bishop and Chapman, 1970). However, it is quite distinctive, and, like several other isolated teeth recovered more recently from the Ngorora Formation (~12.4–12.5 Ma), it may have closer affinities with earlier Miocene catarrhines, such as *Afropithecus* (Hill and Ward, 1988; Hill, 1994).

Clearly, the hominid fossil record is exceedingly sparse before 4 Ma, and we know almost nothing about the anatomy and paleobiology of hominids prior to 4.5 Ma. The only way in which the fossil record can be improved is by finding additional specimens from existing localities that sample this time period or, perhaps more importantly, by stepping up the search for productive new localities in unexplored regions of Africa, such as the Manonga Valley, where fossiliferous deposits of the right age are likely to be found or are known to occur.

3. Why Are There No Hominids in the Manonga Valley?

Several possible explanations can be given for why no fossil hominids have been recovered from the Manonga Valley: (1) The geographical distribution of hominids did not extend as far south as Tanzania during the late Miocene–early Pliocene; (2) the ecology of the Manonga basin was not suitable to support early hominid populations at this time because (a) hominids were restricted in their habitat preferences or (b) the ecology of the Manonga Valley was in some way different from that of hominid sites in Kenya and Ethiopia; (3) hominids were an extremely rare component of the fauna, and their remains have not yet been recovered; and (4) hominids were locally common, but (a) they did not inhabit ecosystems favoring their preservation, (b) there was a selective taphonomic bias against their remains being preserved as fossils compared with other mammals, or (c) their remains are preserved as fossils, but we have been searching in the wrong parts of the basin.

I suspect that it is a combination of several of these factors. A brief consideration of the evidence from the Manonga Valley, and from other sites of similar age in Africa, allows us to rule out some options, but there are still several remaining possibilities. A review of these is instructive for possible interpretations of the ecological and geographic distribution of early hominids.

It is a distinct possibility that hominids had a restricted geographic range during the late Miocene and early Pliocene. Their known geographic distribution prior to 4.0 Ma is limited to sites in Ethiopia and Kenya associated with the East African Rift valley (if the purported hominoids from Sahabi are excluded from consideration). Could it be that hominids originated in this region, and were then limited to a relatively restricted range until just before 3 Ma, when they appear for the first time in Chad and southern Africa? There is some evidence (at least of a negative kind) from sites in other parts of Africa dated at 4–6 Ma to support this hypothesis. In addition to the Manonga Valley, no hominids have been recovered from this time period from the Western Rift of Uganda and Zaire, North Africa (Wadi Natrun, and possibly also Sahabi), or South Africa (Langebaanweg). It could be argued that the intensity of the research effort and the quality of the preservation is much higher at sites in the Eastern Rift valley, and that this has contributed to the successful recovery of fossil hominids. There is certainly some justification for this argument. However, given the size of the faunal collections from the Manonga Valley and the Western Rift, as well as the remarkably well-preserved and meticulously collected fossils from Langebaanweg, it is difficult to accept that the absence of hominids in these particular samples is simply a matter of preservation or collecting technique.

I am more inclined to accept, at present, that early hominids may have been geographically restricted to the rift valley region in Kenya and Ethiopia during the late Miocene and early Pliocene. This seems a reasonable hypothesis given the evidence currently available. Perhaps there is something unique about the ecology of the developing rift valley that lies at the root of hominid origins. Only detailed comparisons of the geology and paleoecology between sites in the Eastern Rift valley and those from other parts of Africa will allow us to test this idea. Unfortunately, if this scenario is the correct one, the asymmetric nature of the negative evidence logically means that there is no possibility of ever effectively demonstrating it to be so, no matter how much effort we put into paleontological research at sites outside the rift valley. By contrast, a single discovery of a fossil hominid in the Manonga Valley will necessitate a major rethinking of the proposed hypothesis. However, there are several other possible ways to explain the absence of hominids in the Manonga Valley.

For instance, there might be an important ecological distinction between sites that could imply that early hominids had a particular habitat preference. At first glance this does not seem to be a likely alternative. Preliminary data on the paleoecology of sites older than 4 Ma suggest that hominids were able to occupy a diversity of habitats. At Lothagam (~4.7–6.2 Ma) the paleoecology appears to have been closely similar to that inferred for the Ibole Member in the Manonga Valley (Harrison, this volume, Chapter 4). The vegetation consisted predominantly of dense woodland with broad tracts of gallery forests located along the banks of rivers and other permanent sources of water (Leakey *et al.*, 1996). Similarly, the ecology of Aramis in the Sagantole Formation of the Middle Awash (4.3–4.5 Ma) has also been reconstructed as closed woodland, although the rarity of aquatic elements in the fauna may indicate somewhat drier conditions than those at Lothagam (WoldeGabriel *et al.*, 1994). At the site of Kanapoi (3.9–4.2

Ma) dry, possibly open woodland or bushland conditions are indicated by the fauna, although the presence of a large river system may have supported a gallery forest along its flanks (Leakey *et al.*, 1995). Evidence from Laetoli, at a slightly younger date (3.5–3.8 Ma), suggests a predominantly dry grassland and open woodland setting, possibly with more densely wooded areas nearby (Harris, 1987; Andrews, 1989). We can draw two main conclusions from these data. First, early hominids appear to have been rather eclectic in their habitat preference; they are found at sites with ecologies that are inferred to range from moist woodland or forest settings to rather dry grasslands and open woodlands. Second, the paleoecology at sites such as Lothagam or Aramis is basically similar to that inferred from the Manonga Valley, with no indication of a profound ecological distinction that would serve to exclude hominids.

Although we can probably rule out the possibility that major ecological differences existed between the Manonga Valley and contemporary hominid-bearing sites in Kenya and Ethiopia, it is not possible to establish whether or not more subtle environmental or vegetational differences may have been influential in determining hominid distribution patterns. For example, hominids may have been constrained by the geographic distribution of particular plant species that were an important component of their diets. If this is the case, it will be exceedingly difficult to tease this out using paleontological evidence. However, some clues might be gained from the comparative study of other taxa from these sites. Some importance might be attributed to the observation that cercopithecids are found commonly at sites in association with early hominids, while they tend to be much rarer elements of the fauna at other sites. At Aramis, for example, monkeys are remarkably abundant, and they compose over 30% of the vertebrate fauna from the site (WoldeGabriel *et al.*, 1994). Cercopithecids are also quite common at Lothagam, Lukeino, Kanapoi, and Laetoli (Leakey and Delson, 1987; Hill *et al.*, 1985, 1992; Leakey *et al.*, 1995). They also occur at the early Pliocene sites of Wadi Natrun and Sahabi in North Africa, but are relatively uncommon components of these faunas (Szalay and Delson, 1979; Boaz and Meikle, 1982). The late Miocene site of Menacer (= Marceau) in Algeria is exceptional, however, in that the fauna (without hominids) is dominated by cercopithecids (Szalay and Delson, 1979; Thomas and Pether, 1986). By contrast, six isolated teeth represent the total complement of cercopithecids from Langebaanweg, the Manonga Valley, and from late Miocene–early Pliocene sites in the Western Rift of Uganda and Zaire (Hooijer, 1963; Senut, 1994; Grine and Hensley, 1981; Harrison and Baker, this volume, Chapter 13). The correlation between the relative abundance of cercopithecids and the occurrence of hominids certainly suggests that ecological or environmental factors are responsible for the association. It may be significant, in this regard, that cercopithecids become much more abundant and taxonomically diverse in both South and East Africa from the mid-Pliocene onwards, just at the time when the hominid fossil record is also beginning to pick up pace (Leakey *et al.*, 1996).

Another important factor that could account for the apparent absence of fossil hominids in the Manonga Valley is that they may have been very rare elements in the East African faunal community throughout the late Miocene and early

Pliocene. This is confirmed by the paleontological evidence, and is especially noticeable for sites older than 4.5 Ma. Even at Lothagam, where an intensive program of fossil collecting has been implemented in recent years, few hominid specimens have been recovered compared to the abundance and diversity of other large mammals (Leakey *et al.*, 1996). If hominids were very rare elements of the fauna during the later Neogene (they represent less than 0.3% of all large mammals at Lothagam, but combining data from all sites of this age in Africa, hominids constitute less than 0.01%), then on the grounds of probability alone, we might expect them to be missing from the fossil record, even at sites within their geographic and temporal range. Although the rarity of hominids from this time period makes the task of searching for them an extremely frustrating business, it also implies that early hominids probably occupied a very specialized niche. Research on the relative abundance and community structure of late Miocene mammals in Africa, using comparative data from modern faunas, could well prove fruitful for reconstructing the ecology of early hominids.

We may yet discover the remains of fossil hominids in the Manonga Valley, and if we do, these are most likely to come from previously established sites. Since 1990, WMPE (Wembere–Manonga Paleontological Expedition) has systematically prospected most areas in the center of the basin, and we are confident that we have now identified most of the productive localities. Perhaps the most promising sites for future research are those at Shoshamagai and Inolelo. These sites have produced well-preserved fossils, including partial skeletons, from the oldest fossiliferous beds in the Manonga Valley (~5.0–5.5 Ma), and we continue to add new species to the faunal list each season.

In conclusion, the absence of hominids from the fossil record in the Manonga Valley can be explained as a consequence of the fact that either hominids are very rare components of the East African fauna during the late Miocene and early Pliocene, or hominids were geographically restricted to a region of the rift valley in Kenya and Ethiopia at this time, and their range did not extend far enough south to encompass the Manonga Valley. Either way, this has important implications for interpretations of the ecology and zoogeography of the earliest hominids, and further research is needed on the detailed community structure and distribution of African faunas from the later Neogene.

4. How Will We Recognize a Hominid if We Find One?

A more mundane, but no less important, consideration of our research in the Manonga Valley is the problem of how to recognize a hominid if we find one. This is not as easy as it might seem. Many of the craniodental features previously employed as characteristics of hominids, such as a well-developed metaconid on P₃, a simple occlusal pattern on the cheek teeth, thickened enamel on the molars, and a relatively shallow and robust mandible, are also typical of many late Miocene hominoids from Eurasia, including *Griphopithecus*, *Graecopithecus*, and *Sivapithecus*, and these may be inferred to represent primitive features of great apes and humans (see Andrews, 1995). There appear to be few

derived craniodental characters that serve to distinguish early hominids. The development of an incisiform canine of reduced size appears to be the most significant specialization shared by all hominids. If only isolated teeth and jaw fragments of early hominids are found it may be difficult to establish their affinities. For this reason, attribution of the specimens from Lukeino and Lothagam has proved problematic (Kramer, 1986; Hill and Ward, 1988; Ungar *et al.*, 1994; Hill *et al.*, 1992; Hill, 1994; Leakey *et al.*, 1996), and their hominid status might best be considered provisional. All that can be stated with certainty is that they are hominoids with relatively thick-enameled molars. It should be noted, in this regard, that thick-enameled hominoids from Africa have been traditionally recognized as hominids, while those from Eurasia are just apes. However, unless relatively complete cranial or postcranial remains are recovered it may be difficult to tell whether we are truly dealing with a hominid or a more conservative member of the clade comprising all of the African hominoids.

5. Conclusions

Research in the Manonga Valley has contributed significantly to an improved understanding of the taxonomic diversity, evolutionary history, paleoecology, and zoogeography of faunas from the late Neogene of East Africa. The region also has the potential to yield important new finds that could document the earliest stages of human evolution, and help to explain the ecological and biogeographic factors associated with the initial differentiation of hominids. The main findings and conclusions of the Manonga Valley project that relate to issues of hominid origins can be summarized as follows:

1. The sequence of fossil-bearing sediments in the Manonga Valley, with an estimated age range of 4.0–5.5 Ma, samples a critical period of time between 4 Ma and 7 Ma that is poorly represented in sub-Saharan Africa. Paleontological collections from the Manonga Valley, therefore, contribute significant new information toward improving our limited understanding of the taxonomic diversity, evolutionary history, paleobiology, and paleoecology of fossil mammals in East Africa during the late Miocene and early Pliocene.
2. The location of the Manonga Valley at the southern end of the Eastern Rift valley extends the geographic range of faunas from this time period. Contemporary faunas are known from North Africa, the Eastern Rift in Kenya and Ethiopia, the Western Rift in Uganda and Zaire, and South Africa. Detailed comparisons of these faunas might allow us to recognize possible provincial or ecological differences in Africa at this time.
3. Faunas from the late Miocene and early Pliocene of Africa are especially significant because this is a period of time that witnesses a significant change in the composition of the mammalian community. Faunas dated between 5 Ma and 7 Ma are characterized by the first appearance of a number of groups of mammals of “modern aspect.” Hominids also apparently make their initial appearance at this time. As a consequence, detailed

study of the dynamics of this major faunal change could provide important clues to understanding the factors underlying the differentiation and subsequent divergence of the hominid lineage from the last common ancestor of African apes and humans.

4. Given the paucity of hominid finds from the late Miocene and early Pliocene of Africa, the Manonga Valley has the potential to yield new finds that could contribute significantly to an improved understanding of their anatomy and paleobiology. Even if hominids are not found in the Manonga Valley, study of the faunas might eventually allow us to gain valuable insight into the ecological and biogeographic factors that led to the initial differentiation of hominids in Africa.
5. A number of possible explanations have been given for why hominids do not occur in the fossil record of the Manonga Valley: (a) The geographic distribution of hominids did not extend south as far as Tanzania at this time; (b) the geographical range of hominids extended into northern Tanzania, but ecological factors excluded hominids from occupying the Manonga basin; and (c) hominids were an extremely rare component of the fauna throughout this time period, and the chances of finding their remains in the fossil record are very remote.
6. Even if fossil hominoids are recovered from the Manonga Valley at a later date, it may be difficult to identify them as members of the hominid clade. Isolated teeth and jaw fragments offer relatively few characteristics that can be used to distinguish early hominids from later Miocene Eurasian hominoids, or from the inferred primitive morphotype for African hominoids. Relatively complete cranial and postcranial remains will undoubtedly be required to establish the affinities of purported hominids from the late Miocene of Africa, but given the paucity of finds currently known from this time period, this may be an overly optimistic expectation.

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