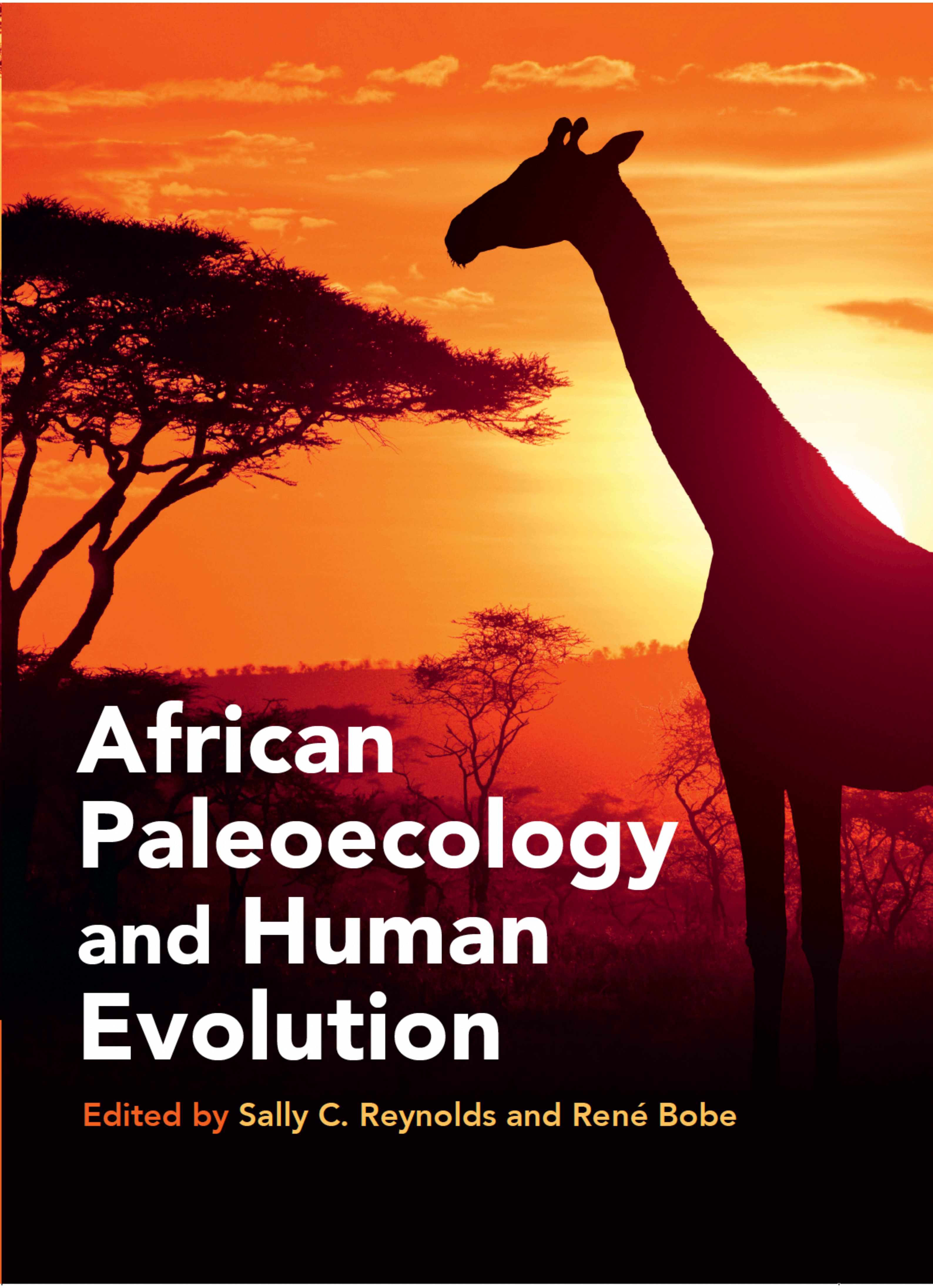

African Paleoecology and Human Evolution

Edited by Sally C. Reynolds and René Bobe

African Paleoecology and Human Evolution

Humans evolved in the dynamic landscapes of Africa under conditions of pronounced climatic, geological, and environmental change during the past 7 million years. This book brings together detailed records of the paleontological and archeological sites in Africa that provide the basic evidence for understanding the environments in which we evolved. Chapters cover specific sites, with comprehensive accounts of their geology, paleontology, paleobotany, and their ecological significance for our evolution. Other chapters provide important regional syntheses of past ecological conditions. This book is unique in merging a broad geographic scope (all of Africa) and deep time framework (the past 7 million years) in discussing the geological context and paleontological records of our evolution and that of organisms that evolved alongside our ancestors. It will offer important insights to anyone interested in human evolution, including researchers and graduate students in paleontology, archeology, anthropology, and geology.

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Context and Environments of the Lower Pleistocene Hominins of Peninj, Tanzania

Denis Geraads, Ignacio de la Torre, and Christiane Denys

History of Research

In the 1880s, Gustav Fischer was the first European to see the Oldoinyo Lengai volcano (Dawson, 2008) and, with Joseph Thomson, to visit Lake Natron (Gregory, 1921). The first systematic geological studies in the area were carried out by Carl Uhlig, who in 1904 surveyed the Manyara–Natron fault and noted the asymmetry of this sector of the rift (Dawson, 2008). Guest (1953) mapped and studied the volcanics of Lake Natron, and Baker (1963) compared the lacustrine beds of lakes Magadi and Natron. However, it was only in 1959 when Mary Leakey (1984: 124) drove across the area and realized the paleoanthropological potential of the area.

The Leakeys confirmed by aerial reconnaissance in 1963 the interest of West Natron, and in 1964 a field expedition in the area was led by Glynn Isaac and Richard Leakey (Isaac, 1965). The only hominin remain so far discovered in the area belongs to this very first expedition in 1964, when a mandible of *Paranthropus boisei* was discovered in Plio-Pleistocene sediments of the Peninj river (Leakey and Leakey, 1964). Isaac (1965) mapped systematically the West Natron sediments, and documented the existence in Pleistocene deposits of vertebrate remains and Acheulean sites. Preliminary reports on the geology and archeology of Peninj (Isaac, 1965, 1967) were followed by the first radiometric dating of the sequence (Isaac and Curtis, 1974), which situated the Peninj assemblages among the earliest Acheulean sites worldwide.

Fieldwork at Peninj resumed in September 1982, when G. Isaac, A. Mturi and M. Taieb co-directed a new field project, with archeological, geological, and paleontological components (Figure 31.1). The untimely death of G. Isaac in 1985 prevented publication of his results, but a detailed study of the sedimentology, geochemistry, and other aspects of the Lake Natron basin were published by Taieb and Fritz (1987). The paleontological field work was conducted by E. Chacha, D. Geraads, and B. Hanson, who collected a number of large mammals and other vertebrates; B. Hanson also coordinated systematic bulk sampling at some selected localities in various levels of the Humbu Formation. Systematic collecting was also undertaken at Kipalagu, an archeological site in the upper part of the Humbu Formation. Geraads (1987a) published an

Figure 31.1 G.Ll. Isaac and E. Chacha at the site of the *Paranthropus boisei* mandible in 1982.

account on the large vertebrates collected in 1963, 1964, and 1982, except the primates and suids, which were supposed to be studied at Berkeley and Dar-es-Salaam, respectively. No report on these latter groups has been published so far, so our account here for Primates and suids is based upon very sketchy notes and photos.

Geological survey and fieldwork organized by M. Taieb, N. Thouveny and P. Manega were conducted in 1984 in the Kipalagu area. During this survey, the Moinik and Humbu Formation sections were sampled for paleomagnetism (Thouveny and Taieb, 1986, 1987). In addition, washing and screening of about 450 kg of sediment from the Basal Sandy Clays below the Main Humbu Tuff and the Gabbia limestone were performed (Denys, 1987b).

A new phase of archeological research was initiated in the mid-1990s (Dominguez-Rodrigo et al., 2009b), which is still ongoing (Dominguez-Rodrigo et al., 2014b).

Geographic Setting

The Peninj area is located in the Lake Natron basin, Tanzania. Lake Natron lies on an elongated depression that runs North-South (approximately S2°05 to S2°35 and E35°–36°) as a southern continuation of the Magadi Basin in Kenya (Figure 31.2). The present lake is around 20 km wide and 50 km long, with an approximate surface area of 1039 km^2 and an average altitude of 608 m above sea level (Vincens and Casanova, 1987), and is very shallow (3–4 m depth) and saline, with a high evaporation rate (Dawson, 2008).

Lake Natron is surrounded by five volcanoes (clockwise from the north: Shombole, Gelai, Lengai, Embagai, and Sambu), one of which (Oldoinyo Lengai) is still active. Four permanent rivers flow into the lake. In the north, the Engare Nyiro feeds Lake Natron from Kenya; the Engare Sero enters into the lake from the southwest; the Peninj and the Moinik rivers flow into the lake from the west, and cut through Plio-Pleistocene sediments.

Plio-Pleistocene deposits have been reported on the western part of Lake Natron only, across the Peninj and Moinik river courses. Deposits extend from the Precambrian hills to the west to the area close to the lake shoreline. Fossiliferous sediments are particularly relevant in three areas across the Peninj river: Maritanane-Type Section, closest to Lake Natron; MHS (also known as Bayasi-South Escarpment), in the middle course of the Peninj river; and RHS (Mugulud-North Escarpment), upper in the fluvial course of the Peninj river (Figure 31.2).

Geological Context

Structurally, Lake Natron is located in the northern Tanzania section of the Gregory Rift Valley. Like other basins of the northern Tanzania Rift Valley, Lake Natron is not enclosed within opposed faults, but is a half-graben rift basin with a maximum depth of 3.3 km (Dawson, 2008) that lies between the Archaean Tanzanian craton and the reworked craton margin (Neukirchen et al., 2010). Two major episodes of faulting took place in the area of Lake Natron (Macintyre et al., 1974); the first produced the accommodation space for the deposition of the Peninj

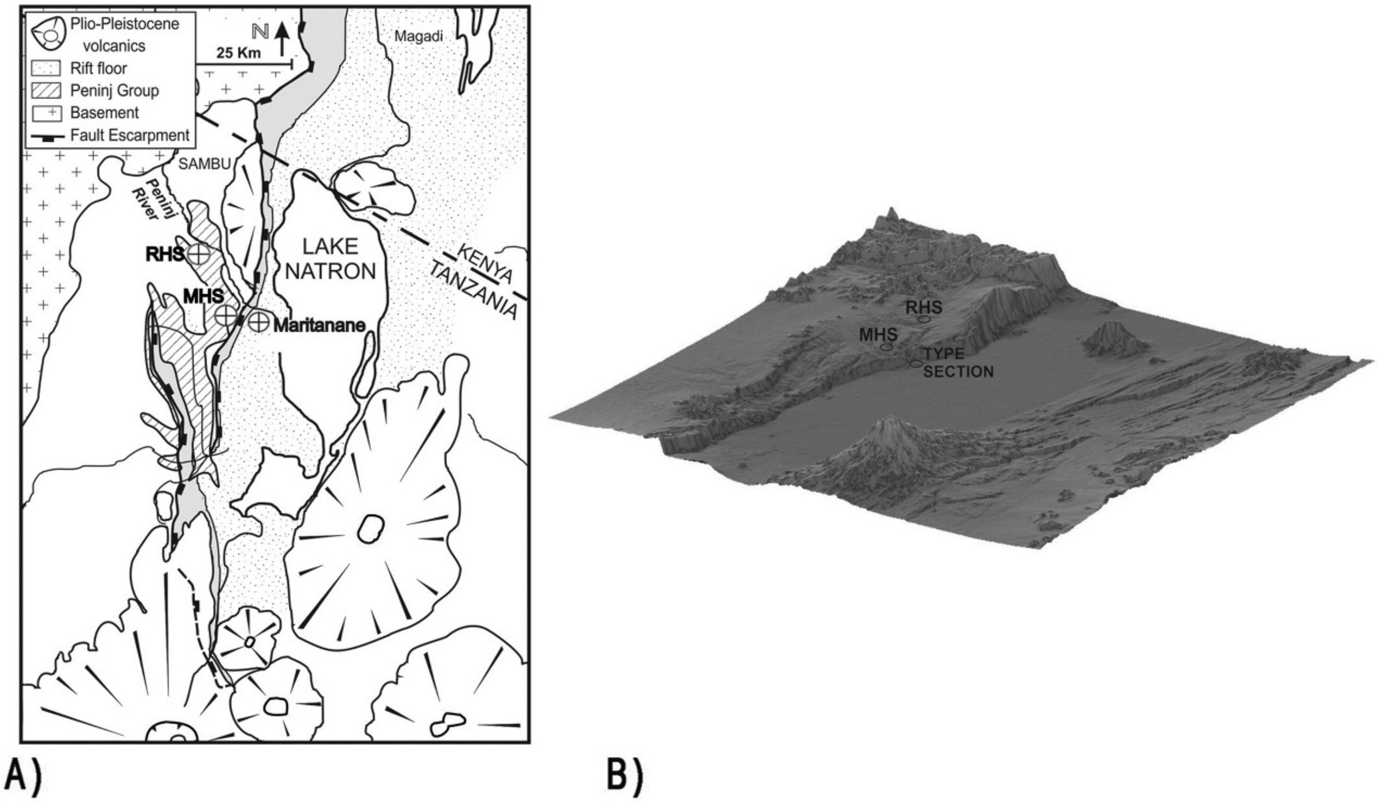

Figure 31.2 (A) Map of Lake Natron and Lake Magadi basin (adapted from Luque, in Mora et al., 2003). (B) Digital elevation model of Lake Natron, with the fossiliferous areas mentioned in the text.

Group into a shallow fault-bounded basin. The second and main faulting episode occurred between 1.2 and 1.15 million years ago, and created the escarpment of the Manjara–Natron Fault (Macintyre et al., 1974), which caused the termination of the Peninj Group sedimentation (Isaac and Curtis, 1974).

The Precambrian basement (quartzites, gneisses, and quartz micaschists) is exposed in the Sonjo fault, and is separated from Plio-Pleistocene basalts and nephelinites derived from the Sambu and Mosonik volcanoes (Isaac, 1967). These lavas were deposited in a fault-generated shallow depression and fill up most of the basin. The Sambu lavas are more than 250 m thick and are overlain by the Hajaro Beds, which contain sediments and lavas (Isaac, 1967). Between the Precambrian hills eastwards to Lake Natron, extensive clastic deposits with interbedded tuffs and lavas lie on top of the Sambu and Hajaro Beds, forming the Peninj Beds (Isaac, 1965) or Peninj Group (Isaac, 1967), which are the main fossiliferous deposits in Lake Natron.

The Peninj Group (Figure 31.3), as defined by Isaac (1967), corresponds to *ca*. 100-m thick fluvial and lacustrine sediments deposited in a wide and shallow basin, previous to the major faulting that created the escarpment of the Manjara–Natron Fault. Isaac (1967) distinguished two major units within the Peninj Group, namely the Humbu Formation and the Moinik Formation. The Humbu Formation consists of clays and sands, which vary laterally and contain basaltic tuffs and flows, and is largely deltaic. The Moinik Formation sits conformably on top of the Humbu Formation. It consists of sands, clays, and trachytic tuffs and lavas, and is largely lacustrine, although there is considerable lateral variation, with lacustrine deposits dominating in the east and south, and alluvial and deltaic facies in the northwest (Isaac, 1967).

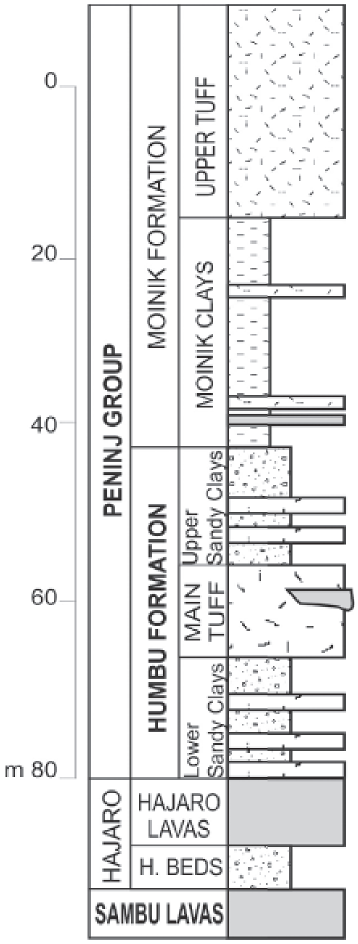

Figure 31.3 General stratigraphic column of the Peninj Group (adapted from Luque, in Mora et al., 2003).

Within the Peninj Group, it is the Humbu Formation that yields most of the archeological and paleontological evidence. Isaac (1967) subdivided the *ca*. 40-m thick Humbu Formation into three members (see also Icole et al., 1987; Luque et al., 2009). At the bottom, the Basal Sandy Clays (BSC) Member contains basaltic tephra and coarse-grained alluvial sands. This is overlaid by the Main Humbu Tuff (MHT, 1.6 m thick), which contains numerous fish and gastropod remains, and which to the south includes a lava flow (Wa-Mbugu basalt) with normal polarity. It is overlain by the Middle Zone (MZ) that contains numerous root casts, followed by the Upper Sandy Clays Member (USC; 20–30 m thick), which lies on top of the Main Humbu Tuff and caps the Humbu Formation. It contains a variety of facies, including channels, fluvial and deltaic environments, and lacustrine conditions. This upper member of the Humbu Formation is the richest in archeological terms within the Peninj Group.

Geochronology

Radiometric dating of the Peninj beds has proven difficult, and disparate – and often contradictory – results exist. The first K/Ar dates of the Peninj sequence were obtained by Isaac and Curtis (1974), who privileged an interpretation of the Moinik Formation basalt at 1.35 My, the Sambu lavas at 3.5 ± 0.46 My, and the Wa-Mbugu basalt at 1.91 My. Manega (1993) dated by $^{40}Ar/^{39}Ar$ the bottom of the Humbu Formation (1.72 My), and the base (1.33 My) and the top (1.06 My) of the Moinik Formation. More recently, Deino et al. (2006b) used $^{40}Ar/^{39}Ar$ to place the Wa-Mbugu basalt at 1.19 ± 0.03 My, and the tuff at the top of the Moinik Formation at 1.01 ± 0.03 My. Given that the Moinik Formation was deposited before the Manjara–Natron Fault offset the deposits (Isaac, 1967), and that such episode of major faulting is dated at 1.2–1.15 My (Macintyre et al., 1974), an interpretation of the whole of the Humbu Formation as older than 1.33 My (Isaac and Curtis, 1974; Manega, 1993) is probably more consistent than placing the post Wa-Mbugu units at <1.19 My (Deino et al., 2006b).

Paleomagnetism (Thouveny and Taieb, 1986, 1987) has not settled radiometric discrepancies, especially concerning the Wa-Mbugu, whose correlation with the Olduvai positive event is unlikely (see below). Tephra correlations between Olduvai Gorge and Peninj are also uncertain, as basaltic tuffs from the Humbu Formation are not comparable with those from Olduvai, and the Moinik trachytic tephras could only be correlated with Olduvai Bed IV (McHenry et al., 2011).

Archeology

The archeological record of the Peninj Group was first reported by Isaac (1965, 1967), and has been the subject of a number of monographic volumes in recent years (de la Torre and Mora, 2004; de la Torre, 2006; Dominguez-Rodrigo et al., 2009b, 2014b). Isaac (1965, 1967, 1981–1982) documented fossils and artifacts in three geographic areas across the Peninj river; in the northernmost outcrops (by the Sambu foothills), Isaac (1965, 1967) found the Acheulean site of MHS – later renamed as Mugulud (Isaac, 1981–1982) – which is stratigraphically located at the top of the Humbu Formation/bottom of the Moinik Formation (de la Torre, 2006; Dominguez-Rodrigo et al., 2009b). Further south, Isaac (1965, 1967) excavated another Acheulean site (MHS, later renamed as Bayasi), located in the USC Member of the Humbu Formation. Closer to the shoreline of Lake Natron and on the hanging wall of the Sambu Fault that offsets the Peninj Group, Isaac (1967) located the Type Section or Maritanane (Isaac, 1981–1982). Here, fossils are found in the BSC Member – e.g., the *Paranthropus boisei* mandible (Leakey and Leakey, 1964) – the Main Humbu Tuff and the USC Member of the Humbu Formation (Denys, 1987b; Geraads, 1987a; Dominguez-Rodrigo et al., 2009b). Stone tools are reported in the USC Member of the Humbu Formation and in the Moinik Formation (de la Torre and Mora, 2004; de la Torre, 2006; Dominguez-Rodrigo et al., 2009b).

In the Type Section/Maritanane, archeological occurrences are found throughout the whole of the USC Member of the Humbu Formation, albeit most is surface material (de la Torre, 2006, 2009). Fossils and artifacts are particularly clustered in the denominated ST Site Complex (Dominguez-Rodrigo et al., 2002, 2009b; Mora et al., 2003; de la Torre and Mora, 2004), where some mammal bones are cut-marked (Dominguez-Rodrigo et al., 2002, 2009b) and cores and flakes predominate (de la Torre and Mora, 2004). Although handaxes are yet to be found, hand axe flakes may exist in the ST Site Complex (de la Torre, 2006, 2009), and handaxes are found elsewhere in the Type Section. Therefore, despite the predominance of cores and flakes, it is plausible to attribute the whole of the archeological sequence of the USC Member to the Acheulean technology (de la Torre, 2009), rather than to the Oldowan (de la Torre et al., 2003).

While in the deltaic environments of the Type Section/Maritanane fossils are relatively abundant, bone preservation in the MHS and RHS areas is poorer. This contrasts with the lithic assemblages, which are much denser in the middle course of the Peninj River, and contain large concentrations of handaxes (Isaac, 1967; de la Torre, 2009). The MHS and RHS assemblages show attributes typical of the early Acheulean, i.e., the manufacture of handaxes that are often flaked unifacially and that show limited shaping and asymmetrical platforms (de la Torre et al., 2008). Albeit attributed to the same Acheulean techno-complex as the Type Section/Maritanane assemblages, the considerably higher density of artifacts and abundance of handaxes in the MHS and RHS areas when compared to the deltaic settings may be a reflection of distinct technological and subsistence activities by Lower Pleistocene humans across the varied landscapes of the Peninj river (de la Torre, 2009).

Fauna

Based on our own field notes, on bovid identifications by Gentry (in Isaac, 1967) and Gentry and Gentry (1978a, 1978b) of specimens that we have not seen, and on unpublished field notes by B. Hanson, we were able to combine a catalog of 380 identified large vertebrates, of which 353 are mammals, and within which 344 were identified by D.G. to family level or below. In addition, there are many fragments collected by bulk sampling procedures, but they have not been entered in the catalog. The micromammals were obtained after sieving the sediment with a 0.2-mm mesh in the field and in the laboratory, and sorted under the microscope. Rodents, primates, and lagomorphs were identified by C.D., while Soricomorpha and Chiroptera were identified by P.M. Butler. In total, 276 microvertebrate skeletal elements were found among which rodents and shrews predominate (NR = 255). A short account of the faunal taxonomic composition, updated from Denys (1987b) and Geraads (1987a), is given below.

Mammalia

Primates – Cercopithecidae: Cf. *Cercopithecoides kimeui*. Besides the well-known mandible of *Paranthropus boisei* (Leakey and Leakey 1964), there is no evidence of more than three primate species. An unidentified colobine, represented by a mandibular fragment with two teeth, is the same size as those present at Olduvai.

Theropithecus oswaldi. An unpublished skull, associated mandible and some limb bones, found by B. Hanson in 1982, as well as some isolated teeth, probably represent this species.

Galago sp. A single upper right canine was recovered by screening (Denys, 1987b) and may have affinities with *G. senegalensis*, also found at Olduvai Bed I and Omo Member G.

Carnivora – Viverridae: an unidentified viverrid milk tooth was identified by P.M. Butler (pers. comm.).

Hyaenidae: *Crocuta crocuta* cf. *ultra*. This is a close relative of the modern spotted hyena, relatively common in the African Plio-Pleistocene; a mandible is more primitive than the modern form in the presence of metaconid on the lower carnassial tooth.

Felidae: *Panthera pardus*. A leopard skull is one of the most valuable Peninj fossils, and probably the most complete *Panthera* specimen from the Plio-Pleistocene of East Africa.

Canidae: *Lupulella* cf. *adustus*. A single maxilla is more similar to this species than to *L. mesomelas* in its large M2, but species identification is tentative.

Rodentia – Muridae: This is by far the most abundant family. *Thallomys quadrilobatus* is the most abundant rodent. Besides isolated molars, a half anterior skull and a lower mandible show typical characters of this species found at Olduvai Bed I, Bed II, Omo F and G.

Arvicanthis primaevus is represented by isolated molars whose characters match those of specimens described from Olduvai Bed I, but differ from modern representatives.

Aethomys cf. *lavocati* is represented by a single juvenile molar very similar to the Olduvai Bed I specimens.

Mus sp. is smaller than *M. petteri* from Olduvai Bed I and Bed II and larger than the very small modern *M. minutoides*.

Nesomyidae: *Saccostomus* cf. *mearnsi* is represented by a single broken upper M1, which was further identified following taxonomic revision of the modern species as well as the Olduvai Bed I fossils (Denys, 1992).

Dendromus sp. is very small when compared to specimens of Olduvai Beds I, II and modern East African representatives. It could be very close to modern *D. mystacalis*, but the genus is in need of taxonomic revision.

Myoxidae: *Graphiurus* sp. is the oldest representative of the genus in East Africa, but based upon a single upper molar species identification remains tentative.

Soricomorpha – cf. *Suncus infinitesimus* were represented by 12 isolated teeth which agree closely in size with modern *S. infinitesimus* and with *S. leakeyi* from Olduvai. It differs from *S. leakeyi* in the absence of postentoconid ledge on lower m1–m2, but has a smaller lingual cingulum of M1. Another Soricomorph indet. was also found, but remains unidentifiable (P.M. Butler, pers. comm.).

Chiroptera – cf. Rhinolophidae: a single molar obtained from the BSC by screening may be attributed to this family of bats (P.M. Butler, pers. comm.).

Lagomorpha –*Lepus* sp. is represented by a broken lower mandible with p3–m1, an isolated M3, and upper molars obtained by screening of the sediment. They differ somewhat in size from modern *L. capensis* and Omo E, F, and G specimens attributed to this species.

Proboscidea – Elephantidae: *Elephas recki* cf. *recki*. Several more or less complete teeth are clearly identifiable as a much derived form of this common African species. They are definitely more hypsodont than those of *E. recki atavus* from Olduvai Bed I and lower Bed II, and even than those of *E. recki ileretensis* from upper Bed II (Beden, 1979).

Perissodactyla – Rhinocerotidae: *Ceratotherium simum*. A virtually complete skull, found in 1982, is more similar to the modern "white" rhino than to the East African Pliocene *C. mauritanicum* (Geraads, 1987a, 2005). There is no evidence of *Diceros*.

Equidae: "*Hipparion*" (s.l.) cf. *cornelianum*. Three-toed African equids are usually assigned to *Eurygnathohippus* (Bernor et al., 2010), but this is debatable (Eisenmann and Geraads, 2007).

Equus sp. Monodactyl equids are more common, but their remains are too fragmentary for species assignment.

Cetartiodactyla – Hippopotamidae: *Hippopotamus* cf. *gorgops*. This is the most common species in terms of number of specimens, and probably also in terms of biomass, but most fossils come from the archeological site of Kipalagu.

Suidae: *Kolpochoerus olduvaiensis*. An unpublished female complete skull is of a derived stage of this lineage (Harris and White, 1979), and a few other specimens are probably of the same species.

Metridiochoerus cf. *andrewsi*. Most suid remains probably belong to a species of *Metridiochoerus* that is intermediate in size between *M. andrewsi* and *M. compactus* (see, e.g., Cooke, 2007, figures 7–8), thus similar to *M. hopwoodi*. However, an M3 lacks the pillar isolation of this species, and precise identification must await study of the material.

Giraffidae: *Sivatherium maurusium*. A few remains, including a well-preserved snout and a horn piece, can be assigned to this large, buffalo-like giraffid.

Giraffa cf. *camelopardalis*. A few teeth and some limb-bones are of a large *Giraffa* that is more robust than the late Pliocene *G. jumae* (see Geraads et al., 2013a), and which could be an ancestor of the modern form.

Giraffidae indet. A single tarsal bone attests to the occurrence of another smaller giraffid.

Bovidae: *Tragelaphus strepsiceros grandis*. This is a large relative of the greater kudu, known from Middle Bed II to Bed IV at Olduvai.

Taurotragus sp. The eland is represented by a single molar.

Pelorovis sp. Fragmentary remains of a large buffalo cannot be identified to species.

Kobus cf. *kob*. A close relative of the common kob is present throughout the sequence.

Hippotragus gigas is represented by a single horn-core.

The alcelaphins are the most common and diverse bovids. In addition to many dental remains unidentifiable beyond tribe level, a number of more or less complete horn-cores and cranial remains can be assigned to four species: *Parmularius angusticornis*, *Megalotragus kattwinkeli*, *Connochaetes taurinus prognu*, and *Damaliscus niro*.

Aepyceros cf. *melampus*. Several impala horn-cores and dental remains cannot be separated from the living form.

Among the Antilopini, *Antidorcas* (the springbok), is the most common genus; it resembles the Olduvai form, but could be more derived toward the modern *A. marsupialis*, and can be identified as *A.* cf. *recki*.

A few *Gazella* horn-cores are similar to those of an unidentified Olduvai species.

Ndessokia (1987) also reported *Sylvicapra*, but none of the fossils that we have seen can be assigned to this genus.

Reptilia

Crocodylidae: *Crocodylus* cf. *anthropophagus*. It is likely that the two species tentatively distinguished by Geraads (1987a) are in fact one and the same. The most noticeable skull feature is the upturned postero-lateral squamosal angle, one of the characters defining *C. anthropophagus* from Olduvai (Brochu et al., 2010). Given the close chronological and geographic proximity of Olduvai and Peninj, this attribution is likely, but only a full study of the Peninj material could confirm it. The virtually parasagittal orientation of the lateral borders of the cranial table distinguishes it from *C. thorbjanarsoni* Brochu and Storrs, 2012 in the Turkana basin.

Chelonia indet. A number of tortoise shell fragments have been collected, especially from bulk sampling, but are yet to be identified; there is no evidence of a giant form.

Serpentes – Colubridae indet. Three different types were recorded (J.-C. Rage, pers. comm.), as well as other isolated vertebrae of Serpentes indet., all from the BSC sieved material.

Amphibia – Anura indet. were also represented by long bones (J.-C. Rage, pers. comm.) found in the screened material from BSC.

Pisces – Pisces indet.: a few small fish teeth were found in the BSC sieved material.

Biochronology

All of the Peninj large mammals (Table 31.1) are also present at Olduvai, and it is with this nearby site that comparisons should be made. Gentry and Gentry (1978a, 1978b) correlated the Middle Zone with Middle or Upper Bed II, and further research

Table 31.1 Distribution of the Peninj large mammals across the sequence.

	BSC	MZ	USC	Unknown
cf. *Cercopithecoides kimeui*				+
Theropithecus oswaldi		+		
Galago sp.	+			
Viverridae indet.	+			
Crocuta crocuta cf. *ultra*	+			
Panthera pardus	+			
Lupulella cf. *adustus*		+		
Elephas recki cf. *recki*	+	+	+	
Ceratotherium simum		+		
"Hipparion" (s.l.) cf. *cornelianum*			+	
Equus sp.	+	+	+	
Hippopotamus cf. *gorgops*	+	+	+	
Kolpochoerus olduvaiensis		+	+	
Metridiochoerus cf. *andrewsi*	+	+		
Sivatherium maurusium		+		
Giraffa cf. *camelopardalis*		+	+	
Giraffidae indet.		+		
Tragelaphus strepsiceros grandis	+	cf.	+	
Taurotragus sp.	+			
Pelorovis sp.		+	+	
Kobus cf. *kob*	+		+	
Hippotragus gigas				+
Parmularius angusticornis		+		
Megalotragus kattwinkeli		+	+	
Connochaetes taurinus prognu	+	+	cf.	
Damaliscus niro		+	+	
Aepyceros cf. *melampus*	+		+	
Antidorcas cf. *recki*	+	cf.	+	
Gazella sp.	+			

supports this proposal. The Peninj *Elephas* is decidedly more hypsodont than that of Olduvai Bed I and Lower Bed II, as the hypsodonty index of a molar fragment from the BSC reaches 202; even though the validity of the subspecies recognized by Beden (1979) is questionable (Ferretti et al., 2003a), there is no doubt that elephants point toward an age younger than Bed I. *Ceratotherium* is similar to *C. simum* and more derived than *C. mauritanicum*, which precedes *C. simum* in East Africa in its strongly oblique molar lophs (Geraads, 2005). The suids have not been studied, but if the *Metridiochoerus* is effectively intermediate between *M. andrewsi* and *M. compactus*, it could be positioned close to Olduvai Middle to Upper Bed II. Among the bovids, *Tragelaphus* is larger than that from Bed I, *Megalotragus kattwinkeli* is present in Bed II but is not known from Bed I, and the Peninj *Parmularius* is definitely *P. angusticornis*, rather than the Olduvai Bed I *P. altidens*. Thus, the conclusion that the Peninj large mammals biochronologically correlate with Middle or Upper bed II is supported. The only argument against this correlation would be the identification of *Theropithecus* as *T. oswaldi oswaldi* by Frost and Delson (2002); according to them, this subspecies, also present at Olduvai Beds I and Lower Bed II, is more primitive than *T. oswaldi leakeyi* from Upper Bed II; only a full study of this material could confirm this taxonomic assignment, which is debatable, given the very large size of the Peninj *Theropithecus* fossil.

Some rodent species like *T. quadrilobatus* and *A. primaevus* are found both in Peninj and Olduvai Bed I and Lower Bed II, as well as at Omo Shungura Mb F and G, while *A. lavocati* is also found at Olduvai Bed I; we can thus compare the evolutionary stages of these taxa. Figure 31.4 plots the M1 and m1 of various fossil and modern *Arvicanthis*; we observe that the Peninj lower m1s are among the smallest ones, close to modern *A. somalicus* and Olduvai Bed I and East Turkana *A. primaevus*. They differ from the *A. primaevus* from Lower Bed II that are larger and from modern and fossil *A. niloticus* from Upper Bed II. *A. primaevus* could represent the ancestral species leading to the divergence between *A. somalicus* and *A. niloticus*. Morphological characters indicate that the early modern *A. somalicus* appears at Olduvai Bed IV (*ca.* 0.8 Ma) and that *A. niloticus* appears at Olduvai Upper Bed II; this suggests that the cladogenesis dates at least to 1.4 Ma and that Peninj is older than this level but younger than Upper Bed I (1.79 Ma). In preserving ancestral *A. primaevus* characters, the Peninj molars suggest an age between Upper Bed I and lower Middle Bed II for the BSC (Denys, 1987b). The Peninj *Thallomys* and *Aethomys* also bear similar characters and the same size as the fossil *T. quadrilobatus* and *A. lavocati* recovered at Olduvai Bed I and Lower Bed II. The fact that the Peninj *Mus* sp. differs from *Mus petteri* present at the base of Bed II and the absence of some Muridae like *M. minor*, *Oenomys olduvaiensis*, and *Zelotomys leakeyi* at Peninj also suggests an intermediate age of BSC between the base and the top of Bed II sites (HWK and FCW localities; Table 31.2).

As a whole, and as was already apparent in earlier papers (Denys, 1987b; Geraads, 1987a), some discrepancies remain concerning the biostratigraphic ages provided by the Peninj large and small mammals. While large mammals suggest a correlation with Middle or Upper Bed II of Olduvai, small mammals may indicate an earlier age. Incomplete sampling and/or evolutionary stasis probably played a role; in any case, the Peninj mandible remains among the last known *Paranthropus*, although it is probably not younger than the Olduvai BK II fossils.

Table 31.2 Distribution of small mammals across the Peninj and Olduvai sequences (after Butler and Greenwood, 1976; Jaeger, 1976, 1979).

Species	BSC	Olduvai Upper Bed I	Olduvai Lower Bed II	Olduvai Upper Bed II
Thallomys quadrilobatus	+	+	+	
Arvicanthis primaevus	+	+	+	*A. niloticus*
Aethomys cf. *lavocati*	+	+	+	
Mus sp.	+	*M. petteri*	*M. petteri*	
Graphiurus sp.	+			
Dendromus sp.	+	+	+	
Saccostomus cf. *mearnsi*	+	+		
Cf. *Rhinolophus* sp.	+			
S. infinitesimus	+	*S. leakeyi*		

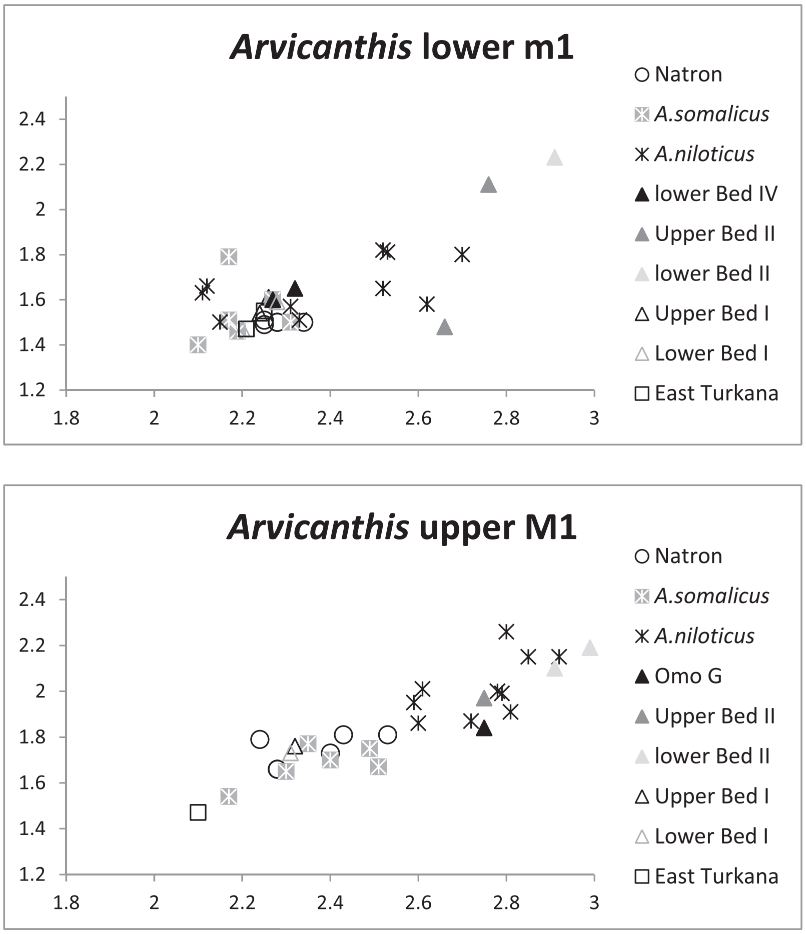

Figure 31.4 Scatterplots of the length × width proportions of fossil and modern *Arvicanthis* spp. (A) Lower m1; (B) upper M1. Measurements in mm.

Taphonomy

Systematic collecting at selected localities from various levels in 1982 recovered a total of 595 specimens. Table 31.3 provides percentages of the various anatomical elements per sample plot (numbered 82A through 82I). There are important differences in the proportions of elements, but there is no obvious trend through the sequence. The heavy fragmentation of most specimens is noticeable, in accordance with the deltaic conditions that prevailed during most of the time of deposition, implying significant water transport of most specimens. However, there is also evidence of deposition in lower-energy settings; for instance, the *Panthera* skull at the base of the BSC could not have been transported for a long distance, and the same is true of other relatively complete skulls, such as those

Table 31.3 Number of collected fossils and percentages of anatomical elements in the 1982 sample plots, arranged by stratigraphic order.

	Level	Sample total	Horn-cores	Dental elements	Vertebras	Epiphyses	Limb bone shaft fragments	All others (mostly bone fragments)
Sample plot 82B	USC	42	0	69	0	2	0	29
Sample plot 82C	USC	27	0	3	0	4	4	89
Sample plot 82D	USC	46	2	2	0	24	11	61
Sample plot 82E	MZ	75	0	11	1	5	12	71
Sample plot 82F	MZ	84	1	5	7	12	0	75
Sample plot 82A	MZ	78	13	1	4	5	13	64
Sample plot 82G	BSC	42	5	38	0	0	7	50
Sample plot 82H	BSC	24	0	8	0	0	0	92
Sample plot 82I	BSC	177	0	14	9	28	16	33
Total		*595*	*2*	*15*	*4*	*14*	*9*	*56*

Table 31.4 Taphonomic and paleoecological parameters of the BSC small mammals fauna in comparison with selected predation assemblages. Average PR is calculated from Dodson and Wexlar (1979) as the mean bone representation for all skeletal elements (original data on skeletal representation were taken from Denys, 1987b). The Gerbillinae/Murinae ratio is adapted from Fernandez-Jalvo et al. (1998). Data for *B. lacteus* and *B. africanus* are from Andrews (1990) and Denys (1997), those for *G. genetta* are from Denys et al. (1999 and unpublished).

	BSC	*B. africanus*	*B. lacteus*	*G. genetta*
% digested incisors	65.1	57	25	35
Average PR	23.4	28.8	58.6	40.7
Gerbillinae/Murinae ratio	0	0–0.4	1–3	0.5
N rodent species	7	4–9	1–4	5

of *Ceratotherium* and *Kolpochoerus*. Ndessokia (1987) also observed that few bones seem to have been transported over long distances. Significant parts of suid and hippo limbs were also recovered from Kipalagu.

Because all small vertebrates obtained by screening were recovered from a small surface (10 m^2) of the BSC, we infer that they all were subjected to the same taphonomic history. Usually microvertebrate concentrations result from predation. Here, the potential prey species are small, from about 10 g (*Mus*, *Suncus*) to 2–3 kg (*Lepus*). We observe a wide spectrum of prey including snakes, shrews, amphibians, Lagomorpha, Rodentia, small primates; such a wide spectrum is generally observed for large birds of prey like *Bubo*, *Asio* spp., some eagles, as well as some mammalian Carnivora such as *Genetta* or medium-size Canidae (Andrews, 1990; Denys et al., 1996; Denys et al., 1999). Most of the prey are nocturnal or semidiurnal, which suggests a nocturnal predator. Denys (1987b) found a 23.4 percent average bone representation percentage (PR), which is lower than what is known for *Bubo lacteus* and *Genetta*, but is similar to *Bubo africanus* (Table 31.4). The fragmentation is very high, but may also been accentuated by the sieving process. However, there is a good representation of skull fragments, vertebrae, and phalanxes. There is a lack of some long bones (tibia, mandible) and very low proportions of femora, humeri, radii, ulnae, pelvis, and scapulae, which suggest slight hydrodynamic sorting (Denys, 1987b). New re-examination of the material shows clear evidence of the characteristic polishing and epiphyses alterations resulting from digestion (according to Andrews, 1990) both on long bones and teeth (Table 31.4). The percentage of digested elements was analyzed only upon incisors, and 65.1 percent showed evidence of digestion; digestion was light for 48.9 percent of them, against 24.4 percent for which it is moderate, 24.4 percent strong, and only a single incisor showing extreme digestion (2.4 per cent). All epiphyses also show evidence of light to moderate digestion. These values may correspond to accumulation by the spotted eagle owl (*Bubo africanus*) and are higher than for *Genetta*. Other taphonomic alterations include, e.g., low weathering and polishing, potential burning, and carbonate coating in some large bones.

Paleoenvironment

We have computed the proportions of the large mammals in the Humbu Formation, either considered as a whole (344 identified mammals, of which 109 have no precise stratigraphic provenance), or divided for convenience into a lower part (BSC + MHT + MZ), and an upper part with the USC only, with comparable numbers of identified specimens (respectively, 121 and 114). The main difference is that the upper part of the sequence contains more hippos, but they are mostly from Kipalagu, and their abundance might have a local significance only. By contrast, the scarcity of hippos in the lower part may be an artifact of field collection strategies, as often occurs in East Africa. We have not included them in the graph of Figure 31.5A.

As a whole, relative abundances of the diverse families do not differ from the usual ones in other late Pliocene or early Pleistocene East African sites. Bovids make up more than half of the total, with Suidae, Elephantidae, and Equidae also being common. Tooth preservation in this latter family is favored by their robustness, but their abundance is the first indication of an open landscape. The number of specimens in non-bovid families is low, and therefore inferences must be drawn with caution. We should note the absence of any brachyodont form apart from *Giraffa*, well-known to feed upon *Acacia* trees in open savannas.

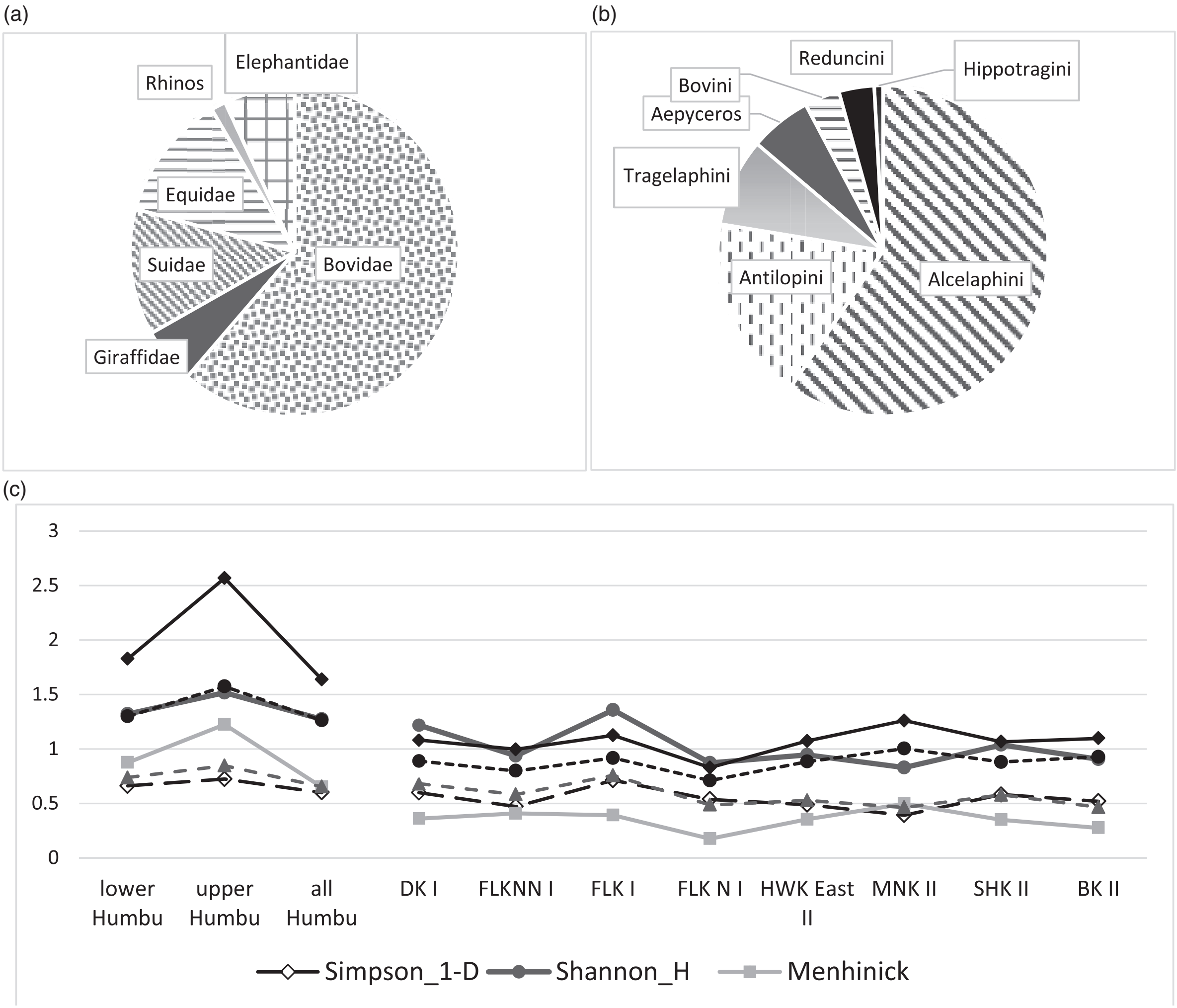

Figure 31.5 (A) Proportions of large mammals in the Humbu Formation. (B) Proportions of bovid tribes in the Humbu Formation. (C) Values of some bovid diversity indices at Peninj and in some Olduvai sites (Olduvai data from Gentry and Gentry, 1978a, 1978b).

This absence is not too significant, as in fact such brachyodont forms are virtually unknown in the East African Pleistocene, with the exception of the small Cercopithecidae. The latter are the best indicators of forest, and their virtual absence here attests to a minimal wood cover.

The proportions of bovid tribes (Figure 31.5B) support such inferences. As documented by Vrba (1980), Alcelaphini and Antilopini are indicators of open, dry environments. At Peninj, they amount to about 75 percent of the total number of bovids, so that the overall picture was certainly that of an open savanna. On the other hand, other bovids indicating somewhat distinct environments are not uncommon. Tragelaphini favor more closed settings, *Aepyceros* prefers the savanna/woodland ecotone, and the Reduncini suggest presence of wetlands; these bovids show that the landscape was probably not a uniform savanna. The overall similarity with Olduvai is obvious because of the taxonomic similarity and general dominance of the same two tribes; for instance, HWK II East (Lower and Middle Bed II), is very similar in terms of bovid proportions. However, proportions are far from uniform at Olduvai, with some sites, especially in Bed I, having many reduncins, or alternatively virtually yielding only alcelaphins and antilopins (Gentry and Gentry, 1978a, 1978b). On the whole, however, the dominance of alcelaphins and antilopins at Peninj is less sharp than at Olduvai. This is reflected in the Peninj diversity indices, several of which have higher values than in Olduvai (Figure 31.5C). Some assumptions should be made prior to interpreting these results. First, we must keep in mind that sample size is low, although the presence of several specimens of impala, an antelope virtually unknown at Olduvai, demonstrates a real difference. We also assume that the fossil abundances roughly reflect those of the biocenosis, i.e., that they are not biased by hominid selection and/or taphonomic processes. Absence of hominid selection (outside of archeological sites) is supported by the lack of systematic association between faunal remains and artifacts in the assemblages collected in the 1960s–1980s; taphonomic processes certainly altered the proportions (e.g., preserving preferentially alcelaphin teeth because of their robustness), but we may surmise that the same factors acted at Olduvai. Thus, even though conclusions remain tentative, and although the meaning of these diversity indices is far from fully understood, it is not unreasonable to assume that they reflect a more diverse

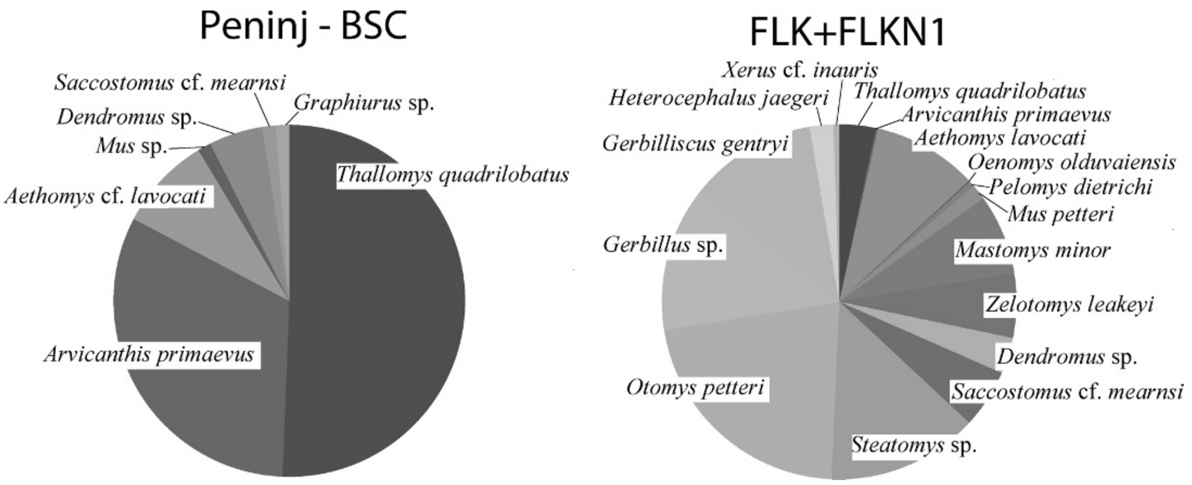

Figure 31.6 Proportions of BSC rodent species based upon the mandible and molar frequencies, compared to Olduvai Upper Bed I (FLK + FLKN sites, after Jaeger, 1976, 1979).

ecological setting than at Olduvai. The two sites are geographically quite close, but Olduvai is presently located at a significantly higher elevation (*ca*. 1500 m instead of *ca*. 700 m at Peninj).

Differences observed between the lower and upper parts of the Humbu Formation are few and of doubtful significance, given the low numbers of specimens. The upper part has fewer suids and more elephants and equids, but the proportions of the bovid tribes are similar.

On the whole, the faunal indications agree with those provided by the pollen and phytolith assemblages, which point to a savanna grassland with xeric grasses, where trees and shrubs of *Acacia*, *Commiphora*, and *Salvadora persica* were scarce, similar to the present-day vegetation (Barboni, 2014). Herbivores must have been dominated by C_4 eaters (including *Paranthropus* – van der Merwe, 2013), but these arboreal plants must have been able to also sustain giraffes, and probably tragelaphins at least.

Micromammal communities from the BSC have been compared with modern ones. Most of the rodents and shrews indicate the presence of savanna during the deposition of the Humbu Formation. Three taxa are arboreal or semi-arboreal (*Thallomys*, *Graphiurus*, *Galago*) and *Thallomys* is associated with *Acacia*. *Aethomys* is considered as a bush rodent. *Suncus*, amphibians, and *Dendromus* are indicators of water proximity. *Saccostomus* is found in woodland savanna and floodplains. *Arvicanthis* and *Lepus* are grazers, which indicates grassland areas and a relatively open savanna environment, in agreement with paleoecological inferences provided by Bovidae and other large mammals. The absence of Gerbillinae (*Gerbillus* and *Gerbilliscus*) and of some Murinae like *Mastomys* and *Otomys*, which are very abundant at Olduvai Bed I (Figure 31.6), may be explained either by differences in predators/prey specificity and/or by the altitude. A complete absence of Gerbillidae has been recorded only in lowland rainforest and montane forests of Africa (Denys, 1999), but it is not in agreement with the presence of numerous savanna species in Peninj. Due to the absence of true lowland forest Murinae species in BSC, the Gerbillinae/Murinae ratio is here probably biased by predators' dietary habits. It has been shown that *Bubo lacteus* favors Gerbillinae in its diet (Andrews, 1990; Denys, 1997) and was supposed to be one of the accumulators of Olduvai Bed I small mammals (Fernandez-Jalvo et al., 1998), whereas *B. africanus*, which we consider here as the most probable accumulator for BSC, avoids Gerbillinae in its diet. Both *Bubo* spp. predators catch fewer Murinae prey than *Tyto* spp. (barn owls; Denys, 1997). This may explain differences between the Olduvai Bed I and Peninj assemblages better than a difference in the type of vegetation. The absence of *Otomys* at Peninj compared to its abundance at Olduvai Bed I (Figure 31.6) may be explained by the altitudinal differences between the two sites. Today *Otomys* is a savanna genus and most of the recognized East African species live in highlands. Denys (1999) found that the Peninj rodent community has its highest affinities with modern Somali–Masai savanna (eight common genera) but also with Zambezian (seven), southwest arid (seven) and Highveld (six) savannas of South Africa. The same result was obtained for Olduvai Middle and Upper Bed I, and Lower and Upper Bed II, which confirms continuity through time of the savanna environment of Northern Tanzania.

Conclusion

While dating problems are still unsolved, the early Acheulean sequence and the main fossiliferous sequence in the Humbu Formation are most likely 1.3 million years or older. The vertebrate fauna from Peninj testifies to an environment similar to, but not identical with, those of Olduvai, and provide important insights into the dynamics of the paleoecology of the early Pleistocene in northern Tanzania. Despite the need for further paleoecological, archeological, and radiometric investigations, Peninj remains a key place for understanding the late survival and final demise of *Paranthropus*, and early *Homo* adaptations associated to the emergence of the Acheulean in East Africa.