Chapter 9

Faunal Change in Eastern Africa at the Oldowan – Acheulean Transition

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Abstract The Early Pleistocene Transition from the Oldowan to the Acheulean in eastern Africa was roughly contemporaneous with a number of other events commonly assumed to be connected with hominin evolution. I review here the large mammal evidence, well documented in several major eastern African sites. Definite conclusions are hard to reach because of temporal gaps in the fossil record, and very patchy history of many lineages, but I conclude that, although some groups do show some turnover during this period, most of them did not change more than before or after it. We may conclude that this cultural change did not seriously impact the faunal assemblage. In addition, we may surmise that, since climate change at this period, if any, did not seriously impact the fauna, it is unlikely to have played a major role in human evolution at that time.

Keywords Mammalian assemblage • Early Pleistocene • Ethiopia • Kenya • Tanzania

9.1 Introduction

The site of Melka Kunture, about 50 km south of Addis Ababa in the Ethiopian highlands, contains a number of archaeological floors ranging from the Oldowan to the Late Stone Age, which document several major technological transitions (Gallotti 2013 and references therein; see also www.melkakunture.it/index.html). The earliest of them, the Oldowan–Acheulean transition, is illustrated by the localities of Garba IV and Gombore I (Morgan et al. 2012; Gallotti 2013, and references therein). The various localities of Melka Kunture also yield numerous faunal remains that allow reconstructing part of the faunal assemblage living nearby, even though selection by hominins and/or taphonomic biases certainly altered the representation of the biocenosis (Geraads 1979, 1985a). This co-occurrence of artifacts and faunal remains offers a valuable opportunity to document their evolutions side by side, in the frame of eastern African prehistoric and faunal evolution.

9.2 A Period of Major Changes?

During the middle part of the Early Pleistocene, from c. 1.9 to 1.5 Ma (following Gibbard et al. 2010, I regard the Pleistocene as beginning at 2.6 Ma), a number of important changes in human taxonomic composition, anatomy, and behavior are observed in eastern Africa:

(1) Succeeding ancestral *Homo habilis* (FAD 2.8 Ma, Villmoare et al. 2015), new species of the genus *Homo* appeared more or less simultaneously in the Upper Burgi Member of the Koobi Fora Formation of Kenya, at slightly more than 2 Ma (Joordens et al. 2013). These are *H. rudolfensis* and the first representatives of the *erectus* group, usually called *H. ergaster* in eastern Africa. *Homo erectus* appeared soon afterward if its earliest example is KNM-ER 2598 from just below the KBS tuff (Lepre 2014). Taxonomic assignment of these early specimens is debated, but they seem to document hominin diversification, although the possibility that they merely illustrate intraspecific variation must be considered (Lordkipanidze et al. 2013).

(2) Brain size steadily increased in hominins starting in the earliest Pliocene, with no sudden jump in hominin endocranial volume during the 1.9–1.5 Ma period (contra Maslin et al. 2014). Early *Homo* was not very different from *Australopithecus* in endocranial volume,

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but what did happen at that time was a change in the slope of the time vs. volume curve. Appearance of some large brains was primarily linked with an increase in body mass (Ruff et al. 1997; Hublin et al. 2015).

(3) The *Australopithecus*—*Homo* transition was associated with a change in diet. On the whole, there was a trend toward incorporation of more and more ^{13}C-enriched food over time, but with considerable variation among regions and individual specimens (Cerling et al. 2013a; Sponheimer et al. 2013). As observed by these authors, in *Paranthropus* there is no doubt that this was linked to high reliance on C_4 plants, but in *Homo* it may be due to meat consumption of C_4-eating herbivores. The proportion of meat in the diet remains unknown, but Aiello and Wheeler (1995) and Braun et al. (2010) suggested that it was a contributing factor to increasing brain size.

(4) What we know of the cultural changes derives mostly from lithic technology, and the transition from the Oldowan to the Acheulean that took place during this interval is certainly a major one. It is first documented at Kokiselei 4 in West Turkana (Lepre et al. 2011) and Konso-Gardula in Ethiopia (Asfaw et al. 1992; Beyene et al. 2013), both at ca. 1.75 Ma; this transition is distinctly younger at Olduvai (de la Torre and Mora 2013). At Melka Kunture, it occurs at Garba IVD (Gallotti 2013).

(5) At about 1.8 Ma, hominins are first recorded in Eurasia, with Dmanisi in Georgia being the most securely dated site (Lordkipanidze et al. 2013). The beginning of the human expansion into Eurasia is often considered as a cultural event, but there is no evidence that it was, in contrast to more recent, deliberate migrations involving a human decision. The geographic ranges of all species expand and shrink for purely ecological or geographical reasons, and it is either a change of this nature or an improvement of their ecological flexibility that allowed humans to spread to Eurasia. The idea that climate change or failure to compete with Acheulean makers “forced” the makers of the Oldowan industry to leave Africa is biological nonsense: just like any other species, hominins expanded their range out of Africa as soon as they were able to do so.

(6) In addition, there were global and regional changes in the climate, vegetation, topography, and hydrological system. It is well known that global temperatures further dropped from their earliest Pleistocene values, the glaciated areas enlarged, and savannahs expanded at the expense of closed country (even though the change was neither regular, nor continuous, nor Pan-African). Maslin et al. (2014) noted that a number of eastern African lakes appeared or became deeper during this period, although Lepre (2014) questioned this dating and the correlation with other climatic events.

A recurrent issue is precise dating; there are a number of rich sites in eastern Africa, but the chronological calibration of some of the most relevant sites is still imperfect. This is true of Olduvai Bed II (in contrast to Bed I; Sanistreet 2012) or, at the time of writing, of the earliest sites of Melka Kunture. In addition, the definitions of *Homo* and its various species, or of the Acheulean, vary with authors. There is also evidence that some of the above-mentioned events are diachronic in eastern Africa (as noted, the Acheulean seems to appear later at Olduvai than at Konso and West Turkana). At least three of these events are definitely not synchronous, because the earliest *Homo* out of Africa, at Dmanisi and other sites, was still using an Oldowan technology and was still small-brained (Agustí and Lordkipanidze 2011; Lordkipanidze et al. 2013).

It is likely that these changes are interrelated to some extent and, although the hypothesis of a single triggering factor is probably an oversimplification, environmental changes are often regarded as heavily bearing on human evolution (Maslin et al. 2015, and references therein). If this is true, we may expect that the large mammal fauna of which hominins were part was similarly impacted, even if not necessarily to the same degree. We may also expect that emergence of new hominin species modified the ecosystem, including the fauna, and probably more and more so as technology and behavior allowed our ancestors to increase their impact on the environment.

Therefore, analyzing faunal changes help to shed light on various aspects on human biological and cultural evolutions. In particular, did faunas change more (or less) before or after this period than during it? If they did, were these changes synchronous with any of the other changes, and are they causally related, or at least correlated?

I shall review briefly below the main groups of large mammals, but it should be borne in mind that even though Early Pleistocene eastern African large mammal faunas are relatively well documented in sites such as Olduvai and Peninj in Tanzania, Rawi, Kanam, Koobi Fora, and West Turkana in Kenya, Omo, Konso-Gardula, and Melka Kunture in Ethiopia, a relatively complete fossil history is known for a few lineages only. Unfortunately, some rich sites (especially in the Middle Awash) are still mostly unpublished.

I have chosen not to put too much weight on frequently used observations such as first appearance datum (FAD) and last appearance datum (LAD). First, they are meaningful only for taxa that have a relatively continuous record. In addition, even for these taxa, it is usually hard to draw precise boundaries between closely related genera and species, so that in fact the only sharply defined events are FADs that correspond to immigration (e.g., *Equus*), and LADs that correspond to extinctions of a lineage. I believe that most often the use of these "data" is dictated more by the need to provide a basis to some objective treatment than by the wish to reflect biological reality.

9.3 A Review of the Evolution of the Main Groups

Carnivores are always rare, so that sampling certainly accounts for a large part of inter-site differences. If a turnover is to be recognized, it is probably c. 1.4 Ma rather than earlier, as the Okote Member of Koobi Fora is the youngest eastern African stratum with the large civet *Pseudocivetta* (also present at Garba IVE at Melka Kunture: Geraads et al. 2004a) and the otter *Torolutra* (Werdelin and Lewis 2013a). Saber-toothed felids of the genera *Megantereon* and *Homotherium*, as well as the "pseudo-machairodont" *Dinofelis* also went extinct in eastern Africa around that time (Werdelin and Peigné 2010). It is tempting to believe that the demise of these formidable predators left open a niche that *Homo* could partly fill (or, alternatively, that they failed in their competition with *Homo*), but *Homotherium* at least survived at Tighenif in Algeria until c. 1 Ma (Geraads 2016), and much later in Europe, showing that coexistence with our ancestors was possible. The only extinctions that occurred around 1.9 Ma were those of the large otters *Enhydriodon* and *Hydrictis gudho*, last recorded in the Upper Burgi Member of Koobi Fora (Werdelin and Lewis 2013a), but these taxa are quite rare. It is also around that time that the modern spotted hyena *Crocuta crocuta* replaced its smaller ancestor *C. dietrichi*, and became the most common large carnivore in Africa.

The date of appearance of the iconic African felids is not known with certainty. Cheetahs were present in the Pliocene, but it is likely that some of their highly specialized adaptations for fast running in open landscapes appeared more recently, perhaps in relation with savannah expansion (Geraads 2014). True leopards appeared in the Early Pleistocene of Olduvai Bed I, together with *Panthera leo*, although identifications at species level (Petter 1973) should perhaps be regarded with caution. They also coexisted with their saber-toothed cousins.

Werdelin and Lewis (2005, 2013b) and Lewis and Werdelin (2007) analyzed the evolution of eastern African carnivore assemblages in the Plio-Pleistocene and concluded that species richness decreased after a peak at 3 Ma, with a second, lower peak of diversity between 2 and 1.5 Ma, but acknowledged that this second peak is probably a sampling artifact due to the richly sampled Olduvai Bed I.

Ungulates make up the bulk of large mammal faunas, so that one would expect their chronological ranges to be better known, but species delineation is often imprecise. Because of their aquatic habits, hippos are among the most frequently encountered ungulates in eastern African, water-deposited open-air sites, but their species identification is difficult. This certainly explains apparent discrepancies in abundances in the Turkana basin, where they have been studied in some detail (Gèze 1985; Harris 1991a). The affinities of the most common lineage are still uncertain, so that it is better left as aff. *Hippopotamus* (Weston and Boisserie 2010). Aff. *H. protamphibius* is common throughout the Omo sequence; early representatives were hexaprotodont (with six lower incisors), but they progressively became tetraprotodont (four lower incisors) during the latest Pliocene. The canines remained relatively small. In the nearby Koobi Fora Formation, a contemporaneous tetraprotodont form has been called aff. *H. karumensis*, but we are probably dealing with the same lineage (Harris 1991b; Weston and Boisserie 2010). It evolved into a diprotodont form in the later part of the sequence, in the KBS Member of the Koobi Fora Fm, whose contemporaneous deposits are poorly fossiliferous at Omo (Shungura Fm Members H-J). Meanwhile, during the Early Pleistocene, new lineages of large hippos appeared and became dominant; they resemble the modern *Hippopotamus amphibius*, with large canines and four lower incisors. The most commonly reported Pleistocene eastern African form is *H. gorgops*; through time, its orbits and occipital became more and more elevated above the skull roof, obviously an adaptation to its aquatic life, but it is hard to understand why the closely related, contemporaneous *H. amphibius* did not develop these characteristics to the same degree. These lineages probably diverged in the Early Pleistocene, but the precise date will probably remain uncertain, as early representatives of both species cannot easily be told apart. Last, one (or more) species of pygmy hippo is known from the Turkana basin as late as the time of Shungura Member L and Okote Member, Olduvai Bed II (Harris 1991a), and Gombore I at Melka Kunture. In any case, there is no evidence of a major change in hippopotamid fauna in the 2–1.5 Ma range.

Suids have been much studied in eastern Africa (Harris and White 1978; Cooke 2007; Bishop 2010) but most lineages evolved continuously, with no major gap in morphology, and speciation events, either anagenetic or cladogenetic, are hard to date with precision, making attempts to define FADs somewhat arbitrary. In the genus *Kolpochoerus*, which some authors recognize as early as the Early Pliocene (but see Pickford 2012), the teeth remained relatively primitive, with premolars of normal size, and third molars that never reached the lengthening and degree of complexity seen in some other genera. The most common lineage is that of *K. limnetes* (or *K. heseloni* if the holotype of *K. limnetes* does not belong to this genus)—*K. olduvaiensis* (called *K. paiceae* by Souron 2012), the latter being the most derived member of the genus, with longer and more hypsodont third molars, although it was not more of a grazer (Harris and Cerling 2002) than another species, relatively common in Middle Pleistocene sites, *K. majus*, which is probably ancestral to the living giant forest hog, *Hylochoerus*. *Kolpochoerus majus* differs from the main lineage in retaining primitive features in the dentition, which looks like a mere enlarged version of Pliocene ones. This suggests an omnivorous diet, but the $\delta^{13}C$ of the only two analyzed specimens is close to 0 (Bedaso et al. 2010), as in pure grazers, showing that it probably fed mostly on grasses. The earliest record of *K. majus* is from the lower part of the Konso sequence, at c. 1.9 Ma (Suwa et al. 2003; Beyene et al. 2013), and it is perhaps also represented by fragmentary remains in the lower levels of Garba IV. Cooke (2007) and Souron (2012) place the transition from *K. limnetes* to *K. olduvaiensis* (or *K. paiceae*) at about the same period (Member J of the Shungura Fm at Omo, KBS Member of Koobi Fora). In any case, the transition between the two forms is gradual (Souron 2012, Fig. 2.18) and if *Kolpochoerus* changed its diet, it was certainly earlier than the Early Pleistocene (Souron 2012, Fig. 3.4).

The genus *Metridiochoerus* includes several species, one of which certainly gave rise to the modern warthog, *Phacochoerus*. The main species is *M. andrewsi*, known since the earliest Pleistocene, and common through most of the Early Pleistocene. Three other species, with hypsodont third molars, *M. modestus*, *M. hopwoodi*, and *M. compactus* have their FADs at about 2 Ma (Upper Burgi or KBS Members of Koobi Fora; uppermost part of Shungura Mb G). They were quite rare at that time, but may become more common later on, especially at Konso around 1.5 Ma (Suwa et al. 2014); they all survived into the Middle Pleistocene (Cooke 2007). The third molars of *M. compactus* consisted of tall simple pillars, as in the warthog, and this species was also remarkable in its huge canines. There is no doubt that these suids were, like *Kolpochoerus*, mostly grazers adapted to open environments, as also shown by their carbon isotopic values (Harris and Cerling 2002; Cerling 2015); thus, this grazing diet is at least 2 Ma old.

Ecologically, *Metridiochoerus* seems to replace *Notochoerus* that belongs to another subfamily but had a similar dental morphology, with longer and more hypsodont third molars than in *Kolpochoerus*, showing that environmental factors were perhaps less important than interspecific competition. *Notochoerus* becomes uncommon after c. 2 Ma, until its extinction c. 1.8 Ma (it is last recorded in the KBS Member of Koobi Fora and Shungura Member H; Cooke 2007). On the whole, the Suidae do show some turnover during the 2–1.5 Ma period, but none of the taxa replacements is of great magnitude.

Giraffids were not very abundant elements of the ungulate faunas in terms of number of individuals, but because of their large size they might have formed a significant part of the animal biomass. They include at least two species of *Giraffa*, of different sizes but morphologically similar to the modern giraffe, plus the genus *Sivatherium*, a very large form with buffalo-like proportions but as least twice as heavy (Harris et al. 2010a and references therein). It is known from the early Pliocene until the Middle Pleistocene at least, but it may be that it evolved toward more grazing habits (Cerling et al. 2015). Abundance data are lacking for most sites, but it was still common at Anabo Koma in Djibouti, at c. 1.5 Ma (Geraads 1985b), showing that it was not seriously affected by ecological changes in the course of the Early Pleistocene. The evolution of *Giraffa* is still imperfectly understood. *Giraffa jumae* has been reported throughout the Early Pleistocene; it may be that the transition between *G. gracilis* and the modern species *G. camelopardalis* occurred during the Early Pleistocene; it involved an increase in size and premolar molarization, but no major evolutionary change (Geraads et al. 2013).

No camel is known in eastern Africa between the earliest Pleistocene and latest Pleistocene (Harris et al. 2010b), but *Camelus* was always so rare there before historic times that this might be a sampling artifact.

The Bovidae (cattle, buffaloes, antelopes, goats, and gazelles) were by far the most common and most diversified group of large mammals in the African late Neogene, and for decades (Vrba 1995) they have repeatedly been used to examine effects of climate change. Most of them belong to tribes that mainly occur in Africa.

The Bovini are the main exception, as they are widespread in the Old World; they were chiefly represented by the genus *Syncerus* that includes the modern African buffaloes, and by its long-horned cousins of the genus *Pelorovis*. *Syncerus* was infrequent, but the history of *Pelorovis* is better known. The genus is first recorded from the top of the Hadar sequence (Geraads et al. 2012). Afterward, *P. turkanensis*, whose horns remain of moderate length, is progressively replaced by *P. oldowayensis*, whose horns may have spanned up to 3 m from tip to tip. It has been recorded from Middle Bed II of Olduvai and from the KBS Member of Koobi Fora (Gentry and Gentry 1978; Harris 1991b). At Melka Kunture, it is known from Simbiro, where it might have coexisted with *P. turkanensis*, also present in this locality although perhaps not in the same level. Besides these buffaloes, a close relative of the aurochs, of the genus *Bos*, is known from the latest Early Pleistocene of Buia in Eritrea (Martinez-Navarro et al. 2010) and the earliest Middle Pleistocene of Asbole in the Lower Awash (Geraads et al. 2004b) but this immigration of a Eurasian form remained localized.

Of the spiral-horned antelopes of the tribe Tragelaphini, large forms are better known than small ones, perhaps because their horn cores preserve better. The greater kudu, *Tragelaphus strepsiceros*, probably descended from the Hadar *T. lockwoodi*, is known throughout the Pleistocene (Gentry and Gentry 1978). Another kudu-like form, *T. gaudryi*, is known throughout the Omo sequence (Gentry 1985; Bibi and Kiessling 2015). The most significant event during the time interval considered here was that the lineage of the large *T. nakuae*, whose horns are only slightly spiraled and is abundant in the Plio-Pleistocene of Ethiopia and Northern Kenya, virtually disappeared without descent after the KBS Member of Koobi Fora (Harris 1991b); however, its extinction might be as late as Shungura Member J or K according to Bibi and Kiessling (2015). Geraads and Coppens (1995) showed that this species must have had habitat preferences similar to those of the impala, *Aepyceros*, the abundance of which seems to have been unaffected at that time. We may tentatively surmise that *T. nakuae* was replaced by the eland (*Taurotragus*), which appeared in the late Early Pleistocene (Gentry and Gentry 1978).

The smallest antelopes of the tribes Neotragini and Cephalophini (dik-diks and duikers) are so rare in most sites, certainly because of taphonomic or collecting biases, that no firm conclusion can be drawn from their presence/absence, but dik-diks may have been as common as today. This is not true of the gazelles (tribe Antilopini), a group with northern affinities, whose abundance in eastern Africa is recent; their fossil representatives in that region are not sufficiently well known to reconstruct the history of the genus *Gazella*. *Antidorcas recki* is the extinct eastern African form of the South African springbok; it is best known from Olduvai, but fluctuations of its abundance there were more related to local conditions than to chronology (Gentry and Gentry 1978). Other groups with northern affinities, the Caprini and Ovibovini, were extremely rare. One of the most commonly found antelopes is the impala, *Aepyceros*, with several species of rather uniform morphology. The modern species, *A. melampus*, prefers the woodland-savannah ecotone; it is absent from Ethiopia today, and from Melka Kunture, but there was no obvious trend in the abundance of this genus through the Pleistocene.

Reduncins include today the kobs, waterbucks, and relatives (*Kobus*) and reedbucks (*Redunca*). They are dwellers of wet grasslands, even swamps, so that their abundance is an indicator of moist, open environments, and varies therefore with the local context; no general trend can be recognized, at least until c. 1.5 Ma, after which time they were never the dominant bovid group again. No major change in taxonomic composition occurred in the first part of the Early Pleistocene, as the ancient forms *Kobus ancystrocera*, *K. sigmoidalis*, and *Menelikia* have been reported until at least the top of the Omo sequence. *Kobus sigmoidalis* has even been recorded from the Middle Pleistocene of Konso (Suwa et al. 2003) but its daughter species *K. ellipsiprymnus*, the modern waterbuck, appeared at c. 2 Ma (Gentry and Gentry 1978; Gentry 1985). The common kob *K. kob* is known throughout the period considered here, but becomes common only during its later part (see below).

Hippotragins (oryx, sable, and roan antelopes) were not very common as fossils and are not easy to identify to species. The most common one was *Hippotragus gigas*, known throughout the Olduvai sequence (Gentry and Gentry 1978) and still present at Buia at c. 1 Ma (Martinez-Navarro et al. 2004).

The alcelaphins include, among other species, the modern wildebeest, hartebeest, topi, and blesbok, living in large herds emblematic of the modern eastern African savannahs. They underwent a spectacular radiation in the Early Pleistocene, with probably at least 20 species, five or more of which being sometimes found in the same layers. However, it is only after c. 1.5 Ma that they are commonly the dominant antelopes, although relative abundances must be computed with caution because their teeth preserve better than those of other bovids (probably because they are more robust, but this important issue has never been investigated).

The wildebeest (*Connochaetes*) lineage dates from the earliest Pleistocene (Gentry 2010) and was first represented by a species with slender horn cores of more or less circular cross-section, of which a local subspecies is abundant at Garba IV at Melka Kunture, *C. gentryi leptoceras* (Geraads et al. 2004a). In the second half of the Early Pleistocene, around 1.5 Ma, it was replaced by its descendant with shorter, stouter horn cores, closer to the modern blue wildebeest, *C. taurinus* (Gentry 2010, and references therein).

Megalotragus was an extinct genus close to *Connochaetes* but of larger size and with less divergent horns, probably related to giant South African forms. With its two eastern African species, *M. kattwinkeli* and *M. isaaci*, it is known through the whole Early Pleistocene, without any obvious trend in its abundance (Harris 1991b; Gentry 2010).

Parmularius was another extinct genus, already present in the Pliocene, with a long face and rather short horn cores inserted far above the orbits, as is the case for the hartebeest. In the Pleistocene, it is best known from Olduvai, where both *P. rugosus* and *P. angusticornis* appeared in Lower Bed II, at c. 1.6 Ma, succeeding their likely ancestor *P. altidens* (Gentry and Gentry 1978; Gentry 2010).

Damaliscus remains imperfectly known, perhaps because its horn cores are less diagnostic than those of other alcelaphins. It certainly appeared in the Early Pleistocene, and two species with slightly spiraled horns were present around 1.5–1.7 Ma at Olduvai (*D. agelaius*) and Melka Kunture (*D. strepsiceras*); the "*Parmularius* cf. *pandatus*" from the lower part of the Konso sequence (Suwa et al. 2003) was perhaps related. Slightly later, after 1.5 Ma, a species with large, curved, but non-spiraled horns became relatively common until the Middle Pleistocene, *D. niro* (Suwa et al. 2003; Gentry 2010). The modern species are unknown before the Middle Pleistocene.

Beatragus, with its extremely long horns reminiscent of those of the impala, appeared at the Plio-Pleistocene boundary but is never common; it survives today as the endangered hirola, *B. hunteri* (Vrba 1997; Gentry 2010).

Numidocapra (including *Rabaticeras*) was a Pan-African but poorly known form with horn cores that were almost parallel at their bases but were slightly spiraled in a direction opposite to that of most antelopes (clockwise in the right horn). It is known at Olduvai and Anabo Koma in Djibouti (and Aïn Hanech in Algeria) at c. 1.7–1.5 Ma, but was too rare for its chronological range to be estimated (Bonis et al. 1988). It could be the ancestor of *Alcelaphus*, the hartebeests, which are now among the most abundant African antelopes but are not known before the Middle Pleistocene; the report of this genus from FwJj20 dated to c. 1.95 Ma (Braun et al. 2010) is probably erroneous.

On the whole, even though it may be that several species, especially alcelaphins, appeared at that time, the period from 2 Ma to 1.5 Ma clearly does not document a major change in the ecological preferences of bovid assemblages; changes in their taxonomic composition occur throughout this period, and if some turnover is to be recognized, it is more probably close to 1.6–1.5 Ma, i.e., after the appearance of the Acheulean.

The Perissodactyla, or odd-toed Ungulates, include the Equidae, Rhinocerotidae, and Chalicotheriidae (no tapirs are known in Africa). They passed the climax of their diversity long before the Pleistocene. Among the Equidae, the three-toed hipparions had been, together with antelopes, the dominant ungulates in the Late Miocene, but no longer played this role after the Pliocene, at which time their diversity had already decreased. Their systematics is still controversial (African forms are often called *Eurygnathohippus*, but the monophyly of this genus is disputable), and the fragmentary remains that form the bulk of the collected fossils do not help much in recognizing evolutionary events (Bernor et al. 2010, and references therein). They survived until the Early/Middle Pleistocene boundary at Gombore II at Melka Kunture (Geraads et al. 2004a) and at Konso (Suwa et al. 2003), but went extinct soon afterward. The FAD of the monodactyl equids of the genus *Equus* is the earliest Pleistocene at c. 2.2 Ma, but here again, a consensus on the species content has not been reached. After c. 2 Ma, *Equus* became more and more abundant relative to hipparions, but it would perhaps be naive to assume that the rise of *Equus* was the cause of the rarefaction and eventual extinction of the three-toed forms, which had been so successful and widespread for 10 My.

The rhinos were very similar to the modern *Diceros bicornis* ("black" rhino), a browser, and *Ceratotherium simum* ("white" rhino), a grazer, so that relative abundances of these genera provide indications on the vegetation. At the beginning of the Pleistocene, *Ceratotherium* still had relatively unspecialized teeth, prompting inclusion in a distinct species (*C. mauritanicum* in my opinion), but during the course of the Early Pleistocene hypsodonty increased and its molars became more similar to those of the modern species (Geraads 2010, and references therein). However it would be an oversimplification to link this change with an increasingly open habitat, because this evolution occurred later in North Africa although this region was probably still more open, because it was accompanied by a shortening of the metapodials unexpected in an open country form, and because isotopes show that Late Pliocene *Ceratotherium* was already a grazer (Bedaso et al. 2013; Cerling et al. 2015).

The last perissodactyl was the elusive chalicotheriid *Ancylotherium*, once called the "gorilla-horse", a survivor from the Miocene, with its long forearms and clawed paws, perhaps adapted to feeding on bark, lianas or soft trunks. Its last known occurrence is at Konso-Gardula, at c. 1.3 Ma (Suwa et al. 2003).

Of the Proboscidea, the most distinctive was *Deinotherium*, with its downturned lower incisors, no upper tusks, and lophodont molars resembling those of tapirs more than those of elephants, in accordance with a pure leaf diet. Little changed since the Miocene, it disappeared at c. 1.4 Ma in the Turkana basin (Harris et al. 1988; unpublished Omo catalogue). Elephants include the genus *Loxodonta*, to which the present-day African elephant belongs, but was a rare genus in the Pleistocene, and the much more common *Elephas* (or *Palaeoloxodon*), a relative of the present-day Asian elephant. The evolution of the Pleistocene species *Elephas recki* was chiefly marked by an increase in hypsodonty, and in the number of plates that make up the molars, allowing its use in biochronology. However, this evolution seems to have followed a gradualistic model with no recognizable bursts of evolution (Beden 1979, 1983). The species disappears from the African fossil record in the Middle Pleistocene.

Leaving aside rare groups like the hyraxes and aardvarks, the last taxon to be considered are the Primates. Apes (other than hominins) are unknown in the African Early Pleistocene but their virtual absence as fossils strongly suggests that a taphonomic factor, probably their forested environment, mitigated against fossilization, or that relevant sediments have not been found yet, but they were certainly present somewhere. The largest monkey was the terrestrial *Theropithecus oswaldi*, a relative of the modern gelada baboon of the Ethiopian highlands. Its lineage is documented since the Pliocene, with a regular evolution until its extinction toward the end of the Middle Pleistocene when it reached the size of a female gorilla (Jablonski and Leakey 2008; Jablonski and Frost 2010). Its diet incorporated more and more C_4 grasses through its history, but this change is continuous (Cerling et al. 2013b). Another species of the genus, *T. brumpti*, restricted to the Turkana basin, disappears after mid-Member G of the Shungura Fm and is unknown from the Upper Burgi Member at Koobi Fora, so its extinction is not posterior to 2 Ma (Frost 2007). Other baboons were less common and included *Parapapio*, which went extinct at c. 1.4 Ma after it gave rise to modern baboons of the genus *Papio*. It was also around that time, after the Okote Member of Koobi Fora, that the large terrestrial colobines *Cercopithecoides kimeui* and *C. williamsi* disappear, together with the arboreal *Rhinocolobus turkanensis* and the papionin *Lophocebus*, the latter now restricted to Western Africa (Jablonski and Leakey 2008; Jablonski and Frost 2010). *Paracolobus mutiwa* is a rare form known only from the Turkana basin. It is known at Omo only until Member G, but overlying sediments are poorly fossiliferous; at Koobi Fora there are only two specimens from the Upper Burgi, so that the LAD of 1.88 Ma (Frost 2007) is based upon slender evidence. *Colobus freedmani* Jablonski and Leakey 2008 is known by a few specimens from the Okote Member of Koobi Fora, c. 1.5 Ma. Thus, on the whole, although there is certainly some renewal of the cercopithecid fauna in the Early Pleistocene, it is not restricted to a particular period.

9.4 Quantitative Analysis

In addition to changes in taxonomic composition, faunal assemblages evolve through changes in abundances of the various taxa. In order to evaluate them, I have calculated the number of specimens of the main taxa of large mammals in the best-documented area, the Turkana basin, from roughly 2.2–1.3 Ma, using the available catalogues. I have divided the basin into its three main research areas and into three successive time periods (Fig. 9.1). I have excluded the carnivores that are too rare to be significant, and the hippos and proboscideans because they were not systematically collected. Still, it should be remembered that several biases may distort the results. A major one is the identification bias: some taxa have been studied in more detail in some areas than in others; some taxa were studied by different specialists who came to different conclusions; some taxa were not fully entered in the catalogue. Another one is the difference in collecting strategies, which may operate even within the same project area (Alemseged et al. 2007). Such biases certainly explain some of the most obvious gross differences, such as the seemingly high frequency of hominins in the Natoo Member, due to the virtual absence of other Primates in the database, or the high peaks of some bovid species. In addition, some of the apparent changes are restricted to some parts of the basin only and probably reflect local conditions only.

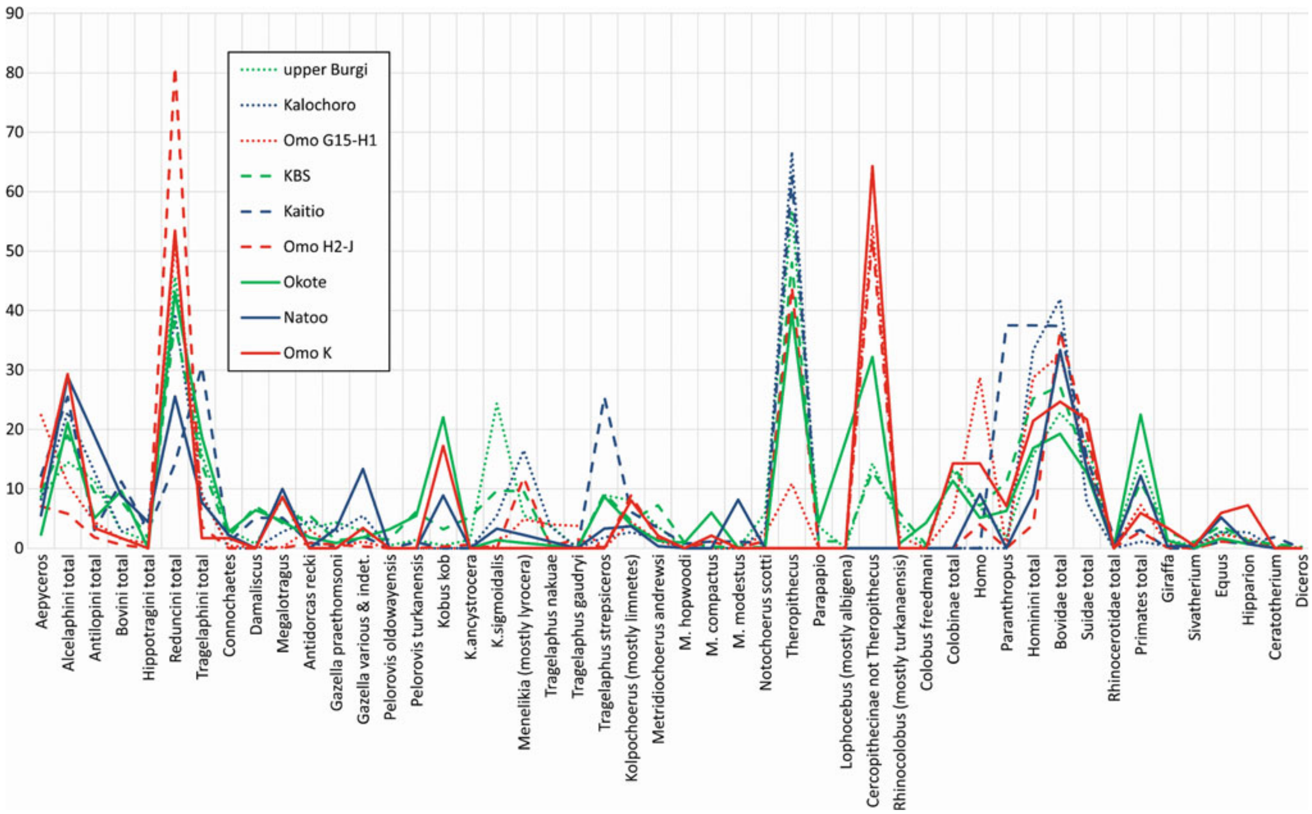

Fig. 9.1 Frequencies of the main taxa of large mammals in the Turkana basin in the Early Pleistocene. Values for individual bovid taxa are calculated as their percentage of all identified bovids; for suids, of all suids; for primates, of all primates; for other taxa (10 taxa to the right of the graph), of all large mammals excluding Proboscidea, Hippopotamidae, and Carnivora. Koobi Fora in green, West Turkana in blue, Omo Shungura in red. Each area has been divided into three successive time units that are roughly contemporaneous through the three areas; the oldest one is represented by a dotted line, the intermediate one by a dashed line, the youngest one by a continuous line, so that any trend in the whole basin should follow this order, irrespective of the color. Compiled from the Turkana database (courtesy of R. Bobe) and the Omo catalogue. The database contains no entry for non-hominin Primates in the Natoo Member, so that their number was artificially set to their average proportion in other members

Besides this, changes in abundances showing the same pattern through the whole basin are few. The sharpest one is the greater frequency of *Kobus kob* after c. 1.6–1.5 Ma, but other bovids do not display consistent patterns. Among suids, as noted above, the disappearance of *Notochoerus* in the youngest time slice is the terminal event of its earlier rarefaction; it may have made room for *Metridiochoerus compactus* that probably had similar ecological requirements. On the whole, however, Fig. 9.1 shows that even within this single basin, differences between research areas are at least as important as those that occur through time.

This lack of major change during the 2–1.5 Ma period is in agreement with some recently published results. For instance, Hakala (2012) calculated that from the Upper Burgi to the KBS and Okote Member at Koobi Fora, the proportions of the bovid tribes remained more or less the same, with only a slight increase of alcelaphins and a slight decrease of antilopins; these members are also very close in a factor analysis (Bobe et al. 2007). Similarly, Itoh et al. (2015) note that “These characteristics and size of the *K. sigmoidalis* horn cores from the Konso Formation were relatively constant during the Konso Formation range from interval 1 (∼1.9 Ma) to interval 5 (∼1.3 Ma)”. On the whole, bovids suggest a rather steady environment over that period of time. From a detailed analysis of abundances and appearance/extinction patterns in eastern Africa, Frost (2007) concluded that the period between 3.5 and the early Middle Pleistocene, noticeable by the abundance of *Theropithecus*, is relatively stable (Frost 2007, Figs. 10, 11), except for a modest renewal at c. 2 Ma (Delson 1984; Frost 2007, Fig. 7). Cerling et al. (2015) analyzed isotopic values of a large number of mammals across the Plio-Pleistocene and placed the major change at c. 2.35 Ma. Last, Bibi and Kiessling (2015) concluded that “speciation and extinction proceeded continuously throughout the Pliocene and Pleistocene”. They add that “a single origination pulse may be present at 2.0–1.75 Ma”, but acknowledge that this pulse might be an artifact of the fossil record, in agreement with the above-mentioned lack of fossiliferous strata below Olduvai Bed I and the Upper Burgi Member.

9.5 Conclusion

As noted above, the quality of the fossil record is highly dependent on the existence and richness of fossil sites, so that FADs and LADS often reflect these parameters more than real evolutionary events (see, e.g., Behrensmeyer et al. 1997). In particular, appearance of several taxa at c. 2–1.8 Ma is obviously correlative of the existence of the rich deposits of the KBS Member and Olduvai Bed I, while the apparent extinctions at c. 1.5–1.4 Ma correspond with the end of the fossiliferous sequences of Omo Shungura and Koobi Fora. Attempts to estimate appearance or extinction dates and faunal turnover can note this incompleteness of the fossil record, but there is no way to reconstruct missing data.

What emerges from the above review, however, is that the transition from the Oldowan to the Acheulean is not associated with a major turnover of large mammal faunas. Kovarovic et al. (2013) have also shown that at Olduvai, faunas from the lower Bed II at c. 1.75 Ma do not much differ from those above the Lemuta tuff if the taphonomic difference in body weight profiles is taken into account; both mostly sampled woodland habitats. We may conclude, not only that this cultural transition was not triggered by a change of faunal assemblages, but also that the cultural transition did not seriously impact the large mammal assemblage as a whole. It may be, however, that the change in behavior associated with Oldowan–Acheulean transition had a significant influence on some particular taxa, and that certain ungulate species were exterminated during this period (even if this is unlikely). At a somewhat larger scale, Lewis and Werdelin (2007) link the decrease of carnivore diversity after 2 Ma to the entry of *Homo* into the carnivore guild and believe that, although our ancestors were certainly unable to compete directly with large predators, they may have interfered with them in scavenging activities (see, e.g., Ferraro et al. 2013).

Thus, it seems that there is no well-supported evidence for a link between the Oldowan–Acheulean transition and a faunal turnover. It is interesting to observe that Behrensmeyer et al. (1997) were also unable to find definite support for the widely accepted change between 2.8 and 2.5 Ma, corresponding to the emergence of *Homo*. This relative independence between the fauna and key events of human evolution is also apparent in the fact that the first known humans out of Africa were virtually unaccompanied by other large mammals, because the fauna from Dmanisi and other sites in the Caucasus, according to the few available publications (O'Regan et al. 2011; also Amirkhanov et al. 2014, and references therein), is almost totally Eurasian in character (so that it is hard to escape the conclusion that it is the ability to use stone tools that allowed *Homo* to explore this new environment).

If there is no major change in the composition of the large mammal assemblage, obviously this period is ill-suited to search for correlations between possible climate or environmental changes and biological evolution in this group, but in any case it does not provide support for an effect of external factors on its biological and cultural evolutions at that time. In this context, the challenge of finding an extrinsic cause to human diversification and biological and technological advances at that time remains open.

The impact of climate change on biological evolution is the current paradigm. A recent example is provided by Bibi and Kiessling (2015: 10626) who, without analyzing any extrinsic parameter, "conclude" that "global climate drove large mammal evolution at the million-year timescale". In fact, it is extremely hard to demonstrate. For instance, Faith and Behrensmeyer (2013) observe that "…problems of temporal and spatial scale are known to plague analyses of turnover relative to climate change, and this could explain why some studies fail to observe climatic effects on turnover". One might ask why such an elusive correlation is often taken for granted; it may be that the high concern about present-day climate change prompts researchers to overemphasize its impact on faunas, but it is also obvious that this high concern drives funding toward climate-related issues.

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