



The environment of the Ethiopian highlands at the Mid Pleistocene Transition: Fauna, flora and hominins in the 850–700 ka sequence of Gombore II (Melka Kunture)



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ABSTRACT

Environment, climatic change and human evolution have been debated over the last 50 years giving special attention to the Plio-Pleistocene sites of the Rift Valley. In this paper we discuss the environment and the limits of hominin adaptability based on evidence from Melka Kunture, at 2000 m asl on the Ethiopian highlands, and specifically on the ~850 ka to ~700 ka sequence at sub-site Gombore II. Human fossils and multiple Acheulean occurrences, as well as hippo remains and footprints, combined with palynological analysis, provide a highly detailed chronological resolution of the changing local environmental conditions during the last ~150 ka of the MPT (Mid Pleistocene Transition), including the sequence of events after a volcanic eruption. Layers containing footprints and fossils are evidence of near-continuous occupation by hippos and their recolonization of the area after a disruptive volcanic eruption. Conversely, Acheulean implements and human fossils suggest that peopling by hominins occurred at a different and discontinuous pace even when the flora and fauna were re-established and the environment was rather stable. Most notably, the assembled evidence points to the limits of *Homo erectus s.l.* adaptability. Apparently, this hominin could no longer live at 2000 m asl when the climate deteriorated during glacial isotopic stage 20, becoming markedly colder than it is today, but re-colonized the area when the climate turned warmer again during isotopic stage 19.

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1. Introduction

Over the last 50 years, long Plio-Pleistocene sequences have been researched in East Africa, focusing on the Rift Valley and dramatically changing our knowledge of human evolution and our understanding of climate change. This led to the ongoing debate on the characteristics of the environment where early hominins evolved, which is usually understood as having been of savanna-type (e.g. [Lepre, 2014](#); [Passey et al., 2010](#)). Here we shall discuss human settlement in a very different environment, i.e. Pleistocene evidence from Melka Kunture (8°42'N; 38°35'E), at 2000 m asl on the Ethiopian highlands. In the same general area, in 1960–1990

the average monthly temperature was between 16.5 °C and 20.5 °C, while annual precipitations were close to 1000 mm ([Climate Change Knowledge Portal, accessed 9/25/15](#)). We will track hominin presence or absence as a proxy of human adaptability at the Mid Pleistocene Transition (MPT) ([Elderfield et al., 2012](#); [Head and Gibbard, 2005](#)), when the dominant periodicity of climate cycles shifts from 41,000 to 100,000 years, and ice-caps were accumulating at northern latitudes. We will use the detailed information available for over ~150,000 years at Melka Kunture, in Ethiopia's Upper Awash Valley, specifically at sub-site Gombore II. We acquired archaeological, paleontological, ichnological and palynological information, reconstructing changes on a finer chronological scale than is often available.

In our analysis of the 850,000- to 700,000-year stratigraphic sequence of Gombore II, encompassing the last ~150 ka of the MPT, we shall focus on the evidence left by hominins and

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hippopotamuses. While they impacted differently on the environment, this happened in a lasting way in both cases, thus allowing comparisons. Human fossil bones are rarely preserved, but lithic productions are enduring proxies of hominin activity. Hippo bones, being much bigger than hominin ones, fossilized better. Furthermore, the common hippo (*Hippopotamus amphibius*), being a very large animal with relatively small feet, leaves deep footprints and trails when walking over unconsolidated fine sediments (Chansa et al., 2011; Eltringham, 1999; Field, 1968). Fossil footprints and tracks – which can be produced by a number of species – are important in providing snapshot evidence of the evolution of paleolandscapes. They have been discovered at Plio-Pleistocene African sites extending over sizeable areas, as at Laetoli (Leakey, 1987), or occurring repeatedly at various stratigraphic levels, as at Koobi Fora (Bennett et al., 2014) and Gombore II (reported below).

The sequence at Gombore II also documents two volcanic eruptions. A first one happened at ~875 ka, and a second one, that will be discussed in detail, at ~700 ka, when distal ash flows or ash-cloud surges expanded into the Upper Awash Valley, modifying the fluvial lacustrine environment. Recent fieldwork brought to light well-preserved tracks linked to hippo activity that we use as proxies of animal life. Hippo footprints left in volcanic deposits that were still malleable are evidence of these animals' reoccupation, after a disruptive event, of a resilient environment where vegetation had reappeared. Accordingly, hominins could be expected to be present as well. The detailed stratigraphic sequence makes it possible to check whether and when co-existence actually occurred, and to draw conclusions about hominin recovery. This in turn makes it possible to address the subject of peopling by hominins in the Middle Pleistocene, and whether it was driven by the same factors that affected hippo occupation. The palynological analysis, reconstructing past vegetation and past climatic conditions, allows to figure out if global cooling at the MPT affected *Homo erectus* s.l. peopling of the Ethiopian highlands.

2. Gombore II

2.1. Regional setting

Gombore II is part of the cluster of sites that make up the archaeological area of Melka Kunture, which is located in a semi-graben depression of the Upper Awash Valley, on the western border of the Main Ethiopian Rift (Chavaillon and Berthelet, 2004) (Fig. 1). Volcanoes rising at a distance of 30 km or more were active from the Pliocene on (Mohr, 1999). The volcanic deposits made it possible to establish a detailed chronology of the complex archaeological record through radiometric dating (Morgan et al., 2012). The Pleistocene landscape here consisted mostly of meanders, small tributaries and still bodies of water (Kieffer et al., 2004; Morgan et al., 2012; Raynal et al., 2004). Ash-flow emplacement clogged up the streams, thus contributing to the development of shallow ponds and pools.

From 1965 to 1998, a French archaeological mission directed by Jean Chavaillon made extensive surveys and excavations in the area of Melka Kunture (Chavaillon and Piperno, 2004). In 1999, the Italian Archaeological Mission took over this research; since 2011, it has been directed by one of the authors of this paper (M.M.).

Consistently with the nomenclature established by Chavaillon, each archaeological site in this area is identified by the name of the gully it is located in, plus a consecutive number.

2.2. Archaeology and the history of studies

The Lower and Middle Pleistocene stratigraphic sequence in the Gombore gully has been described (Raynal et al., 2004), and has

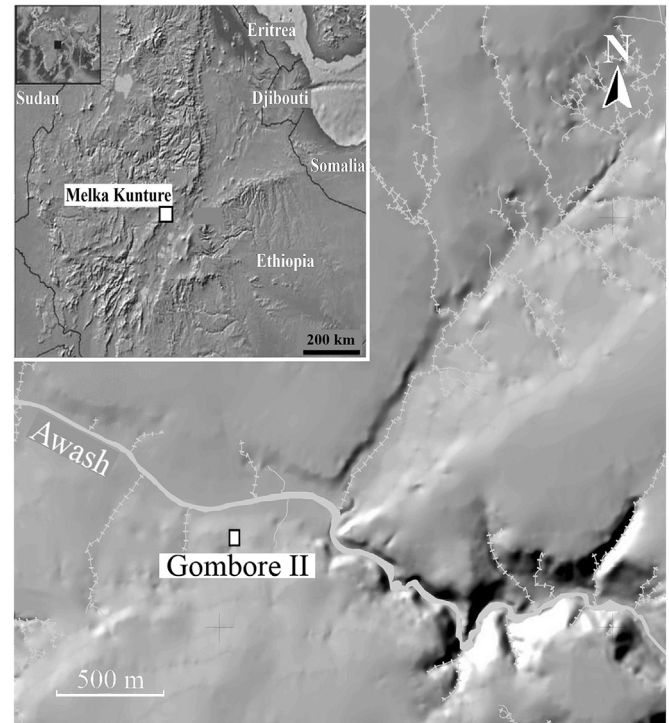


Fig. 1. The location of Gombore II in the Upper Awash Valley. Insert: Melka Kunture on the shoulder of the Main Ethiopian Rift, from the map of Ethiopia and neighbouring countries.

been dated by tephrochronology (Morgan et al., 2012). Further chronological constraint is provided by the Matuyama-Brunhes boundary, which was identified by Tamrat et al. (2013). The sequence starts at Gombore I with Oldowan layers pre-dating 1.4 Ma. Slightly more than 100 m away upstream is Gombore II, which includes several sub-sites (Gombore II-1, Gombore II-3, Gombore II-4, Gombore II-5, Gombore OAM) (Fig. 2), that all lie at the same level above a tuff unit with reverse polarity, dated 875 ± 10 ka (in this paper, the ages of these sub-sites have been rounded to 850 ka). Rich Acheulean assemblages excavated over a total area of ~140 m² are associated with a faunal population dominated by *Hippopotamus* cf. *amphibius* (Gallotti et al., 2010).

Site Gombore II-2 is at the top of the sequence discussed here, less than 10 m from the closest excavated part of Gombore II-1, but 5 m higher up in the stratigraphy. A volcanic tuff with normal polarity situated in this uppermost part of the sequence is dated to 709 ± 13 ka, i.e. the beginning of the Middle Pleistocene (Morgan et al., 2012).

In 1974 a controlled collection of exposed materials was carried out at Gombore II-2, and a shallow stratigraphic test trench was made. Since the lithics and hippo bones found here were apparently associated, Chavaillon (1978) nicknamed it the “Hippo Butchery Site.” Field research was resumed in 1993 and again in 1995, when a total of 26 m² were excavated. More lithics and hippo bones were discovered, but were published only on a preliminary way (Chavaillon and Berthelet, 2004). In order to collect updated information, in 2012–2015 the Italian team carried on new excavations over ~35 m², documenting a stratigraphic sequence more complex than expected. A step-like trench was also dug, starting from the level reached in 1995 at Gombore II-2 and reaching the archaeological level of Gombore II-1. At a linear distance of about 30 m, a second stratigraphic sequence, Gombore X, which had been revealed by gully erosion, was cleared and documented. This made

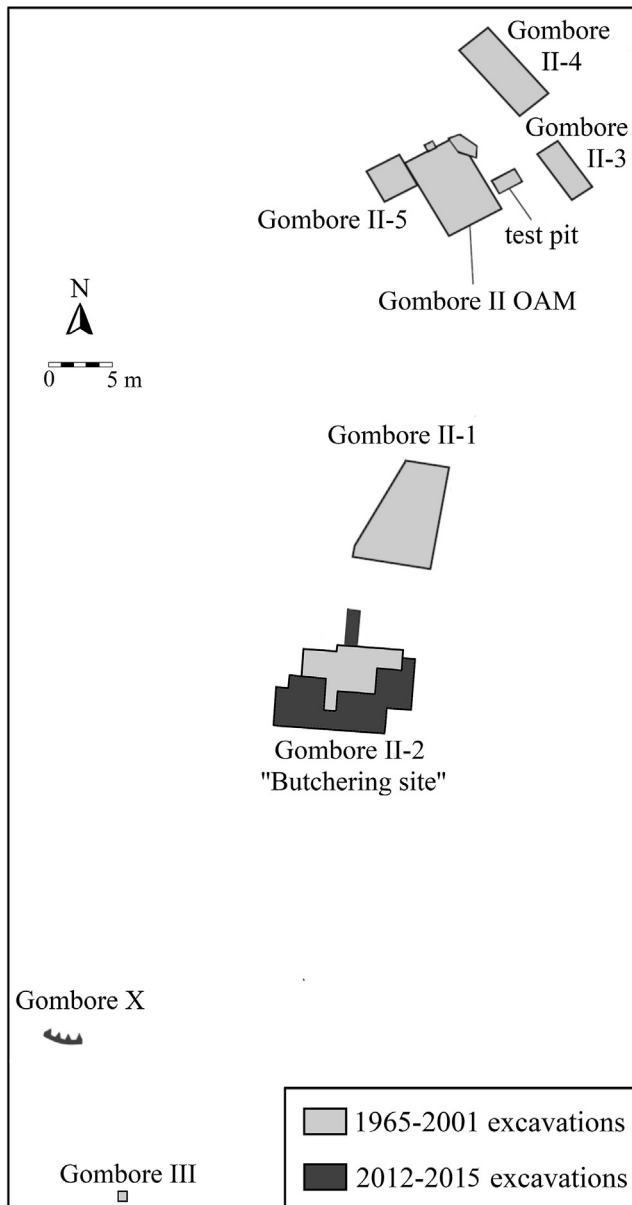


Fig. 2. General map of the excavated areas at Gombore II, together with the natural section of Gombore X and with the test excavation at Gombore III (modified after Gallotti et al., 2010, Fig. 5).

it possible to obtain the complete record of a ~5 m depth profile between the layers dated ~850 ka and ~700 ka.

The uppermost part of the stratigraphic sequence of the gully is found at Gombore III, about 40 m south of Gombore II-2. Gombore III was one of the first sites discovered at Melka Kunture, and was tested by Chavaillon in 1965. An archaeological layer is in the fluvio-lacustrine deposits on top of the ~700 ka ash flow, which was originally labelled “tuff D” (SI 1).

2.3. The stratigraphic sequence

According to the combined information provided in Gallotti et al. (2010) and our own fieldwork, the following stratigraphic sequence is recorded on top of the 875 ± 10 ka lower ash flow, proceeding from bottom to top (Fig. 3):

- Unit 1 (200 cm): fluvial silty, sandy and gravelly sediments with lenses of obsidian gravels at the top, including a Middle Acheulean layer rich in pebbles and cobbles, locally split into two sub-layers; a few small redeposited obsidian flakes are present in coarse sands just above the archaeological level.
- Unit 2 (210 cm): clays and silts (containing hippo remains), which indicate deposition in slowly-flowing water, interrupted by a phase of sand accumulation. At the top of Unit 2, evidence of erosion and soil development.
- Unit 3 (80 cm): silty-sandy lenses, occasionally including pumices and redeposited pyroclastic elements. At the interface with the clays of Unit 2, a rich pollen spectrum was extracted from sample Gombore 173 (Bonnieffille, 1972) that we now place at the bottom of Unit 3. Tamrat et al. (2013) detected the Matuyama-Brunhes boundary within the Unit, providing chronological constraint at ~0.78 Ma. Fauna and lithics are present at various levels. At the top is the “Hippo Butchery Site” (Gombore II-2), containing Acheulean lithic artefacts (SI 2), also discovered at Gombore X (SI 3).
- Unit 4 (70 cm): silty sediments of volcanic origin dated to 709 ± 13 ka, including two distinct beds separated by diatom-rich lenses (SI 4). At the base are lithics and bones displaced from the uppermost part of Unit 3.
- Unit 5 (80 cm): sandy fluvial sediments with load structures, bone fragments and one cobble with percussion marks. Capping them are interbedded and consolidated sandy and silty sediments, containing poorly preserved archaeological and faunal remains in the top layer, which is the present-day surface layer. This layer corresponds to site Gombore III, briefly described in the literature as containing Acheulean industry in consolidated sands and gravels (Chavaillon and Piperno, 2004; Chavaillon et al., 1974) (SI 1).

2.3.1. Palynological analysis

Pollen samples were collected in the 1960s, and were carefully positioned in the stratigraphic sequence, as it was known at that time. The positions attributed then fit quite precisely with the stratigraphy described most recently and used in this paper. Eleven samples were taken along the 0.875–0.7 Ma stratigraphic succession, and 8 more samples from above the 0.7 Ma ignimbrite. In pollen extraction, acids (HCl and HF) are used to remove the mineral fraction. This step is followed by rinsing with hot water and treatment with diluted KOH to remove humic acids. The residue from the chemical processing is then placed in glycerin and coloured with safranin for microscope observation. Unfortunately, in most samples pollen preservation was very poor. Only two samples turned out to contain a sizeable number of grains. The sample was identified by comparing it with a 7000-specimen reference collection of pollen from present-day plants, focusing on East African vegetation. Detailed information on stratigraphy, sampling and sample treatment is available in Bonnieffille (1972).

At the interface of Unit 2 with Unit 3, a rich pollen spectrum with a total of 573 pollen grains was extracted from sample Gombore 173. Pollen from trees and shrubs account for 10% of the total, with almost 20 identified shrub or tree taxa. There is a low percentage of *Juniperus* pollen, whereas *Maesa* appears, this being a common tree in the Shewa forests. The occurrence of Ericaceae (mountain heather) is worth noting. Ebenaceae, *Croton*, *Pterolobium*, with *Acacia* and *Carissa edulis*, associated with the shrubby *Heteromorpha* (Umbelliferae), point to the existence of a dense and diversified woody bushland in the area. Pollen from several Asteraceae species dominates (75%) the herbaceous pollen count and accounts for 67% of the total pollen count. This fits with an evergreen bushland that is normally found above the forest belt,

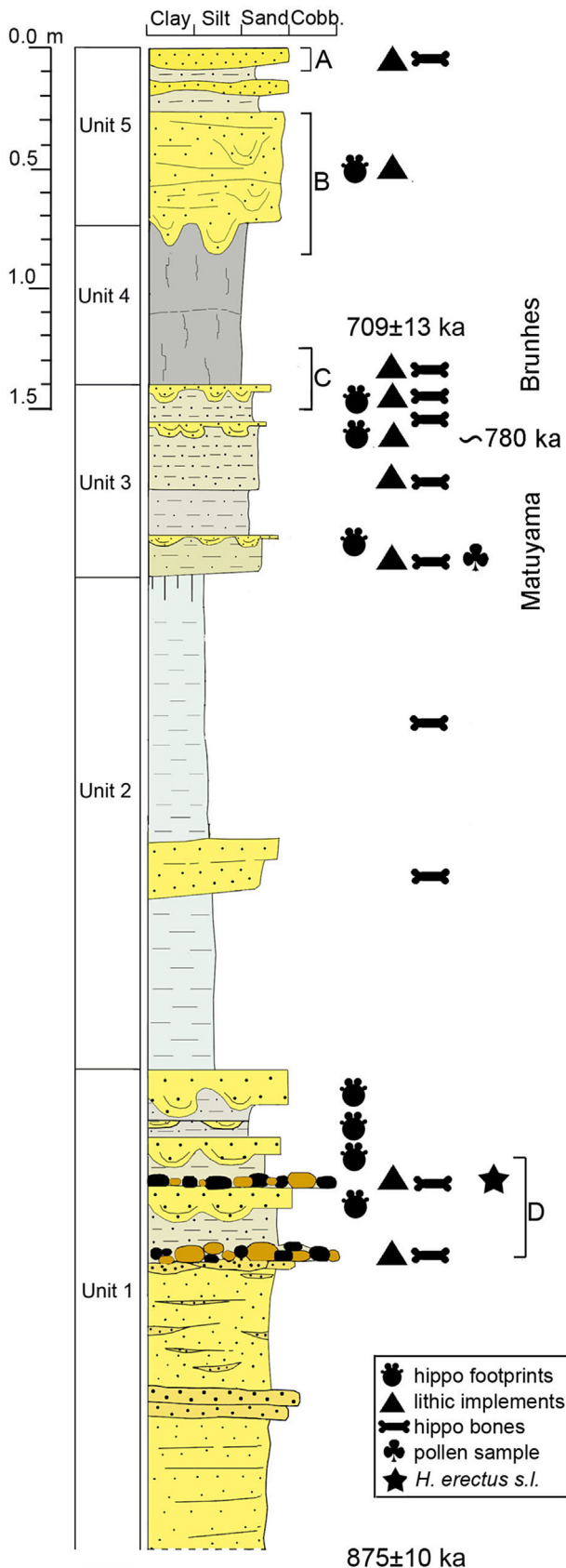


Fig. 3. Composite sedimentary sequence of Gombore II-2, Gombore X, Gombore II-1 and Gombore OAM. A: the uppermost Acheulean layer of Gombore II-2, at the same level as Gombore III; B: the newly excavated hippo footprints and trail at Gombore II-2; C: the so-called Acheulean "Hippo Butchery Site" at Gombore II-2; remains displaced

indicating climate conditions that were definitely drier and colder than they are today.

Another rich pollen spectrum, totalling 565 pollen grains, was extracted from sample Gombore 349. This was the sediment that filled the medullar cavity of a long bone fragment found at Gombore III, post-dating Gombore II-2 and the sequence described here. We include it for comparison purposes. The spectrum shows a rich and diversified arboreal component comprising 28 tree and shrub taxa. Most of the trees are the same as those found in sample Gombore 173. New occurrences in pollen composition, such as *Sapium* (Sapotaceae), *Fagaropsis* (Rutaceae), *Diospyros* (Ebenaceae), and *Osyris* (Santalaceae), a tall herb, indicate a fairly humid forest with a dense canopy (17.5%).

2.3.2. The deposition of the ~700 ka ash-flow (Unit 4)

Optical and petrographic observations (e.g. Fig. SI 4a) of Unit 4 deposits, i.e. of the ~700 ka volcanic sediments, show that both beds are made up of relatively loose sediments consisting of volcanic clasts embedded in a silty matrix. X-ray powder diffraction patterns indicate that the volcanic minerals are potassium-feldspar and quartz with subordinate plagioclase; the silty matrix is essentially composed of mixed-layer illite-smectite clay minerals. The X-ray diffraction pattern does not show any calcium carbonate peak. SEM analyses provide more information; selected images are shown in Figs. SI 4b to SI 4d. All the volcanic clasts (feldspars and quartz grains) have more or less rounded shapes, suggesting a certain degree of transportation, probably over a short distance. Abundant diatoms (Fig. SI 4c) account for up to ~20–25% of the sediment (Fig. SI 4c). Late depositions of Mn-oxides are occasionally observed (Fig. SI 4d); at the hand-specimen scale, they appear as very thin, blackish layers. The combined petrographic and mineralogical observations suggest the sedimentation of an ash fall in a body of still water. The diatoms indicate that sedimentation was interrupted between the deposition of the first bed and that of the second.

3. Load and erosional features produced by hippos

During the recent excavations we noted a number of load and erosional features that had previously escaped attention and that we eventually related to the impact of Pleistocene hippos.

The original surface of the ~700 ka ash flow (Unit 4) is sub-horizontal and fairly uniform. All over we found a number of features that had been filled by sands from the layer above. Viewed from above, their outlines range from sub-circular to elliptical. Some of them, being set in the walls of the excavation, had been cut through, resulting in vertical sections. Their shape is generally columnar, often expanding into toe-like lobes in the lower half (Fig. 4). Crushed silty-sandy lenses in the sectioned infillings suggest that the sediment had been pressed down into the ignimbrite layer.

We removed the sandy infilling from one of the better preserved features and made a positive plaster cast of it. In other cases, we chiselled away the ignimbrite surrounding the imprints and obtained freestanding natural casts made up of consolidated sands and silts. The moulds and casts provided detailed 3D models of the legs and feet of a large mammal. Its legs, documented for a length of

from this layer are also found at the base of the ~700 ka ash-flow; D: the Middle Acheulean layer at Gombore II-1, Gombore OAM and minor sub-sites, locally split into two lenses. Sample 27-08, dated to 875 ± 10 ka, and sample 27-09, dated to 709 ± 13 ka (Morgan et al., 2012), were extracted respectively just below Unit 1 and in the middle of Unit 4. The Matuyama/Brunhes reversal has been recognized in Unit 3 by Tamrat et al. (2013).

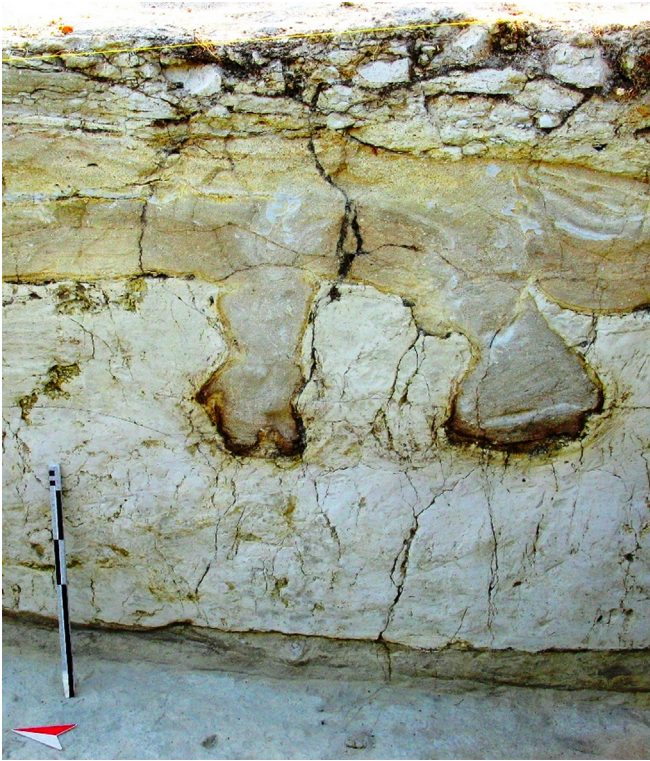


Fig. 4. Sectioned hippo footprint along the eastern excavation wall at Gombore II-2 (Scale bar = 50 cm).

over 20–35 cm, were columnar in shape and ended with four toes. The two central toes slant slightly away from each other, while the two lateral ones are more outspread (Fig. 5).

The casts and sections point unambiguously to a massive artiodactyl with four well-developed functional toes on each foot: a characteristic unique to hippos (Eltringham, 1999; Fisher et al.,

2010). Moreover, the morphology of these footprints is characterized by a plantar surface with multiple, poorly developed cushion-like convexities (Fig. 5c), that make it possible to distinguish hippos from elephants and rhinos. Elephant footprints are oval-to-round in shape, their surface is concave and they have four barely distinguishable toes (or toenails) in front. Conversely, rhino prints, though likewise elliptical in shape, have only three toes (or toenails); the central one is the largest. Furthermore, hippos abounded at Melka Kunture, but elephants are little represented and Rhinocerotidae remains are extremely rare (Geraads et al., 2004, in press).

The pressure exerted on deformable ground by massive hippos walking on it produced the load structures we observed, which are actually footprints. They sink from variously superposed sandy lenses. Some of them reach the volcanic deposit and warp it. Two exceptionally deep ones sink 50 cm down into the ash flow. This is positive evidence that at the time the water-saturated volcanic deposit was not yet fully consolidated.

In the SW of the area excavated in 2014, the sand-filled footprints are clustered and often superimposed on each other, merging into indistinct features. This part of the area turns into a channel-like depression up to 2 m wide, with a concave bottom and an asymmetrical profile: the eastern side is bank-like, going straight down from the surface of the volcanic deposit to 0.4 m deep; the western side is smoother, sloping gradually 0.2 m below the top of the tuff (SI 5). This is an erosional feature, exposed over 6 m in length, in which the footprints converge; it continues along the excavation walls (SI 5, bottom). Taking the behaviour of present-day hippos as an analogue, we interpret this feature as a paleo hippo trail, like the one identified in Olduvai (Ashley and Liutkus, 2003).

At Gombore X, hippo footprints occur in the same layer as at Gombore II-2; they were left by animals walking over the ~700 ka ash flow and the capping sand lenses.

3.1. Footprints encountered during previous excavations

After identifying fossil footprints at Gombore II-2 and Gombore

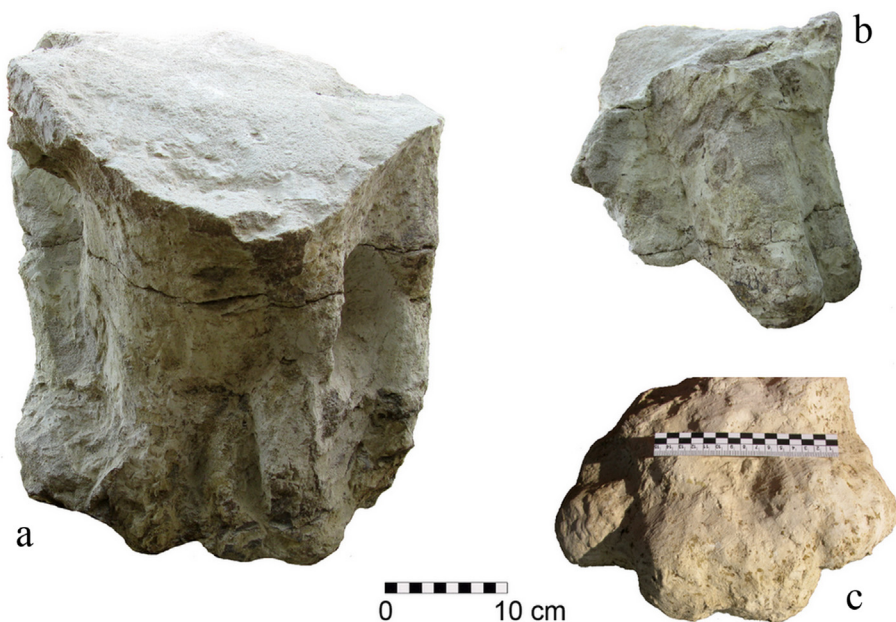


Fig. 5. Gombore II-2: Casts of hippo prints excavated in Unit 5 of Fig. 3: a-b) free-standing natural casts of consolidated sediment; c) plaster cast of an emptied footprint, with the plantar face upwards.

X, we re-analysed the archived photos taken by Chavaillon and his team, the walls of previous excavations, and published drawn records.

At Gombore OAM, we located gravitational bioturbations along the excavation walls that match those at Gombore II-2. They sink down from and are included in at least three distinct layers in the laminated sandy deposits that cap the ~850 ka Middle Acheulean layer. In particular, they include a 23 cm-wide columnar element ending with three toe-like appendices (Fig. 6). Like other large ones (SI 6), it is definitely a hippo footprint.

Other hippo prints had been found at Gombore II-1, as recorded in 20th-century pictures (SI 7). Here the Middle Acheulean layer is split in two by a sterile sand deposit. These footprints are evidence that, during the period when the intermediate sands were accumulating, hippos were walking around on ground that was still soft. More bioturbations occur in the capping silts and sands, at no fewer than three separate levels, possibly corresponding stratigraphically to those at Gombore OAM.

Summing up, footprints were discovered during current and past excavations in 8 different levels, above as well as under the clays of Unit 2.

4. A changing environment at the Mid Pleistocene Transition

The combined archaeological, paleontological, mineralogical, ichnological and palynological evidence makes it possible to reconstruct a detailed sequence of events.

At Gombore II, after the ~875 ka volcanic eruption, more than 1 m of silts and sands were deposited, with channel lag on top. A stream eroded the riverbanks. Lithics and animal bones that were lying around were eventually redeposited and piled up. Taken as a whole, this is a Middle Acheulean deposit extending over an area

estimated at ~1000 m². Many lithic tools have been unearthed (Fig. 7). According to Gallotti et al. (2010), the Gombore OAM assemblage lay abandoned on a bank before being displaced and jumbled by the stream, probably more than once. The substantial number of pebbles and cobbles suggests a relatively high-energy deposition, understood as having had a polygenic history. The embedded paleontological and archaeological material attests to environmental resilience after the ash flow submerged the area. At the top, much finer-grained laminated silt and sand layers point to the re-establishment of a low-energy environment, while hippos trampled the ground at nearby Gombore II-1. The stream acquired new energy and was again able to carry cobbles. Locally, fauna and lithics were redeposited, as they were at Gombore OAM and Gombore II-1, in the latter case together with human remains, i.e. two skull fragments of *Homo erectus* s.l. (Chavaillon and Coppens, 1986; Chavaillon et al., 1974) (Fig. 8), recently considered a candidate for the ancestral occurrence of *Homo heidelbergensis* (Profico et al., 2016).

A new cycle of low-energy deposition began. Sands accumulated, and footprints at various levels provide direct evidence of ongoing animal life. Hominins, however, do not seem to have been around anymore. Eventually ~2 m of clays were deposited in two successive cycles. A body of still water was thus in existence during long periods of time. There were some hippos, and they died nearby, as the finding of a few bones indicates. There is no hint of any hominin presence either in the clays (that is, when the environment was truly aquatic) or in the intermediate sands. According to pollen results, shortly after these cycles the area was still surrounded by evergreen bushland, a type of vegetation found today above the forest belt, at higher altitudes than Melka Kunture's. The vegetation points to climate conditions that were much drier and colder than they are today, and than they had ever been earlier, as

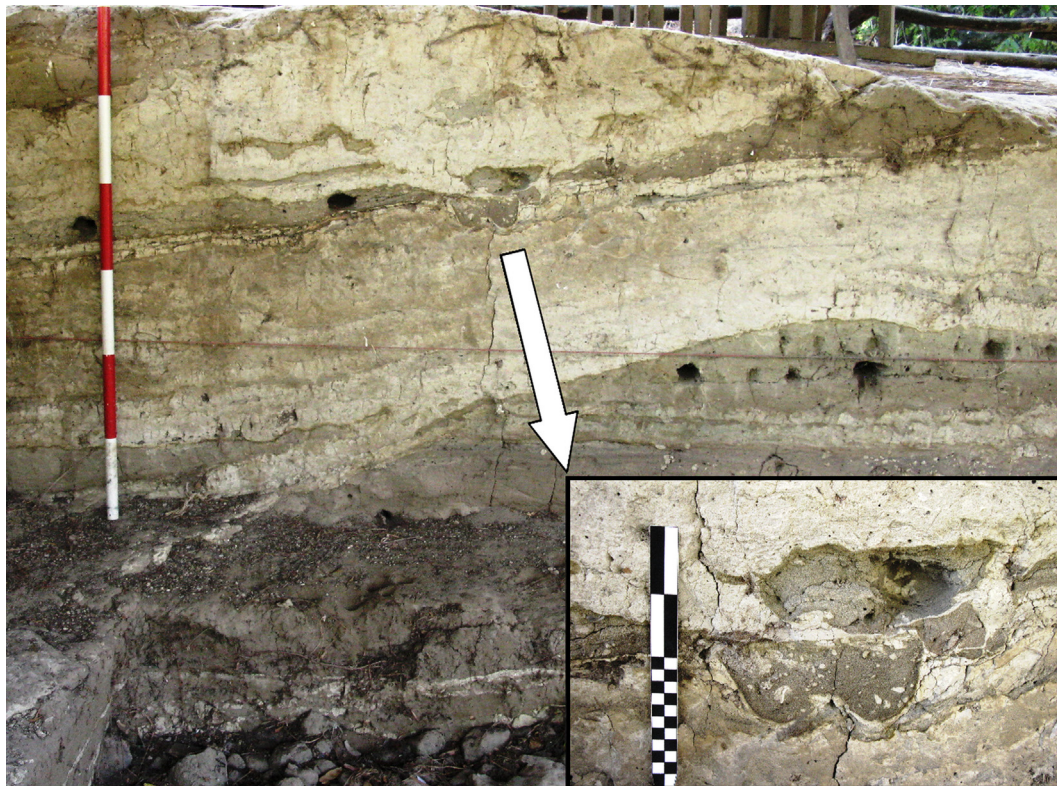


Fig. 6. Gombore OAM: a sectioned hippo footprint in the west wall of the excavated area, above the ~850 ka archaeological layer; today it is a museum exhibit. The footprint shown in the photo insert is 23 cm wide; it was impressed in a silt layer and eventually filled up with sand. The three lobes correspond to three of the animal's four toes.

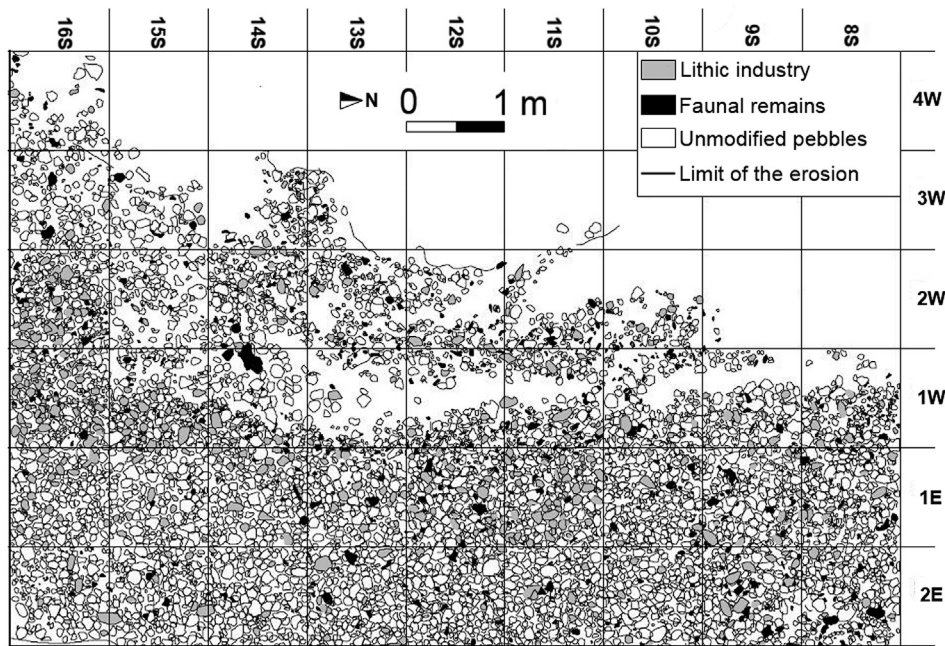


Fig. 7. Gombore II-1: planimetry of the excavated area, with the 1 m × 1 m grid (modified after Gallotti et al., 2010).



Fig. 8. Gombore II-1: Fragment of a left parietal bone of *Homo erectus* s.l. at the time of discovery in 1973 in the upper lens of the ~850 ka Middle Acheulean layer (hitherto unpublished photo; archives of the Archaeological Mission).

we know from Oldowan and earlier Acheulean layers (Bonnefille, 1972; Geraads et al., in press).

Changes occurred when the area later became drier again, and soil started to develop, indicating warmer climate conditions. After an erosion phase, more sands accumulated, ending with the layer including the “Hippo Butchery Site.” There is also evidence of hominin presence again, starting with a single core found at Gombore X, at the bottom of a layer of redeposited volcanic ashes in Unit 3. More Acheulean tools, including handaxes, as well as hippo remains, have been discovered eroding from several overlying sand layers (SI 3). Hippos continued to stay in the vicinity. Their fossil remains have been found at Gombore X, while at Gombore II-2 sands piled up and footprints were preserved. Archaeological evidence accumulated steadily. At the “Butchery Site,” well-preserved hippo bones account for most of the remains and are associated with Acheulean implements, thus providing ample archaeological and paleontological evidence. More lithics and hippo bones have

been found eroding out of the natural section of Gombore X. Between such occurrences, hippos once again impressed their footprints on sandy deposits. In all, we recognized three layers containing hippo footprints in Unit 3.

A dramatic disruption occurred at ~700 ka, when an ash flow submerged the gullies. Remains lying on the ground were moved by and partially incorporated in the spreading ashes. No articulated skeletal remains such as would suggest that the animals had been caught in the ash flow have been found here; there were probably safer areas in the vicinity to which animals could flee.

The detailed stratigraphy shows that diatoms proliferated in silica-rich waters before erosion probably redeposited the ash flow in a second bed. In a relatively short span of time, a hippo population re-established itself. The animals impressed new footprints on sand lenses that might have accumulated in few seasons above the uppermost water-saturated volcanic deposit. In their nighttime travels to and from grazing grounds they gradually eroded a trail: a proxy of the re-organization of the environment. Life was once again sustainable for many large animals, including individuals whose legs could measure as many as 35 cm in diameter. Their footprints are found at the same level at both Gombore II-2 and Gombore X, suggesting that a sizeable stretch along the riverbank, or possibly along a dead meander, had been re-colonized by a successful population. Archaeology is very scarce, but one cobble with percussion marks points to human activity nearby.

We find much less evidence of hippo activity and significantly more archaeology when the uppermost Unit 5 is eventually deposited, extending to and encompassing Gombore III, which has been investigated by Chavaillon. At the later site, after an Acheulean layer post-dating 0.7 Ma had deposited, the pollen composition indicates the presence of grasslands in the vicinity of a diversified forest with taxa pointing to an Afromontane rain forest growing under fairly humid conditions. Warmer and wetter climate conditions had been re-established.

4.1. Volcanic eruptions and resilience

Scientific monitoring of resilience following volcanic eruptions

in modern times provides comparative information for Pleistocene events. In 1943 the Parícutin volcano in the Mexican highlands started erupting and blanketed the landscape with 25 cm to 100 cm layer of ashes over an area with a radius of nearly 10 km (Burt, 1961; Egger, 1948, 1959). Few grass species were able to survive when the ash cover was thicker than 75 cm, but more were alive when it was less than 50 cm thick. Plants were quickly re-established after wind and water eroded away the ash. However, 50 years later the plant cover was still thin (Lindig-Cisnerosa et al., 2006). In 1991, the Hudson volcano in Patagonia produced a blanket of ash, but within a few months' time wind and rain had removed much of the suffocating cover over extensive areas (Pearson, 1994). Sixteen months after the eruption, the vegetation did not appear to have been severely affected. The Mount St. Helens eruption in 1980 caused wholesale destruction, but most of the pumice and ash cover was less than 30 cm thick. Larger animal species suffered greater mortality than smaller ones. However, the animals classified as “large” were actually medium-sized species: mountain goats, deer, elk and bears, not to mention human beings (Dale et al., 2005). Twenty-five years after the catastrophe, fauna and flora had recovered to a significant degree.

The modern evidence enabled WoldeGabriel et al. (2000) to work out an overall reconstruction of past environmental devastation in the Ethiopian Rift after volcanic events. However, Pleistocene archaeology cannot provide the kinds of details available for historic times. In the case of hippos, there is no modern analogue for their behaviour after eruptions. Grasses constitute most of their diet, even if meat eating and even cannibalism are known to occur (Eltringham, 1999). At night, away from the water, today's hippos graze on grasses growing in higher pastures. Throughout the Melka Kunture sequence, the local vegetation belonged to the “Dry evergreen Afromontane forest and grassland Complex,” with varying proportions of grasslands and high-altitude forests (Geraads et al., in press). At archaeological sites, the ~700 ka tuffs is 0.5–1 m thick, suggesting that grasses were totally blanketed over and suffocated by the ash flow. However, this data comes from parts of the landscape where the ash flow had been channelled. On slightly higher ground, the ash blanket must have been thinner and the vegetation may not have been totally wiped out. Nevertheless, we may take it for granted that the eruption had catastrophic effects on vegetation, on fauna (including hippos, which are grazers), and on any hominin group living within their range.

5. Discussion

The Gombore II sequence lasted over 150,000 years, including periods of erosion as well as of clay accumulation, which cannot be pinpointed precisely in time. However, several undisturbed layers of footprints impressed in silts and sands, together with multiple archaeological and paleontological occurrences, suggest shorter and well-defined periods. This, in turn, makes it possible to track with comparatively fine chronological resolution the multiple returns of life, including hominin presence, after environmental disruptions, related to volcanic events and/or to changing climatic conditions.

The ~850 ka Middle Acheulean layer extensively records hominin presence and activity. Later on, however, while the hippos continuously left plain evidence of their presence during quiet phases of laminated sand deposition (upper part of Unit 1), and then during clay deposition in ponds or meanders when the climate turned cold (Unit 2), hominins do not seem to have been around anymore. They became part of the archaeological landscape again after the area dried out. Thenceforth the record they produced constantly co-occurs with hippo remains and prints. Accordingly, they were living at a short distance from hippo herds. At least five

archaeological episodes of co-occurrence are well documented in the stratigraphic sequence up to and including the so-called “Hippo Butchery Site.” Seasonal or otherwise cyclic returns of hominin groups are a distinct possibility.

The ~700 ka ash flow interrupted this pattern. Its impact on hippos does not appear to have been a lasting one, for they returned when the reworked volcanic deposit was still in a plastic state, after erosion had probably removed ash from higher ground. The hippos' tramping back and forth between resting places near or in the water and re-established grazing grounds gradually modified an area where sands were accumulating, and eventually wore a trail through it.

The cobble with percussion marks found at Gombore II-2 is a discreet sign of the presence of hominins; it also points indirectly to their avoidance of watery environments. When the area dried out, hominins returned; Acheulean implements litter the ground not far below its present-day level and were also discovered at Gombore III. Later, under warm and wet climate conditions, dense forest vegetation developed.

The dated tuffs and the Matuyama-Brunhes boundary impose age constraints on the lithostratigraphic units and related archaeological evidence. This, in turn, allows their age to be reconciled with the known age of marine isotope stages at the MPT (Head and Gibbard, 2005; Elderfield et al., 2012; Lisiecki and Raymo, 2005). At ~850 ka, the extensive Middle Acheulean deposit of upper Unit 1 is related to hominin activity during MIS 21. Unit 2, capped by a layer containing pollen from vegetation characteristic of cold and dry mountain environments, fits well with MIS 20. Unit 3 was being deposited at the time of the Matuyama-Brunhes boundary, which happened during MIS 19, at ~780 ka, and at 773 ka according to the revised chronology of Channell et al. (2010). Hominins started once again leaving their marks on the record. Unit 3, containing more archaeological evidence, apparently continued to be deposited during the double cold peak of MIS 18, which is also well documented in the Eastern Mediterranean (Almogi-Labin, 2011), and which was interrupted by a warmer oscillation. The so-called “Hippo Butchery Site” provides further evidence during MIS 17, while the dated tuff making Unit 4 at ~700 ka likewise corresponds to this isotope stage. Unit 5, the Acheulean of Gombore III, and the dense forest vegetation that developed later, cannot be attributed to any specific isotope stage.

In other gullies of Melka Kunture the chronological resolution is lower. Upstream of the Awash River, on the right bank, in the Simbiro gully a major stratigraphic sequence with Acheulean layers pre-dates 878 ± 14 ka (Morgan et al., 2012) (contra Tamrat et al., 2013, who mistakenly place the dated layer at the base of the sequence), and accordingly is not relevant here. In the double Garba gully, conversely, sedimentation occurred in parallel with Gombore gully. The record assembled by Chavaillon and his team so far suggests a similar dearth of archaeological evidence at the MPT (Chavaillon et al., 1979; Chavaillon and Berthelet, 2004) above the tuff dated at 869 ± 20 ka by Morgan et al. (2012). This is also the case in the Kella valley, on the opposite side of the Awash River, which has a Middle Pleistocene sequence ending at 726 ± 18 ka.

6. Conclusions

The record of Melka Kunture makes it possible to expand the search for human origins to higher elevations of East Africa where Afromontane forest, bushland and grassland developed.

The evidence assembled to date indicates that there were periods when hominins were not part of the picture, at least not in the sequence we investigated. This was definitely the case after the ~850 ka archaeological layer had been deposited and a bushland developed in a definitely cold climate.

Re-peopling occurred later, during MIS 19, and accordingly when the climate was turning warmer again. Apparently, cyclic returns to the area were established and continued during the two cold oscillations of MIS 18, which are known to have been of limited amplitude and included a warmer period. Human settlement was then interrupted by the ~700 ka eruption. After this catastrophic event, the hippos seem to have returned relatively quickly. In modern hippo populations, dramatic fluctuations due to poaching, habitat encroachment or drought have been followed by new surges of population in the next 20–30 years (Kanga et al., 2011; O'Connor and Campbell, 1986). In the case of hominins, the recovery was slower, but new evidence occurs at the very top of Unit 5.

Overall, at the MPT hominin peopling and hippo population dynamics proceeded at a different pace. While the hippos left near-continuous evidence all over the sequence, at 2000 m asl the uninterrupted cold and dry spell of MIS 20 seems to have imposed insurmountable limits to *Homo erectus* s.l. adaptation. Conversely, later the warmer climate of MIS 19 allowed hominins to return often to the Gombore gully. It may have also happened during the cold phases of MIS 18, and certainly did during MIS 17. The ~700 ka volcanic eruption, however, definitely marks an interruption, and hominins took quite a while to adjust to it.

Author contributions

M.M. designed the project and wrote the paper. F.A. (excavations and ichnology), R.B. (palynology), D.D.R. (volcanology) and R.T.M. (stratigraphy) conducted research.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quascirev.2016.07.033>.

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