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A Middle Pleistocene hippo tracksite at Gombore II-2 (Melka Kunture, Upper Awash, Ethiopia)

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ABSTRACT

In this paper we describe exceptionally well-preserved evidence of hippo activity at Gombore II-2, a 700,000 year-old site at Melka Kunture, at 2000 m asl in the Ethiopian highlands, in the Upper Awash Valley. We excavated and made casts of footprints that had been left after a volcanic eruption. The 3D casts provide a detailed record of the outer anatomy and soft tissues of Pleistocene hippos. They reveal for the first time the shape of the legs and feet of the animals. Gombore II-2 also provides information on the behavior of past hippos. This prominent species of the African wildlife affects the vegetation and the landscape, and acts as a geomorphological agent. The animals wallow beside bodies of water and erode deep trails linking them to pastures. At Gombore II-2 the trampling marks converge toward an erosional feature that we interpret as a fossil trail, documenting an early Middle Pleistocene behavior similar to that of today. Signs of trampling and erosional features interpreted as hippo trails have also been described in Pliocene and early Pleistocene levels at Olduvai and Koobi Fora. We further underline that the hippo population of this tract of the valley was resilient and re-established itself not long time after the volcanic eruption.

1. Introduction

Hippopotamus amphibius, the common hippo, is a prominent and locally dominant sub-Saharan species (Field, 1968; Eltringham, 1999; Chansa et al., 2011). Living in groups, or "schools" (Eltringham, 1999), of up to several dozens of adults, these animals have a strong impact on the environment, both direct and indirect. At night, they leave the wallows, ponds and rivers where they spend most of the daytime, and set off to forage to places that may be a few km away. They tend to follow established trails to the same grazing spots, where they pluck the grass with their lips, producing characteristic closely-cropped patches known as "hippo lawns" (Lock, 1972). They also act as geomorphological agents, wallowing beside bodies of water where they enlarge and deepen their favorite resting places. Being huge animals—an adult weighs 1.5 ton or more—with relatively small feet (Eltringham, 1999), their trampling back and forth along the same trails erodes the ground into long shallow trenches that are easily recognizable in the landscape and sometimes become real gullies. As time goes on, the trail floors get harder and harder, and retain their profile even when flooded by seasonally rising waters. The geomorphological impact of hippos and the channeling of water along their trails has been described both in the Ngorongoro crater (Tanzania) and in the Okavango Delta (Botswana), where hippos are viewed as "ecosystem engineers" (McCarthy et al., 1998; Deocampo, 2002; Mosepele et al., 2009).

As in the present, hippos were a feature of past sub-Saharan wildlife. In East Africa their fossil remains are frequently unearthed at Pleistocene archaeological sites. At Koobi Fora, early evidence of hominin-hippo interaction was also discovered: cut-marks were identified on 1.5 Ma-old hippopotamid bones (Bunn, 1994; Pobiner et al., 2008). A "hippo turnover" occurred at ca.1 Ma, when *Hippopotamus* became the dominant hippopotamid group in Africa (Boisserie and Gilbert, 2008).

Here we will focus on evidence subsequent to this event. We will describe in detail new Middle Pleistocene evidence discovered at Melka Kunture, when *Hippopotamus* was a permanent part of the landscape.

1.1. General introduction to Melka Kunture

Melka Kunture, a cluster of archaeological sites extending along the Upper Awash Valley on the Ethiopian highlands (Fig. 1), is well suited to provide evidence of past hippo behavior. The Pleistocene environment was characterized not only by the slow-flowing Awash river, which meandered in a half-graben depression, but also, at least seasonally, by a variety of abandoned meanders and still bodies of water (Raynal et al., 2004). Furthermore, the landscape was modified repeatedly by

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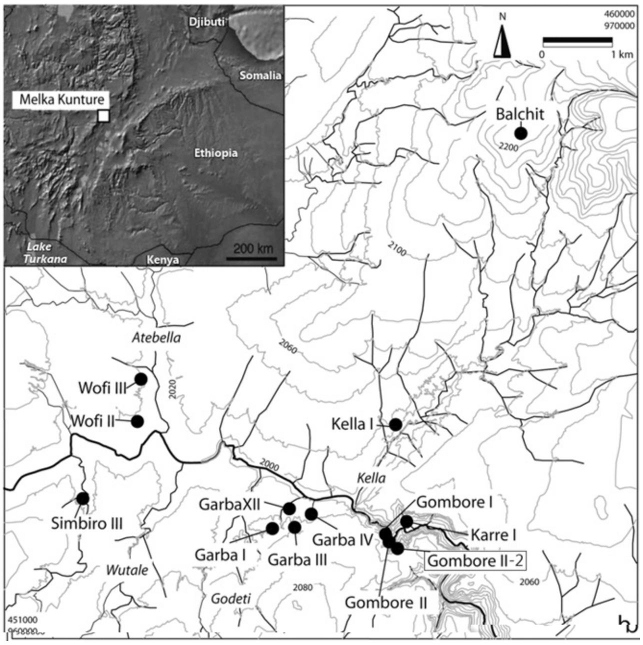

Fig. 1. The main archaeological sites of Melka Kunture, including Gombore II-2. Insert: Melka Kunture, in the Main Ethiopian Rift.

the thick volcanic ash fallout, which clogged the streams and led to the formation of shallow ponds and pools. Starting at ca. 1.7 Ma, the vast archaeological record includes a number of Oldowan, Acheulean, Middle Stone Age and Late Stone Age sites (Chavaillon and Berthelet, 2004; Piperno et al., 2008; Mussi et al., 2014). The fauna discovered at sites close to the main river is invariably dominated by hippos determined as *Hippopotamus* cf. *amphibius* (Geraads et al., 2004; Gallotti et al., 2010; Geraads et al., 2017).

The Melka Kunture sites are named after the gullies and valleys where they are located, i.e. the tributaries of the Awash that drain the area, many of them seasonally. The name of the gully or valley is followed by the consecutive Roman numeral identifying the specific site. Exceptionally well-preserved evidence of hippo activity, including footprints, was recently discovered at Gombore II-2, a 700,000 year-old site of Melka Kunture which is part of a geological sequence documenting environmental change at the Mid-Pleistocene Transition (Mussi et al., 2016). The record described here in detail was produced on layers of volcanic ashes soon after volcanic eruptions. It also makes it possible to address questions related to hippo population resilience.

1.2. Gombore II-2, location and history of excavations

Archaeological surveys and excavations were first undertaken in the area of Melka Kunture by Gérard Bailloud (1965), and then by Jean Chavaillon, who directed the French Archaeological Mission from 1965 to 1998. Since 1999, research at Melka Kunture has been under the responsibility of the Italian Archaeological Mission, first directed by Marcello Piperno and, since 2011, by one of the authors of this paper (M.M.).

Gombore II-2 is a site at the top of the early and Middle Pleistocene stratigraphic sequence of Gombore gully, on the right bank of the Awash River (Egels, 1971; Chavaillon and Berthelet, 2004; Gallotti et al., 2010; Kieffer et al., 2004; Morgan et al., 2012; Mussi et al., 2016; Raynal et al., 2004). The archaeology was first investigated in 1974, when members of the French team noticed some fossils eroding from the top of the gully (Chavaillon and Berthelet, 2004).

A test stratigraphic excavation grid just 20 cm deep was dug over 7 m^2. Outside the grid, a systematic collection of exposed materials was also made over another 7 m^2 area. A total of 126 objects were collected: 49 lithic implements and 77 faunal remains, most of which were hippo bones. After preliminary determinations by Denis Geraads, at least two individual hippos were identified, together with some giraffid and equid remains (Chavaillon, 1975, 1976). The site, currently called Gombore II-2, was named at the time "Gombore IIA".

More excavations were planned for the 1980s, but were delayed because of the difficult political situation in Ethiopia at that time (Chavaillon, 1981–1982). New research eventually started again in 1993. In 1993 and 1995, Jean-Luc Boisaubert excavated 26 m^2. More lithic industry was discovered, together with fossil hippo bones (Chavaillon and Berthelet, 2004). Since 2001, the area excavated by the French team has been open to tourist visits, together with casts of the bone and lithic finds, and a panel suggesting that this had been a prehistoric hippo butchering site (Chavaillon and Piperno, 2004).

In 2012, the Italian team started a new project aiming to gather updated information. This led to the discovery that the stratigraphic sequence was more complex than expected. For one thing, on top of the already researched archaeological site was a previously unrecorded layer displaying the features discussed below.

1.3. Gombore II-2, stratigraphy and dating

Raynal et al. (2004) provided a detailed description of the stratigraphic sequence of Gombore gully, from the early and Middle Pleistocene, while absolute dates are available in Morgan et al. (2012) for episodic volcanic deposits alternating with fluvio-lacustrine deposits. Close to the Awash and almost at the river's present-day level, the earliest site is Gombore I, containing Oldowan lithic industry. Just 100 m upstream lies Gombore II, which includes several sub-sites (Gombore II-1, Gombore II-3, Gombore II-4, Gombore II-5, Gombore OAM), all of them just above a tuff unit dated by $^{40}Ar/^{39}Ar$ to ca. 875 ka (Morgan et al., 2012). Thousands of Acheulean lithic implements were found with faunal remains. The record was dominated by *Hippopotamus* cf. *amphibius*, as was the case everywhere else at Melka Kunture (Gallotti et al., 2010).

Gombore II-2 was discovered in the upper part of the sequence, 5 m higher up in the stratigraphy than the other Gombore II sub-sites. In 2013, 2014 and 2015, we re-excavated the uppermost 1.5 m of the sequence described below. A volcanic layer at the top of the succession is dated by $^{40}Ar/^{39}Ar$ to 0.709 ± 0.013 Ma (MK27-09), i.e. at the beginning of the Middle Pleistocene (Morgan et al., 2012). It lies atop the layer where we discovered the features described in this paper.

2. Materials and methods

2.1. Recent stratigraphic excavations

The main archaeological area of Gombore II-2 was re-investigated over a total of roughly 35 m^2, extending southward the previously researched area (Fig. 2). The general 1x1m grid of the area had been established in the last century by the French team, and was documented in the literature (Chavaillon and Berthelet, 2004). We followed it, and the related nomenclature, identifying each square meter by a consecutive letter and number (Fig. 2).

The excavation method is the one called "décapage horizontal": the deposit is removed progressively one thin layer at a time. Every feature observed in the ground is carefully isolated using scalpels and small brushes. This meticulous and time-consuming method revealed features of different sizes and shapes in the upper part of a volcanic layer just below the one dated 700,000 years ago. They had been filled by sand from the overlying deposit.

The features, which had gone unnoticed during the 20th-century excavations in the adjacent area, were quite deep, up to 50 cm. They were also visible in the vertical and horizontal sections of previous excavations. Bag- or bell-shaped, they sometimes even included toe-like protrusions.

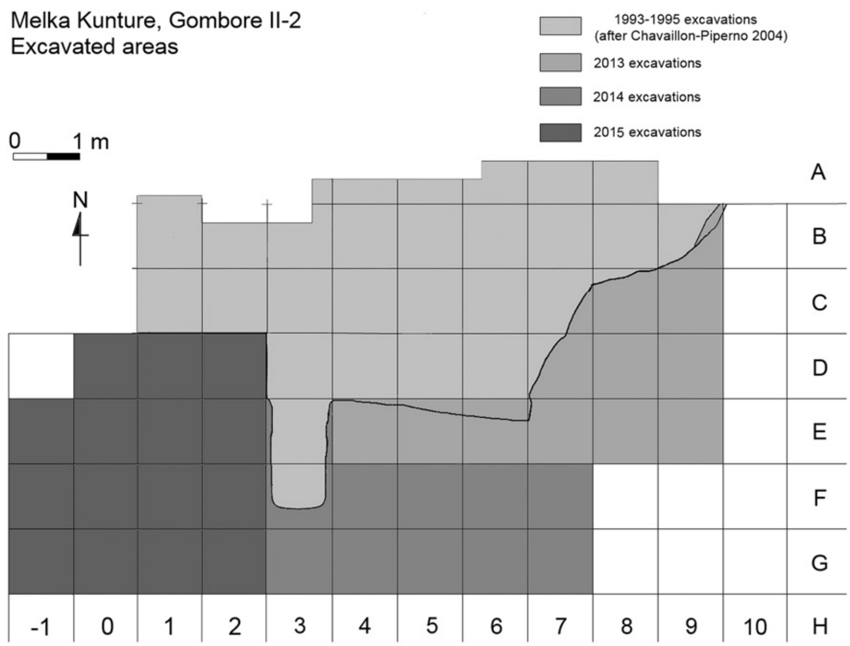

Fig. 2. Gombore II-2: excavation grid.

To make casts of some of these shapes, they were emptied of the sand that had filled them and refilled with plaster. When the plaster was dry and hardened, the volcanic sediment around it was removed, leaving us with a free-standing cast which we could then extract from the deposit. Natural casts were also made directly, leaving in place the concretioned sandy fill and scraping away the surrounding volcanic deposit. In several instances this made it possible to preserve the exact shape of the hollow feature. In order to remove the casts safely, they were consolidated with Paraloid diluted in acetone at a 10% concentration.

Once the surface of the volcanic deposit was completely visible, the excavated features were drawn on graph paper, and also recorded by photogrammetry. The vertical walls, i.e. the sections enclosing the excavated area, were recorded by laser scanning.

Conventional drawings were made both of the general planimetry and of the emptied or free-standing natural casts. The vertical walls and the emptied or exposed features, were rendered graphically. The scale was 1:5 or 1:10, depending on their size and details.

Photogrammetry was produced by pictures of the paleosurface taken from zenithal elevations. A detailed lithostratigraphic analysis was carried out along the standing wall of the excavation.

3. Results

3.1. Stratigraphic and palaeoenvironmental reconstruction

From bottom to top, four lithostratigraphic units were recognized (Fig. 3). Unit 4 is the lowermost one. It is composed of plane-laminated sandy and silty-sandy fluvial sediments with signs of bioturbation. This layer, more than 25 cm thick, contains bones and lithic industry (Middle Acheulean).

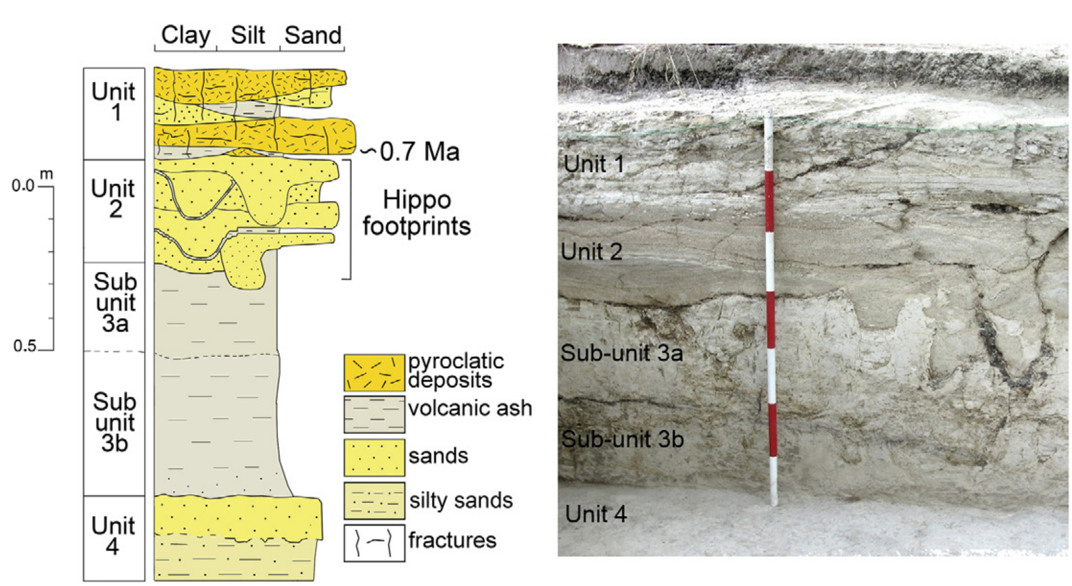

Fig. 3. Gombore II-2, stratigraphic units. Concise log (left); stratigraphy readable on the excavation walls (right).

Unit 3, a volcanic deposit, is c. 80 cm thick. Raynal et al. (2004) described it as a dacitic cinereous tuff deposited in water. At first sight the tuff looks like a single massive beige-gray unit, but upon detailed inspection a division into two subunits appears: Sub-Unit 3b and Sub-Unit 3a, separated by a thin irregular surface. Both sub-units are mainly composed of volcanic silty-clayey sediments. Sub-Unit 3b, the lower one, is mainly silty-sandy at the bottom and turns silty-clayey toward the top. This sub-unit is a distal deposit of an ash cloud surge that entered a watery environment. Scattered bones and lithics remnants are concentrated at the base, locally mixing with sand. This is evidence that the ash-flow moved, carried and redeposited materials lying on the surface of the underlying Unit 4. Sub-Unit 3a, the upper sub-unit, is characterized by silty-clayey sediments that probably originated from erosion of the volcanic deposit outcropping in the surrounding area. Alternatively, it could have been a second ash cloud entering in water shortly after the first one. At the bottom, just above Sub-Unit 3b, there are lenses of both broken and well-preserved diatoms that are evidence of a short period of water stagnation. Sub-Unit 3a contains the load structures described below.

Unit 2, up to 50 cm thick, is made of coarse volcanic sand levels interbedded with thin silty levels. The deposit is heavily bioturbated and shows planar cross-stratification.

Unit 1, the uppermost unit, is composed of interbedded and deeply fractured sandy and silty sediments with reworked pumices dated at c.700,000 years ago (Morgan et al., 2012). On the top of this 30 cm-thick layer is a partly eroded archaeological layer nearly level with the present-day ground surface.

3.2. Description of the load structures

The top surface of tuff Unit 3 (ca. 0.7 Ma) is usually sub-horizontal and slightly slanting from NW to SE. However, in the central and north-western portion of the excavated area, the level's surface deepens into a channel-like depression 1.4–2 m wide (Figs. 4, 5). This erosional feature runs from NW to SE. It was exposed over 6 m in length, and is truncated in the middle and at both ends; at the southern end it continues beyond the excavated area, while in the central part and in the northern extension it was truncated by the 1995 excavation. The bottom of this erosion structure is concave and uniform, and sinks as much as 0.4 m deeper than the original surface of the ignimbrite.

On the whole surface of this volcanic flow, we recognized a number of sand-filled disturbances with circular or elliptical shapes 15 to 60 cm in diameter. In some areas, the features are found at some distance from each other, while elsewhere, as in squares F5–F6, they are grouped closely together (Fig. 4). They cluster in the central-western part of the excavation, merging into the channel-like depression described above. At the bottom of the channel, the features are packed so closely together that they cannot be distinguished as separate entities. The sand infill now consists of continuous, irregularly shaped and superimposed lenses, while the ignimbrite is almost completely eroded (Figs. 4, 6).

Along the excavation walls, some features had been sectioned more or less vertically. They are column-shaped, often expanding into semi-circular lobes at the bottom. Two features on the eastern wall are exceptionally long; they sink 50 cm into the ignimbrite from the lowest lenses in fluvio-lacustrine Unit 2 (Fig. 7A). One ends with three toe-like lobes. In the sectioned infilling we also noticed crushed silty-sandy lenses, as if the sediment had been pressed down into the ignimbrite layer.

Most of the stratigraphy contains evidence of heavy load disturbance. Along the walls, there are sectioned columnar features and sectioned bioturbated paleo-surfaces. The silty-sandy lenses in Unit 2 have been churned, and the surface of the tuff (Unit 3) has been crushed and compressed downwards. The overlying sands have then quickly filled the gaps and holes. Inside the channel-like depression which continues on the southern wall, the discrete columnar features merge into a kind of palimpsest (Fig. 7B).

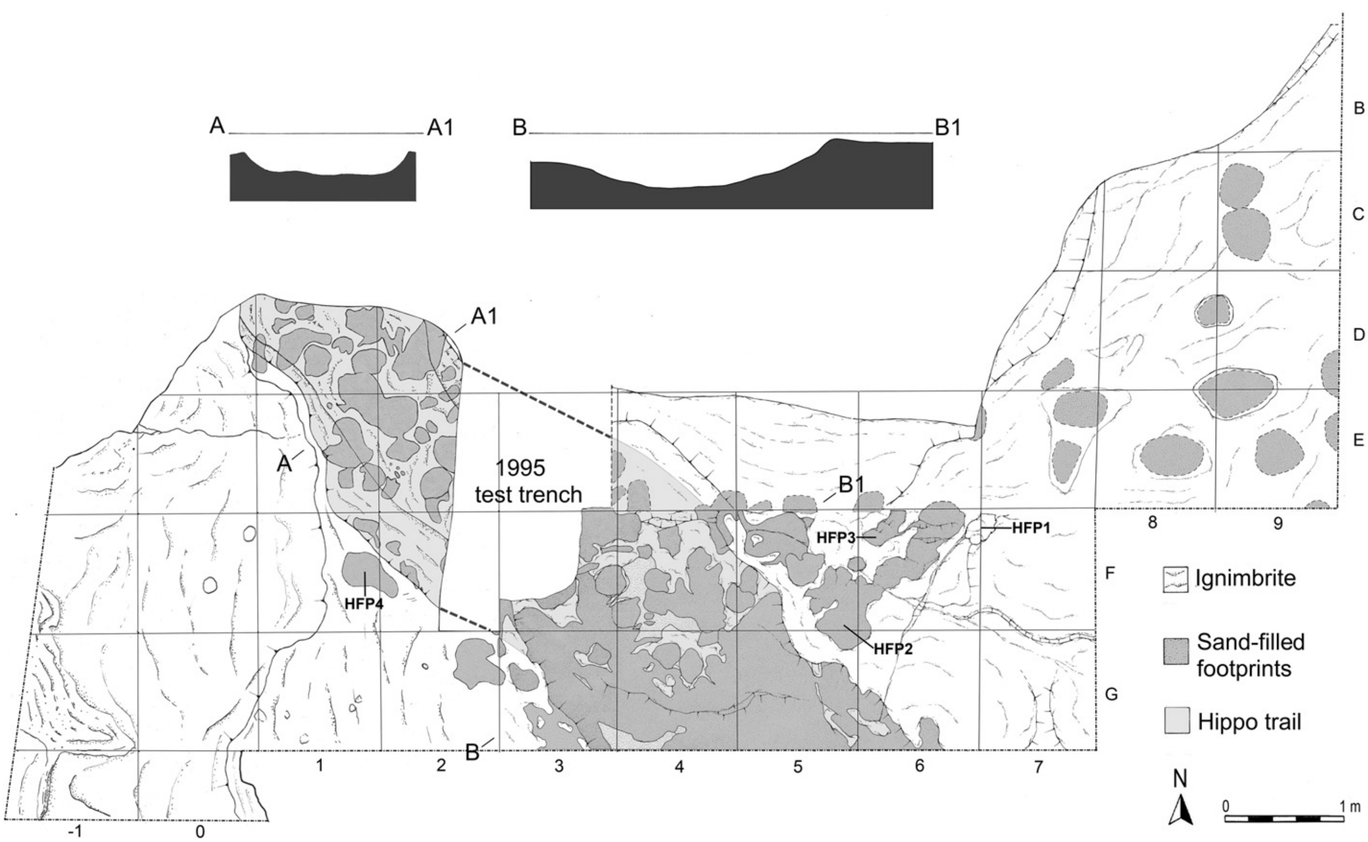

Fig. 4. General planimetry of the surface of Unit 3, showing the channel-like structure and the described features. Above, profiles of the channel (drawing by F. Altamura and N. Tomei).

Fig. 5. The channel-like structure found in 2014, viewed from the west.

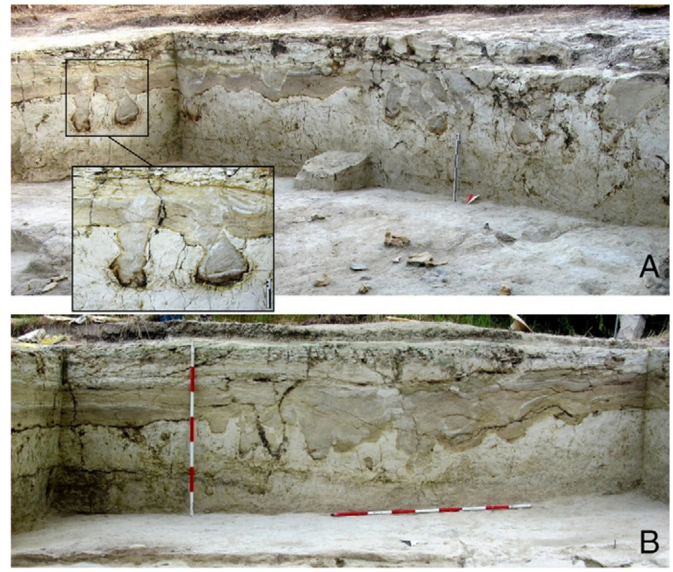

Fig. 7. Views of the excavation walls: A) south-eastern sections of 2013 excavation; B) southern section of 2014 excavations.

Some of the better-preserved discrete features were excavated to obtain a detailed 3D model. In one instance (Fig. 4: HFP1), a feature was cleared of its sandy infill. A 30 cm-deep bell shape appeared in the ignimbrite; its base widened to 35 × 30 cm. Laterally, this lower part was shaped as 4 toe-like lobes separated by thin, sub-vertical walls of sediment (Fig. 8A–B); it had apparently been produced by a heavy animal treading over unconsolidated deposits. We made a positive plaster cast of the feature. The smooth bottom surface had multiple, scarcely developed cushion-like convexities and looked like the bottom of a big mammal's foot (Fig. 8C).

We also isolated other features by scraping away the surrounding ignimbrite to obtain free-standing natural casts of consolidated sands and silts (Fig. 4: HFP2, HFP3, HFP4). This fine sediment infill is made up of lenses that were crushed downwards by a heavy load. It also includes some ignimbrite that was stirred up from below. The exposed three-dimensional features are columnar in shape, 20–35 cm high, and expand into semi-circular lobes and appendices in the lower half (Fig. 9).

One of the best-preserved natural casts, HFP2 (Fig. 4; Fig. 9, top row), is quite large and displays four such lobes arranged in a semi-radial pattern: the two central ones slant slightly away from each other, while the two lateral ones are more outspread. The columnar part measures 35 cm in diameter and slants 40° in a north-south direction.

Another natural cast, of a feature in squares F1–F2 (Fig. 4: HFP4), has four elongated appendices on its south-western side which depart from a columnar portion slanting NE-SW. In all, it measures 55 × 42 cm, and sinks 30 cm into the tuff surface (Fig. 10A–C).

Stratigraphically, the features start in Unit 2, sinking down from different sub-layers. Several times they reach and enter the tuff layer (Unit 3), but never start in it. The volcanic deposit was been warped by heavy pressure from higher up in the sequence, which suggests that it was still in a plastic and malleable state when the load structures were produced. It is a palimpsest of events that happened at different times during the gradual accumulation of the silty and sandy lenses from Unit 2.

4. Discussion

4.1. Identification of animals that made the tracks

The morphometric features of the footprints described here all refer to a large mammal whose feet each had four weight-bearing toes. These slightly elongated appendices are roundish, departing from a convex, elliptical plantar surface. The candidates for identification as track-makers are elephants, rhinos and hippos.

Elephants and rhinos are both recorded at Melka Kunture, though in small numbers. *Elephas recki recki* is associated with the Oldowan of Garba IV (Geraads et al., 2004). A single rhino bone fragment was discovered at Gombore II OAM, one of the sub-sites of Gombore II dated at ca. 850,000 years ago, at a lower stratigraphic level than Gombore II-2 (Gallotti et al., 2010). However, elephants produce elliptical footprints without noticeable toenail marks, while rhino footprints are

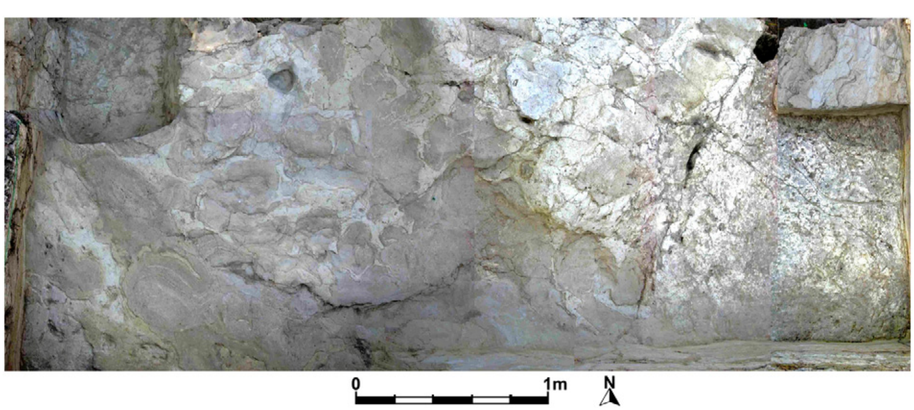

Fig. 6. Orthophotomosaic of Unit 3 surface as exposed in 2014 (by F. Altamura and N. Tomei).

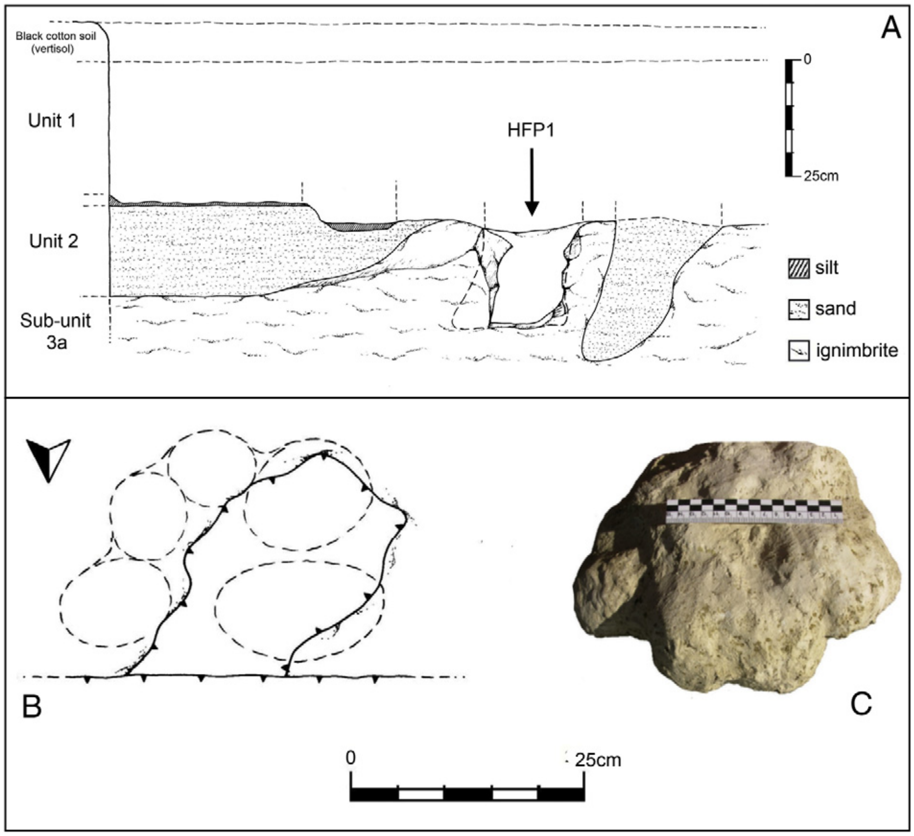

Fig. 8. Hippo footprint HFP1: A) section documented along the southern limit of squares E6-7; B) planimetry of the footprint; C) plantar view of the plaster cast made in the emptied hole (drawing by N. Tomei).

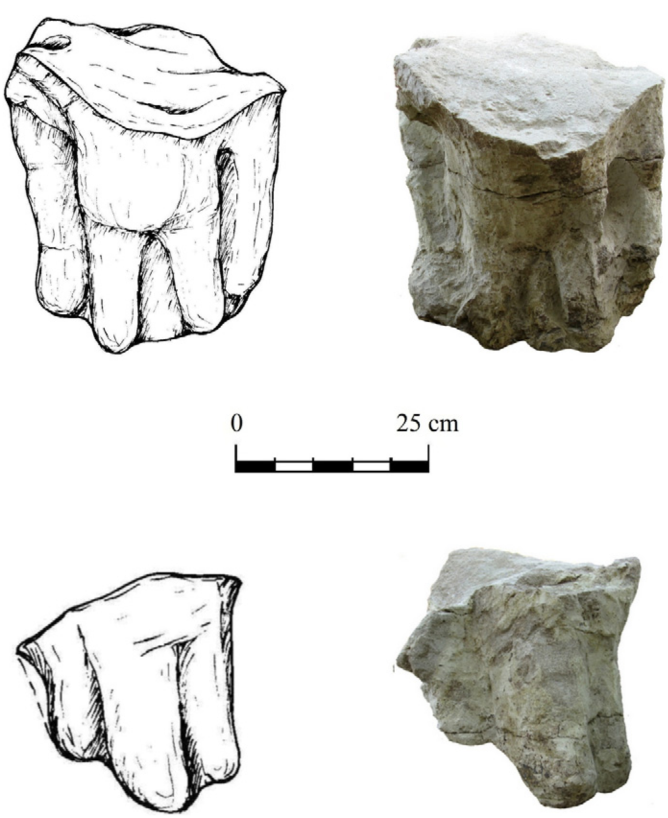

Fig. 9. Hippo footprints HFP2-3: graphic rendering and views of the natural track casts of HFP2 (above) and HFP3 (bottom) (drawing by N. Tomei).

characterized by the imprints of the animals' wide and short three front toes (Leakey, 1987).

The footprint dimensions and the foot morphology are largely consistent with those of Middle Pleistocene and modern hippos (Laporte and Behrensmeyer, 1980; Behrensmeyer and Laporte, 1981; Fisher et al., 2007, 2010; Bennett et al., 2014). The attribution to *Hippopotamus* is the only one coherent with the tracks discovered at Gombore II-2. Furthermore, in terms of biomass and fossil record, hippo remains actually dominate the entire geo-archaeological sequence of the Gombore gully and, overall, of Melka Kunture. The paleo-environment of the Melka Kunture half-graben was an ideal one for hippo populations. Based on geomorphological indicators, Gombore II-2 formed on the side of the slow-flowing paleo-Awash or of one of its tributaries, close to marshes and ponds.

Hypothetical or well-documented hippo tracks from the Pleistocene that would allow comparisons are only recorded at Olduvai and Koobi Fora. At Olduvai (Tanzania), a few isolated footprints were discovered in a Plio-Pleistocene clay deposit (Ashley and Liutkus, 2003; Bennett et al., 2014). These footprints are 10–25 cm wide and 15–40 cm deep, but are scarcely detailed and cannot be given any specific attribution.

At Koobi Fora (Turkana Basin, Kenya), a track-filled surface dating back to 1.4 Ma was researched and exposed at different spots over several dozens of meters. In Central and North Gaji 10, about 90 footprints of vertebrates, including hominins, were investigated (Behrensmeyer and Laporte, 1981). Twenty-three are interpreted as having been produced by hippos. Generally speaking, they are circular depressions up to 38 cm deep. In only a few instances there are also the typical prints of 4 toes and toenails. The larger footprints are attributed to adult *Hippopotamus gorgops*, the smaller ones (18–20 cm) to young specimens or to the pygmy *Hippopotamus aethiopicus* (Behrensmeyer and Laporte, 1981; Bennett et al., 2014). The paleoenvironmental reconstruction

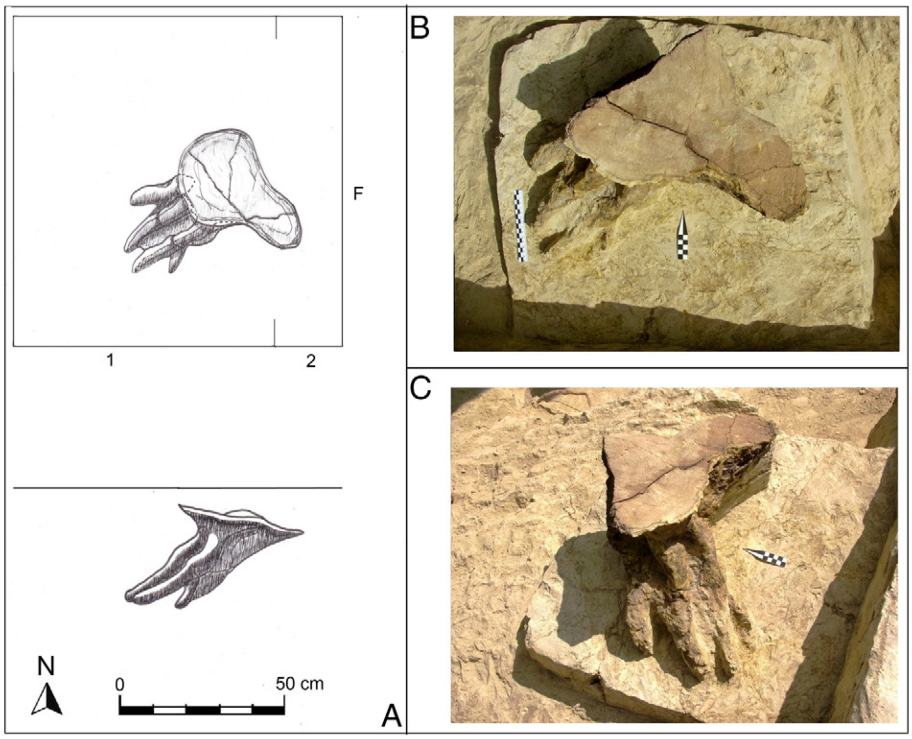

Fig. 10. Hippo footprint HFP4: A) planimetry and rendering of the footprint; B–C) zenithal and lateral view of the natural track cast.

suggests shallow waters and random walking over a surface submerged under 10 cm or so of water.

Another paleosurface of the same period, Gaji 10 South, was discovered about 70 m away. It contains 240 individual tracks, but no well-defined trackway (Bennett et al., 2014). The prints are 5.9–26.9 cm long and 7.3–29.9 cm wide, suggesting swimming hippos. The water was deep enough to allow the animals to keep afloat, so that they did not press all their weight into the surface, producing instead various types of partial footprints. A "punting" gait scratched the bottom, and generally only the toes impressed into the muddy substrate, leaving elongated tracks. This is very different ichnological evidence than the one produced by ambulatory type motion, as at Gombore II-2.

There is no reference database of measured hippo prints (Bennett et al., 2014). We will use information from Olduvai and Koobi Fora for some informed guesses. At Gombore II-2, the bioturbations at the surface of Unit 3 are 15 to 60 cm in diameter. However, the sediment was mechanically distorted as the hippos walked over and sank into it. This is clear from the sectioned footprints on the excavation trench walls (Fig. 7). Accordingly, we will take into account not the measurements at the top, but only those available at the bottom of footprints, whether sectioned or excavated (true tracks and natural track casts, sensu Bennett and Morse, 2014). The largest plantar surface measures about 30 × 35 cm, which is slightly more than the largest ones found at Koobi Fora (Bennett et al., 2014). The leg prints sink about 50 cm, which likewise exceeds the reported evidence from Koobi Fora. Some of the hippos at Gombore II-2 could well have been exceptionally large animals. Smaller footprints, including the smallest ones (diameter: 15 cm), could have been left by young animals. Attributing them to the pygmy *Hippopotamus aethiopicus* is an option, but an unlikely one, as this species is a tentative identification at Melka Kunture, based on a single tooth in much earlier layers, at ca. 1.7 Ma (Geraads et al., 2004).

The morphology of the plantar surface is the same as that of present-day animals. On one side of the plantar pad there are the lobe-shaped imprints of the four toes: two central ones and two lateral ones slightly behind them. In the natural casts, the slant of the feet suggests that the tracks were left by hippos that were slipping in the mud and had most of their weight on their toes. We would underline the fact that at Gombore II-2 the toes are spread out, possibly due to the foot's biomechanical reaction to sinking.

4.2. Superimposed trampling surfaces

To allow ichnosurfaces to be produced and preserved at all, the sediments must have specific properties related to fine texture, plasticity, humidity, contrasting lithological characteristics of superimposed layers, and burial rate (Laporte and Behrensmeyer, 1980; Ashley and Liutkus, 2003). Animal size and trampling rate are also important. This only happens under unusually favorable circumstances, as was the case at Gombore II-2. Unit 3 is the outcome of an ash-cloud surge that modified for a while the morphology and sedimentation in the area. The exposed surface at the top of this unit was quickly buried by sand (Unit 2). Footprints were pressed into plastic and deformable ground all over Unit 2. The lithological contrast with the underlying ignimbrite allowed bioturbations to be produced when hippos trampled heavily on a surface which was still rather unconsolidated, usually using the same preferred trail.

The footprints were produced in succession, as evidenced by the stratigraphic sequence. This is better recorded in the excavation walls at the intersection of row G and row 2, as cleaned in 2014 (Fig. 11). The two earliest trampling phases are documented by isolated footprints, which were pressed onto the surface of the tuff which at time was slightly concave (Fig. 11, trampling phases 1 and 2). By then, less than 20 cm of fluvio-lacustrine deposits had accumulated. Real trampling happened later, when up to 20 cm more of sands and silts had piled up (Fig. 11, trampling phase 3). This was the time when the tracks started to cluster, eroding a 2 m-wide channel. Elsewhere and at the same stratigraphic level, footprints found at some distance from each other suggest that they were left by one or more hippos occasionally wandering around. The animals walking on the top of a still relatively thin layer of silt did not always sink very deep, in which case the tuff layer below was not directly reached. Its surface, however, indirectly

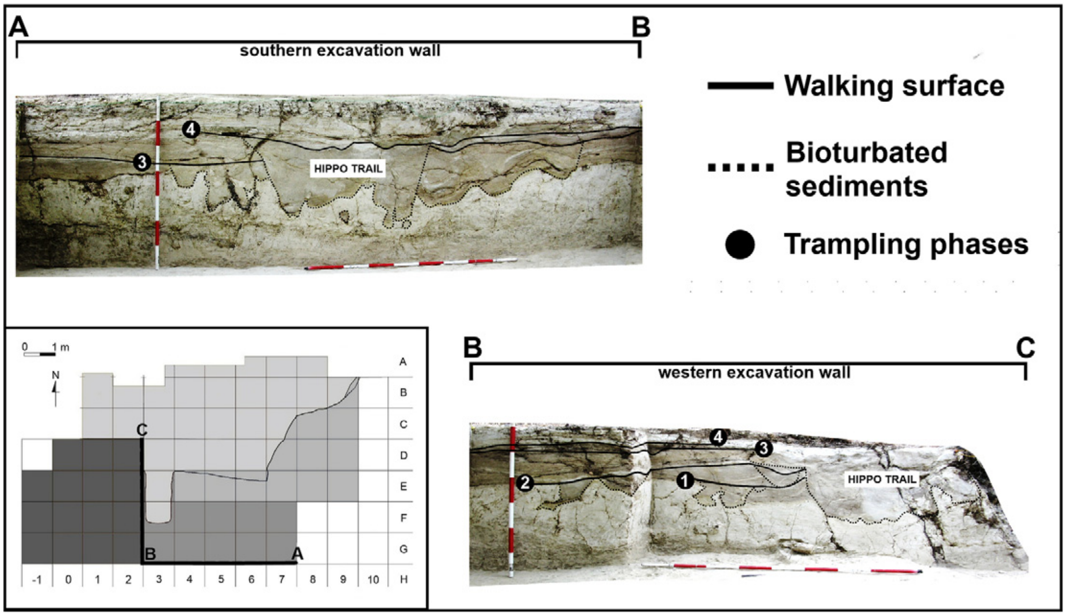

Fig. 11. The southern and western excavation walls in 2014. The four superimposed walking surfaces and related bioturbated sediments are highlighted.

strained by the load, became deformed, and undertracks were eventually produced.

The channel itself documents a last trampling episode, when more sands were deposited and sporadic seems to have ceased (Fig. 11, trampling phase 4). The eroded area deepens to a maximum of 0.7 m, and also gets narrower (1.2 m). The sediment filling was the outcome of the churning and rechurning of the same deposits that had already been trampled upon in the previous phase.

4.3. Behavior of Middle Pleistocene hippos

The scientific literature describing the behavior of present-day *Hippopotamus amphibius* provides detailed evidence on how their trails are produced and gradually eroded (McCarthy et al., 1998; Eltringham, 1999; Deocampo, 2002). Schools of hippos (male and female adults and young individuals) gradually shape them, walking regularly back and forth along the same path from the water where they rest during the day to grazing grounds at night. Over time, a radial or dendritic web of trails develops, stretching up to 2–3 km from the river or lake. Hippos are heavy animals with relatively small feet and they compress the path they walk on. In the end, the ground is eroded and a ditch is produced, usually 1 to 5 m wide, and up to 1 m deep (McCarthy et al., 1998; Deocampo, 2002). Close to the bodies of water the hippos spend their days in, the trails are quite deep and seasonally flooded. At a distance, and closer to the grazing grounds, they branch out into narrower paths, wide enough for only one animal.

The channel-like depression at the top of Unit 3 (Fig. 4; Fig. 12) matches perfectly the kind of trails described above, suggesting that Pleistocene hippos behaved just as their modern counterparts do. Its width (max. 2 m) and depth (max. 0.7 m) are within the known variability range. The superimposed prints we have documented are further direct evidence that hippos had gotten used to following this trail.

The dimensions fit well with those of a segment of the trail near the body of water. Individual prints discovered a short distance away suggest single hippos occasionally wandering around, as is well documented in present-day and past records (Laporte and Behrensmeyer, 1980; Behrensmeyer and Laporte, 1981; Cohen et al., 1993; Ashley and Liutkus, 2003; Bennett et al., 2014).

Before the discovery at Gombore II-2, only one fossil hippo trail had been reported, in the Plio-Pleistocene deposits of Olduvai Gorge in Tanzania (Ashley and Liutkus, 2003). However, the evidence there is much less detailed. This trail is a U-shaped erosional feature, 1.2 m wide and 0.6 m deep, which was noticed in a natural section. A load structure warped the local basal clays, and overlying clays had eventually filled the depression. Prints are not reported, and the length of the feature was not investigated. Trails made by Plio-Pleistocene mammals are also mentioned elsewhere at Olduvai (Leakey, 1971), as well as at Koobi Fora (Laporte and Behrensmeyer, 1980) and Laetoli (Leakey and Hay, 1979; Leakey, 1987), but none is positively recognized as having been made by hippos.

4.4. Resilience of Middle Pleistocene hippo populations

Unit 3 is an ash-cloud surge deposit; i.e., the eruption occurred in a relatively distant volcanic center (Mussi et al., 2016). Accordingly, the flow had relatively low energy, speed and temperature when it reached the area of Melka Kunture. Nonetheless, it significantly affected the local environment. Severe impacts on vegetation have been observed during recent eruptions (e.g. MacMahon et al., 1989; Pearson, 1994).

Fig. 12. The hippo trail found at Gombore II-2. In the foreground, view from N-W of the portion of hippo trail, with a bioturbated surface, which was unearthed in 2015. In the background, the trail continues beyond the southern wall of 2014 excavations.

We surmise that the ashes were probably not distributed uniformly. Spreading out from the distant volcanic center, they may have been channeled along the gullies. On relatively higher grounds, such as hippo pastures, the vegetation could have been covered less thickly. The two sub-units of Unit 3 are separated by lenses of diatomite, indicating that some calm water had accumulated briefly. This points to some stasis between two volcanic events. Alternatively, we interpret Sub-Unit 3a as ashes eroding from the banks of the clogged channel and re-depositing on top of Sub-Unit 3b.

It is known from reports of recent volcanic eruptions that the removal of ashes by a natural agent influences directly and very positively the re-establishment of vegetation. This was the effect of rain after the Parícutin volcano started erupting in Mexico in 1943 (Burt, 1961), and of wind and rain in the case of the Hudson volcano eruption in Patagonia, in 1991 (Pearson, 1994).

At Gombore II-2, hippos started walking around on the volcanic deposit when it was still in an unconsolidated, plastic state. The lack of any erosion or pedogenesis affecting the top of Unit 3 further suggests that the area's hydrographic system was re-established rather quickly. There has been no eruption in modern times in any area with a hippo population, so no direct observation could be made. However, it is known that smaller animals are most directly affected by volcanic events, and also that aquatic environments are more resilient than others (MacMahon et al., 1989). We surmise that hippos, being large and leading a semi-aquatic life, had better chances of recovering.

Dramatic fluctuations are known to occur in contemporary hippo populations, both because of anthropic impacts caused by poaching and habitat encroachment, and because of natural events such as droughts (Lewison, 2007; Zisadza et al., 2010). However, when favorable conditions return, population crashes may be followed by rapid surges. For instance, hippo density in Zimbabwe's Gonarezhou National Park increased three-fold in just over 20 years between, 1958 and 1980 (O'Connor and Campbell, 1986), and in Kenya's Masai Mara National Reserve likewise between 1971 and 2006 (Kanga et al., 2011).

No animal species other than hippos is recorded at Gombore II-2 soon after the eruption. Only later on, after the trail had been abandoned and Unit 1 had accumulated, are herbivores and medium- and small-sized species (including hominins) found within an archaeological horizon.

5. Conclusions

The ichnosurfaces, footprints and casts of Gombore II-2, fairly precisely dated to 700,000 years ago, provide unusual details on the outer shape of hippos' legs and feet, including the plantar pad and the position of the toes as the animals walked with their feet sinking into the deposit. The behavior of present-day *Hippopotamus amphibius* includes the routine use of a preferred path, which eventually erodes the ground. The fossil trail of Gombore II-2, where most of the prints converge, provides direct evidence that this behavior had already developed in the Middle Pleistocene. Circumstantial evidence further suggests that the resilience of modern hippo populations to catastrophic events was probably also typical of the ancient Upper Awash hippos, which quickly re-occupied an area devastated by a volcanic event.

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