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Tracks made by swimming Hippopotami: an example from Koobi Fora (Turkana Basin, Kenya)

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ABSTRACT

Here we report an ichnological surface close to Koobi Fora, Kenya in palaeontological collecting Area 103. The surface is marked by hominin tracks, as well as many traces from large animals. A southern excavation of the surface some 70 m from the hominin tracks displays a diverse range of animal track typologies, most of which appear to have been made by a four digit animal moving via punting or bottom walking in a shallow water body. Due to the track morphology and the associated fossil record, the non-hominin tracks are interpreted as being made by hippopotami, potentially including pygmy species or juveniles. The track typologies are explained using modern analogue observations of hippopotami sub-aquatic locomotion. This work provides important environmental context for adjacent hominin tracks and fossils, as well as providing the first recorded description of fossilized swim tracks made by mammals. The site has implications for the interpretation of swim tracks in the geological record particularly the widespread and controversial tracks made by sauropods and other dinosaurs.

Keywords: ichnology, hippopotamus, swim tracks, swimming dinosaurs

Highlights:

- Ichnological context for hominin footprint site GaJi10, Koobi Fora (Kenya)
- First recorded example of swim tracks made by hippopotami
- Implications for the interpretation of swim tracks in the geological record made by sauropods and other dinosaurs.

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1.0 Introduction

Inferring the range of locomotory capabilities of animals from the traces they leave provides opportunities for insight into the kinematics of extinct species, however it is not without its challenges. Given the appropriate geological conditions, the locomotion of terrestrial animals can leave a clear record of their footfall, allowing for inferences on foot morphology, biomechanics, gait and plantar load (Lockley and Meyer, 2000; Falkingham, 2014). Those with an aquatic or semi-aquatic habit provide a greater challenge, since not only are the tracks often incomplete due to partial contact, but discrete trackways (or more accurately swimways) are frequently absent and different biomechanical models apply due to the micro-gravity environment provided by water (Coughlin and Fish, 2009).

Fossil swim tracks are commonly reported for turtles and crocodilians (e.g., McCrea et al. 2004; Avanzini et al. 2005; Milan and Hedegaard, 2010), which is perhaps unsurprising given their respective lifestyles. What is perhaps less intuitive is that there is a substantial record of purported swim tracks of dinosaurian origin in the literature. Despite being highly adapted for terrestrial locomotion, a wide range of dinosaur taxa appear to have left sub-aqueous swim tracks, including theropods (Coombs, 1980; Milner et al., 2006; Ezquerra et al., 2007; Xing et al., 2013) and sauropods (Ishigaki, 1989; Lockley and Rice, 1990). Oddly, ornithischian dinosaurs are conspicuous by their absence in the swim-track record.

Dinosaur swim tracks often attract controversy, because it is difficult to explore the swimming capabilities of extant taxa with no modern analogue. Romilio et al. (2013) interpreted the Lark Quarry tracksite, Australia, as containing many swim-traces potentially made by ornithopods, but this was later refuted by Thulborn (2013). The sauropod manus-dominated trackways that were frequently interpreted as having been made by the large, long-necked animals ‘punting’ off the bottom with their forelimbs are now thought, in light of several studies, to be the results of issues of preservation– artefacts of underfoot pressures resulting from centre of mass position and substrate consistency (e.g., Vila et al., 2005; Falkingham et al., 2011).

We find it interesting that despite the wealth of dinosaur swim tracks reported, there is as yet no record of swimming tracks produced by mammals or birds (Milner and Lockley, in review). To be able to link such tracks with trackmakers for whom there is a modern analogue, or closely related taxa, would be of immense help in identifying the morphological characteristics of tracks made by swimming animals compared with those made on land. A number of mammals, including hippopotami, are known to ‘bottom walk’ and they may provide an alternative source of insight into the sub-aquatic locomotion of larger extinct animals such as dinosaurs.

In this context we report an ichnological surface in the Okote Member of the Koobi Fora Formation (Turkana Basin, Kenya) which contains tracks of swimming hippopotami (Figs 1 and 2). Not only is this an important set of tracks in their own right, given the existence of hominin tracks on the same surface (Behrensmeyer and Laporte, 1981; Bennett et al., 2009), but they provide evidence of the type of ichnological variability associated with punting locomotion and therefore provide a useful analogue with which to interpret the traces left by sub-aquatic extinct species such as dinosaurs.

2.0 Excavations and methods

The site (GaJi10) lies on the southern edge of the Koobi Fora Ridge in the paleontological collecting zone known as Area 103 (Fig. 1). The excavations described here lie on the western flank of a north-south strike-parallel dry valley in beds of the Okote Member (Koobi Fora Formation; Brown and Feibel, 1991). The eastern valley side is formed by an indurated sandstone layer which dips between 15° and 18° to the west. Excavations were made from the valley floor into the western valley side, along bedding surfaces dipping to the west into the slope and were therefore limited in east-west extent by the rapid increase in overburden (Fig. 2A-D). The original excavation of Behrensmeyer and Laporte (1981; c. 4 m by 4 m) was re-excavated in July 2008 (Bennett et al., 2009) and a further excavation (13 m along strike and 3 m wide) on the same ichnological surface was made 70 m to the south, down valley in January and July of 2009 (Fig. 1). The surface outcrop of the Akait Tuff provides a visible datum allowing the tracked surface to be traced and correlated between excavations. A further small excavation 20 m to north of the original excavation was also made. These excavations are referred to as GaJi10 North, Central and South with the central site being that of Behrensmeyer and Laporte (1981; Fig. 1). In addition to exposures in the excavation walls, geo-trenches were dug at locations of opportunity and described using the facies codes of Miall (1977).

The site was surveyed using a Leica System 500 (SR530) dGPS with a vertical accuracy of ± 30 mm. Track surfaces were excavated and cleaned before being photographed and digitised using an optical laser scanner (Vi900 Konica-Minolta Scanner; Bennett et al. 2009). Scan data was captured in Konica-Minolta Polygon Editing Tool and either output as a cdm file for subsequently manipulation in Rapidform 2006 or output as XYZ point clouds in asc format. The point cloud data was viewed in Foot Processor, a piece of bespoke freeware [http://footprints.bournemouth.ac.uk/] that allows rapid visual editing of XYZ data files in order to: (1) rectify tracks to the orthogonal plane; (2) rotate and mirror tracks; (3) crop extraneous material from tracks; (4) create contour plot, place landmarks and measure inter-landmark distances; and (5) converts the files if required to csv format for use in ArcGIS. Photographs of the surface were georectifed using surveyed control points and merged in ArcGIS for the purposes of mapping.

The submerged locomotion of two female common Nile hippopotami (*Hippopotamus amphibius*) was videoed through the side of a glass walled tank at the Adventure Aquarium in Philadelphia in 2008. Video was used to observe the range of locomotion styles displayed and short segments of video footage were analysed frame-by-frame where the hippopotami moved parallel to the glass tank wall. It is appreciated that this may not be wholly typical of natural hippopotamus behaviour but is at least indicative and complimentary to the observations of Coughlin and Frank (2009).

3.0 Stratigraphic context and lithofacies

3.1 Stratigraphic context

Behrensmeyer (1970) provided an initial description of the sediments in the Koobi Fora region in which she documented the presence of approximately 160 m of lacustrine sediments overlain by fluvial facies (Vondra et al., 1971; Bowen and Vondra, 1973). This lithostratigraphy was refined by Brown and Feibel (1986) on the basis of inter-bedded and increasingly dated tuffs (McDougall et al., 1992; Brown et al., 2006; McDougall and Brown, 2006). The current consensus is that the Koobi Fora Formation (~4.3 Ma to 0.6 Ma) encompasses the entire Plio-Pleistocene and is subdivided into eight members defined on the basis of volcanic ash horizons (Brown and Feibel, 1986). The KBS and Okote members which out crop in Area 103 record the gradual silting up of a former lake within the rift floor between 2.0 Ma and 1.5 Ma (Brown and Feibel, 1986, 1991; Lepre et al., 2007). The base of the KBS Member is defined by the KBS Tuffs dated to 1.869 + 0.021 Ma (McDougall and Brown, 2006) and the boundary to the Okote

Member by the Okote Tuff with an interpolated age of 1.56 + 0.05 Ma being overlain within a few metres by the Lower Koobi Fora (1.476 + 0.013 Ma) and the Koobi Fora Tuff (1.485 + 0.014 Ma; Brown and Feibel, 1986, 1991; McDougall and Brown, 2006).

Units of the Okote Member in Area 103 dip to the east and south east at between 5° and 18° and are cut along strike by a series of listric normal and reverse faults forming a series of escarpments and cuesta with a north-south axis and dry river beds between (Lepre et al., 2007; Fig. 1C). On the basis of unit conformity GaJi10 is believed lie within a single fault block separated from others by two prominent river valleys (Fig. 1C). The tuff that outcrops at GaJi10 in the valley floor and excavations was originally identified by Behrensmeyer and Laporte (1981) as the Kobi Fora Tuff, but has on the basis of the geochemical correlations reported in Bennett et al. (2009) been re-assigned to the Akait Tuff (1.43 ± 0.01 Ma; Brown et al., 2006; Bennett et al., 2009) placing it firmly within the Okote Member.

3.2 Lithofacies and palaeoenvironment

The lithofacies at selected sites in Area 103 was documented by Behrensmeyer (1975) and within the underlying KBS Member more recently by Lepre et al. (2007). This is supplemented here by the description of a number of geo-trenches and excavations (Figs 1-4). On the basis of the lithofacies present, four broad facies associations have been identified and are summarised in Table 1. They are consistent with previous interpretations of the KBS and Okote members which envisage a low energy fluvial-lacustrine system with both short-term seasonal and millennial scale water variations (Behrensmeyer, 1975; Brown and Feibel, 1991; Lepre et al., 2007). Behrensmeyer (1975) interprets the lithofacies in Area 103 as being those of a delta flat on the margins of large lake fed inland by a more stable fluvial system. In contrast Brown and Feibel (1991) favour a more complex and laterally variable facies model in which the size of the lacustrine element is more restricted and/or absent especially in the upper KBS and Okote members.

What is clear from the lithofacies observed here is that: (1) the landscape was relatively low lying with palaeosol development in drying-wetting conditions (Wynn 2004); (2) subject to seasonal/millennial regressions (episodes of desiccation) and transgressions of shallow water bodies, with a complex and variable geometry of unknown size; (3) transgressive elements are associated with stromatolites (Abel et al., 1982), mollusc horizons (Williamson, 1981, 1982) and shoreline facies (Renaut and Owen, 1991); and (4) these water bodies were fed by a range of broad, shallow, laterally variable channels subject to fluctuating flow regimes with low flow and sediment re-working punctuated by episodes of high sediment/water discharge. There is no direct evidence in the vicinity of GaJi10 of a deep water lake facies although there is a limited outcrop of laminated clay, equivalent to the deep water facies of Lepre et al. (2007), in an adjacent fault block. Figure 5 provides a schematic summary of the type of environment envisaged with the key features being the local complexity and the presence of numerous water bodies whether small lakes, river lagoons or channels.

This landscape was rich in a diverse range of vertebrate and semi-aquatic fauna and has yielded a plethora of vertebrate remains. Behrensmeyer (1975) suggests that the skeletal remains around Area 103 contained a higher proportion of aquatic and semi-aquatic fauna consistent with her interpretation of a delta plain. Table 2 provides a summary of surface skeletal elements recovered along a transect running from KMN ER1808 in the east and GaJi14 in the east via a series of bone walks (Fig. 1). This data takes no account of potential preservation bias of individual skeletons, or multiple sampling from one skeleton, and therefore provides only an approximation of the species present not necessarily their abundance on the landscape. The faunal list is similar to that reported by Brehensmeyer (1975). The terrestrial vertebrates are dominated by bovids and suids, while the aquatic and semi-aquatic finds predominantly consisted of hippopotami and crocodiles. The faunal list is consistent with a diverse and rich ecosystem dominated by numerous small and varied water bodies in a landscape subject to seasonal and decadal change.

4.0 Ichnology

4.1 Tracks: GaJi10 (Central and North)

This surface (c. 12 m^2; Figs 1 and 2D, E) was originally excavated by Behrensmeyer and Laporte (1981) and contains over 89 distinct impressions (200-380 mm deep) identified as the tracks of large vertebrates. According to Behrensmeyer and Laporte (1981) 22 had morphology similar to that of modern hippopotamus and three distinct trails associated with hippopotami walking in shallow water. The inference of shallow water (<100 mm deep) was based on the presence of wading bird tracks. The larger tracks (250 to 320 mm) were attributed to the large fossil hippopotami, *Hippopotamus gorgops*, while the smaller ones (180 – 200 mm) were thought to be either juveniles or pigmy species, (*Hippopotamus aethiopicus)*. Both species of hippotami are known from the fossil record of the Koobi Fora region (Harris et al., 2008). This surface was re-excavated in 2008 and while a small part of the front edge had been lost to erosion the rest was intact (Bennett et al., 2009). The non-hominin tracks take the form of deep amorphous, crudely circular craters (Figs 2D-E and 6B). In some the presence of four digits with nail impressions can be identified consistent with the interpretation proposed by Behrensmeyer and Laporte (1981). A small excavation to the north (GaJi10(North); Fig. 1) approximately one metre by three metres in the same surface revealed one clear four digit track with nail impressions (Fig. 2F). In all these cases the entire plantar surface of tracks is visible suggesting that track makers were walking normally on the surface and the water depths to shallow to allow buoyant locomotion.

4.2 Tracks: Description – GaJi10 (South)

In 2009 a larger excavation was opened up to the south in the same surface as that excavated by Behrensmeyer and Laporte (1981; Figs 1, 2B, C and 7). The surface has little relief and is composed of consolidated, partially lithified, fine silt with no apparent spatial variation in grain size. The tracks, approximately 240 individual examples, are exclusively non-human and randomly distributed with no evidence of identifiable trackways.

Figures 7-11 provide an overview of the typical track typologies present (See Supplementary Figures S1-9). The tracks range in width from 73 to 299 mm with a mean of 188 mm, and length which varies from 59 to 269 mm with an average of 143 mm (Fig. 8A-B). Each track is composed of a maximum of four digits and we recognise five main typologies, although none are mutually exclusive:

1. Type One (Figs 9A, F, H, M, L, 10A and 11A). These tracks typically have four well-defined parallel/aligned digits, with toenail marks visible in some tracks. The central two digits are more prominent than the lateral and medial ones and their extent is often exaggerated either as the digits scratch at the surface during first contact with the substrate or as the foot leaves contact with the surface and are dragged forward. To the rear of the track a central pad impressions is sometimes visible (Fig. 9I), although in many cases this is obscured by the proximal movement of sediment within a track (Fig. 8E) and the fact that in most cases there appears to be an inclined plane of contact between the indenter and the substrate. This often results in tracks with a marked longitudinal asymmetry in the direction of travel. Some of the tracks (Fig. 11A) have a two stage form; a broader imprint of all four digits, including proximal pad, into which the two central digits have been imprinted further during the later stages of contact. The individual toes are distinct and there is no obvious evidence of webbing between them, although in some examples the two central toes merge to form a single impression.
2. Type Two (Fig. 9G). In a limited number of cases the lateral and medial toes are not visible and the track is dominated by just two digits. The digits are truncated by a steep rear track wall often showing evidence of a rim structure. There is a variation between these tracks and that of Type One suggesting that they are formed by the same species of track maker, just that the contact between the substrate and the foot is limited to the central two digits.
3. Type Three (Figs 9B, J, P and 10B). In these tracks the lateral and medial toes are visible but tend to form oval-shaped impressions to the rear of the central digits which are also shorter.
4. Type Four (Figs 9C, E and 11B). These tracks consist of up to four shallow (10 to 40 mm), oval- or tear-shaped prod-like impressions, sometimes containing distal toenail impressions, distributed around a broad arc giving the appearance from above of a crown. The marks are made by vertical or sub-vertical contact between the digits and the substrate; the exact plan-form shape is probably controlled by the angle of contact with and the degree of forward drag as the digits lift from, the substrate. The overall width and spacing of the digits is much greater than in the other track typologies and they form a radial rather than parallel pattern. While the best examples contain four impressions, the surface is covered locally by partial examples indicative of vertical contact between one or more digits (Figs 9K, N and 11B).

5. Type Five (Figs 9O and 10C, D). A wide variety of complex forms exist associated with the overtracking (or partial overtracking) of one or more track. In some cases these complex forms consists of deeper (20 -40 mm) elongate craters, traverse to the long axis of individual discernible tracks and containing multiple and superimposed impressions, apparently made by laterally adjacent feet. The examples in Figure 10C, D are the simplest consisting of two tracks set side by side, separated laterally by between 245 mm and 316 mm and backed proximally by a clear ridge. Other examples are more irregular and there is evidence of multiple tracks within the elongated crater.

Tracks occur in close juxtapositions with a variety of orientations (Fig. 7) and often overlap, but do not form clearly identifiable trackways. There is however a preponderance of tracks with a west-east direction of travel across the excavated surface (i.e. across the shortest axis) and given greater excavation width it might be possible to link tracks more systematically. Individual tracks are associated to varying degrees with proximal displacement rims (10 to 30 mm high) and show a proximally rather than vertically directed plantar force consistent with the longitudinal asymmetry present in many of the tracks. No systematic variation in track typology allows for the identification of manus or pes tracks; suggesting either a predominance of manus/pes contact or more likely a common foot anatomy. While some tracks are clearly made by adjacent feet (Fig. 10 C, D) others are too closely spaced (Fig. 9J, K) and potentially represent examples of manus and pes tracks in close juxtaposition supporting the contention that there is a lack of anatomical variation between the manus and pes of the print maker. A range of track widths are associated with any given track depth, and depth does not correlate with width of the track digits and by assumption with body size of the print maker (Fig. 8C-D). Instead one may hypothesize that depth is linked to the degree of applied contact pressure and/or variations in the consistency of the substrate. In Figure 11C it is possible to deduce several cross-cutting tracks of varying size; the well-defined Type One track on the left is superimposed on a much larger Type Four track providing direct evidence of multiple individuals and animal sizes. The distribution of track sizes (Fig. 8A-B) shows a continuous distribution.

The tracks described here have a different but potentially cognate typology from the crater-like impressions found at GaJi10 (Central and North; Fig. 6) interpreted by Behrensmeyer and Laporte

(1981) as being those of walking hippopotami. The presence of four digits with nails is common to both and while the tracks at GaJi10 (South) are generally smaller there is some overlap in sizes (Fig. 8A). They do not resemble the tracks of crocodiles or turtles (cf. Avanzini et al., 2005; Milàn and Hedegaard, 2010; Romano and Whyte, 2010) which are the only other plausible track makers given the fauna present as identified in the bone surveys (Table 1). The observed topological differences between the tracks at GaJi10 (South) and those at GaJi10 (Central) are therefore interpreted as due to differences in locomotion with those at GaJi10 (South) being swim tracks. This interpretation is consistent with the lack of discernible track ways and the typological variation present caused by different patterns of bottom-contact. The implication here is that water depth increased to the south of GaJi10 (Central) giving rise to different locomotor styles. The absence of desiccation structures on the surface is also supportive of a subaqueous interpretation. Behrensmeyer and Laporte (1981) noted the presence of a wading bird (Fig. 6A) and bovid tracks at GaJi10 (Central), all of which are absent at this site consistent with the increased water depth and the interpretation made here.

Hippopotami have distinctive four digit feet as shown in Figure 12A. Detailed anatomical dimensional data for hippopotami is not available making size comparisons difficult but individual hippo tracks (250-290 mm wide) have been described by Ashley and Liutkus (2002) although their focus was on terrestrial trails/trackways (1.2 m wide and over 0.6 m deep) linking hippo pools and grazing meadows. Behrensmeyer and Laporte (1981) report sizes of 250 to 320 mm for the larger tracks which partially overlap with the dimensions reported here, although their smaller tracks (180-200 mm) do fall within the range of observed dimensions (Fig. 8A). Notwithstanding the different mode of locomotion between the two sites, it is possible to speculate that the track maker at GaJi10 (South) may have been the pygmy hippopotami (*Hippopotamus aethiopicus*; Harris et al., 2008) or alternatively it may reflect the presence of calves. The occurrence of two superimposed tracks of very different sizes (Fig. 11C), despite the typological differences, is perhaps more consistent with the latter. Little is known about the habitats of these extinct hippopotami and whether pygmies would use the same water body as larger species, although not necessarily at the same time. Modern pygmies (*Choeropsis liberiensis*) have more prominent nails/claws and do not have webbing between the toes (Eltringham, 1999) which is consistent with the tracks described here, although it must be noted that pygmy hippopotami are not particularly social animals (Eltringham, 1999) and the abundant presence of tracks may therefore be an issue. There is nothing to say however how many hippopotami generated the assemblage of tracks since the surface represents a time averaged record and the length of time over which imprinting occurred is not known. The range of sizes present (Figs 8A, B and 11C) does suggest that more than one individual was involved.

5.0 Discussion

The tracks and associated ichnofacies described here provide the first accounts of a mammal swim record. They are important not only because of the human tracks which have been found on the same surface (Behrensmeyer and Laporte, 1981; Bennett et al., 2009), but also because they provide important information with which to help interpret swim tracks of extinct animals such as sauropods and tetrapods.

GaJi10 (Central) contains a hominin trackway attributed to *Homo erectus* by Behrensmeyer and Lapotre (1981), a conclusion tentatively confirmed by their re-analysis (Bennett et al., 2009), although more than one hominin is known to have been present on the landscape 1.5 Ma (Spoor et al., 2007; Dingwell et al., 2013). In comparison to the slightly older tracks at Ileret 40 km to the north, the tracks are very poorly defined anatomically and add little to the discussion of foot morphology across the *Australopithecus* to *Homo* transition (Bennett et al., 2009; Crompton et al., 2012). This almost certainly reflects the poor imprinting and preservation conditions of a sub-aqueous site. The tracks in the GaJi10 trail transition from large craters to more shallow and better formed tracks and may suggest that the track maker emerged from deeper water to shallow or sub-aerial conditions. The tracks described from GaJi10 (South) are 70 m down valley and appear to represent much deeper water in that the hippopotami tracks represent swimming/punting rather than ambulatory type motion. Water depth is hard to estimate and depends on the body mass and stature of the hippopotami present. The Common Hippopotamus (*Hippopotamus amphibius*) is typically between 150-165 cm high (Males 1,475 kg; Females 1,360 kg) with pygmy hippos about half that height (Eltringham, 1999) and given that they like to be able to rest on the bottom while breathing at the surface water depths could range from as little 0.5 to as much as 1.6 metres deep. Blowers et al. (2012) found that in artificial enclosures, hippopotami preferred water depths of 0.6 to 1.0 m.

On land and in shallow water hippopotami use a lateral sequence walk which ensures that there are three limbs in contact with the ground at all times to maintain stability (Hildebrand, 1989). When running they use a trotting gait in which diagonally opposite legs swing in unison (Hildebrand, 1989). In water however Coughlin and Frank (2009) observed an unstable galloping gait in which the forelimbs extend in unison providing for extended unsupported intervals; a mode of gait referred to as 'punting'. This involves the limbs pushing off the substrate for alternating phases of thrust and glide through the water (Koester and Spirito, 2003; Martinez et al. 1998). Coughlin and Frank (2009) found that as horizontal speed increases the time interval between periods of ground contact decreases as one might expect and the vertical displacement or rise between each period of ground contact decreases. More ground contact is associated with greater rise (Coughlin and Frank, 2009).

The authors' videoed the motion of two female Nile *Hippopotamus amphibius* through the side wall of their tank at the Adventure Aquarium Philadelphia in 2008 (See Supplementary Information). Two different types of motion were observed (Fig. 12). In the first type the hippopotami move in a hybrid form, neither in a classic trot or gallop. Periods of glide, in which the limbs were folded limply beneath the body (Fig. 12B), were separated by substrate contact via a single extended forelimb (Fig. 12C), on occasions this was followed by a hind limb although not necessarily the diagonally opposite foot. In fact the glide was often maintained by contact with a single forelimb in which only the digit tips made contact. Where greater control was needed, for example when the two hippopotami were in close contact a more stable and conventional trot was observed in which diagonally limbs moved in unison. During phases of glide, especially with increasing speed, a single forelimb was often the only point of contact as noted by Coughlin and Frank (2009) the amount rise and fall between steps was minimal. This type of motion contrasts with the other observed in which the hippopotami thrust upwards towards the water surface using both hind feet placed firmly apart (Fig. 12D). In some cases limbs return to the same spot, thrusting upwards again, while at others times there may be some forward motion such that the limbs make contact further forward.

These types of motion and behaviours are consistent with the tracks at GaJi10 (South). Type One tracks represent situations where the foot is placed flat on the substrate, thrusting off principally through the central two digits cause them to be impressed into the substrate and for sediment to be pushed in a proximal fashion. At other times forward glide is maintained by contact with only the extended digits moving vertically or sub-vertically into the substrate to create prod-like marks (Type Three Tracks). Variations between plantigrade and digitgrade placement of the feet account for the range of track typologies. The capacity for this range of different motions is reflected in the myology of hippopotami limbs explored in detail by Fisher et al. (2007, 2010) in relation to pygmy hippopotami. Specifically they outline the presence of musculature which allows for control of the degree of separation of the digits. The short powerful limbs and musculatures are also highly adapted to punting type locomotion. The near-placement of tracks, off-set by just a few tens of millimetres, may represent the passage of both manus and pes limbs in the form of the one-sided trot observed by the authors. Thrusting upwards often from a static or semi-static position leads to the double tracks spaced apart backed proximally by more substantial rim structures.

As illustrated above, swim tracks involve an understanding of the physical influence of water depth, current flow directions (or lack of current flow as in this case) and substrate consistency, alongside the biological influences of animal size, foot/limb morphology of feet and limbs, buoyancy, and different swimming behaviours (Milner and Lockley, in review). Here the critical control on track morphology appears to be swimming behaviour and both the flexibility and control of the digit's musculature. There is no doubt that where the centre of mass or locomotion style of an animal leads to the differential application of force that critical substrate yield strengths may lead to the selective formation and track sampling as argued by Falkingham et al. (2011), but this may not account for all cases as we have illustrated here, where tracks can be linked to an extant analogue. The observations here are consistent with those of Milner et al. (2006) in that swim trackways can sometimes be distinguishable (Ezquerra et al. 2007; Romilio et al. 2013; Xing et al. 2013), but are more commonly absent if linking tracks is extremely challenging, especially where several animals are involved or they pass repeatedly over a spot as for example in a constrained water body or one with a favoured water depth for habitation.

6.0 Conclusion

We have documented an ichnosurface characterised by a wide range of track typologies interpreted here as being formed by a species of hippopotami moving in a shallow water body. The size range of these tracks may represent a combination of adult, juvenile or pymgy hippopotami. The track typologies are consistent with a range of locomotor strategies associated with punting or bottom walking. They reflect the unique characteristics of the hippopotami foot with four weight bearing digits. Typologies vary from tracks where the plantar surface has been largely in contact with the substrate and the load is directed vertically as well as laterally, to others which consist of prod-marks where the digits have touched the ground vertically or sub-vertically and have been made in balancing an unstable pattern of gait or to maintain forward momentum of the glide. It is not possible to separate manus from pes tracks due to similar morphologies. Tracks occur singularly and in close juxtaposition with slight lateral and forward offsets suggesting that the feet in contact are laterally congruous. Direct observations do not show a predominance of a trot or a gallop type motion but a mixture of the two. In other cases double tracks with clear separation of manus/pes are indicative of thrusting from the substrate in which both limbs are placed side by side. Clear swimways are not apparent but the predominant direction of movement seems to be across the narrow width of the excavation. It is not clear whether these tracks were made by a multitude or a few individuals. It is very possible that only a few individuals could build up this complex pattern of tracks over time. While some of the variation in track sizes may be due to variation in the foot dimensions of the individuals, some of it is likely to result from typological variation.

The significance of this paper lies in the first description of mammalian fossil swim tracks, providing environmental context for nearby hominin tracks and linking track morphology to the known/observed punting behaviour of a large animal. As such, these tracks provide an important analogue in aiding the understanding of swim tracks in extinct species such as sauropods or theropods.

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Figure and Table Captions

Figure 1. Location and site maps. **A.** General over view showing the line of transect for the faunal analysis, drainage and general strike and dip of the outcropping beds. Hominin marker sites are also shown. **B.** Detailed topographic map for the GaJi10 based on a primary field survey using a Lecia System 500 (SR530) dGPS. The outcrop of the Akait Tuff is shown. **C.** Cross-section transverse to strike between GaJi14 and the famous hominin site of KMNER1808.

Figure 2. Photographs of GaJi10. **A.** General overview of the excavation of GaJi10 (Central) showing the scanning rig in action. Note the dip of the bedding into the slope and away from the valley floor. **B.** General overview of the excavation of GaJi10 (South). **C.** Ichnological surface at GaJi10 (South). **D-E.** Ichnological surface at GaJi10 (Central) both in overview and close-up. **D.** Single print at GaJi10 (North). **G.** Hippopotami prints in cross-section with the south wall of GaJi10 (Central). **H.** Track from GaJi10 (South) showing the striated substrate caused by the proximal movement of the trackmaker's foot across the surface. **I.** Double track at GaJi10 (South), note the rim structure immediately behind the print. **J-L.** Ichnological surface of GaJi10 (South) showing the general pattern of tracks.

Figure 3. Sedimentary logs for geo-trenches in the vicinity of GaJi10. Log locations can be found in Figure 1 and the key to the facies codes in Table 1.

Figure 4. A. Sketch of the rear wall of GaJi10 (South). See Table 1 for code to the facies logs. B. Sedimentary log through the rear wall of the excavation GaJi10 (Central).

Figure 5. Schematic visualisation of the landscape around GaJi10 based on the lithofacies analysis.

Figure 6. Contour maps derived from optical laser scans of selected tracks on the ichnological surface at GaJi10 (Central).

Figure 7. Map of the ichnological surface at GaJi10 (South).

Figure 8. **A-D.** Dimensions of the tracks found at GaJi10 (South) measurements are taken from landmarks placed on digital scans analysed in Foot Processor. **C.** Longitudinal cross-section of Track in Figure 9M.

Figure 9. **A-P.** Photographs of typical tracks from GaJi10 (South). See text for detailed description of individual tracks.

Figure 10. **A-D.** Selected scans of track complexes, warm colours represent areas of elevation.

Figure 11. **A-C.** Contour maps created in ArcGIS for selected tracks and track assemblages. Contour interval is 1 mm.

Figure 12. Selected photographs of two Nile *Hippopotamus amphibius* through the side wall of their tank at the Adventure Aquarium Philadelphia in 2008 showing an anatomy of a right front foot (**A**) and various styles of punting behaviour (**B-D**). See the text for detailed description..

Table 1. Lithofacies documented in the vicinity of GaJi(10) see Figures 3 and 4 for associated sediment logs. Modified lithofacies codes after Mail (1977): Dmm = massive diamict; GRt = trough cross-bedded granule gravel; GRh = horizontally bedded granule gravel; GRfu = normally graded granule gravel; GRm = massive granule gravel; Su = fine to coarse shallow scours and cross-stratification sand; Sh = horizontally stratified sand; Sm = massive sand; Sr = rippled sand ;Sl = parallel laminated sand ;Sd = deformed sand beds; Fm = massive silt/clay; Fl = laminated silt/clay; …(p) = weathered/palaeosol.

Table 2. Faunal data for six parallel 25 m transects running from GaJi 14 in the west through GaJi10 to KNM-ER-1808 in the east (Fig. 1). All surface bone specimens where flagged and surveyed and identified by Dr Jack McCoy and Dr Stephen Merrit. Data collection was in July 2008. (Source: Personal Communication Dr Jack McCoy.

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Facies Association	**Component Facies**	**Architecture**	**Description**	**Interpretation**
FA-1	Su, Sh, St, GRh, GRm, GRt, GRfu, Sm(p), Dmm	Varies laterally and vertically over a range of distances. Broad sheets infilling shallow troughs (0.5 to 1 m thick) over 10 to 100 m. Scours and small cross-cut channels locally.	Sheets containing: multiple cross-cutting scours and small channels (<0.5 m wide) of coarse sand and granule gravel (0.1-0.4 m thick); trough cross sets; normally graded granule gravel to medium sand units; .palaeosols (<100 mm - >2.5 m thick; columnar and polished peds); occasional units (0.2 - 0.5 m) of diamict with soft-sediment clasts; and occasional silting lines and fine-grained rip-up clasts and palaeosol peds. Distinctive oolitic, stramolites and indurated carbonate horizons occur in places.	Low energy fluvial environment consisting of a series of shallow troughs and channels at a range of scales. At the largest scale, broad sand dominated troughs with a range of sinusoidal bedforms and dunes. At a smaller scale there are multiple erosional channels and scours re-working abandoned channel and trough floors during periods of low flow. Channel instability with rapid lateral erosion during peak flows, with palaeosol formation on exposed bars and adjacent slopes. The presence of occasional diamict units indicates debris or hyperconcentrated flows typical of periodic high energy floods.
FA-2	Fm, Sl, Sh, Sr, Fm(p), Dmm	This association consists of multiple, thin (typically <0.3 m) sheets extending over 100s of metres laterally.	Massive silt units (50-500 mm) inter-bedded with thin beds of parallel laminated and rippled fine to medium sand with scoured bases and draped upper contacts. Upper surface of silt units often show evidence of desiccation cracks and surface weathering verging towards palaeosols. Above punctuated by laterally extensive sheets of sand (0.2-0.5 m) thick have cemented to form prominent marker horizons. Contain stramatolites small nodular domes and mamal (50-150 mm diameter). Diamict units occur as tabular sheets and include soft-sediment clasts and sand stringers. Some thicker units of medium sand may contain mollusc horizons, particular where they overlie desiccated silt surfaces.	Flat, planar sediment surfaces subject to oscillations in water level with periodic desiccation of thick silt units typical of shallow lacustrine or lagoonal conditions receiving varying water supply either due to seasonal variations in water flow or switching /migration of feeder channels. This gives a distinct couplet of sediment with thin coarse units indicative of water and sediment inflow punctuated by periods of quiet water where silts settle and the water level falls, revealing desiccated surface. This wetting and drying leads to algal growth structures. More widespread flood events involve the transgression of medium to coarse sand with isolated mollusc shells. Lake margins or lagoonal system.
FA-3	Sh, Sd, Sm, Su, Fm, Fm(p)	Either sheets of mollusc rich sand 0.2 to 0.6 m thick extending laterally along strike for tens if not hundreds of metres, although the shell concentrations varies rapidly both vertically and laterally. The facies can also be found in filling scours and smaller channels (<5m wide).	Units containing commuted mollusc shells (10-95%) set in matrix of massive medium/coarse sand. Mollusc concentration typically has inverse grading or shows evidence of soft-sediment deformation. Mollusc units infill desiccation cracks in underlying units. Occasional in fill small scours (0.5 m wide). Rippled, laminated and graded sand units plus massive mollusc free sand units form prominent and laterally extensive inter-beds. Hummocky cross-stratification present locally. Tabular, domal and nodular carbonate concentrations occur locally especially on the upper surface of units.	Shoreline or near shore units with winnowed, re-worked mollusc horizons concentrated as lag deposits. Migration of carbonate through leaching of ground waters to form nodules and other carbonate concentrations. Part of transgressive lake episodes.

FA-4	Fm, Fl	Tabular sheets of appear to be of limited lateral extent, infilling troughs and channels	Massive or weakly laminated clay with manganese and iron staining. Draped basal contacts and occasional granule gravel dropstones. Little evidence of palaeosol formation, although near-surface units may be over printed with modern soil formation	Deep water infilling abandoned channels, pools or larger water bodies.
FA-5	Su, Sl, Sh, GRh, Sr	Planar sheets with broad trough like geometry over 10 t0 100 m+	Multiple units often forming fining upwards sequences culminating in thicker, more massive silt units. Range of ripple cross lamination plus climbing ripples. Local soft-sediment deformation; rip-up clasts including tuff in places; asymmetrical infills to broad troughs; multiple alternating units of silts, fine sand with thicker units of medium to coarse sand. Very occasional small scale scours. Trough cross laminations in sand and silt, usually small. Diverse range of bedforms; relatively high energy sheet like deposits Multiple gaded units; 1- 5 mm individual units making up 0.3 m packages scours; contorted laminations	Broad shallow channels to inflow across shallow lake floor; graded units present but little evidence of sediment gravity flows more limited; mostly tractional currents; couplets limited. Shallow water deposits under sheet flow in troughs or near shore lacustrine environments

Table 2. Faunal data for six parallel 25 m transects running from GaJi14 in the west through GaJi10 to KNM-ER-1808 in the east (Fig. 1). All surface bone specimens where flagged and surveyed and identified by Dr Jack McCoy and Dr Stephen Merrit. Data collection was in July 2008. (Source: Personal Communication with Dr Jack McCoy)

	Bovid	**Suid**	**Equid**	**Elephant**	**Primate**	**Carnivore**	**Camel**	**Bird**	**Giraffe**	**Terrestrial Sub-Total**
Transect 1	48	5	4	0	6	0	0	0	0	63
	49%	5%	4%	0%	6%	0%	0%	0%	0%	
Transect 2	39	12	5	2	1	1	1	0	0	61
	46%	14%	6%	2%	1%	1%	1%	0%	0%	
Transect 3	27	6	2	0	0	0	0	0	0	35
	47%	11%	4%	0%	0%	0%	0%	0%	0%	
Transect 4	43	14	10	1	0	0	0	0	0	68
	33%	11%	8%	1%	0%	0%	0%	0%	0%	
Transect 5	36	15	8	0	0	0	0	1	0	60
	38%	16%	9%	0%	0%	0%	0%	1%	0%	
Transect 6	41	9	15	4	0	0	0	0	0	69

	34%	7%	12%	3%	0%	0%	0%	0%	0%	
Totals	234	61	44	7	7	1	1	1	0	356
	40%	10%	8%	1%	1%	0%	0%	0%	0%	

	Hippo	**Croc**	**Fish**	**Turtle**	**Aquatic/semi Sub-Total**	**Total Specimens All Taxa**
Transect 1	21	7	4	2	34	97
	22%	7%	4%	2%		
Transect 2	11	7	2	3	23	84
	13%	8%	2%	4%		
Transect 3	14	4	2	2	22	57
	25%	7%	4%	4%		
Transect 4	43	11	5	5	64	132
	33%	8%	4%	4%		
Transect 5	21	6	5	2	34	94
	22%	6%	5%	2%		
Transect 6	31	11	8	3	53	122
	25%	9%	7%	2%		
Totals	141	46	26	17	230	586
	24%	8%	4%	3%		