

Tracks, Trails and Trampling by Large Vertebrates in a Rift Valley Paleo-Wetland, Lowermost Bed II, Olduvai Gorge, Tanzania

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The impact of large vertebrates on the sedimentary record in an East African groundwater-fed wetland in Ngorongoro Crater, Tanzania, is used as a modern analog to interpret an ancient (Plio-Pleistocene) wetland record in Olduvai Gorge, Tanzania. The 3 km² wetland at Olduvai is characterized by massive silty claystones produced by intense vertebrate trampling, as well as trails by vertebrates frequenting the wetlands and isolated footprints that represent a “snapshot in time.” Based on modern analogs, a paleo hippo trail (1.2 m wide and 0.6 m deep) in the Plio-Pleistocene wetlands is interpreted as a frequently used corridor between hippo pools (days) and grazing meadows (nights).

Groundwater-fed wetlands are low energy environments where the physical record appears to be dominated by plant and animal activity. The bioturbation record reflects a number of interacting factors such as substrate texture, moisture content, sedimentation rate, frequency of flooding, type of animals present, trampling rate, and post-depositional changes (compaction). Lithofacies in both the modern and ancient wetlands include muddy sandstone (drainage channels) and silty claystone (vegetated and nonvegetated mud flats). Organic-rich sediments eventually oxidize, eliminating most evidence of the habitat. Modern wetlands have organic-rich mud and peat, whereas the ancient analog has siliceous earthy claystones that contains plant remains, bone fragments, pollen, phytoliths, and localized beds of diatomite. Thus, the physical record of vertebrate bioturbation in conjunction with paleontological and lithological records provides crucial information on the ecology of ancient wetland environments.

Keywords hippo trail, trampling, paleo-wetland, Olduvai Gorge

INTRODUCTION

Groundwater-fed wetlands may occur in any low ground (lake margins, river flood plains and deltas), basically wherever the water table intersects the surface. Wetlands are also associ-

ated with impervious materials (perched groundwater) or linked to geological structures (faults or bedrock systems) that are natural conduits for flow. Thus, in certain geological contexts wetlands may be small isolated features and occur separately and distinct from major water bodies. Freshwater wetland records have been neglected as a focus of study, particularly in arid and semi-arid environments, despite the fact that they are and have been important ecologically as a water resource (Ashley, 2001). Arid to semi-arid environments receive 500–1000 mm precipitation annually but can experience 2000–3000 mm annual evaporation. The logical affinity of fauna to dependable, potable water suggests that wider recognition of ancient wetland deposits could lead to discovery of previously overlooked paleontological records.

The multiplicity of geological settings in which wetlands occur creates a variety of depositional contexts for wetlands, and yet there is a dearth of basic description of their distinctive sedimentological record. There are several reasons why groundwater-related environments have not been widely recognized.

1. There is a misconception that groundwater discharge always produces travertine and sinter deposits. Many springs and groundwater seeps, particularly cool ones (<30°C), have little to no associated mineral deposits (Quade et al., 1995; Deocampo, 2001).
2. Most spring deposits are restricted in size (few m²) and thus could be overlooked during fieldwork.
3. Preservation potential of wetland peats and organic-rich sediments is low. Organic-rich sediment oxidizes with time, unless preserved in an acidic (<5.5 pH), anoxic environment (Thompson and Hamilton, 1983; Quade et al., 1998).
4. Some ancient groundwater-fed wetland deposits have been misinterpreted as floodplains, deltas, or marshy fringes of lakes (Hay, 1976). However, the location of rivers and lakes can shift laterally with time, whereas

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groundwater-fed wetlands that are controlled by topography or underlying geology are expected to maintain a relatively fixed location.

A large interdisciplinary research effort, OLAPP (Olduvai Landscape Paleoenvironmental Project), to reconstruct a Pliocene landscape (~25 km wide) spanning a narrow window of time (~50 ka) (Blumenshine and Masao, 1991), provided an excellent opportunity to study a paleo wetland. Geologic mapping and sedimentologic description provided the basis of paleoenvironmental reconstruction of a number of Pliocene deposits within the paleontologically rich Olduvai Gorge, Tanzania, which included alluvial fan, fluvial plain, lake margin, ephemeral stream, and playa lake, in addition to a large wetland (Ashley and Hay, 2002) (Fig. 1). The wetland was 3 km² and appears to have been mainly ground-mentation of bioturbation to groundwater-fed wetland systems.

The wetland deposit is characterized by vertebrate bioturbation that yielded structureless silt and earthy claystones, distinct trails of superimposed tracks, and isolated footprints. Although vertebrate bioturbation has been recognized previously as an important process, the paleoenvironmental interpretations were associated with sedimentation in depositional systems such as volcanoclastic (Leakey and Hay, 1979), lake margin (Laporte and Behrensmeyster, 1980; Renault et al., 1986; Hay et al., 1986; Cohen et al., 1993; Decampo and Ashley, 1999), fluvial (Haynes, 1985; Holliday, 1995), deltaic (Behrensmeyster and Laporte, 1981), and coastal (Van der Linde and Andrews, 1969) environments. There is now a need to extend the documentation of bioturbation to groundwater-fed wetland systems.

logical studies will be reported elsewhere.

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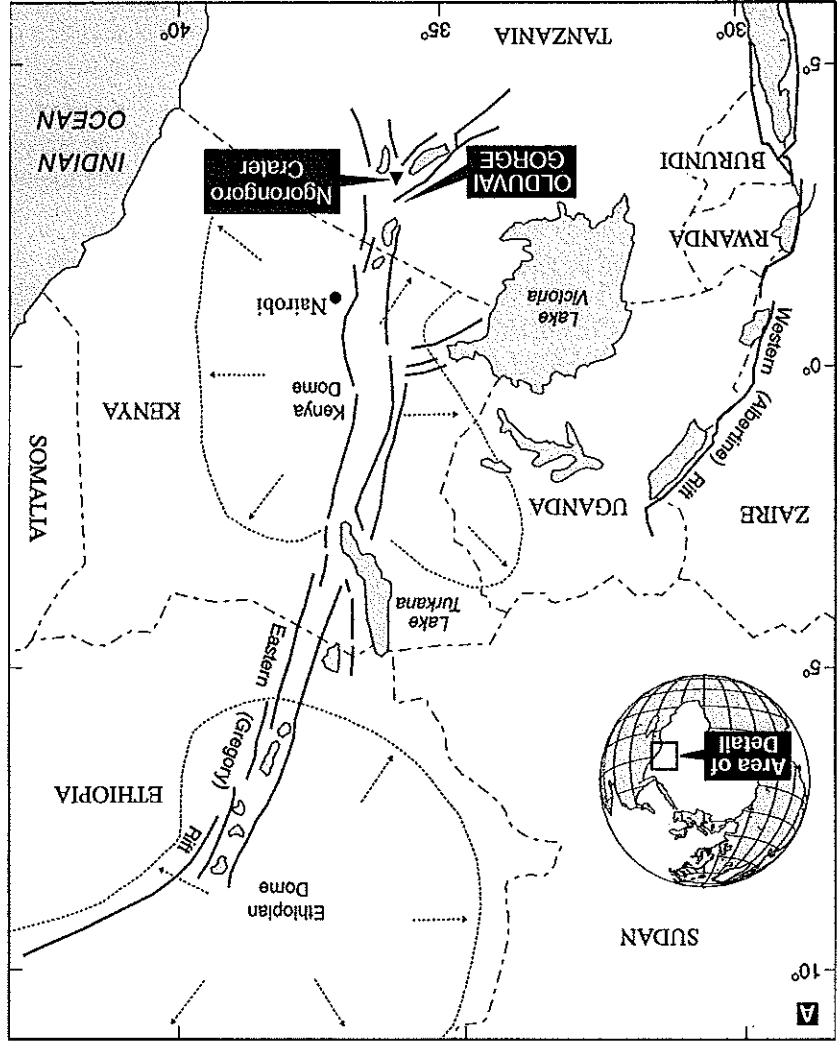


FIG. 1. A regional location map of the Eastern (Gregory) and Western (Albertine) rifts in East Africa depicts the location of Olduvai Gorge on the west margin of the Eastern rift and Ngorongoro Crater at a bifurcation of the rift, both in northern Tanzania.

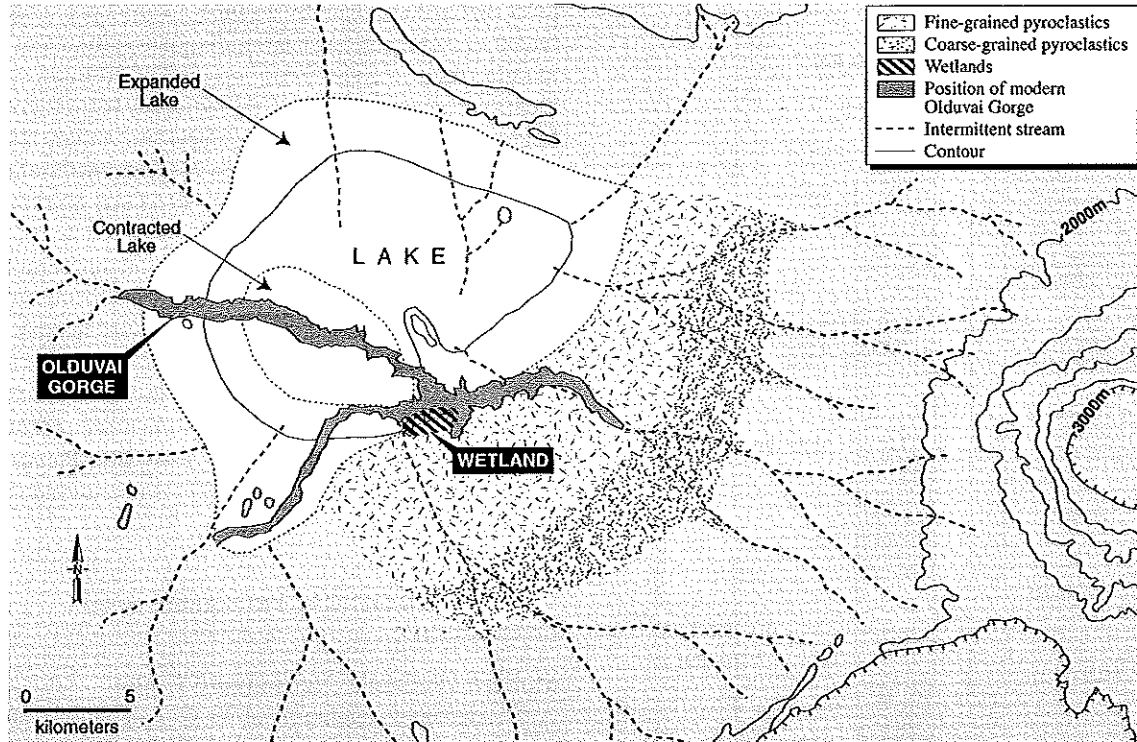


FIG. 2. Paleogeographical reconstruction of the Olduvai Basin during early Pleistocene time (modified from Hay, 1976). The area covered during lake expansions and the location of the groundwater-fed wetland that developed on the southeastern margin of the lake are depicted. The outline of the modern Olduvai Gorge is shown for reference.

The objectives of this paper are to: (1) summarize the geologic and sedimentologic context of groundwater-fed wetland deposits in a semi-arid setting based on observations from an ancient and a modern environment, (2) describe the characteristic bedding and structures formed by vertebrate reworking of the substrate, and (3) discuss preservation potential of large terrestrial mammal bioturbation that is relatively common in the modern environment, but rarely recognized in the geological record.

GEOLOGICAL SETTING

Modern Wetlands, Ngorongoro Crater

Ngorongoro Crater is the caldera of a large trachytic volcano located in the East African Rift, northern Tanzania, about 40 km from Olduvai Gorge, and provides a good modern analog for ancient groundwater-fed wetlands (Deocampo and Ashley, 1997; Deocampo and Ashley, 1999) (Fig. 1). The caldera collapsed approximately two million years ago creating an internally drained basin, 23 km wide at the top and ca. 15 km in diameter in the "crater" bottom. About 20,000 large animals use the area for food and water. The lake in the center of the caldera has varied in size and chemistry since the late Pleis-

tocene and at present is best described as a playa (Pickering, 1965; Hay, 1976; Deocampo, 2001). Two perennial rivers drain into the caldera, and many active springs are scattered throughout the basin. These areas of groundwater discharge support extensive wetlands and provide potable water for thousands of animals daily (Estes and Small, 1981).

The spring-wetland site used in this study, Mti Moja, is a persistent groundwater source located in the center of the caldera. Freshwater flows from the spring orifice over nearly one kilometer; gradually evaporating to a brine (Deocampo and Ashley, 1999; Deocampo, 2001). A ca. 10,000 m² wetland occurs in the freshest part near the spring and is a well-established habitat for hippos (Deocampo, 2002b). The wetland has a spring drainage channel carrying low velocity flows and pools of standing water (excavated by the hippos). Other subenvironments include marsh as well as vegetated and unvegetated mud flats. A black rhino calving ground is nearby on slightly higher ground.

Plio-Pleistocene Wetlands, Olduvai Gorge

Olduvai Gorge is an incised river valley draining from the eastern Serengeti Plain toward the Eastern Rift valley (Fig. 1). The Gorge exposes a two-million year record across a 50

posit that is dominated by a saline-alkaline playa lake that fluctuated episodically over several kilometers of the lake margin (Figs. 2, 3). A 3 km² spring and wetland complex was identified near the base of the adjacent Ngorongoro Volcanic Highland (Ashley, 1996; Decampo and Ashley, 1999). In addition to pyroclastic airfall from Ngorongoro, sediments were transported into the basin by both wind and intermittent runoff (rivers and mudflows).

The groundwater-fed spring and wetland complex is adjacent to the lake, sometimes physically separated from the lake and sometimes inundated by it. Lake level changes were likely driven by both short-term (seasonal to decades) and longer-term (Milankovitch-scale) changes in the hydrologic budget (Ashley and Driese, 2000). The sedimentary record contains a rich faunal and cultural record of early Plio-Pleistocene vertebrates and hominids (Leakey, 1971; Blumenstine and Masao, 1991).

SEDIMENTOLOGICAL PROCESSES AND LITHOFACIES

Modern Wetlands, Ngorongoro Crater

The wetland vegetation varies with depth of water; duration of inundation, and salinity. But, ephemeral wet meadows commonly have *Cynodon*, the marsh contains *Scirpus* and *Cyperus* species, and *Typha* is present in more permanently wet areas. Sediments are fine-grained, organic-rich, 10–20% loss-on-ignition (LOI), silty to sandy clays. They are composed of aluminum clays and biogenic amorphous silica, as well as abundant plant remains (localized root mat and peats) (Decampo, in press). Occasionally a track of a single animal is preserved (e.g., Fig. 4A), but typically the muds are heavily pummeled by foot traffic (e.g., Fig. 4B, C).

Additional lithofacies forming in the modern sedimentary environment range from carbonate (springhead deposit) to muddy sand (spring drainage channel) to silty and alkaline clay (evaporative mudflats and playa lake) to very sandy muds (sub-aerial sedimentation). The coarse fraction is probably eolian detritus sourced from deflation of adjacent de-vegetated areas. Sands are a mixture of tuffaceous minerals, weathered lithic fragments of locally derived lava and Pleistocene carbonates, as well as reworked diagenetic lacustrine calcite. In freshly desiccated areas of the playa lake margin, efflorescent crusts of iron and halite are common, although these are rapidly reworked by bioturbation and wind. Clays are generally illitic with minor smectite interstratification, with Mg-smectite, consistent with diagenesis under saline-alkaline conditions (Hay, 1976; Decampo, 2001).

Modern Bioturbators

The majority of large vertebrates utilizing the spring/wetland complex, at least seasonally as a water source, are ungulates (wildbeest, black rhinos, gazelles, wart hogs, buffalo, zebras) and elephants (Estes and Small, 1981). Carnivores (lions,

FIG. 3. A representative stratigraphic section (ca. 5 m thick and 1 m wide) from the early Pleistocene lake-margin wetlands, Olduvai Gorge, is comprised of tuffs and interbedded claystones: green smectitic claystone deposited in a saline-alkaline lake and siliceous "early" claystone deposited in the groundwater-fed wetlands. The bedding contacts are lithologically sharp, but are commonly irregular and undulating; these surfaces are interpreted as having been bioturbated by large animals frequenting the wetlands.

kilometer-wide rift-platform sedimentary basin that was located on the western margin of the main rift valley (Ashley and Hay, 2002). The shallow sedimentary basin was situated between Precambrian basement (west) and the Plio-Pleistocene Ngorongoro Volcanic Highland (east). The basin fill, that is now disrupted by rift-parallel faults, is thin (100 m), and comprised of interbedded primary airfall tuffs, reworked volcanic-clastic sediments, and locally quartzo-feldspathic sediments (Hay, 1976).

Paleoenvironmental reconstruction of a short (~50 kyr) interval of time starting at ~1.75 Ma revealed a semi-arid landscape within a closed depression (Hay, 1976, 1990; Ashley, 2000). The interval is recorded as a 6-m thick sedimentary de-

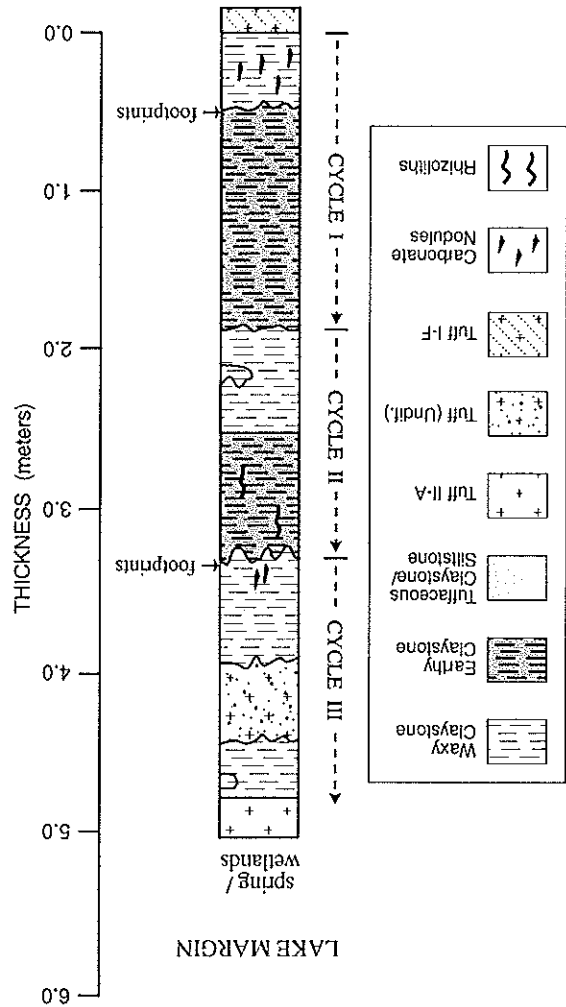


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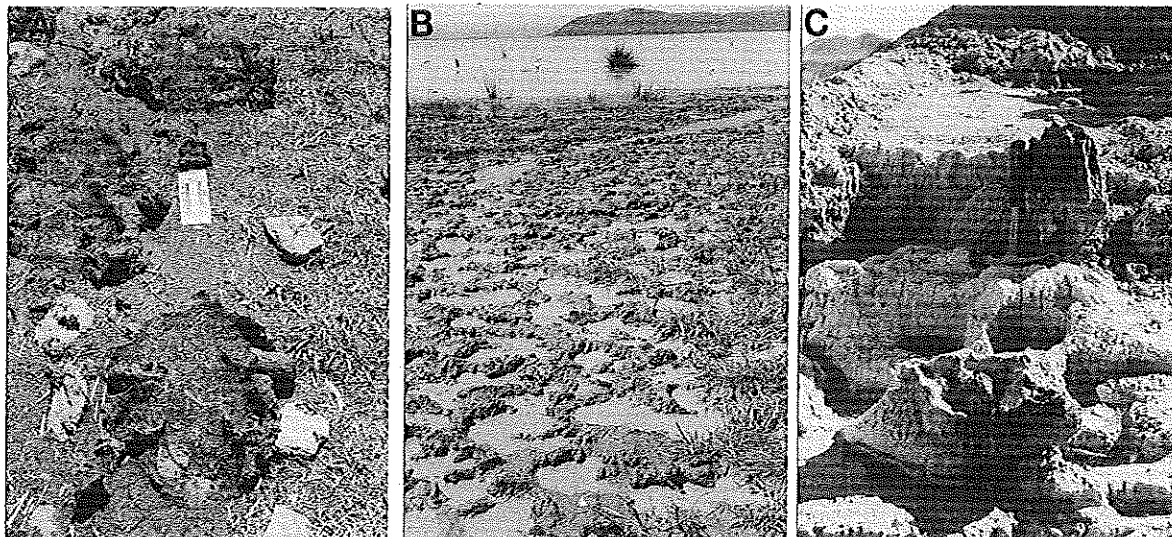


FIG. 4. A. Lake Baringo, Kenya. Tracks of a single hippo moving from top to bottom of photo. The manus (front) print is modified by the pes (hind) print. Substrate is a moderately moist, silty claystone. Width of individual prints ranges from 25–29 cm. Length of stride is ca. 100 cm. Scale is 4 cm. B. Hippo habitat. Intensely bioturbated mudflat, with minor vegetative cover. Substrate is a saturated, silty to sandy mud. This modern mudflat is a reasonable analog for ancient deposits in C. C. Early-Pleistocene record, Olduvai Gorge. Bedding plane surfaces at top of siliceous “earthy” claystones commonly reveal footprints of large vertebrates. (See Color Plate 1 at the end of this issue).

hyenas, vultures, jackals, etc.) may also frequent the area. Hippos (*Hippopotamus amphibious* Linnaeus) are the only large vertebrate resident. Another potential permanent wetland dweller is the crocodile (*Crocodilus niloticus* Linnaeus) (Ross, 1989), and although they occur in other groundwater wetland settings in the rift, crocodiles require a larger more stable freshwater environment than currently exists at Ngorongoro Crater. The area of standing freshwater (pools) is small, and the adjacent playa lake is relatively dynamic and thus not ecologically dependable on an annual basis (Deocampo, 2002a).

Hippo adults generally weigh between 1000 and 1500 kg, but may reach 4000 kg and thus can have significant impact on the substrate (Marshall and Sayer, 1987). An adult hippo eats about 18 kg of grass (dry weight) per day (Lock, 1972). Hippos are semi-aquatic, spending most days partially submerged in pools (5–50 m in diameter) that they often excavate for themselves. They are gregarious and travel in groups to and from grazing sites (Fig. 5A). Most vertebrates frequenting the wetlands tend to follow higher ground, except hippos that tend to seek low grounds. Because of this behavior the hippo trails are usually partially filled with water, and the associated sediment is either saturated or very moist (Fig. 5B). They plod along the trail squeezing mud up and out of the depression, creating a mud levee (Fig. 5C). Additional sediment is likely excavated and carried away on hooves of the animals. At low water levels, the mud levees and mud banks desiccate and crack (Fig. 5D). Claystone blocks slide back into the incised trail, and eventually the trail is infilled by mass movement, windblown sediment, and lake sediments brought in by rising playa lake water.

Crocodiles are reptiles that live for several decades and grow to 3–5 m, or greater, in length. They frequent the shallows of lakes and marshes, where the shallow water allows for the penetration of sunlight and results in a diverse fauna (Ross, 1989). These reptiles are mainly nocturnal hunters and spend most of their day basking in the sun (Ross, 1989). They utilize the wetlands for food, as protection from carnivores, and to maintain thermal stability. Their diet consists of a wide variety of animals, from frogs, birds, fish, small mammals, and insects, to larger prey such as buffalo, hippos, zebras, antelopes, and wildebeest (Ross, 1989). Although they feed in the wetlands, they nest and lay eggs on slightly higher, better drained terrain nearby. Their footprints (Fig. 6A, B) and tail prints (Fig. 6C) are common in the environs of wetlands that are associated with stable bodies of standing water.

Plio-Pleistocene, Olduvai Gorge

During low lake levels a large groundwater-fed wetland, fed by precipitation at higher elevations on the Volcanic Highland (>1500 m above the basin floor), developed on the southeastern margin of the Olduvai basin (Fig. 2). Small springs likely erupted along the slope and at the base of a volcanoclastic fan. Localized carbonate deposits composed of masses of micrite (1–3 m² in diameter and ca. 30–50 cm thick) record the former presence of springs (Liutkus, 2000). The wetland covered >3 km² and is represented by siliceous earthy claystone. Earthy claystones are interbedded with green waxy claystones, interpreted as saline-alkaline lake sediments by Hay (1976). During high lake levels the playa lake covered the wetlands area drowning the marsh. Figure 3 depicts 2-1/2 lake cycles in a rep-

TABLE 1
 Plio-Pleistocene 4-meter thick paleontological record of interbedded freshwater-wetland and lake sediments, MCK, lowermost Bed II, Olduvai Gorge, Tanzania.

Thickness (m)	Lithology	Environment	Taxon
0.2	Tuff	Subaerial	No fossils
0.2	Reworked tuff	Subaerial	Mammal, bovid
0.1	Waxy claystone	*Lacustrine	Mammal, reptile
0.8	Earthy claystone	Wetland	Mammal, carnivore, suid, equid, bovid, aves
0.3	Waxy claystone	*Lacustrine	Reptile, mammal, bovid
0.3	Earthy claystone	Wetland	Aves, bovid, rhino, equid, bovid, mammal
0.7	Tuffaceous claystone	Mud flat	Aves, bovid, hippo, mammal
1.0	Earthy claystone	Wetland	Aves, bovid, mammal
0.2	Waxy claystone	*Lacustrine	No fossils
0.2	Tuff	Subaerial	No fossils

Fossil identification by Amy Cushing (Cushing, 2002).

*Lacustrine-waxy claystone deposited in a lake, but fossils may be younger mixed in following lake recession.

and having minimal post-depositional compaction enhances preservation potential. Well-preserved footprints are relatively rare in the geological record of wetlands, whereas massive sediments are more common. Thus, the long term picture within a wetland is one typified by relatively low energy, fluctuating water availability and a high rate of trampling relative to the rate of sedimentation.

Paleoecological implications

Hippos (*Hippopotamus amphibius*) are important to the ecology of permanent wetlands in Africa and have significant environmental impact (Olivier and Laurie, 1974). They have been known to affect drainage avulsions in the Okavango Delta, Botswana and Ngorongoro Crater, Tanzania, by creating incised channels during daily excursions from permanent deep water pools used during the day to adjacent grazing areas utilized at night (McCarthy et al., 1998; Deocampo, 2002b). These trails lead away from the wetlands and criss-cross adjacent terrain (Fig. 5C, D). They represent significant topography in this otherwise flat terrain. They can be up to a few km long and range between 0.5 and 1 m wide and 0.5 to 1 m deep—much deeper, narrower, and straighter than one would expect from a fluvial incision.

The trough exposed at Olduvai (Fig. 7) is similar in shape, scale, and context to hippo trails commonly found at modern water holes (Deocampo and Ashley, 1997; McCarthy et al., 1998; Deocampo, 2000) (Fig. 5B, C, D). To our knowledge this is the first hippo track to be documented in Plio-Pleistocene sediments.

Modern hippos may well be occupying the same ecological niche and expressing similar behavior of an extinct group of large vertebrates, the amyodonts, that evolved in North America and later spread into Europe and Asia (Colbert, 1969). *Amyodont* (Eocene) and *Metamyodont* (Oligocene) were large, heavy vertebrates with short, broad feet and are fire-

trails retention of the impression. High sedimentation rate and frequent flooding events increase the potential for print preservation, because fresh prints are covered and buried before extensive modification can occur. Finally, limited post-depositional modification, for example compaction, increases the likelihood of preserving delicate structures, such as invertebrate trace fossils or human footprints (Leakey and Hay, 1979).

In summary, ideal conditions for recording individual footprints and trails are moderately moist, silty sediments, with a low rate of animal activity (trampling) relative to rate of sedimentation (Fig. 8). Covering the sedimentary structure quickly

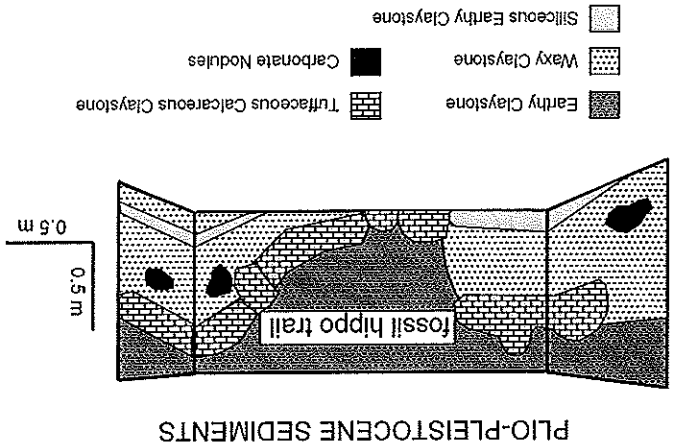


FIG. 7. Ancient hippo trail (1.75 million years old). An excavation exposes lake-margin stratigraphy of interbedded waxy claystone, earthy claystone and tuffaceous claystone. Carbonate deposits were found nearby indicating a spring or groundwater seep. A U-shaped depression (1.2 m wide and 60 cm deep) is eroded into the sediments. The depression was later infilled by earthy claystone. Based on modern analogs, this depression is interpreted as a hippo trail.

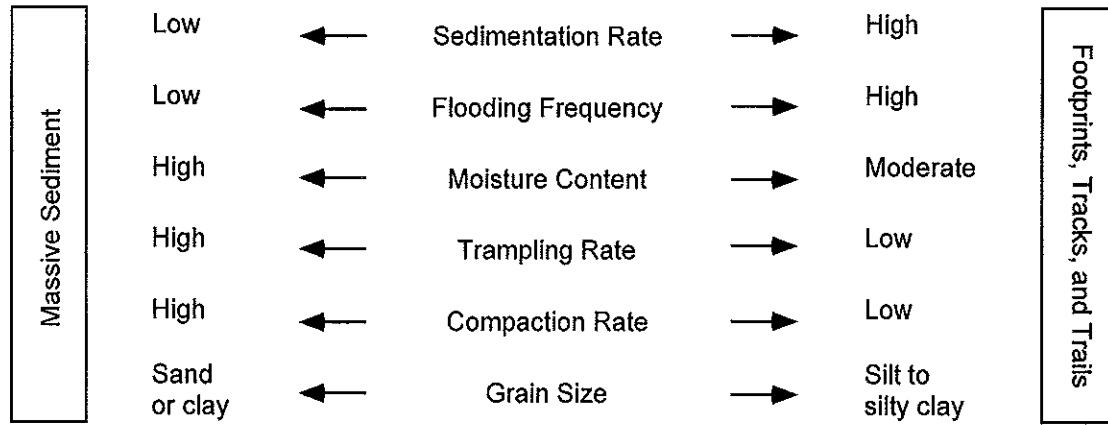


FIG. 8. Environmental factors that affect the nature of a vertebrate bioturbation record in groundwater-fed wetlands

quently found in stream-channel deposits, indicating that they may have been water-lovers like the modern hippopotamus.

Unusually narrow (1–2 m) and 1m deep incisions in river channel banks and levees have been noted in the 55 Ma Lower Eocene Willwood Formation (in the Big Horn Basin, Wyoming) and are difficult to interpret in terms of natural fluvial processes (M. J. Kraus and A. J. Pulham, pers. comms.). These incisions could represent trails of large vertebrates moving to and from the river channel and sources of food. *Coryphodon*, a large pig or hippo-like member of an extinct group known as pantodonts, had a herbivorous diet and would have been at home in swampy habitats (Rose, 2001). It had tusklike canines and broad, crested molars to feed on vegetation, and is a reasonable ancient analog for the Plio-Pleistocene hippos at Olduvai and modern hippos at Ngorongoro Crater, Tanzania.

CONCLUSIONS

1. Groundwater-fed wetlands are low energy environments where the physical record appears to be dominated by biological processes. Sedimentation rates are generally low and plant and animal activity relatively high.
2. The wetland bioturbation record reflects a number of interacting factors, such as substrate texture, moisture content, sedimentation rate, frequency of flooding, types and numbers of animals present, trampling rate, and post-depositional changes (compaction).
3. Organic-rich wetland sediments in semi-arid regions may oxidize and thus all that remains are vestiges of the former habitat: localized carbonate and diatomite deposits, sandy and silty claystones, and siliceous earthy claystones containing plant remains, bone fragments, pollen, and phytoliths. Vertebrate bioturbation leaves a physical record that can provide indirect information on the ecology of the paleoenvironment despite the loss of organic remains.

4. The impact of large mammals on the wetland sediment record is pervasive and ranges from thoroughly bioturbated sediments pummeled by thousands of hooves to trails of superimposed tracks and discrete footprinted surfaces.

5. A paleo hippo trail (1.2 m wide and 0.6 m deep) was interpreted in the Plio-Pleistocene wetland deposits based on comparison to modern analogs.

6. Preservation potential of the massive bedding (intense trampling) is excellent and is likely to occur in most circumstances. However, preservation of footprints or trails requires a rapid burial to record the “snapshot in time.” Dramatic change in sedimentary regime occurs rarely in wetland environments, particularly those isolated from rivers or lakes.

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