

Short communication

IMPLICATIONS OF A NEW AFF. *HIPPOPOTAMUS KARUMENSIS* MANDIBLE FROM THE KOOBI FORA FORMATION, TURKANA BASIN, KENYAIan J. Wallace¹, Meave G. Leakey^{1,2} and Louise N. Leakey^{1,2}¹Department of Anthropology, Stony Brook University, Stony Brook, New York 11794, USA
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ABSTRACT: The phylogeny of the East African Hippopotamidae is problematic. A particularly controversial relationship is that between aff. *Hippopotamus protamphibius* and aff. *Hippopotamus karumensis* from the Pliocene and Pleistocene of the Turkana Basin (Kenya and Ethiopia). Various hypotheses have been proposed, including (1) that the species are sister taxa derived from a common ancestral hexaprotodont species, (2) that they are time-successive segments of a single anagenetic evolutionary lineage, and (3) that aff. *Hippopotamus karumensis* represents a branch of an evolving aff. *Hippopotamus protamphibius* lineage. A major obstacle to determining which of these evolutionary scenarios is the most parsimonious is the unknown degree to which the two species co-occurred. Here we describe a new aff. *Hippopotamus karumensis* mandible from the Upper Burgi Member of Koobi Fora Formation, east of Lake Turkana (Kenya), that represents the earliest occurrence of this species yet to be documented. The presence of aff. *Hippopotamus karumensis* in this member implies a lengthy period of sympatry with aff. *Hippopotamus protamphibius* that makes an anagenetic relationship between these species improbable. It is also unlikely that the species derived from a common hexaprotodont since there is currently a lengthy time gap between the earliest occurrences of the two species. The most parsimonious interpretation is that aff. *Hippopotamus karumensis* represents a branch of an evolving aff. *Hippopotamus protamphibius* lineage.

Keywords/phrases: *Hippopotamidae*, *Plio-Pleistocene*, *Turkana Basin*

INTRODUCTION

The family Hippopotamidae was diverse and abundant in the Turkana Basin (Kenya and Ethiopia) from the late Miocene through the Pleistocene. Hippopotamids are among the most common mammals at various East African paleontological sites of this age, including most early hominin localities. However, the phylogeny of Hippopotamidae is problematic. Recognizing this, Boissarie (2005) published the first cladistic analysis of Hippopotamidae, in which he shows that most East African hippopotamids formerly attributed to *Hexaprotodon* Falconer and Cautley, 1836 (abbreviated *Hex.*), are in fact more closely related to members of *Hippopotamus* Linnaeus, 1758 (abbreviated *H.*). Nevertheless, a number of issues remain unresolved. A particularly controversial relationship is that between Plio-Pleistocene specimens from the Turkana Basin previously assigned to *Hex. protamphibius* (Arambourg, 1944) and *Hex. karumensis* (Coryndon, 1977) and referred by Boissarie (2005) to aff. *H. protamphibius* and aff. *H. karumensis*. The consensus view is that these species are closely related. However, some consider them to be sister taxa

derived from a common ancestral hexaprotodont species (Coryndon, 1976; 1977; Harris, 1978; Gèze, 1985), others have interpreted them as possible time-successive segments of a single anagenetic evolutionary lineage (Harris, 1991), and recently aff. *H. karumensis* has been suggested to represent a branch of an evolving aff. *H. protamphibius* lineage (Harrison, 1997; Weston, 2000; Boissarie, 2005).

The earliest occurrence of aff. *H. protamphibius* is in the early or middle Pliocene, whereas aff. *H. karumensis* first appears in the late Pliocene or early Pleistocene, depending on which fossil samples are assigned to these taxa (Harris, 1991). The degree to which they overlapped in time is unclear and is an issue that is central to disagreements surrounding their evolutionary relationship. An obstacle to resolving this issue is the uncertain taxonomic status of certain tetraprotodont material from the Upper Burgi Member of the Koobi Fora Formation (Kenya), a time interval between 2.08–1.87 Ma (McDougall and Brown, 2006; Joordens *et al.*, 2013). This material has been interpreted as representing late occurrences of aff. *H. protamphibius* (Maglio, 1971) as

well as primitive examples of aff. *H. karumensis* (Harris, 1978; 1991; Gèze, 1980; 1985).

Difficulty in assigning the Upper Burgi Member material to a particular taxon stems from the fact that aff. *H. protamphibius* and aff. *H. karumensis* are morphologically very similar in most respects (Gèze, 1980; Harris, 1991; Boisserie, 2005). Neurocrania are short and globular with well-developed postorbital constriction, a large sagittal crest, laterally expanded supraorbital processes, and orbits that are elevated to varying degrees above the cranial vault. Viscerocrania have marked postcanine constriction relative to the laterally expanding upper canine apophyses and robust zygomatic arches. Both taxa are brachydont with very similar molar morphologies. Both also possess comparatively gracile postcrania with relatively long and slender limbs. The overall body size of aff. *H. karumensis* is larger than that of aff. *H. protamphibius*, but the species overlap in their respective ranges.

Diagnostic characteristics of the species are primarily in the mandible and lower anterior dentition. First, aff. *H. protamphibius* is tetraprotodont with four lower incisors (Arambourg, 1944), whereas aff. *H. karumensis* is diprotodont with two (Coryndon, 1977). Some have opted to recognize early hexaprotodont and tetraprotodont morphs of aff. *H. protamphibius* and aff. *H. karumensis*, respectively (Gèze, 1985; Harris, 1991); however, such lumping of primitive and derived forms assumes a close relationship between the groups that has never been satisfactorily demonstrated via cladistic methods or otherwise. We therefore recognize the original definitions of these species and consider the number of lower incisors to be of diagnostic value. Second, the species differ in the position of the canines relative to the incisor row (in dorsal view). Boisserie (2005) observed that in aff. *H. protamphibius* the anterior borders of the canine alveoli are anterior to the incisor alveoli, whereas in aff. *H. karumensis*, the canines are more anteriorly placed such that the posterior borders of the alveoli are anterior to the incisor alveoli. While this distinction is generally valid, we would argue that in some unequivocal specimens of aff. *H. karumensis*, such as the holotype (KNM-ER 798; Fig. 2.8 in Harris, 1991), the posterior borders of the canine alveoli are level with, rather than anterior to, the incisor row. Nevertheless, the canines are always situated more anteriorly in the mandible in aff. *H. karumensis*. Third, the transition between the anterior and ventral faces of the symphysis forms a gentle angle in aff. *H. protamphibius* and an abrupt angle in aff. *H. karumensis* (Boisserie, 2005). Numerous other

distinctions have been drawn (Harris, 1991), but many of these lack consistency.

Multiple tetraprotodont hippopotamid species are currently recognized from the Upper Burgi Member (Harris, 1991), including *H. gorgops* (Dietrich, 1928), and aff. *H. aethiopicus* (Coryndon and Coppens, 1975), both of which are rare. The tetraprotodont specimens variously assigned to both aff. *H. protamphibius* (Maglio, 1971) and aff. *H. karumensis* (Harris, 1978; 1991; Gèze, 1980; 1985) are by far the most common. Additional specimens collected in recent years by members of the Koobi Fora Research Project bring the total number of mandibles from this group to a minimum of 15. In most respects, these fossils are morphologically very similar to aff. *H. protamphibius* (Coryndon, 1976; 1977). Besides having four lower incisors, the lower canines are situated posteriorly relative to the incisors and the anterior and ventral faces of the symphyses form gentle angles (*e.g.*, KNM-ER 1395; Fig. 2.10 in Harris, 1991). Coryndon (1976) claimed that these fossils could not be assigned to aff. *H. protamphibius* due to the small size of their canines and the diastema between their lower central incisors, but these features have since been documented in aff. *H. protamphibius* (*e.g.*, KNM-ER 944; Fig. 2.6 in Harris, 1991).

As explained by Harris (1991), the assignment of the Upper Burgi Member material to aff. *H. karumensis* is largely a product of historical circumstance stemming from the fact that aff. *H. protamphibius* was originally recognized from the lower members of the Shungura Formation (Ethiopia) whereas aff. *H. karumensis* was described based on specimens from members directly above the Upper Burgi (*e.g.*, KBS and Okote). Because members of the Koobi Fora Formation below the Upper Burgi (Lonyumum through Lower Burgi) had yielded few hippopotamid specimens, and because the sample from above was so rich, S.C. Coryndon, who undertook the initial study of the Koobi Fora Hippopotamidae, considered the material in terms of "early" and "typical" aff. *H. karumensis*. An alternative interpretation might be to describe this material in terms of aff. *H. protamphibius* and aff. *H. karumensis*.

Here we describe a new hippopotamid mandible from Koobi Fora that has bearing on the identity of these Upper Burgi Member tetraprotodonts as well as implications for the evolutionary relationship between aff. *H. protamphibius* and aff. *H. karumensis*. Insights gleaned from the new mandible have broader implications for hippopotamid paleobiology during the Plio-Pleistocene of the Turkana Basin.

MATERIALS AND METHODS

Description and interpretation of mandible

Material

KNM-ER 47950, a partial mandible with right I1 and P4–M2 and left I1 (Fig. 1). The specimen was found *ex situ* by I.J.W. during fieldwork in 2008.



Figure 1. Dorsal view of the KNM-ER 47950 hippo mandible. Arrows indicate the position of the incisor alveoli (incisors not pictured).

Locality and horizon

Area 131, Karari Ridge, east of Lake Turkana, northern Kenya (N 4° 6' 56", E 36° 23' 3"). Upper Burgi Member, Koobi Fora Formation (Brown and Feibel, 1986).

Description

The mandible is relatively complete (Fig. 1), though discovered in many fragments. The reconstruction of the specimen is ongoing; many small fragments remain, particularly from the ascending rami and condyles. Nevertheless, sufficient reconstruction of the symphysis, corpora, and canine processes has been completed to warrant a preliminary description of the fossil. The mandible is robust with a tall and massive symphysis. The anterior face is steeply inclined and forms an abrupt angle with the ventral face. A weakly overhanging incisor alveolar process displays the diprotodont condition. Incisor alveoli extend to the posterior border of the symphysis. Sagittally, the dorsal face of the symphysis is horizontally to weakly inclined and it is curved

mediolaterally. Though slightly distorted, the ventral face of the symphysis appears relatively flat in the sagittal and mediolateral planes. The symphysis extends posteriorly to the level of the P3 alveoli. Canine processes are well developed and project anterolaterally. The posterior borders of the canine alveoli are level with the incisor row. The incisors are procumbent with large, circular cross sections. The I1–I1 diastema (39 mm) is wider than the mesiodistal diameter of the lower incisors (~35 mm for both right and left I1). The cheek tooth rows are anteriorly subparallel, but converge posteriorly and the molars become inclined lingually, though these features could be exaggerated by distortion of the fossil. The corpora become taller and thinner posteriorly. Cheek teeth are heavily worn and the specimen lacks P1 alveoli. The right P4 is rectangular and set at an angle to the midline of the ramus.

Attribution to *aff. Hippopotamus karumensis*

Attribution of KNM-ER 47950 to *aff. H. karumensis* is supported by its diprotodont condition, anteriorly positioned canine alveoli, and an anterior face of the symphysis that forms an abrupt angle with the ventral face. A feature of the fossil that distinguishes it from most *aff. H. karumensis* specimens is that its symphysis only extends posteriorly as far as the P3 alveoli (rather than to P4 or M1), but because this characteristic has been documented in certain unequivocal specimens of *aff. H. karumensis* (Harris, 1991), including the holotype (Coryndon, 1977), it cannot be used to exclude it from this species.

Simple mandibular metrics are of limited utility in attributing KNM-ER 47950 to either *aff. H. protamphibius* or *aff. H. karumensis*, due to overlapping values for the two taxa (Table 1).

Table 1. Mandibular measurements of KNM-ER 47950 compared to the range of values of *aff. H. protamphibius* and *aff. H. karumensis*.

Species	Measurements			
	M1	M2	M3	M4
KNM-ER 47950	96	117	335	39
<i>aff. H. protamphibius</i>	63–104	111–151	231–308	11–48
<i>aff. H. karumensis</i>	43–109	103–183	231–360	36–117

Note: Measurements to nearest mm. M1, height of the symphysis; M2, sagittal length of symphysis; M3, width across canine processes; M4, width across I1–I1 diastema. Comparative data are from Boissier and White (2004).

The symphyseal height and length, as well as I1–I1 diastema length, fall within the known ranges of variation for both species. However, the width

between the anterior tips of the canine processes falls outside the range of aff. *H. protamphibius*, but within the range of aff. *H. karumensis*, therefore adding some quantitative support to the attribution of KNM-ER 47950 to aff. *H. karumensis*.

DISCUSSION

Additional Upper Burgi Member diprotodont material

In an inventory of the hippopotamid material from the Koobi Fora Formation housed at the National Museums of Kenya, Harris (1991) described all documented specimens of aff. *H. karumensis* from the Upper Burgi Member as tetraprotodont. However, during an examination of this material by one author (I.J.W.), it was noted that an aff. *H. karumensis* hemisymphysis (KNM-ER 1402) from the Upper Burgi Member of Area 123 displays the diprotodont condition, thus adding support to the proposed presence of diprotodont aff. *H. karumensis* in this member. Readers should be aware, however, that the geologic provenance of the mammalian fauna from Area 123 is the subject of an ongoing debate (Gathogo and Brown, 2006; Feibel *et al.*, 2009). Nevertheless, noteworthy features of the fossil include its overall robusticity, the posterior extension of the symphysis to the P4 alveolus, and the abrupt angle formed between the anterior and ventral faces. The canine alveolus is unfortunately not preserved.

Implications

The new mandible described here represents the earliest documented occurrence of aff. *H. karumensis sensu stricto* (*i.e.*, diprotodont). Previously, the appearance of diprotodont aff. *H. karumensis* in the Koobi Fora Formation was thought to have occurred in the upper part of the KBS Member, coincident with, or subsequent to, the last appearance of the tetraprotodonts commonly assigned to aff. *H. karumensis* (Harris, 1991). The earliest occurrence west of Lake Turkana is in the Kaitio Member of the Nachukui Formation (Harris *et al.*, 1988), the lateral equivalent of the KBS Member (Feibel *et al.*, 1989). No diprotodont material has been documented from the Shungura Formation (Harris, 1991).

The presence of diprotodont aff. *H. karumensis* in the Upper Burgi Member implies a lengthy period of sympatry between the two morphotypes and likewise makes an anagenetic relationship between them implausible. Anagenetic

change has for decades been an operating assumption for many researchers of East African hippopotamid evolution (*e.g.*, Coryndon, 1970; 1971, 1976, 1977; Gèze, 1980; 1985). Under this paradigm, several allochronic fossil samples have been considered conspecific regardless of their well-documented morphological distinctiveness. While such an approach is appealing in its ability to simplify taxonomy, it appears to have led to incorrect interpretations of the relationship between diprotodont aff. *H. karumensis* from the KBS and Okote Members and tetraprotodonts from the Upper Burgi Member. A general criticism of the approach is that evolutionary changes with enough permanence to be recognized in the fossil record probably reflect speciation events, since, on a geologic time scale, intraspecific differentiation is largely ephemeral (Futuyma, 1987). Another criticism of this paradigm, more specific to its application to East African hippopotamid fossils, is that it downplays the evolutionary importance of morphological characters with great adaptive significance, such as features of the anterior dentition. For the extant common hippo (*H. Amphibious* Linnaeus, 1758), the canines and incisors are critical weapons during clashes over mates, resources, and offspring, which can be fatal (Laws, 1968; Kingdon, 1979; Eltringham, 1999). Likewise, differences between aff. *H. protamphibius* and aff. *H. karumensis* in their anterior dental morphologies likely reflect important social differences arising from distinctive selective pressures (Kingdon, 1979). In sum, we propose that the tetraprotodont fossils from the Upper Burgi Member which have been assigned to aff. *H. karumensis* (Harris, 1978; 1991; Gèze, 1980; 1985) are best assigned to aff. *H. protamphibius sensu* Maglio, 1971).

The inclusion of these fossils into aff. *H. protamphibius* does not impact on the temporal distribution of this taxon in the Turkana Basin since the species is present in the late Pliocene members of the Shungura (Coryndon and Coppens, 1973) and Nachukui Formations (Harris *et al.*, 1988). However, assignment of these fossils to aff. *H. protamphibius* does extend the presence of this species in the Koobi Fora Formation by a minimum of 0.5 Myr. This interpretation is ecologically more realistic than the alternative which posits that two similarly sized species with largely indistinguishable craniodental morphologies simultaneously exploited the Turkana Basin (*e.g.*, Coryndon and Coppens, 1973; Coryndon, 1976; 1977; Gèze, 1980; 1985;

Harris, 1991). Gèze (1985) recognized an additional tetraprotodont taxon from the late Pliocene members of the Shungura Formation (*Hex. shungurensis*) which was similar in its size and general morphology to aff. *H. protamphibius*. However, we tend to agree with Harris (1991) that this taxon represents the female morph of aff. *H. protamphibius*. In addition, it is likely that early Pleistocene tetraprotodont material assigned to aff. *H. cf. karumensis* by Gèze (1985) also represents aff. *H. protamphibius*, for the same reasons warranting the reassignment of the Upper Burgi Member specimens.

The assignment of the Upper Burgi Member tetraprotodont material in question to aff. *H. protamphibius* means that it is improbable that aff. *H. protamphibius* and aff. *H. karumensis* shared an anagenetic evolutionary relationship. It is also unlikely that the two are derived from a common ancestral hexaprotodont species since there is currently a lengthy time gap (*ca.* 0.7 Myr) between the first occurrences of aff. *H. karumensis* (documented here) and the last occurrences of hexaprotodont hippos in the Turkana Basin. The most parsimonious interpretation is that aff. *H. karumensis* represents a branch of an evolving aff. *H. protamphibius* lineage (Harrison, 1997; Weston, 2000; Boisserie, 2005).

Speciation was conceivably facilitated by niche differentiation whereby aff. *H. karumensis* shifted to more lacustrine resources while aff. *H. protamphibius* remained more terrestrially adapted (Coryndon, 1976). An often-cited piece of evidence supporting this hypothesis is the increased elevation of the orbits of certain aff. *H. karumensis* specimens (Coryndon, 1977; Harris, 1991; Boisserie, 2005). However, there are at least three potential problems with this interpretation of niche differentiation. First, elevated orbits are not a common feature among aff. *H. karumensis* crania from below the Okote Member, when the speciation event occurred. This is true even for specimens from the KBS Member (*e.g.*, KNM-ER 1208, 1214, 1308, and 4892). Second, the limb bones of aff. *H. karumensis* remain long and slender, which has been thought to represent an adaptation to territoriality (Coryndon, 1976; Harris, 1991; Harrison, 1997; Weston, 2000). Third, in order for aff. *H. karumensis* to have successfully moved into the lacustrine niche it would have had to compete for resources with *H. gorgops* already occupying that environment (Coryndon, 1976; 1977; Harris, 1991). On the other hand, a study by Harris *et al.* (2008) of the stable isotope ecologies of certain East African fossil

hippopotamids documented that aff. *H. karumensis* and *H. gorgops* were dietarily very similar, indicating that these species may have been able to simultaneously occupy similar ecological (lacustrine) niches. In fact, none of these potential problems are particularly fatal to the hypothesis that the origin of aff. *H. karumensis* was marked by a shift to a more aquatic lifestyle, yet they highlight the need for future research to clarify the differences between the ecological adaptations of aff. *H. protamphibius* and aff. *H. karumensis*.

The recognition of both aff. *H. protamphibius* and aff. *H. karumensis* in the Upper Burgi Member implies substantial diversity among the Hippopotamidae during this time interval. Such diversity is in clear contrast to the Holocene distribution of a single pan-African large bodied species and a geographically restricted small-bodied species (Harris, 1991). The most abundant taxon appears to have been aff. *H. protamphibius*, whereas aff. *H. karumensis*, aff. *H. aethiopicus*, and *H. gorgops* were less common. Indeed, aff. *H. aethiopicus* is represented by only two astragali, which were assigned to this species based on their small size (Harris, 1991). The dimensions of these astragali are, however, only millimetres smaller than fossils assigned to aff. *H. karumensis*, making this evidence equivocal. Excluding these specimens, the earliest evidence for aff. *H. aethiopicus* in the Turkana Basin is during the early Pleistocene (Gèze, 1985; Harris *et al.*, 1988). If one opts to not recognize aff. *H. aethiopicus* in the Upper Burgi Member, however, hippopotamid diversity is still great and requires explanation. More data on the ecological adaptations of the fossil species are needed to accomplish this goal.

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