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Carnivora from the Kanapoi hominin site, northern Kenya

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ABSTRACT

The assemblage from Kanapoi represents the most diverse early Pliocene carnivore assemblage from sub-Saharan Africa. Carnivora from Kanapoi were originally described by Werdelin (2003a), but continuing field work has brought to light significant new material from the site, shedding new light on the earliest post-Miocene radiation of Carnivora in Africa. Most importantly, a second species of *Enhydriodon* has been recovered from the site, including the first specimen to include a large part of the neurocranium. This makes Kanapoi the first site to include two species of this genus. This addition to the fauna will be of prime significance to understanding the ecology and evolutionary radiation of these giant, extinct otters. Other significant new finds include additional material of a wildcat-sized felid. Finds of this group are rare, and the new Kanapoi material adds significantly to our knowledge of the stem lineage of the genus *Felis*, which is widespread in Africa today.

1. Introduction

The Carnivora of Kanapoi were originally described by Werdelin (2003a) on the basis mainly of material collected by National Museums of Kenya expeditions in the 1990s, directed by Dr. Meave Leakey, with some additional specimens from the Harvard University expeditions in the 1960s directed by Dr. Bryan Patterson. Since the end of the 1990s, collecting at Kanapoi has continued on a smaller scale, led by one of us (FKM). This collecting has yielded additional carnivore material from the site, providing some significant additions to the fauna, including the first instance of two species of *Enhydriodon* in the same fauna. We have therefore prepared this contribution, to set these new finds in perspective and to take stock of the Kanapoi carnivoran sample as a whole.

The fossiliferous sediments at Kanapoi belong to the Kanapoi Formation, as defined by Feibel (2003). They consist of three sedimentary intervals: a lower fluviatile interval, a lacustrine interval, and an upper fluviatile interval. The stratigraphy and depositional setting of the Kanapoi sequence are discussed in detail by Feibel (2003). The Kanapoi sequence includes three dated tuffs (Leakey et al., 1998): a lower pumiceous tuff within the lower fluviatile interval, dated 4.17 ± 0.03 Ma, an upper pumiceous tuff just below the upper boundary of the lower fluviatile interval, dated 4.12 ± 0.02 Ma, and the Kanapoi Tuff at the top of the lacustrine interval, dated 4.07 ± 0.02 Ma. All of the carnivore specimens studied herein that have secured stratigraphic positions come from either the lower fluviatile interval or the lacustrine interval, with the exception of KNM-KP36600 (*Homotherium* sp.), which comes from the upper fluviatile interval.

Werdelin (2003a) noted that the majority of published eastern African early Pliocene (taken here as pre-Upper Laetolil beds, i.e., older than ca 3.85 Ma; Deino, 2011) mammal localities have few carnivore fossils associated with them. This is in marked contrast to the several rich Late Miocene localities such as Lothagam (Werdelin, 2003b), Lemudong'o (Howell and García, 2007) and the Lukeino Formation (Morales et al., 2005) in Kenya, and the Adu-Asa Formation in Ethiopia (Haile-Selassie and Howell, 2009). The situation has improved since 2003, however, with, e.g., the publication of carnivores from the informally named Mabaget Fm. overlying the Lukeino Fm. in Kenya (Morales et al., 2005). However, the assemblages from the early Pliocene still remain few and, more importantly, small. Therefore, any additions to these faunas are of great importance to the understanding of the first radiation of carnivores of modern aspect (i.e., post-Miocene) in Africa.

2. Material and methods

The following measurement abbreviations are used in this paper (upper dentition in upper case letters, lower dentition in lower case). LI1, WI1: length and width I1; LI3, WI3: length and width I3; LP4: buccal length P4; LliP4: lingual length P4; LpP4: length paracone P4; LmP4: length metastyle P4; WaP4 width of P4 including protocone; WblP4: width of metastyle P4; LM1: buccal length M1; LliM1: lingual length M1; WM1: greatest width M1; Lc: length

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lower canine; Wc: width lower canine; Lp2, Wp2: length and width p2; Lp3, Wp3: length and width p3; Lp4, Wp4: length and width p4; Lpp4: length of main cusp p4; Lm1, Wm1: length and width m1; Ltm1: trigonid length m1.

Only measurements of the new material are provided here. Measurements of previously described material are given in Werdelin (2003a).

3. Systematic paleontology

Order Carnivora
Family Mustelidae Fischer, 1817
Subfamily Lutrinae Bonaparte, 1838
Tribe Enhydriodontini Pickford, 2007
Genus *Enhydriodon* Falconer, 1868
Enhydriodon ekecaman Werdelin, 2003

Old material: KNM-KP 10034A-C, right C, P4 (Fig. 1A), M1 (Fig. 2A), and m1.

This material was fully described by Werdelin (2003a) and these descriptions will therefore not be reiterated here. Comparisons with new material of *Enhydriodon* from Kanapoi are given below.

Enhydriodon cf. *Enhydriodon dikikae* Geraads et al., 2011

New material: KNM-KP 49887, partial neurocranium (Fig. 3), right and left P4 (Fig. 1B and C) and M1 (Fig. 2B and C), left I3 and ?I1, and numerous cranial and other unidentifiable fragments.

Measurements: LI1: 7.4; WI1: 4.9; LI3: 10.4; WI3: 9.1; LP4: 18.4; LliP4: 16.6; WaP4: 19.5; LM1: a14.7; LliM1: 16.8; WM1: a23.6.

3.1. Description

P4 (based on both left and right specimens) (Fig. 1B and C): The tooth is subrectangular in shape. It is slightly wider than long and the distolingual corner is rounded off. The distal margin of the tooth is damaged in both specimens. At the mesiobuccal corner of the tooth the parastyle, which has a distinct cusp, is set well apart from the paracone, to which it is connected by a distinct preparacrista. The paracone is the largest cusp of the tooth. It is round and has a distinct postparacrista (centrocrista of Van Valen, 1966) leading to the metacone. This crista is not interrupted by a (carnassial) notch. The metacone is set at the distobuccal corner of the tooth. The protocone is double (protocone and protoconule), with the more mesial of the two cusps being the larger. It is set off from the paracone by a wide valley demarcated by a low, blunt crest. The distolingual protocone cusp is smaller and appressed to the larger cusp. Distolingual to this cusp is a third, lower cusp that marks the posteriormost margin of a strong cingulum that extends around the protocone shelf. The hypocone is large and set distobuccal to the cingulum cusp. Whereas paracone, protocone, and metacone have small horizontal wear facets, the hypocone has a strong wear facet that runs obliquely down its mesiolingual face perpendicular to the lingual margin of the tooth.

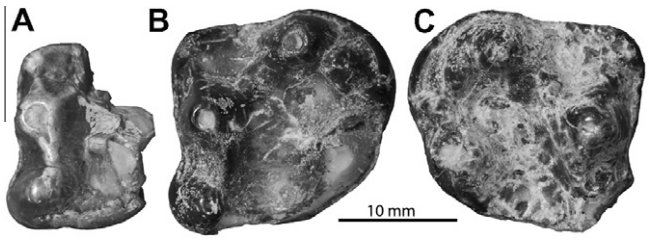

Fig. 1. P4 of *Enhydriodon* spp. from Kanapoi. (A) KP 10034A, right P4 of *E. ekecaman*; (B) KP 49887, right P4 of *E.* cf. *E. dikikae*; (C) KP 49887, left P4 of *E.* cf. *E. dikikae*. See text for detailed comparisons. All specimens in occlusal view with mesial at the top of the figure.

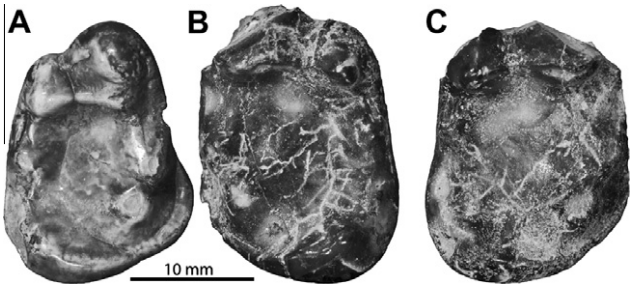

Fig. 2. M1 of *Enhydriodon* spp. from Kanapoi. (A) KP 10034, right M1 of *E. ekecaman*; (B) KP 49887, left M1 of *E.* cf. *E. dikikae*; (C) KP 49887, right M1 of *E.* cf. *E. dikikae*. See text for detailed comparisons. All specimens in occlusal view with labial at the top of the figure.

M1 (based on both left and right specimens) (Fig. 2B and C): The M1 forms an elongated rectangle, with the proximolingual corner cut off. The buccal margin is damaged in both specimens. The paracone is low and connected to the metacone by a low, blunt crest that is interrupted by a shallow notch. The enlarged parastyle seen in some other Enhydriodontini (Werdelin, 2003a) is broken in both left and right specimens. The metacone is lower but longer than the paracone. It is set at or close to the distobuccal corner of the tooth. The protocone and protoconule are subequal in size and height. The hypocone is crest-like and set at the distobuccal corner of the tooth. At the distal margin of the tooth there are also a metaconule set just lingual to the metacone and hypoconule set buccal to the hypocone. Both of these cusps are very low, especially the latter. There is a well-developed cingulum that bounds the protocone and protoconule.

I3 (left): The crown is low and round and has an apical wear facet that is nearly horizontal. The lingual face of the tooth has a well-developed cingulum at the base of the enamel. There is a mediolingual pit that may have been a broken off accessory cusp. The root is much longer than the crown, and nearly straight.

I1? (left): This tooth is mediolaterally flattened and has a low, poorly developed lingual shelf. The apical wear facet is nearly horizontal. The root is broken a few mm below the enamel-dentine junction.

The skull is represented by a large fragment that is broken in the anterior third of the right orbit and in a line extending posteromedially across the frontal (only the posteriormost tips of the nasals are visible) to the medial part of the left orbit, which is entirely missing (Fig. 3). The posterior parts of the nasal passages are visible when the skull is viewed in anterior aspect. The frontal is remarkably flat across its entire preserved width, back to the origin of the sagittal crest. The orbit is relatively shallow and is bordered dorsally by a distinct crest leading to a strong, though not very long postorbital process. The posterior side of the postorbital process is deeply excavated for the temporalis muscle. There is a well developed sagittal crest that extends to the posterior end of the preserved part of the skull. The sagittal crest does not appear to have been very tall, however. On the right lateral side of the skull the crest of the postorbital process is well developed and continues posteroventrally as a distinct ridge to or near the parietal. There is a single fenestra in the lateral wall that likely housed the sphenoid and postpalatine foramina. Posteriorly, the specimen is broken near the anterior end of the parietals.

3.2. Remarks

Werdelin (2003a) described the species *E. ekecaman* from Kanapoi. Since there has hitherto only been found a single species of *Enhydriodon* at any given site, it might be expected that the new