A contextual review of the Carnivora of Kanapoi

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Abstract

The Early Pliocene is a crucial time period in carnivoran evolution. Holarctic carnivoran faunas suffered a turnover event at the Miocene-Pliocene boundary. This event is also observed in Africa but its onset is later and the process more drawn-out. Kanapoi is one of the earliest faunas in Africa to show evidence of a fauna that is more typical Pliocene than Miocene in character. The taxa recovered from Kanapoi are: *Torolutra* sp., *Enhydriodon* (2 species), *Genetta* sp., *Helogale* sp., *Homotherium* sp., *Dinofelis petheri*, *Felis* sp., and *Parahyaena howelli*. Analysis of the broader carnivoran context of which Kanapoi is an example shows that all these taxa are characteristic of Plio-Pleistocene African faunas, rather than Miocene ones. While some are still extant and some went extinct in the Early Pleistocene, *Parahyaena howelli* is unique in both originating and going extinct in the Early Pliocene.

Keywords: Africa, Kenya, Miocene, Pliocene, Pleistocene, Carnivora

Introduction

Kanapoi stands at a crossroads of carnivoran evolution. The Miocene –Pliocene boundary (5.33 Ma: base of the Zanclean Stage; Gradstein et al., 2012) saw a global turnover among carnivores (e.g., Werdelin and Turner, 1996). This turnover is slightly delayed in Africa, with typical Miocene taxa, such as *Ictitherium*, *Hyaenictitherium*, and *Machairodus*, continuing into the earliest Pliocene after they had become extinct elsewhere. This is best seen at Langebaanweg, South Africa (Werdelin, 2006), but such Miocene holdovers are also present in eastern Africa (see Discussion). At the same time, the Kanapoi fauna includes some of the earliest occurrences of Carnivora, such as *Dinofelis*, *Homotherium*, and *Felis*. These taxa subsequently spread, not only across Africa, but also to the Holarctic and, in the case of *Homotherium*, into the Neotropics (Rincón et al., 2011). Thus, Kanapoi is one of the earliest, and to date best studied, sites with a carnivoran association foreshadowing the better known, relatively stable associations of the latest Early Pliocene to Early Pleistocene (Werdelin, 2005; Lewis and Werdelin, 2007; Werdelin and

Dehghani, 2011; Werdelin and Lewis, 2013a, b). In this contribution we will investigate this pattern and its significance in detail.

Material and methods

The Kanapoi faunal list (Table 1) is based on previously published work (Werdelin, 2003a; Werdelin and Manthi, 2012). No new taxa have been recovered since the latter publication. Comparative data have been drawn from our own published work (Werdelin, 2003b; Werdelin and Dehghani, 2011; Werdelin and Lewis, 2013a; Werdelin et al., 2013) and from other published literature (Morales et al., 2005; Howell and García, 2007; Haile-Selassie, 2008; Haile-Selassie and Howell, 2009; Werdelin et al., 2014; Morales et al., 2016). The important site complex of Aramis (dated ca. 4.4 Ma, i.e., slightly older than Kanapoi; WoldeGabriel et al., 2009) represents a special case because the Carnivora from the site have not been published, and the faunal lists that have been published are in part contradictory (WoldeGabriel et al., 1994; White et al., 2009). When published, this fauna will bring additional insights into the early evolution

Family	Genus and species
Mustelidae	<i>Torolutra</i> sp. <i>Enhydriodon ekecaman</i> <i>Enhydriodon</i> cf. <i>dikikae</i>
Viverridae	<i>Genetta</i> sp.
Herpestidae	<i>Helogale</i> sp.
Hyaenidae	<i>Parahyaena howelli</i>
Felidae	<i>Dinofelis petteri</i> <i>Homotherium</i> sp. <i>Felis</i> sp.

Table 1. List of Kanapoi Carnivora

of the African carnivoran guild, likely including first appearance datums (FADs) for several taxa. No Late Pliocene (younger than 3.60 Ma: base of the Piacenzian Stage; Gradstein et al., 2012) have been included in the present comparisons. The faunal lists used are given in the Supplementary Online Material (SOM) Table S1.

The comparisons in this paper will be mainly qualitative. Quantitative estimates of faunal similarity are possible, but due to the small sample sizes such estimates are likely to have large errors and to be misleading. Therefore, we will avoid them here.

The Kanapoi Carnivora and their distribution

In this section the species identified at Kanapoi will be discussed by family and their temporal and geographic distribution reviewed.

Mustelidae: *Torolutra* sp.

Torolutra is represented at Kanapoi by associated fragments of the dentition and axial and appendicular skeleton. The material is poorly preserved. It is adequate to diagnose the genus, but not assign it to any specific species. The genus was first described from Early Pliocene sites of the Nkondo Formation, Western Rift, Uganda (Petter et al., 1991). Its earliest appearance is in the Lower Nawata Member at Lothagam if our reassignment to *Torolutra* of the tooth identified by Werdelin (2003) as *Vishnuonyx angolensis* is correct (otherwise the FAD is the base of the Nkondo Formation). *Torolutra* is subsequently found at several sites ranging from ca. 6 Ma (Lukeino) to >1.56 Ma (KBS Member, Koobi Fora Formation). There is only one species described, *T. ougandensis* (whether *T. angolensis* from Lothagam is distinct from *T. ougandensis* is a moot point at present), although material from Koobi Fora indicates that a second species is present. This genus is the most common piscivorous lutrine in the Plio-Pleistocene

of eastern Africa. It is always found in association with species of *Enhydriodon*, except within the KBS Member. Both otters are clearly associated with permanent large bodies of water. *Torolutra* postcranial material from Kanapoi is within the size range of the living sea otter, *Enhydra lutris*.

Mustelidae: *Enhydriodon* spp.

There is fundamental disagreement regarding the generic status of the African members of the mustelid tribe Enhydriodontini. Some authors (e.g., Morales and Pickford, 2005; cf. also Pickford, 2007)

Figure 1. KNM-KP 49885A and B, *Enhydriodon* cf. *dikikae*, right metatarsals in dorsal view. a) Metatarsal III. b) Metatarsal IV.

assign them to *Sivaonyx*, whereas others (e.g., Werdelin, 2003; Geraads et al., 2011; Werdelin and Lewis, 2013a) assign them to *Enhydriodon*. This contribution is not the place to settle this debate and in the text below we refer taxa to the generic name under which they were first described.

Kanapoi is unique among eastern Africa sites in that more than one species of *Enhydriodon* is present (Werdelin and Manthi, 2012: figs. 1, 2): the giant *E. cf. dikikae* and the smaller *E. ekecaman* (Werdelin, 2003a; Geraads et al., 2011; Werdelin and Manthi, 2012). Both taxa occur in the lacustrine as well as in the fluvial phases of the Kanapoi sedimentary record, so we have no information regarding how they might have partitioned the ecospace. However, they are sufficiently different in size that they may have partitioned the available prey (which is unknown) by size, which is common in Carnivora (Dayan and Simberloff, 1996, 2005). The earlier described *E. ekecaman* is known only from a set of associated teeth, while *E. cf. dikikae* is known from a fragment of the neurocranium, some teeth and a few postcranial elements (Fig. 1).

The first appearance of *Enhydriodon/Sivaonyx* in Africa is at Lukeino (Morales and Pickford, 2005) and the last in the Upper Burgi Member, Koobi Fora Formation (Werdelin and Lewis, 2013a), with the latter being a tentative identification. Eight species of *Enhydriodon/Sivaonyx* have been described from Africa, but sample sizes are small and it is not clear at present how many of these are valid. The two Kanapoi species are morphologically very distinct, however, and may even eventually be placed in separate genera.

A variety of food items have been suggested as potential prey for bunodont otters including bivalves (Pickford, 2007), catfishes (Lewis, 2008), and other armored prey (Geraads et al., 2011). All of these suggestions and more were evaluated thoroughly by the last mentioned authors, who drew the conclusion

Figure 2. KNM-KP 32565, *Genetta* sp., left maxilla fragment with P⁴ and M¹ and posterior part of P³ in occlusal view.

Figure 3. KNM-KP 32826, *Helogale* sp., right partial mandibular corpus with M₁ and posterior part of P₄. a) Lingual view. b) Labial view. c) Occlusal view.

that none was fully satisfactory nor could help explain their extinction.

The locomotion of *Enhydriodon* has also been of great interest. Based on a study of the femur, one of the few elements found across several taxa, Lewis (2008) concluded that *Enhydriodon* from West Turkana and Langebaanweg were locomotor generalists and not specifically aquatic (although she did not rule out some level of semi-aquatic behavior). She found that *Enhydriodon* specimens from Omo and Hadar were unique among mustelids in their morphology: the morphology of the proximal end of the femur was more lutrine-like, whereas its proportions were more like those of femora from terrestrial generalist mustelids. Peigné (2008) studied much more complete material of *Sivaonyx beyi*, a bunodont otter from Chad, and determined that this species was a terrestrial predator based on the high proportion of more general terrestrial features, including limb proportions, and poorly developed aquatic adaptations across the skeleton. Thus, given that *Enhydriodon/Sivaonyx* and relatives are more terrestrial than extant lutrines, it is curious that they are always found in association with permanent bodies of water and are absent from the Upper Laetolil Beds, where no such environmental feature was present.

The Kanapoi metatarsals (Fig. 1) are similar in overall length to those of *S. beyi*. As in *S. beyi* and extant lutrines, the fourth metatarsal is longer than the third. Unfortunately, the relative proportions of the metatarsals to other long bones, an important feature

used by Peigné (2008) to distinguish *S. beyi* locomotion from that of extant lutrines, is unknown.

Viverridae: *Genetta*

Of the Kanapoi collection, only craniodental material can be assigned with confidence to *Genetta* sp. (Fig. 2). The proportions of M_1 and P^4-M^1 suggest that the material belongs to an undescribed species, but more material is needed to confirm this. *Genetta* sp. has been reported from a number of early sites beginning with the Lower Nawata member at Lothagam. Like other small carnivores, it is never common at any site but one or more species of *Genetta* appear to have been present from the Late Miocene to present. This ties in well with discussions of the evolution of the extant radiation of *Genetta* (Gaubert et al., 2004; Gaubert and Begg, 2007), that propose a molecular date for the origin of the genus at around 8 Ma and an origin for *G. genetta* at ca 3 Ma.

Herpestidae: *Helogale*

A mandibular corpus fragment with damaged P_4-M^1 can with some confidence be assigned to *Helogale* sp. on the basis of morphology and size (Fig. 3). This genus is a relatively common fossil at sites where extensive sieving has been undertaken, but is otherwise rare. Molecular data place the origin of the genus *Helogale* around 8-9 Ma (Patou et al., 2009), which is consistent with its first fossil appearance at Lemudong'o (Howell and García, 2007). It is best known from the Upper Laetolil Beds at Laetoli (Werdelin and Dehghani, 2011), where complete skulls and numerous postcranial elements of the extinct *H. palaeogracilis* have been found. The Kanapoi material is not diagnostic to species.

Felidae: *Homotherium*

Kanapoi is one of the earliest occurrences of *Homotherium* worldwide, along with possibly older material from the Lonyumun Member, Koobi Fora Formation (the two overlap in their dates). The Kanapoi material is limited but includes an M_1 as well as elements of the postcranial skeleton (Fig. 4; Werdelin, 2003a: fig. 7). Despite its age, this material has typical *Homotherium* morphology. The origin of the genus is still shrouded in mystery, although it is clear that it is derived from within the *Amphimachairodus* species-group (Werdelin and Flink, in press). Three species of *Homotherium* have been recognized in Africa: *H. problematicum* from Makapansgat Member 3, South Africa (described as *Megantereon problematicus*; Collings, 1972), *H. africanum* from Aïn Brimba, Tunisia (described as *Machairodus af-*

Figure 4. Elements of the manus of *Homotherium* sp. in dorsal view. a) KNM-KP 32558, right metacarpal IV. b) KNM-KP 32820, right proximal phalanx, possibly of digit 3.

ricanus; Arambourg, 1970; Petter and Howell, 1987), and *H. hadarensis* from Hadar, Ethiopia (Petter and Howell, 1988). Whether these represent distinct taxa or to which the Kanapoi material should be referred, is not known pending a revision, but these records demonstrate that the genus was distributed across the African continent in the Pliocene, and it is the most common felid in faunas of that time. *Homotherium* becomes less common in the Early Pleistocene, with

a last appearance datum (LAD) in the Okote Member, Koobi Fora Formation, from which only two associated postcranial elements are known.

Homotherium has been suggested to be relatively more cursorial than most felids and to have had a posture that was somewhat similar to extant spotted hyenas (*Crocuta crocuta*) based on its overall longer limb lengths and its relative limb proportions and morphology (Lewis, 1997; Antón et al., 2005; Lewis and Lague, 2010). All species studied appear to have had decreased rotatory abilities in the forelimb (e.g., Balleisio, 1963; Rawn-Schatzinger, 1992; Lewis, 1997; Antón et al., 2005; Lewis and Lague,

2010). *Homotherium* had limited claw retraction (Rawn-Schatzinger, 1992; Antón et al., 2005), similar to extant cheetahs (*Acinonyx jubatus*), but with retention of manual grasping capabilities (Antón et al., 2005). These features suggest a more open habitat felid, an inference also supported by the relatively long forelimbs (Lewis, 1997).

Previous studies have demonstrated that the postcrania of at least some African representatives differ from representatives in Europe and North America and from each other (Lewis and Lague, 2010; Werdelin and Lewis, 2013a). Unfortunately, these differences occur in elements not yet recovered at Kanapoi.

Figure 5. KNM-KP 49381, left ulna of *Dinofelis petteri*. a) Medial view. b) Lateral view. c) Cranial (anterior) view.

However, the Kanapoi postcranial material falls within the lower size range of *Homotherium* specimens in eastern Africa (Lewis, pers. obs.).

Felidae: *Dinofelis*

The *Dinofelis* at Kanapoi has been assigned to *D. petteri* (Werdelin and Lewis, 2001; Werdelin, 2003a) mainly on the basis of the excellently preserved mandibular corpus KNM-KP 30397 (Werdelin, 2003a: fig. 6). Some postcranial material, including a well preserved ulna, has also been assigned to *D. petteri* (Fig. 5). This species is the geologically oldest named species of *Dinofelis* (Werdelin and Lewis, 2001), but material assigned to *Dinofelis* sp. has been reported from a number of older sites, including the Lower Nawata Member at Lothagam, and Lukeino. *Dinofelis* persists in Africa later than other sabertooth felids, only becoming extinct in the late Early Pleistocene, with a LAD at Kanam East (ca. 1 Ma). The genus clearly originated in Africa, but spread to Eurasia and North America in the Late Pliocene and Early Pleistocene (Werdelin and Lewis, 2001).

Species of *Dinofelis* differed in their adaptations, with some younger species becoming more generalized and *Panthera*-like in their postcranial morphology (Werdelin and Lewis, 2001). The Kanapoi-material, however, belongs to one of the less *Panthera*-like species and is more gracile than later material from eastern Africa (Werdelin and Lewis, 2001). The new ulna discovered in 2007 (Fig. 5) is nearly identical in morphology and size to the less complete ulna described previously from Kanapoi (Werdelin and Lewis, 2001: fig. 7), and confirms the level of gracility in this species relative to its congeners.

Felidae: *Felis*

The genus *Felis* is represented at Kanapoi by a partial mandibular corpus with canine, P_3 roots, broken P_4 and M_1 (Werdelin, 2003a: fig. 4), isolated P_3 and P_4 , and some tentatively assigned postcranial (pedal) elements (Fig. 6). Specimens of *Felis* are extremely rare in the fossil record and the Kanapoi mandibular corpus is the oldest specimen that can be definitively assigned to the genus. “*Felidae* small species” has been reported from the slightly older Aramis and may represent *Felis*, but it is not clear what “small” means in this context. Although fragmentary, the tentatively assigned postcranial material from Kanapoi is consistent in size with a medium-sized extant *Felis* and smaller than that of an extant caracal (*Caracal caracal*) or serval (*Leptailurus serval*). At present the Kanapoi record represents the FAD for *Felis* in the fossil record. This date is consistent with

Figure 6. KNM-KP 40404, elements of the appendicular skeleton of cf. *Felis* sp. a) right calcaneum in dorsal view. b) right proximal phalanx, possibly of the second digit of the pes. These associated specimens show degenerative features due to age.

a molecular date for the origin of the genus at 2.4–4.9 Ma (Johnson et al., 2006).

Hyaenidae: *Parahyaena*

The hyaenid species *Parahyaena howelli* is by far the most common carnivore at Kanapoi. Several partial associated skeletons are known, with material representing all parts of the body (Werdelin, 2003a: fig. 5), suggesting that at least part of Kanapoi represents a den site for this species. *Parahyaena howelli* is emblematic of the transition from the Miocene ‘canid-like Hyaenidae’ to the modern primarily scavenging Hyaenidae, i.e., a transition from a fauna dominated by Hyaenidae types 3–5 to one dominated by type 6 Hyaenidae (Werdelin and Solounias, 1996). Although linked to the extant brown hyaena, *Parahyaena brunnea*, by proportions of the dental apparatus, in particular the upper carnassial, *P. howelli* is less derived than extant species in the weaker development of the premolars and the shorter metapodials. The species is also recorded in the Lower and Upper Laetoli Beds (Werdelin and Dehghani, 2011) and thus at present is restricted to the Early Pliocene.

Taxa not found at Kanapoi

Discussing taxa that are not present from a site may seem to be a futile exercise, especially in view of the small sample sizes available from sites such as Kanapoi. However, there are different categories of ‘not present,’ in that some taxa would be expected to be present if samples were slightly larger, whereas others would not be expected to be present because they a) had become extinct earlier; b) had not

yet evolved; or, most importantly, are absent because of environmental factors or sampling bias.

A taxon that would be expected at Kanapoi but has not yet been recovered is Canidae. This taxon is first recorded in Africa from ca. sediments dated ca. 7 Ma at Toros Menalla, Chad (Bonis et al., 2007) and has been recorded at Lemudong'o, Kenya (ca. 6 Ma; Deino and Ambrose, 2007), Lukeino Formation, Kenya (ca. 6.2-5.7 Ma; Deino et al., 2002) and in the Adu Asa Formation, Ethiopia (vertebrate fossils constrained between 5.77-5.54 Ma; WoldeGabriel et al., 2001), as well as younger sites such as the Upper Laetolil Beds. Overall, however, Canidae are rare in the Plio-Pleistocene record of Africa and it is likely that the family did occur at Kanapoi. As it is, only one specimen very doubtfully referred to Canidae is present in the Kanapoi collection, a damaged proximal ulna fragment.

Another taxon that is present at sites both older and younger than Kanapoi is the ursid *Agriotherium*. However, this taxon is exceedingly rare except at Langebaanweg, South Africa (Hendey, 1980), and a much larger sample size would be necessary to retrieve it at Kanapoi, even if the environment there were suitable for a large bear, which is a moot point since the preferred environment of *Agriotherium* sp. is not known with any certainty.

White et al. (2009) list cf. *Crocota* cf. *dietrichi* in their supplementary material, which if correct would be the FAD for this taxon. However, *Crocota* is rare until the Upper Laetolil Beds, where it is the most common hyaenid, and may have been excluded from Kanapoi by *P. howelli*. While this may seem odd when thinking about extant *Crocota*, *C. dietrichi* is smaller and more gracile than the extant species and has some striped hyena-like features (Werdelin and Lewis, 2013a).

Another taxon that was likely excluded from Kanapoi due to competition with *P. howelli* is *Ikelohyaena abronia*, which is present at earlier and later sites. This taxon is very similar in many respects to *P. howelli* and the two species may have been ecological avatars with no range overlap, much as striped (*Hyaena hyaena*) and brown (*Parahyaena brunnea*) hyenas are today.

There are, of course, many other taxa that might have been present at Kanapoi, including several species of Felidae and any number of small species of the families Herpestidae and Viverridae. With regard to these, however, we do not have enough information to make educated guesses. Among larger carnivorans (>10 kg) the only addition to the fauna that would be expected from extended sampling is Canidae.

Discussion

As noted in the introduction, the Miocene-Pliocene boundary represents a time of major turnover in carnivoran faunas worldwide. In western Eurasia, this turnover event began in the mid-Turolian European Land Mammal Age (MN12; ca. 7.5-6.7 Ma). However, at the end of MN13 (earliest Pliocene, ca. 4.9 Ma) there was an abrupt change in the carnivoran guild, with only a fraction of the MN 13 species appearing in the subsequent MN 14 (Werdelin and Turner, 1996). This change is far less abrupt in Africa, with typically Miocene taxa also present in western Eurasia, such as the hyaenid *Hyaenictitherium* and the ursid *Agriotherium*, lingering for another million years. Other taxa that originated in Africa or southern Asia in the Late Miocene and continued into the Late Pliocene and beyond include the extinct *Enhydriodon* and *Torolutra* and the still extant *Genetta* and *Helogale*.

Kanapoi represents one of the few sites older than 4 Ma that bear witness to this extended turnover. The carnivores there include taxa with widely different evolutionary histories. *Genetta* and *Helogale* evolved in the Late Miocene and are still extant; *Dinofelis*, *Enhydriodon*, and *Torolutra* evolved in the Late Miocene and became extinct in the early Pleistocene; *Felis* evolved in the early Pliocene (tentative FAD at Kanapoi) and is still extant; *Homotherium* evolved in the early Pleistocene (also tentative FAD at Kanapoi) and became extinct in the Early Pleistocene; and *Parahyaena* evolved at the beginning of the Early Pliocene and became extinct near the end of the interval, and is the first post-Miocene African carnivoran to become extinct. This pattern, including constituent taxa with a wide variety of evolutionary histories, is characteristic of transitional faunas, and the Carnivoran guild at Kanapoi provides evidence that it is a prime example of a transitional fauna between the more stable Late Miocene and Late Pliocene-Early Pleistocene faunas.

The causal factors behind the turnover and why it is abrupt in Eurasia and gradual in Africa are not known at present. We may, however, surmise that they are a complex combination of climatic change, land and sea topology, immigration history, and stochastic factors. Some attempts at outlining the pattern of faunal composition and change have been made (e.g., Pickford, 2004; Nieto et al., 2005; Werdelin, 2009), as well as investigations of the general process (Cerling et al., 2011; Fortelius et al., 2016), but this will form a research topic for many years to come.

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